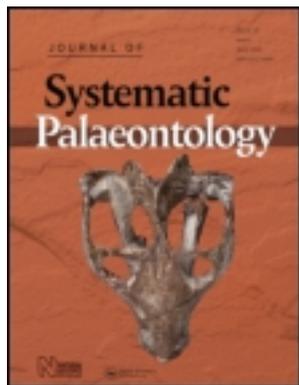


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New information on the anatomy and systematic position of *Dinheirosaurus lourinhanensis* (Sauropoda: Diplodocoidea) from the Late Jurassic of Portugal, with a review of European diplodocoids

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New information on the anatomy and systematic position of *Dinheirosaurus lourinhanensis* (Sauropoda: Diplodocoidea) from the Late Jurassic of Portugal, with a review of European diplodocoids

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Although diplodocoid sauropods from Africa and the Americas are well known, their European record remains largely neglected. Here we redescribe *Dinheirosaurus lourinhanensis* from the Late Jurassic of Portugal. The holotype comprises two posterior cervical vertebrae, the dorsal series and a caudal centrum. Redescription demonstrates its validity on the basis of three autapomorphies: (1) posteriorly restricted ventral keel on posterior cervical vertebrae; (2) three small subcircular fossae posterior to the lateral coel on posterior cervical neural spines; (3) accessory lamina linking the hyposphene with base of the posterior centrodiaepophyseal lamina in middle-posterior dorsal vertebrae. Phylogenetic analysis places *Dinheirosaurus* as the sister taxon to *Supersaurus*, and this clade forms the sister taxon to other diplodocines. However, this position should be treated with caution as *Dinheirosaurus* displays several plesiomorphic features absent in other diplodocoids (including unbifurcated presacral neural spines, and dorsolaterally projecting diapophyses on dorsal vertebrae) and only four additional steps are required to place *Dinheirosaurus* outside of Flagellicaudata. We identify *Amazonsaurus* as the basal-most rebbachisaurid and recover *Zapalasaurus* outside of the South American Limaysaurinae, suggesting the biogeographic history of rebbachisaurids is more complex than previously proposed. Review of the European diplodocoid record reveals evidence for the earliest known diplodocid, as well as additional diplodocid remains from the Late Jurassic of Spain. A Portuguese specimen, previously referred to *Dinheirosaurus*, displays strong similarities to *Apatosaurus* from the contemporaneous Morrison Formation of North America, indicating the presence of a second Late Jurassic Portuguese diplodocid taxon. Along with *Dinheirosaurus*, these Portuguese remains provide further evidence for a Late Jurassic palaeobiogeographic connection between Europe and North America. No dicraeosaurids are currently known from Europe, but rebbachisaurids are present in the Early Cretaceous, with weak evidence for the earliest known representative from the Late Jurassic of Spain; however, more complete material is required to recognize early members of this clade.

Keywords: Dinosauria; Diplodocidae; Lourinhã; Mesozoic; Morrison Formation; Rebbachisauridae

Introduction

The Late Jurassic of Portugal has yielded a diverse dinosaur fauna (de Lapparent & Zbyszewski 1957; Antunes & Mateus 2003; Mateus 2006; Mateus *et al.* 2009), rich in theropods (including *Lourinhanosaurus* and *Allosaurus*), ornithischians (*Dacenturus*, *Draconyx* and *Miragaia*) and sauropods (*Dinheirosaurus*, *Lourinhasaurus* and *Lusotitan*). A number of Portuguese taxa appear closely related to North American dinosaurs from the contemporaneous Morrison Formation, and in several cases workers have proposed that they are congeneric (de Lapparent & Zbyszewski 1957; McIntosh 1990; Wilson & Sereno 1998; Pérez-Moreno *et al.* 1999; Rauhut 2003; Mateus 2006; Mateus *et al.* 2006; Escaso *et al.* 2007; Malafaia *et al.* 2010).

Additional faunal similarities with the Late Jurassic of North America have been noted elsewhere in Europe, with Benson (2008) describing a new species of the theropod *Stokesosaurus* from the UK, previously known only from the USA. There is also putative evidence for the shared presence of closely related lepidosaur species between Portugal and North America (Mateus 2006; Ortega *et al.* 2006; Malafaia *et al.* 2010), as well as plants, mammals, ostracods and other reptiles (Mateus 2006). Alongside geological evidence, these closely related, or shared, occurrences suggest a palaeobiogeographic connection between Europe and North America during or prior to the Late Jurassic (Escaso *et al.* 2007; Benson 2008).

A sauropod skeleton was discovered in 1987 at the Praia de Porto Dinheiro, near Lourinhã, on the western

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coast of central Portugal (Bonaparte & Mateus 1999). The region of Lourinhã is where the vast majority of Late Jurassic Portuguese dinosaur remains have been discovered (Antunes & Mateus 2003). The newly discovered sauropod was briefly reported by Dantas *et al.* (1992) and the remains were subsequently referred to *Lourinhasaurus* (Dantas *et al.* 1998a). This material was later described by Bonaparte & Mateus (1999), who recognized it as distinct from *Lourinhasaurus* and erected the new binomial *Dinheirosaurus lourinhanensis*. These authors considered *Dinheirosaurus* to belong to the Diplodocidae (based on comparisons predominantly with Morrison Formation sauropods), and noted particularly close affinities with *Diplodocus*. A second Portuguese specimen, from Moita dos Ferreiros (Lourinhã), was provisionally classified as aff. *Dinheirosaurus* (Antunes & Mateus 2003).

Dinheirosaurus was listed as *Diplodocoidea incertae sedis* by both Wilson (2002) and Upchurch *et al.* (2004a), with the latter authors noting a lack of derived features of either diplodocids or dicraeosaurids (i.e. the clade Flagellicaudata). Currently, only two cladistic analyses have included *Dinheirosaurus* (Rauhut *et al.* 2005; Whitlock 2011); both of these studies recovered it as a diplodocine diplodocid, although neither analysis was based on firsthand observations of the specimen. Excluding *Dinheirosaurus*, definite diplodocids are currently only known from the Late Jurassic of North America and Tanzania (McIntosh 1990; Upchurch *et al.* 2004a; Remes 2006), although a putative member of this family was recently described from the Early Cretaceous of China (Upchurch & Mannion 2009).

The current study aims to investigate the phylogenetic position of *Dinheirosaurus* through a complete redescription of the type material, including previously undescribed elements. Its position within Diplodocoidea is explored using a modified version of the data matrix of Whitlock (2011). The nomenclature for vertebral lamination of Wilson (1999) is used, supplanting the older terminology utilized by Bonaparte & Mateus (1999). Lastly, we review the European diplodocoid record in order to place *Dinheirosaurus* in its wider stratigraphical and geographical context.

Abbreviations

Anatomy

ACDL: anterior centrodiapophyseal lamina; **ACPL**: anterior centroparapophyseal lamina; **CPOL**: centropostzygapophyseal lamina; **CPRL**: centroprezygapophyseal lamina; **EI**: Elongation Index (Upchurch [1998] = cervical centrum length, excluding condyle, divided by posterior centrum height. Note that height, rather than width, has been used in all EI calculations because the latter cannot be measured on *Dinheirosaurus*); **EPRL**: epipophyseal-prezygapophyseal lamina; **PCDL**: posterior

centrodiapophyseal lamina; **PCPL**: posterior centroparapophyseal lamina; **PODL**: postzygodiapophyseal lamina; **PRDL**: prezygodiapophyseal lamina; **PRPL**: prezygoparapophyseal lamina; **SI**: Slenderness Index (Upchurch [1998] = tooth crown apicobasal height divided by maximum mesiodistal width of crown); **SPDL**: spinodiapophyseal lamina; **SPOL**: spinopostzygapophyseal lamina; **SPRL**: spinoprezygapophyseal lamina.

Institutions

AMNH: American Museum of Natural History, New York, USA; **CM**: Carnegie Museum of Natural History, Pittsburgh, USA; **CPT**: Museo de la Fundación Conjunto Paleontológico de Teruel-Dinópolis, Aragón, Spain; **CUT**: Chengdu University of Technology, Sichuan, China; **DFMMh**: Dinosaurier-Freilichtmuseum Münchhagen, Germany; **IVPP**: Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **MACN**: Museo Argentino de Ciencias Naturales ‘B. Rivadavia’, Buenos Aires, Argentina; **MCF**: Museo ‘Carmen Funes’, Neuquén, Argentina; **MCNV**: Museo de Ciencias Naturales de Valencia, Spain; **MIGM**: Museu Geológico do Instituto Geológico e Mineiro, Lisbon, Portugal; **MIWG**: Museum of Isle of Wight Geology (now Dinosaur Isle Visitor Centre), Isle of Wight, UK; **ML**: Museu da Lourinhã, Portugal; **MLP**: Museo de La Plata, Argentina; **MMCH**: Museo Municipal ‘Ernesto Bachman’, Villa El Chocón, Neuquén, Argentina; **MN**: Museu Nacional, Rio de Janeiro, Brazil; **MNN**: Musée National du Niger, Niamey, Republic of Niger; **MPG**: Museo Paleontológico de Galve, Aragón, Spain; **MPS**: Museo de Dinosaurios – Paleontología, Salas de los Infantes, Burgos, Spain; **MUCPv**: Museo de Geología y Paleontología de la Universidad Nacional del Comahue, Neuquén, Argentina; **NHMUK**: Natural History Museum, London, UK; **NSMT**: National Science Museum, Tokyo, Japan; **OUNH**: Oxford University Museum of Natural History, Oxford, UK; **PALEON**: Glenrock Paleontological Museum, Wyoming, USA; **Pv-MOZ**: Museo ‘Profesor Dr. Juan Olsacher’, Zapala, Neuquén, Argentina; **WDC**: Wyoming Dinosaur Center, Thermopolis, Wyoming, USA.

Systematic palaeontology

Sauropoda Marsh, 1878

Neosauropoda Bonaparte, 1986a

Diplodocoidea Marsh, 1884 (*sensu* Upchurch 1995)

Diplodocidae Marsh, 1884

Dinheirosaurus Bonaparte & Mateus, 1999

Type species. *Dinheirosaurus lourinhanensis*

Dinheirosaurus lourinhanensis

(Figs 1–4, 6–8; see also Bonaparte & Mateus [1999, figs 2–8])

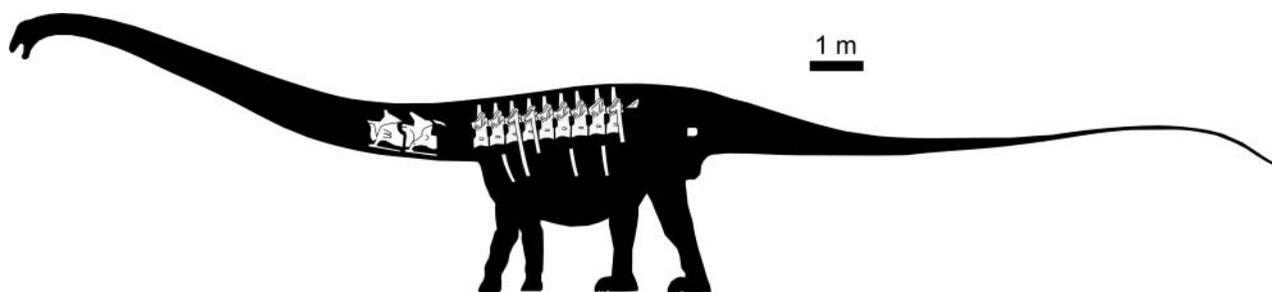


Figure 1. *Dinheirosaurus lourinhanensis* silhouette containing skeletal reconstruction based on ML 414. Scale bar = 1 metre.

Holotype. ML 414 – two articulated cervical vertebrae, nine articulated dorsal vertebrae and the diapophysis of a 10th dorsal vertebra, thoracic ribs, one caudal centrum and several other incomplete centra, distal fragment of pubis, gastroliths.

Revised diagnosis. *Dinheirosaurus* can be diagnosed on the basis of three autapomorphies (marked with an asterisk), as well as a unique combination of characters not seen in other diplodocids: (1) Cv14 possesses a ventral keel restricted to the posterior end of the centrum*; (2) subvertical lamina extends between the ventral surface of the postzygodiapophyseal lamina and the dorsal surface of the posterior centrodiaepophyseal lamina in posterior cervical vertebrae; (3) three small subcircular fossae located posterior to the lateral coel on the neural spine of Cv14*; (4) presacral neural spines are unbifurcated (autapomorphic within Flagellicaudata); (5) dorsal centra maintain the same approximate length throughout the series (autapomorphic within Diplodocidae); (6) robust horizontal accessory lamina links the hyposphene with the base of the posterior centrodiaepophyseal lamina in middle-posterior dorsal vertebrae*; (7) diapophyses project dorsolaterally in dorsal vertebrae (autapomorphic within Diplodocidae).

Locality and horizon. Praia de Porto Dinheiro locality, Lourinhã, Portugal; Amoreira-Porto Novo Member, Lourinhã Formation; late Kimmeridgian–early Tithonian, Late Jurassic (Dantas *et al.* 1998a; Bonaparte & Mateus 1999; Antunes & Mateus 2003; Mateus 2006; Schneider *et al.* 2009).

Additional comments. Only Bonaparte & Mateus (1999) and Upchurch *et al.* (2004a) have previously attempted to provide a diagnosis for *Dinheirosaurus*. Both sets of workers considered the hyposphenal accessory lamina autapomorphic, which is included in our emended diagnosis. Bonaparte & Mateus (1999) also included three dorsal vertebral features that distinguished it from *Diplodocus* in their diagnosis (absence of anterior centroparapophyseal lamina, posterior centroparapophyseal lamina obliquely oriented, lower section of the

neural arch of middle-posterior dorsal vertebrae dorsoventrally shorter in *Dinheirosaurus*); however, differentiating it from *Diplodocus* does not constitute a diagnosis and, additionally, all of these features are either more widespread amongst diplodocids or incorrectly interpreted (see ‘Descriptions and comparisons’ below). Upchurch *et al.* (2004a) regarded the possession of an elongate fossa on the lateral surface of the cervical neural spine as a diagnostic feature, although the latter is also present in *Barosaurus* and *Diplodocus*. The combination of the absence of anterior centroparapophyseal laminae coupled with the presence of prominent posterior centroparapophyseal laminae in the dorsal vertebrae was also considered a local autapomorphy within Diplodocoidea (Upchurch *et al.* 2004a); however, the former lamina is present, albeit weakly, and the presence of the latter lamina is widespread within the clade.

Description and comparisons

The following description of *Dinheirosaurus* is based on personal observations of the holotype (ML 414) and supplements and amends that provided by Bonaparte & Mateus (1999).

Cervical vertebrae

Only two articulated posterior cervical vertebrae are preserved. A third cervical vertebra, articulated with the more posterior of these, was lost during excavation (Bonaparte & Mateus 1999), although a prezygapophysis is still preserved from this latter vertebra. Based on the position of elements in the ground, it seems likely that these were the last three cervical vertebrae in the sequence. Diplodocids tend to have 15 cervical vertebrae (Upchurch 1998; McIntosh 2005); consequently, we refer to them here as Cv13–15. The anteriormost (Cv13) of these three cervical vertebrae is very poorly preserved, so the following description is based entirely on the ‘middle’ cervical vertebra (Cv14) and the prezygapophysis of the posteriormost vertebra (Cv15). The few discernible features on Cv13 do not differ from those observed on Cv14. As a consequence

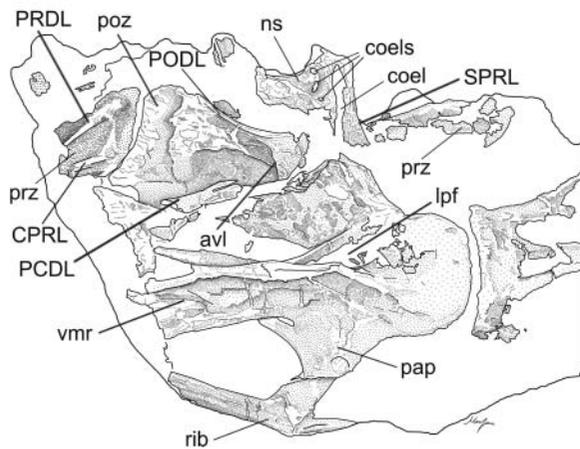


Figure 2. *Dinheirosaurus lourinhanensis* (ML 414) cervical vertebra Cv14 in right lateral view (photograph (top) and line drawing (bottom)). Abbreviations: avl, accessory vertical lamina; CPRL, centroprezygapophyseal lamina; lpf, lateral pneumatic foramen; ns, neural spine; pap, parapophysis; PCDL, posterior centrodiaepophyseal lamina; poz, postzygapophyseal lamina; PRDL, prezygodiaepophyseal lamina; prz, prezygapophysis; SPRL, spinoprezygapophyseal lamina; vmr, ventral midline ridge. Scale bar = 300 mm.

of its mounted position, Cv14 is largely exposed only in right lateral and ventral views (Fig. 2). It is relatively complete, although the neural spine and prezygapophysis are separated from the main body of the vertebra by a prominent break. Measurements are provided in Table 1.

The centrum is strongly opisthocoelous, as in other eusauropods (Upchurch 1995), and has an Elongation Index (EI) value of 2.09. This value is notably higher than in the posterior cervical vertebrae of dicraeosaurids, an indeterminate juvenile diplodocid described by Schwarz *et al.* (2007a; though see Carballido *et al.* (2010a) for an alternative view on the affinities of this specimen), *Apatosaurus* and ‘*Eobrontosaurus*’, but is much lower than in the diplodocines *Diplodocus* and *Barosaurus* (see Table 2). However, it is comparable to the rebbachisaurids *Nigersaurus* and MMCH PV 49 (Apesteguía *et al.* 2010), as well as the larger specimen (CM 879) of the putative basal diplodocoid *Haplocanthosaurus* (Calvo & Salgado 1995; Wilson 2002; Whitlock 2011), suggesting that *Dinheirosaurus* might retain the plesiomorphic diplodocoid state.

As noted by Bonaparte & Mateus (1999), the ventral surface of the centrum is concave transversely, and there is a short, anteroposteriorly oriented keel restricted to the posterior 100 mm of this surface (Fig. 2). Although a ventral keel is present on the cervical vertebrae of a number of basal sauropods, several diplodocoids and some titanosauriforms (Upchurch 1998; Upchurch *et al.* 2004a; Sereno *et al.* 2007; Mannion 2011), these are positioned along the midlength or restricted to the anterior half of the vertebra; consequently, the posteriorly placed keel is here considered an autapomorphy of *Dinheirosaurus*.

The parapophysis is situated on the anteroventral corner of the centrum (Fig. 2); it is excavated dorsally and separated from the lateral pneumatic foramen by a horizontal ridge, as in most neosauropods (Upchurch 1998), although cervical vertebrae of the diplodocid *Tornieria* (Remes 2007, p. 663) and several titanosaurs (Curry Rogers 2005;

Table 1. Measurements of the cervical and dorsal vertebrae of *Dinheirosaurus*. All measurements given in millimetres. An asterisk denotes measurements based on incomplete elements or approximations.

No.	Centrum length (excluding condyle)	Posterior centrum height	Neural arch height	Neural spine height (from top of postzygs)
Cv14	570	273	—	—
Dv2	234	302	—	—
Dv3	229	310	—	—
Dv4	214	305	182	—
Dv5	241	268*	176	—
Dv6	232	299	221	—
Dv7	232	295	212*	400
Dv8	192*	290*	271	—
Dv9	231	275	300	—

Table 2. Elongation Index (EI; cervical centrum length (excluding condyle) divided by posterior centrum height) values for posterior cervical vertebrae of a range of diplodocoid taxa (including putative forms). Note that no measurements were given for *Brachytrachelopan* in the original publication; however, Rauhut *et al.* (2005, p. 670) stated that the cervical centra are the same length or shorter (excluding the condyle) than the posterior centrum height. Museum accession numbers denote those specimens examined by the authors firsthand, or where there may be some ambiguity as to which specimen is being referred to.

Taxon	EI	Cervical no.	Reference
'El Chocón rebbachisaurid' (MMCH-PV 49)	2.26	Cv13	PDM pers. obs. (2009)
' <i>Eobrontosaurus</i> ' (PALEON 001)	1.19	Cv15?	PDM pers. obs. (2008)
<i>Amargasaurus</i> (MACN-PV N15)	1.51	Cv13	PDM pers. obs. (2009)
<i>Apatosaurus louisae</i> (CM 3018)	1.32	Cv14	Gilmore (1936)
<i>Apatosaurus ajax</i> (NSMT-PV 20375)	1.57	Cv14	Upchurch <i>et al.</i> (2004b)
<i>Barosaurus</i>	2.81	Cv15?	McIntosh (2005)
<i>Brachytrachelopan</i>	1.00	Cv12	Rauhut <i>et al.</i> (2005)
<i>Dicraeosaurus</i>	1.09	Cv12	Janensch (1929)
<i>Dinheirosaurus</i> (ML 414)	2.09	Cv14?	This study
<i>Diplodocus</i> (CM 84)	2.55	Cv14	Hatcher (1901)
<i>Haplocanthosaurus</i> (CM 572)	1.57	Cv14	Hatcher (1903)
<i>Haplocanthosaurus</i> (CM 879)	2.07	Cv14	Hatcher (1903)
Juvenile diplodocid	1.62	Cv14?	Schwarz <i>et al.</i> (2007a)
<i>Nigersaurus</i> (MNN)	2.05	Cv11	PDM pers. obs. (2010)

Mannion 2011) lack this excavation. The pneumatic foramen extends most of the length of the centrum (excluding the articular ball) and appears to have been divided near its posterior end by an anteroventrally directed oblique lamina (Fig. 2; Bonaparte & Mateus 1999). However, this region is heavily deformed, limiting further interpretation of the internal morphology of the pneumatic foramen, but it is clear that the foramen is a single structure, unlike the two independent foramina present in rebbachisaurids (e.g. *Limaysaurus* and *Cathartesaura*; PDM pers. obs. 2009).

One prezygapophysis of Cv14 is preserved, projecting anterodorsally beyond the articular condyle and expanding transversely towards its articular surface (Bonaparte & Mateus 1999). As a consequence of its poor preservation, it is not possible to discern other anatomical features; however, the preserved prezygapophysis of Cv15 enables some additional observations (Fig. 2). The ventral surface of this process forms an anteroposteriorly elongate channel in between ventrally directed prezygodiapophyseal (PRDL; laterally) and centroprezygapophyseal (CPRL; medially) laminae (Fig. 2). It is not possible to determine the shape of the zygapophyseal articular surfaces and there is no indication of an epipophyseal-prezygapophyseal lamina (EPRL; Sereno *et al.* 2007; Wilson & Upchurch 2009). There is a short sub-vertical lamina (Fig. 2) which extends between the ventral surface of the prominent postzygodiapophyseal lamina (PODL) and the dorsal surface of the gently anterodorsally inclined posterior centrodiaepophyseal lamina (PCDL). This additional lamina is also present in at least one specimen of *Apatosaurus* (*A. parvus*; UWGM 15556; Gilmore 1936, pl. 31), but appears to be absent in other sauropods; consequently, we consider it a local autapomorphy of *Dinheirosaurus*.

It appears that the neural arch did not reach the posterior end of the centrum, with several centimetres of the dorsal surface of the latter exposed (Fig. 2). In lateral view, the posterior margin of the neural arch is vertically directed at its base, before curving strongly posteriorly to overhang this exposed area.

Steep, posterodorsally oriented spinoprezygapophyseal laminae (SPRL) form the anterolateral margins of the neural spine, but it is not possible to identify spinopostzygapophyseal laminae (SPOL) or epipophyses above the postzygapophyses. The neural spine lacks pre- or post-spinal laminae, as is the case in the cervical vertebrae of most sauropods, with the exception of some titanosaurs (Wilson 1999; Curry Rogers 2005). An anteriorly positioned, dorsoventrally elongate coel is present on the lateral surface of the neural spine, with three smaller subcircular openings located posterior to this (Fig. 2; Bonaparte & Mateus 1999). Cv14 of *Diplodocus* (Hatcher 1901, pl. 3) and the posterior cervical vertebrae of *Barosaurus* (McIntosh 2005, fig. 2.1C) possess a similar dorsoventrally elongate coel, but not the additional smaller openings, which are here considered autapomorphic for *Dinheirosaurus*. These shallow coels are different to the more pervasive lateral openings present in some titanosauriform cervical vertebrae (e.g. *Giraffatitan* and *Qiaowanlong*; You & Li 2009; Mannion 2011), in which the openings are bounded by the PRDL, SPRL and PODL. The two lateral ridges on the neural spine of *Diplodocus* (Hatcher 1901, pl. 3) are not present in *Dinheirosaurus* (Bonaparte & Mateus 1999). The neural spine is dorsoventrally short (unlike in dicraeosaurids) and oriented vertically (Fig. 2), rather than inclined anteriorly as in the posterior cervical and anterior dorsal vertebrae of *Diplodocus* (Hatcher 1901), although this feature is variable within each of the three diplodocoid

clades (Serenio *et al.* 2007). In its dorsal portion, the neural spine is robust and widened transversely; this region is unbifurcated (*contra* Bonaparte & Mateus 1999) and there is no indication of the presence of tapering metapophyses. The lack of bifurcation differs from the condition seen in other flagellicaudatans (McIntosh 1990; Upchurch 1995) and is here considered a local autapomorphy of *Dinheirosaurus*. The dorsal surface of the neural spine is flat along the anterior half, becoming mildly transversely concave posteriorly.

Cervical ribs

A portion of cervical rib is associated with, but detached from, the left parapophysis of Cv14 (Fig. 2). It is exposed in ventral and medial views. The rib clearly lay well below the ventral margin of the centrum, as in all neosauropods (Wilson & Sereno 1998), and the shaft appears to have been directed horizontally backwards. There is a short, slender, tapering anterior process that terminates posterior to the articular condyle of the cervical centrum. As preserved, the shaft terminates close to the posterior end of the centrum (Fig. 2); however, the broken distal surface indicates that the rib probably projected somewhat further posteriorly because there is no sign of the shaft tapering to a narrow point. A number of authors have observed that the cervical ribs of diplodocoids (including the putative basal member *Haplocanthosaurus*) do not extend beyond the end of the cotyle (Berman & McIntosh 1978; Wilson 2002; McIntosh 2005; Sereno *et al.* 2007) and so an elongate distal shaft might be considered autapomorphic for *Dinheirosaurus*. However, *Nigersaurus* (Serenio & Wilson 2005, fig. 5.8; PDM pers. obs. 2010), *Supersaurus* (Lovelace *et al.* 2008), the juvenile diplodocid from the Late Jurassic of the USA (Schwarz *et al.* 2007a), '*Eobrontosaurus*' (Filla & Redman 1994) and even one cervical vertebra of *Diplodocus* (Hatcher 1901, fig. 24), also possess posteriorly extending cervical ribs. It is possible that the cervical rib in Cv14 of *Dinheirosaurus* has been displaced posteriorly (making it appear to extend further than it did in life) or that it narrowed and terminated abruptly; thus, more complete materials will be required to determine whether this apparently elongate rib is a genuine feature.

Dorsal vertebrae

Nine articulated and relatively complete dorsal vertebrae are preserved, as well as the right transverse process of a 10th dorsal vertebra (Fig. 3). As with the cervical vertebrae, only the right lateral and ventral surfaces are fully exposed, although some of the posterior surface of Dv9 can be observed. Measurements are provided in Table 1.

The centra of Dv2–4 are strongly opisthocoelous (it is assumed Dv1 also possessed this condition, but the condyle is not preserved in this element). This anterior convexity is slightly less prominent in Dv5, and is absent (i.e. the anterior articular surface is flat) in Dv6–9 (Fig. 3). In macronarians, middle and posterior dorsal vertebrae are

prominently opisthocoelous (Salgado *et al.* 1997; Wilson & Sereno 1998), and some basal forms possess a mild convexity (e.g. *Cetiosaurus*; Upchurch & Martin 2002, 2003). It has also been claimed that the basal diplodocoid *Amazonosaurus* possesses mild opisthocoely beyond its anterior dorsal vertebrae (Carvalho *et al.* 2003); however, although the absence of parapophyses on the two preserved dorsal centra means that they are clearly not from the anterior-most part of the series, they could still represent Dv3–5 (MN 4559-V; PDM pers. obs. 2009). With the exception of *Supersaurus* (Lovelace *et al.* 2008), the middle and posterior dorsal vertebrae of all diplodocoids (including *Haplocanthosaurus*) are amphiplatyan or amphicoelous (Wilson & Sereno 1998; Upchurch *et al.* 2004a), although location of the transition point between opisthocoelous anterior dorsals and amphicoelous middle dorsal vertebrae varies between, and even within, genera (Upchurch *et al.* 2004b).

The dorsal centra maintain the same approximate antero-posterior length throughout the series (excluding the articular ball in the first five dorsal vertebrae) (Table 1; Fig. 3). In those diplodocids preserving relatively complete dorsal sequences, the middle-posterior dorsal vertebrae are shorter than the anterior ones, i.e. *Apatosaurus* (Gilmore 1936; Upchurch *et al.* 2004b), *Barosaurus* (Lull 1919) and *Diplodocus* (Hatcher 1901). This reduction along the dorsal column is also present in *Haplocanthosaurus* (Hatcher 1903), whereas the posterior dorsal centra of the rebbachisaurid *Limaysaurus* are apparently the longest in the sequence (Calvo & Salgado 1995, p. 22). However, the dorsal centra of the dicraeosaurids *Amargasaurus* (MACN PV N15), *Brachytrachelopan* (Rauhut *et al.* 2005) and *Dicraeosaurus* (Janensch 1929), maintain a relatively consistent length, comparable to *Dinheirosaurus*. Thus, we consider this feature a local autapomorphy of *Dinheirosaurus*, within Diplodocidae.

Dv1 possesses a ventral midline ridge along most of the preserved length of the centrum (Bonaparte & Mateus 1999); this is only weakly developed and restricted to the anterior half of the centrum on Dv2, and is absent on the remaining dorsal vertebrae (Fig. 4). Ventral keels are absent in the dorsal centra of most sauropods, although they are present in *Haplocanthosaurus*, several diplodocids (e.g. *Diplodocus* and *Supersaurus*; Upchurch *et al.* 2004a; Lovelace *et al.* 2008), *Mamenchisaurus hochuanensis* (CUT GCC V 20401: PU & P. M. Barrett pers. obs. 2010), *Euhelopus* (Wilson & Upchurch 2009) and *Barrosasaurus* (Salgado & Coria 2009). Lateroventral ridges are also present in *Dinheirosaurus* (Bonaparte & Mateus 1999), but are restricted to the posterior third of the centrum. These are sharp and well defined in Dv1, but low and rounded in the subsequent dorsal vertebrae, disappearing by Dv6 (Fig. 4). The ventral surfaces of the centra of Dv1–2 are divided into four regions. On either side there is a lateroventrally facing concave region, which lies between the ridge-like ventral margin of the pneumatic foramen and the lateroventral

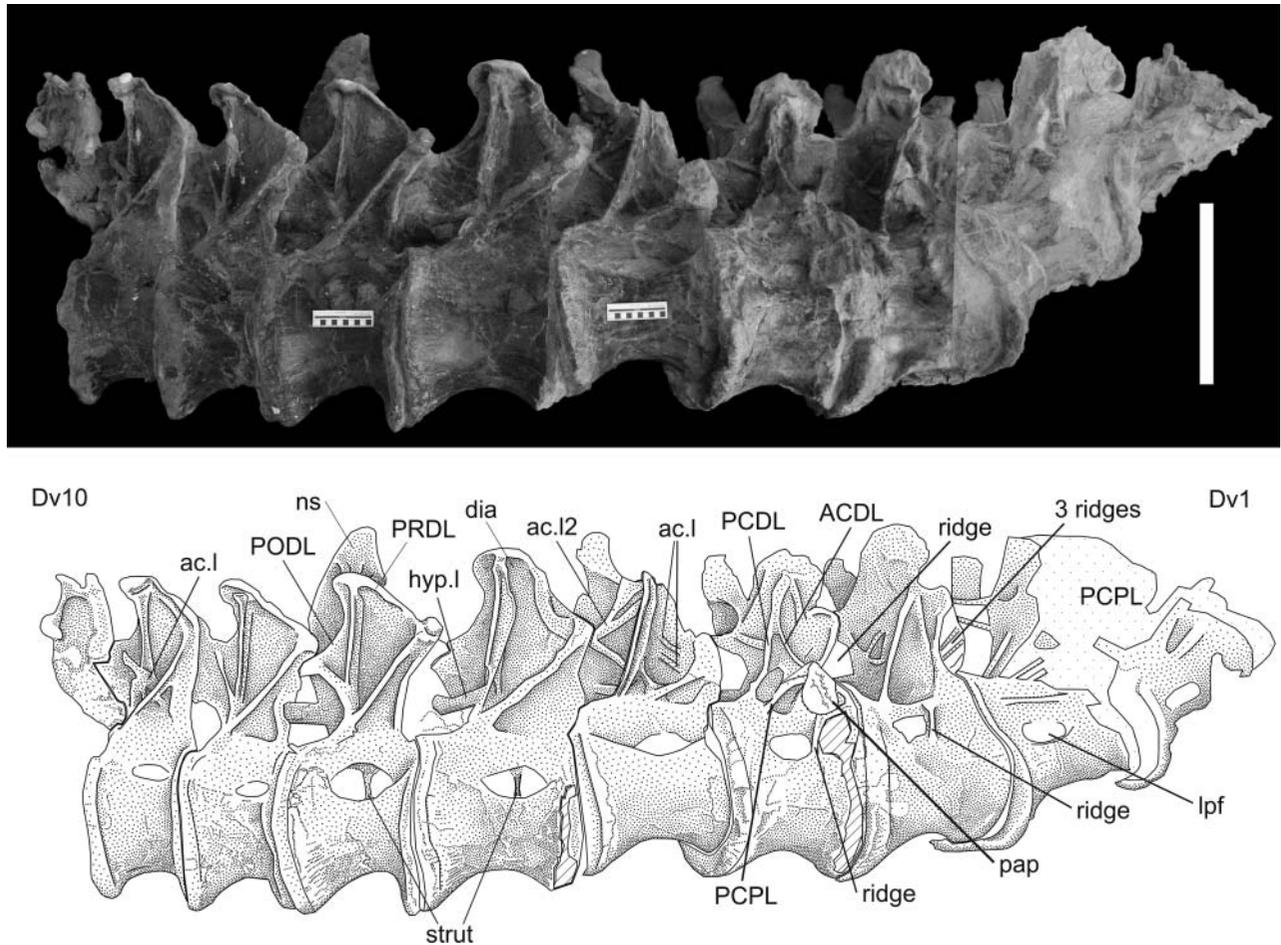


Figure 3. *Dinheirosaurus lourinhanensis* (ML 414) dorsal vertebrae in right lateral view (photograph (top) and line drawing (bottom)). Abbreviations: ACDL, anterior centrodiapophyseal lamina; ac. 1, accessory lamina; ac. 12, accessory lamina 2; dia, diapophysis; hyp. 1, hyposphenal lamina; lp, lateral pneumatic foramen; ns, neural spine; pap, parapophysis; PCDL, posterior centrodiapophyseal lamina; PCPL, posterior centroparapophyseal lamina; PODL, postzygodiapophyseal lamina; PRDL, prezygodiapophyseal lamina. Scale bar = 300 mm.

ridge, and a smaller, transversely concave region between the lateroventral ridge and ventral keel (Fig. 4). Dv3–5 have mildly convex lateroventral surfaces between the pneumatic foramina and ventrolateral ridges, with a broad and slightly transversely concave ventral surface between the two ventrolateral ridges. The ventral surfaces of the remaining dorsal centra are smoothly convex transversely. All of the dorsal centra have dorsally arched ventral surfaces in lateral view as a result of the typical constriction of the centrum between the expanded articular ends.

The lateral pneumatic foramina in *Dinheirosaurus* dorsal vertebrae are filled with matrix, but appear to be moderately deep structures (Fig. 3). With the notable exception of dicraeosaurids, the dorsal vertebrae of most eusauropods possess such lateral excavations (Upchurch 1995; Wilson 2002; Wedel 2003; Mannion 2010). The pneumatic foramen of Dv1 in *Dinheirosaurus* is small and ovoid: anteroposteriorly elongate, but dorsoventrally narrow. In subsequent

dorsal vertebrae, this foramen becomes more anteriorly positioned and throughout the series it is restricted to the dorsal half of the centrum (Fig. 3). The exact morphology of the pneumatic foramina of the anterior dorsal vertebrae is difficult to determine, but they are eye-shaped at least in Dv5–9. Vertically oriented, rod-like struts divide the pneumatic foramina of Dv6 and 7 into approximately equidimensional anterior and posterior portions (Fig. 3; Bonaparte & Mateus 1999). The possession of a dividing strut of bone appears to be extremely rare in sauropods, with only a posterior dorsal vertebra of *Supersaurus* (WDC DMJ-021; PDM pers. obs. 2008) displaying a comparable feature (Fig. 5), although many titanosaurs possess a system of finer internal divisions (Salgado *et al.* 1997). The ventral margins of the pneumatic foramina in *Dinheirosaurus* are defined by a lateral ridge (see above), whereas the dorsal margins are delineated by a rounded ridge that extends posteriorly and a little ventrally from the parapophysis. These dorsal

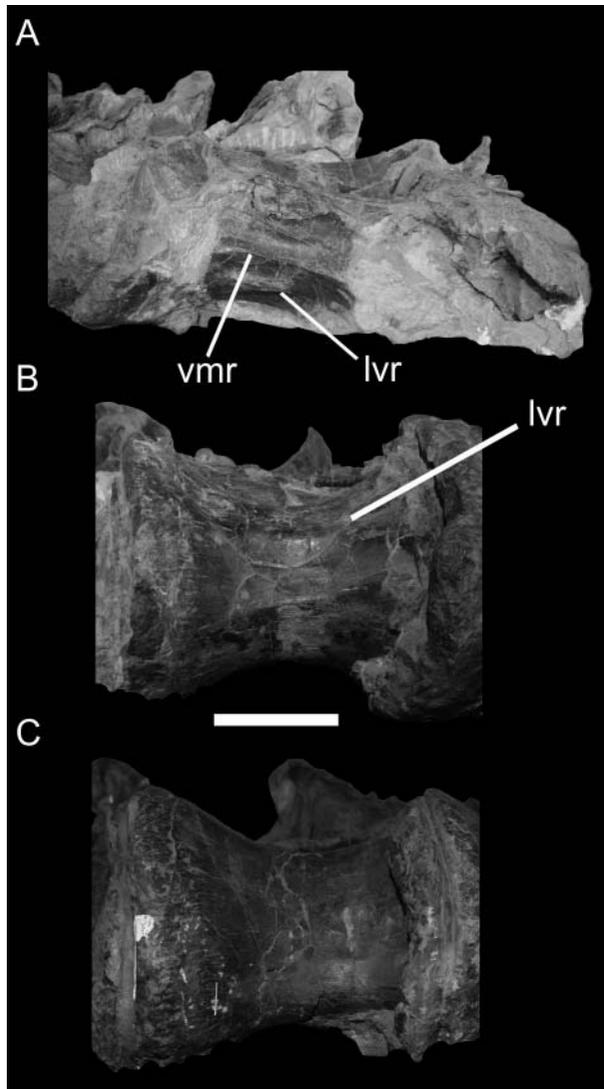


Figure 4. *Dinheirosaurus lourinhanensis* (ML 414) dorsal vertebrae in ventral view: **A**, Dv1; **B**, Dv5; and **C**, Dv7. Anterior is to the right in each image. Abbreviations: lvr, lateroventral ridge; vmr, ventral midline ridge. Scale bar = 200 mm.

ridges are only present on Dv1–2; by Dv3 the parapophysis has moved on to the dorsal portion of the centrum and the ridge no longer defines the dorsal margin of the pneumatic foramen (Fig. 3). On Dv4, the parapophysis lies on the centrum–arch junction (Bonaparte & Mateus 1999) and there is a nearly vertical ridge that extends ventrally from its posteroventral corner to define the anterior margin of the pneumatic foramen (Fig. 3). The parapophysis does not contribute to the margins of the pneumatic foramen on subsequent dorsal vertebrae. Where preserved, the parapophysis is a large, dorsoventrally elongate, roughened area, with a slightly concave articular surface (see Dv4 in particular: Fig. 3).

Bonaparte & Mateus (1999) noted that the posterior centroparapophyseal lamina (PCPL) first appears on Dv4,

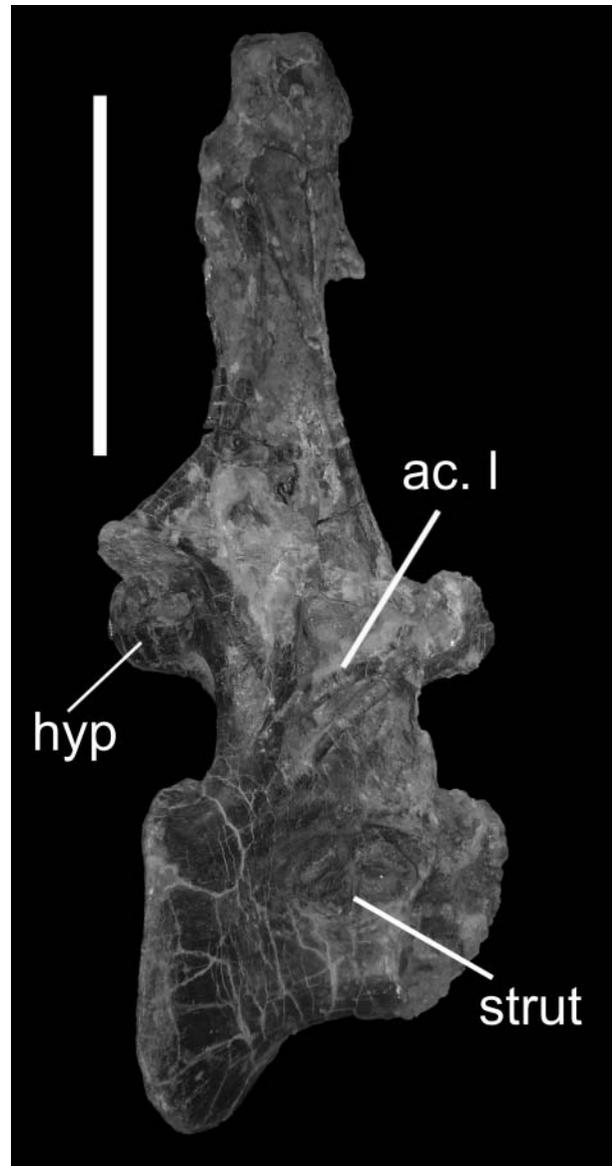


Figure 5. *Supersaurus vivianae* (WDC DMJ-021) posterior dorsal vertebra in right lateral view. Abbreviations: ac. l, accessory lamina; hyp, hyposphene; strut, bony dividing strut. Scale bar = 400 mm.

oriented anterodorsally at approximately 45° to the horizontal; however, there is also a very weak, near-horizontal PCPL on Dv2–3 (Fig. 3). Wilson (1999) suggested that the presence of a PCPL optimizes as a synapomorphy of Titanosauriformes that was independently acquired in diplodocids. Although this lamina is indeed present in the middle-posterior dorsal vertebrae of all diplodocids and most titanosauriforms (Salgado *et al.* 1997; Upchurch 1998; Wilson 1999, 2002; Lovelace *et al.* 2008), it also occurs in a number of dicraeosaurids and rebbachisaurids, and even some non-neosauropods, e.g. *Jobaria* (Upchurch 1998; Wilson 2002; Sereno *et al.* 2007). Therefore, the

presence of the PCPL is more likely to be a synapomorphy of Neosauropoda or a slightly more inclusive clade. Weak, approximately vertical anterior centroparapophyseal laminae (ACPL) appear to be present from Dv5 onwards (*contra* Upchurch *et al.* 2004a), as in most eusauropods (Wilson 1999, 2002); however, preservation in this region is poor in all of the vertebrae.

Three anterodorsally oriented ridges are present on the lateral surface of the CPRL of Dv3; in Dv4, a stout ridge emerges from the anterodorsal corner of the parapophysis before rapidly bifurcating into two short ridges which extend anterodorsally up the lateral surface of the CPRL (Fig. 3; Bonaparte & Mateus 1999). Anterior to this, another ridge extends vertically to support the lateral surface of the prezygapophysis. Thus, it appears that the CPRL bifurcates dorsally (a neosauropod feature; Upchurch *et al.* 2004a) to form a broad, shallow, concave area facing anterolaterally on the lateral surface of the prezygapophysis.

The diapophyses of *Dinheirosaurus* dorsal vertebrae project dorsolaterally throughout the sequence (Fig. 3; Bonaparte & Mateus 1999; *contra* Rauhut *et al.* 2005; Whitlock 2011). A wide array of sauropods possess dorsolaterally projecting diapophyses (e.g. *Cetiosaurus* [Upchurch & Martin 2002, 2003], *Patagosaurus* [Bonaparte 1986b], *Mamenchisaurus* [Young & Zhao 1972], dicraeosaurids [Janensch 1929; Salgado & Bonaparte 1991], rebbachisaurids [Calvo & Salgado 1995] and *Haplocanthosaurus* [Hatcher 1903]), whereas the diapophyses of all diplodocids (as well as some other taxa, e.g. *Brachiosaurus* and *Camarasaurus*) project either horizontally or are only slightly dorsally inclined (Upchurch *et al.* 2004a; Rauhut *et al.* 2005; Sereno *et al.* 2007; Whitlock 2011). This feature is thus considered a local autapomorphy of *Dinheirosaurus*.

There are well-developed centrodiaepophyseal laminae, and the anterior centrodiaepophyseal lamina (ACDL) meets the parapophysis at its posterodorsal margin in Dv1–4 (Fig. 3). The PCDL is larger and more prominent than the ACDL; it extends anterodorsally at approximately 45° to the horizontal on Dv1, becoming steeper and closer to vertical along the dorsal sequence. On Dv2–4, the ACDL and PCDL converge dorsally to form a single ridge that underlies the diapophysis, with a subtriangular coel present between them (Fig. 3). Bonaparte & Mateus (1999) commented that the ACDL appears to be absent in Dv5; however, the relevant region is poorly preserved on this vertebra, but the ACDL is definitely absent from at least Dv6 onwards. Both a PRDL and PODL are present, with the latter becoming increasingly steeply inclined along the dorsal sequence (Fig. 3).

Two ridges descend anteroventrally from the PCDL to the PCPL on Dv5, although only the posterior ridge is well preserved (Bonaparte & Mateus [1999] only described one ridge); these do not appear to be present on Dv6–7 (Fig. 3). A similar morphology seems to reappear on Dv9: a stout rounded ridge runs anteroventrally from near the ventral

end of the PCDL to the PCPL, extending a short distance through the latter. This morphology forms an 'X'-shape in lateral view, although the PCPL arm of this 'X' is much more robust than that of the accessory lamina. An incipient version of this morphology appears to be present on Dv8 too, but the accessory lamina does not pass through the PCPL on this vertebra (Fig. 3). Accessory laminae are also present in this region in middle-posterior dorsal vertebrae of *Supersaurus* (Fig. 5; WDC DMJ-021; PDM pers. obs. 2008), but appear to be absent in other sauropods.

A deep, subtriangular coel is present on the lateral surface of the arch of Dv3–4; this is defined by the ACDL posteroventrally, the PRDL dorsally and the ridge which emerges from the anterodorsal margin of the parapophysis anteroventrally (Fig. 3). On Dv5, the parapophysis forms the anteroventral margin to this coel, whereas on subsequent vertebrae the PCPL forms this margin (with the parapophysis moving up onto the lateral surface of the prezygapophysis). The PCPL also forms the posterodorsal margin of a subtriangular coel on the anterolateral edge at the base of the neural arch on Dv4–9 (Fig. 3; Bonaparte & Mateus 1999).

From Dv2 onwards there are accessory laminae in the infrapostzygapophyseal cavity (i.e. the region between the PCDL, PODL and postzygapophysis). The presence of an accessory lamina in this region is characteristic of the middle-posterior dorsal vertebrae of neosauropods and *Cetiosaurus*, although they are absent in a number of titanosaurs (Upchurch 1998; Upchurch *et al.* 2004a). There are two accessory laminae in Dv5, none in Dv3 or Dv6 (although this may be preservational) and one in each of the remaining dorsal vertebrae (Fig. 3; Bonaparte & Mateus 1999). Both laminae begin near the anterior margin of the postzygapophyseal facet and both meet the PCDL. The lower of the two accessory laminae in Dv5 is the one retained in Dv7–9 and is comparable in position and orientation to other sauropods possessing this feature, descending steeply anteroventrally (Fig. 3). The upper accessory lamina (only present in Dv5) could be regarded as a bifurcation of the PODL; this bifurcation occurs a couple of centimetres anterior to the postzygapophysis and the accessory lamina is directed anterodorsally, at approximately 45° to the horizontal (Fig. 3). Although this second accessory lamina appears unusual and might represent an autapomorphy of *Dinheirosaurus*, its absence on all but one of the vertebrae casts doubt on its utility as a diagnostic character.

Hyposphene–hypantrum articulations are present in the middle-posterior dorsal vertebrae, as in most sauropods, except lithostrotians and rebbachisaurids more derived than *Histriasaurus* (Salgado *et al.* 1997; Upchurch 1998; Wilson 2002; Sereno *et al.* 2007). There is evidence for an incipient hyposphene-like structure beginning on Dv3. The hyposphene in posterior dorsal vertebrae (based on Dv7) is situated a little below midheight of the vertebra (Fig. 3), although poor preservation makes accurate

determination of this difficult. This position is higher than in *Apatosaurus*, and lower than in *Diplodocus* and *Barosaurus*, but is in a similar position to *Supersaurus* (Fig. 5; Lovelace *et al.* 2008). As noted by Bonaparte & Mateus (1999), the middle-posterior dorsal vertebrae possess an unusual, robust and approximately horizontal accessory lamina (Fig. 3). This extends anteriorly from the hyposphene to near the base of the PCDL and is considered an autapomorphy of *Dinheirosaurus*. It is clearly present on Dv5–9 and there is some evidence for its appearance on Dv4, although the relevant region is poorly preserved.

Very little anatomical information can be gleaned from the remnants of most of the neural spines, but Dv5 and 7 provide some details. Neither appears to be strongly compressed anteroposteriorly, possessing triangular cross-sections, and both lack the paddle-shape present in dicraeosaurids and rebbachisaurids, as well as the triangular aliform processes seen in macronarians (Upchurch 1995, 1998; Wilson 2002). The general impression is that the neural spines were directed posterodorsally (Fig. 3), but this may have been affected by crushing and breakage. There is no evidence for bifurcation of the neural spines (*contra* Bonaparte & Mateus 1999), which is unusual as other flagellicaudatans retain a fairly prominent ‘U’-shaped concavity at least up to Dv6 (Hatcher 1901; Gilmore 1936). However, all sauropods possessing bifurcated dorsal neural spines also have bifid posterior cervical neural spines (McIntosh 1990; Upchurch 1998; Wilson & Sereno 1998), which are absent in *Dinheirosaurus* (see above); as such, the absence of dorsal bifurcation is consistent with the cervical morphology. Thus, *Dinheirosaurus* appears to possess the plesiomorphic diplodocoid condition, present in the putative basal form *Haplocanthosaurus* and retained in rebbachisaurids (Calvo & Salgado 1995; Wilson 2002). The neural spine of Dv5 preserves prominent, asymmetrical SPOLs; on the right side it is a single ridge, whereas it seems to bifurcate ventrally on the left side. Lateral laminae are not present on the neural spine of Dv5 (although this may be the result of damage), but there is a thin spinodiapophyseal lamina (SPDL) on Dv7 (Fig. 3). This SPDL bifurcates ventrally, with the anterior branch extending onto the dorsal surface of the diapophysis. Dorsally, it merges into the lateral surface of the neural spine at approximately midheight. Dv7 preserves a prominent postspinal lamina, but this region is poorly preserved in Dv5.

The dorsal half of a previously undescribed neural spine is also preserved (Fig. 6). Although its exact position along the dorsal sequence is unclear, it probably belongs to a middle-posterior dorsal vertebra (possibly Dv8). All of the surfaces are strongly rugose, indicative of strong ligament/muscle attachments. The rugose anterior surface of the spine remains transversely wide throughout its length and does not form a distinct prespinal lamina (Fig. 6A). Towards the ventral end of the preserved portion, a smooth area lies laterally to this central anterior rugosity, form-

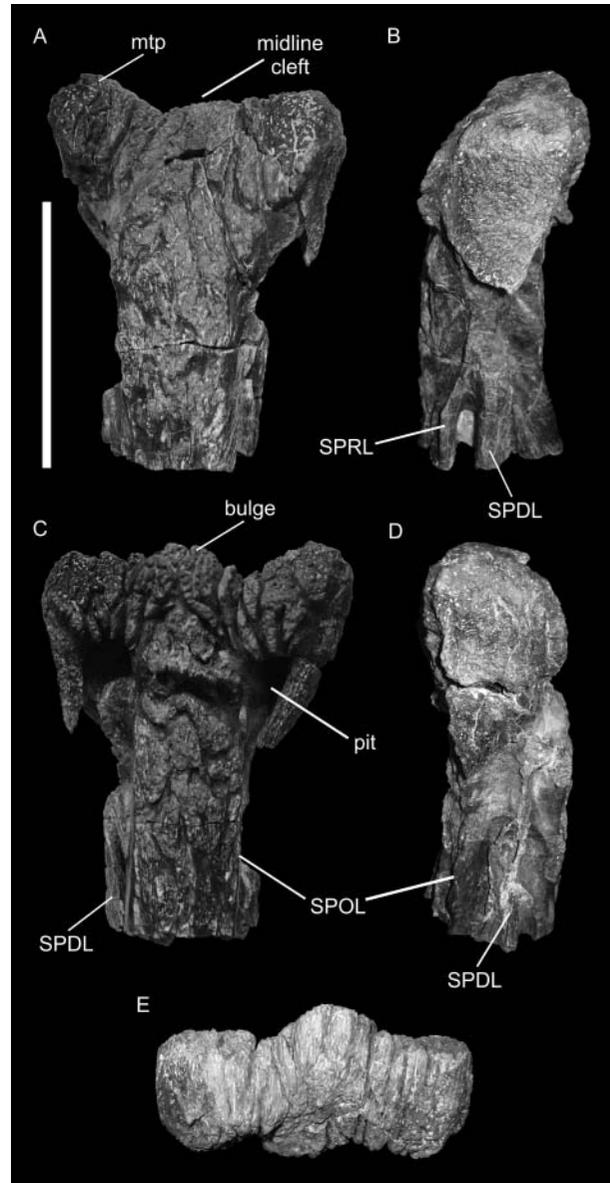


Figure 6. *Dinheirosaurus lourinhanensis* (ML 414) posterior dorsal neural spine in: **A**, anterior; **B**, left lateral, **C**, posterior, **D**, right lateral, and **E**, dorsal (posterior surface at top of image) view. Abbreviations: mtp, metapophysis; SPDL, spinodiapophyseal lamina; SPOL, spinopostzygapophyseal lamina; SPRL, spinoprezygapophyseal lamina. Scale bar = 100 mm.

ing the anterior face of a laterally projecting SPRL. The SPRL curls slightly anteriorly to form a shallow vertical groove between its free margin and the anterior rugosity. It also extends dorsally to merge with what appears to be the base of a broken and much stouter lateral lamina (SPDL). Between the SPRL and the SPDL, a deep vertical slot is present, which is particularly prominent on the left side of the specimen (Fig. 6B). Posterior to the SPDL, there is another smooth area of bone which forms the lateral surface of another ridge or lamina (SPOL). The SPOL is directed

vertically upwards, and in horizontal cross-section the free edge of this lamina points backwards. The smooth lateral surface of the SPOL expands dorsally into a smooth, pit-like area on the posterolateral surface of the spine (Fig. 6C, D). Within the right-hand pit is a small and deep foramen. There is a central rugosity on the posterior surface; this is more prominent towards the midline, becoming a small but sharp ridge near the broken ventral margin of the specimen. Two bulbous projections ('metapophyses') are present on the dorsal surface of the neural spine, one on either side of a shallow, transversely concave central area (Fig. 6A, C, E). A similar cleft is present on the middle-posterior dorsal vertebrae of the diplodocids *Apatosaurus* (*A. excelsus*, *A. louisae* and *A. parvus*), *Barosaurus* and *Diplodocus* (Hatcher 1901; Lull 1919; Gilmore 1936; Ostrom & McIntosh 1966), but is absent in the neural spines of *Supersaurus* (WDC DMJ-021; Lovelace *et al.* 2008) and *Apatosaurus ajax* (NSMT-PV 20375; Upchurch *et al.* 2004b), which possess mildly convex dorsal margins. On the midline, this concave area slopes strongly anteroventrally, and posteriorly it merges into a posterodorsally projecting bulbous process, although this does not extend as far dorsally as the metapophyses (Fig. 6A, C). A comparable bulbous process is also present on Dv8 of *Apatosaurus excelsus* (YPM 1980; Ostrom & McIntosh 1966, pl. 26), but does not appear to be present in other *Apatosaurus* species or other genera. Ventromedially directed processes extend from the lateral margins of the metapophyses and help define the lateral margins of the posterior pits (see above); although incomplete ventrally, it is likely that these processes joined the SPDLs, forming a similar morphology to that seen in *Apatosaurus* (e.g. CM 3018; Gilmore 1936).

Thoracic ribs

A number of previously undescribed thoracic ribs were also found associated with the holotype (Fig. 7; Bonaparte & Mateus 1999).

There are two ribs from the left side of the anterior part of the series. One of these is the proximal plate and top of the shaft (Fig. 7A), whereas the other is the base of the proximal plate and a longer portion from the top of the shaft. The tuberculum is low, and both tuberculum and capitulum possess more prominent ridges than in posterior thoracic ribs (see below). The proximal part of the lateral surface is virtually flat anteroposteriorly, becoming slightly convex distally. Proximally, the shaft has an asymmetrical T-shaped cross-section, with the 'cross-bar' of this 'T' being thin transversely. The short, robust stem of the 'T' forms a medially directed ridge which is situated closer to the anterior margin than the posterior one. This therefore creates two hollows at the proximal end of the shaft, the anterior one being shallower than the posterior one. Passing distally along the shaft, the medial ridge (i.e. the stem of the 'T') gradually widens anteroposteriorly and becomes less prominent so that it fades out into the medial surface of the shaft. Titanosauriform sauropods possess a derived condition in which the shafts of anterior thoracic ribs are widened anteroposteriorly and compressed lateromedially so that they are 'plank'-like (Wilson 2002). Although the incomplete nature of the *Dinheirosaurus* thoracic ribs means that caution is required, the fragments that can be observed suggest that this genus probably possessed the plesiomorphic state.

The proximal end of a right rib from a posterior dorsal vertebra is preserved (Fig. 7B–C). Although slightly

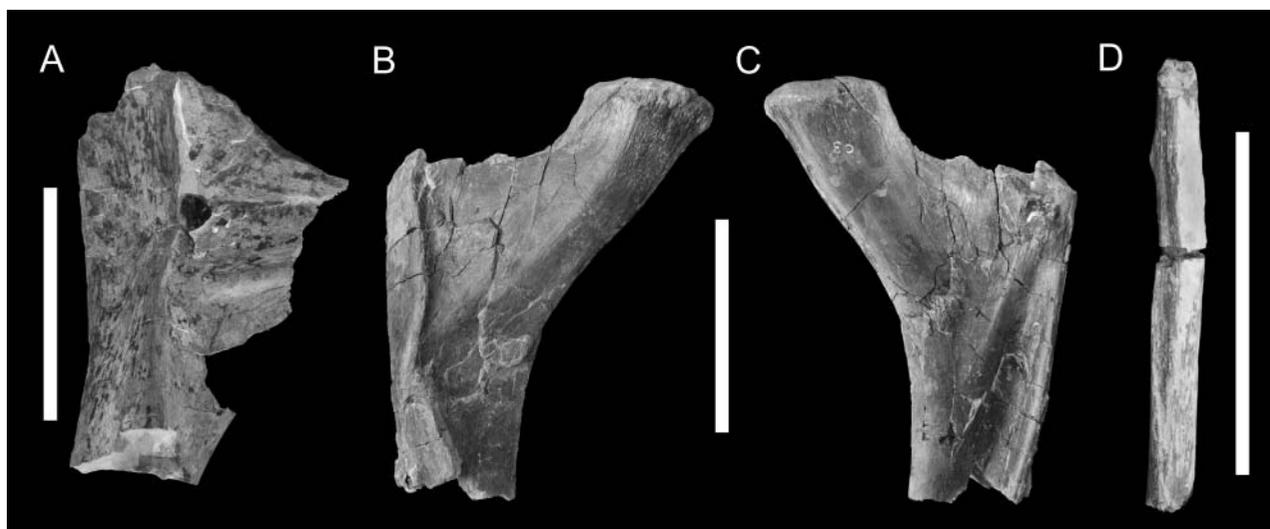


Figure 7. *Dinheirosaurus lourinhanensis* (ML 414) thoracic ribs: **A**, proximal plate of anterior left thoracic rib in posterior view; **B**, proximal plate of posterior right thoracic rib in anterior view; **C**, proximal plate of posterior right thoracic rib in posterior view (same element as B); and **D**, posterior thoracic rib shaft in anterior view. Scale bars = 200 mm.

damaged, the tuberculum is very short dorsoventrally and does not project above the level of the anteroposteriorly thin proximal plate that leads up to the capitulum. In proximal end view, the tuberculum appears to have an approximately rhomboidal or elliptical outline. The capitular process curves strongly dorsomedially and its articular surface faces upwards and slightly medially when the proximal part of the shaft is oriented vertically. This articular surface has an irregular subtriangular outline and is mildly convex both transversely and anteroposteriorly. The posterior face of the capitular process is mildly concave transversely, whereas the anterior face is convex. It has a thickened medial margin and a thin proximolateral edge. The latter connects with the medial edge of the tubercular articular surface, whereas the thickened medial edge becomes anteroposteriorly thinner distally, and eventually merges into the medially directed stem of the 'T'-shaped cross-section at the top of the shaft, as occurs in more anterior thoracic ribs. The posterior surface of the proximal plate is generally concave transversely. This concavity is wide and shallow on the proximal plate, but becomes a narrow, deep slot at the beginning of the shaft. The shallow proximal concavity is divided from the more distal concavity by a rounded dorsolaterally directed ridge. This creates a pocket-like area on the posterior surface of the proximal plate which resembles that in *Euhelopus* (Wilson & Upchurch 2009, fig. 21) and other titanosauriforms, as well as some diplodocids (i.e. *Apatosaurus* [Gilmore 1936] and *Supersaurus* [Lovelace *et al.* 2008]). However, it differs from these taxa in that the ventral part of this pocket is smooth bone that is not pierced by a pneumatic foramen (Wilson & Sereno 1998; Lovelace *et al.* 2008). It is possible that this fossa in the rib of *Dinheirosaurus* represents a developmental and evolutionary precursor to a pneumatic foramen (M. Wedel pers. comm. 2011). The anterior surface of the proximal plate and proximal end of the shaft is also concave transversely, mainly because of the anteriorly directed ridge that forms the remaining portion of the horizontal bar of the 'T'-shaped cross-section. This ridge increases in prominence as it descends from the tuberculum to the top of the proximal part of the shaft.

Another specimen consists largely of rib shaft and its position in the thoracic series is uncertain. Once again, the prominent medial ridge is present and is biased towards the anterior margin, creating an anteromedial and slightly larger posteromedial excavation at the proximal end. Passing distally, this ridge decreases in prominence and gradually approaches the anterior margin so that by the broken distal end the shaft has a laterally compressed, subtriangular horizontal cross-section. This cross-section is formed from a long, straight lateral surface that meets a long, straight medially and slightly posteriorly facing surface at an acute posterior margin. The short anterior margin is slightly concave transversely. Further distally, the posteromedial depression gradually transforms into the broad, flat

medial and slightly posteriorly facing surface. The anteromedial concavity extends distally and as it decreases in width and depth it gradually faces more anteriorly. The anterior margin of the rib bifurcates to form two ridges: the lateral ridge delimits the anterolateral margin, whereas the medial ridge extends down the centre of the anteromedial concavity. These ridges merge with each other close to the broken distal end.

A portion of rib shaft from a posterior dorsal vertebra is also preserved (Fig. 7D). It is transversely compressed throughout its length with a flat lateral surface near the proximal end of the specimen, which becomes very mildly convex anteroposteriorly towards the distal end. The medial surface is much more strongly convex anteroposteriorly near the proximal end but this convexity becomes milder distally. Distally, the shaft becomes more compressed transversely and widens a little anteroposteriorly. The anterior margin is wider than the posterior one at the proximal end. This anterior surface bears a shallow longitudinal groove which seems to fade out at the proximal end, and also fades out distally at approximately three-quarters of the way along the preserved portion of the shaft. Below this, the anterior margin is simply a narrow ridge. A thin, sharp ridge projects posteriorly from the posterolateral margin of the main shaft as a small but separate flange. This feature first appears close to the proximal end of the preserved portion and gradually fades out at about midlength. Below this, the posterior surface is very thin transversely and forms an acute vertical ridge.

Caudal vertebrae

There are several previously undescribed portions of vertebral centra, although anatomical features can only be adequately gleaned from one specimen (Fig. 8). This appears to belong to an anterior caudal vertebra and shows no evidence of fusion to a preceding vertebra, confirming that it is most likely a caudal, rather than sacral, vertebra.

The preserved articular surface of this centrum is moderately concave (Fig. 8A). We interpret this as the anterior surface because the depth of the concavity would be abnormally deep for the posterior articular surface of a sauropod caudal centrum; thus, the vertebra was possibly mildly procoelous as in other flagellicaudatans (McIntosh 1990; Upchurch 1995, 1998). Relative to the expanded articular surface, the middle portion of the centrum is strongly constricted (Fig. 8B–D). The anterior portion of a pneumatic foramen-like opening is present on the left lateral surface and appears to be present on the right side too, but the latter is partially concealed by matrix (Fig. 8C, D). Lateral pneumatic foramina are present in the anterior caudal vertebrae of most diplodocid specimens (Lovelace *et al.* 2008; Upchurch & Mannion 2009), but are absent in other diplodocoids (McIntosh 1990; Upchurch 1995, 1998). The anterior caudal vertebrae of a

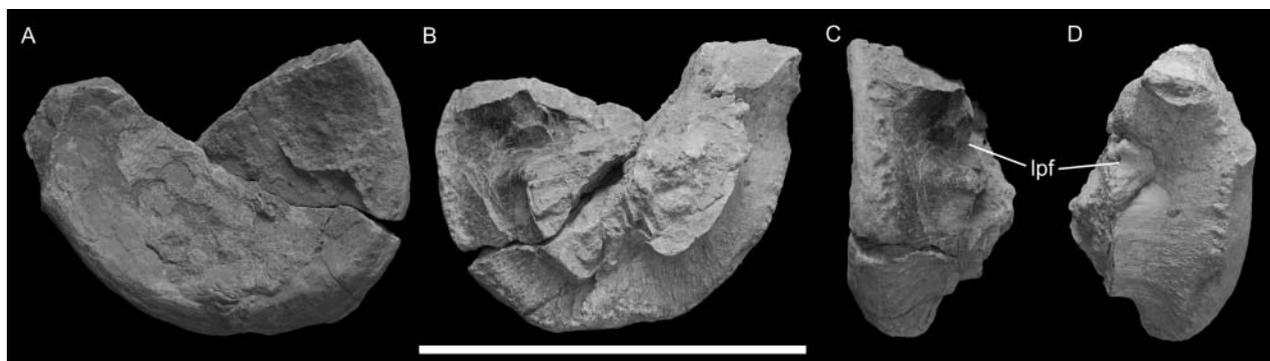


Figure 8. *Dinheirosaurus lourinhanensis* (ML 414) anterior caudal centrum in: **A**, anterior; **B**, posterior; **C**, left lateral; and **D**, right lateral view. Abbreviation: lpf, lateral pneumatic foramen. Scale bar = 300 mm.

number of basal titanosauriforms (e.g. *Giraffatitan*, Janensch 1950; and *Cedarosaurus*, Tidwell *et al.* 1999), *Haplocanthosaurus* (Hatcher 1903) and a basal eusauropod from Madagascar (Mannion 2010) also possess lateral fossae, but these are only gentle excavations. Below this foramen in *Dinheirosaurus*, there is a mildly convex, ventrolaterally facing surface that descends to what appears to be the base of a transversely rounded, longitudinal ridge (Fig. 8B–D). This ventrolateral ridge is present on both sides and the ventral surface in between appears to have been moderately concave transversely, but most of this surface is absent. At the anterior end of the ventral surface there is a broad, D-shaped, rugose area that faces ventrally and slightly posteriorly; this is reminiscent of a single large chevron facet, but the surface is so irregular that its identification is uncertain.

Immediately above the anterior end of the pneumatic foramen, the lateral surface of the centrum expands dorso-laterally in a manner similar to that of the base of a caudal rib (this is best observed on the left side of the specimen) (Fig. 8C, D). The combination of possible procoely, presence of a pneumatic foramen and a caudal rib indicate that this is likely to be a centrum of one of the anteriormost caudal vertebrae and is consistent with interpretations of *Dinheirosaurus* as a diplodocid.

Pubis

A fragment from the distal shaft of a pubis is preserved, but provides no anatomical information.

Gastroliths

More than one hundred gastroliths were found associated with *Dinheirosaurus*, mostly concentrated around the posterior cervical and anterior dorsal vertebrae. These were described in detail by Dantas *et al.* (1998b), and will not be discussed further here.

Additional material referred to *Dinheirosaurus*

Antunes & Mateus (2003) provisionally assigned a middle cervical and a middle dorsal vertebra (both ML 418) from Moita dos Ferreiros, Lourinhã (late Kimmeridgian–early Tithonian), as aff. *Dinheirosaurus*, based on their putative diplodocid affinities. Here we examine these referrals and re-evaluate their taxonomic affinity (Fig. 9). Our description of the dorsal vertebra is based on firsthand observation, but the cervical vertebra was irreparably damaged in the field and our description of that element is based entirely on the figure provided in Antunes & Mateus (2003, fig. 7c). These elements were found in close association.

The cervical vertebra is missing the anterior end of the centrum, but otherwise appears to be complete (Fig. 9A). It is anteroposteriorly elongate and has an EI value of approximately 2.6. An anterodorsally oriented PCDL forms the dorsal margin of an anteroposteriorly elongate lateral pneumatic foramen. The shaft of the cervical rib is not preserved. Prezygapophyses project anterodorsally and there are prominent PRDLs and PODLs (Fig. 9A). The neural spine is relatively low and does not project anteriorly. In terms of its size and neural spine morphology, it most closely resembles Cv7 of *Diplodocus* (Hatcher 1901, pl. 4), though differing in the orientation of the prezygapophyses.

The dorsal vertebra is largely complete, but poorly preserved, and can only be examined in posterior view (Fig. 9B). Its concave cotyle is compressed dorsoventrally, and the height of the neural arch is less than that of the centrum. A hyposphene is present (Fig. 9B), although poor preservation means that it is not possible to tell if the vertebra possesses the autapomorphic accessory lamina seen in *Dinheirosaurus* (see Fig. 3). As in *Dinheirosaurus*, the hyposphene is situated a short distance below midheight of the vertebra (Fig. 9B; note that the dimensions are figured slightly incorrectly in Antunes & Mateus 2003). The diapophyses project mainly laterally

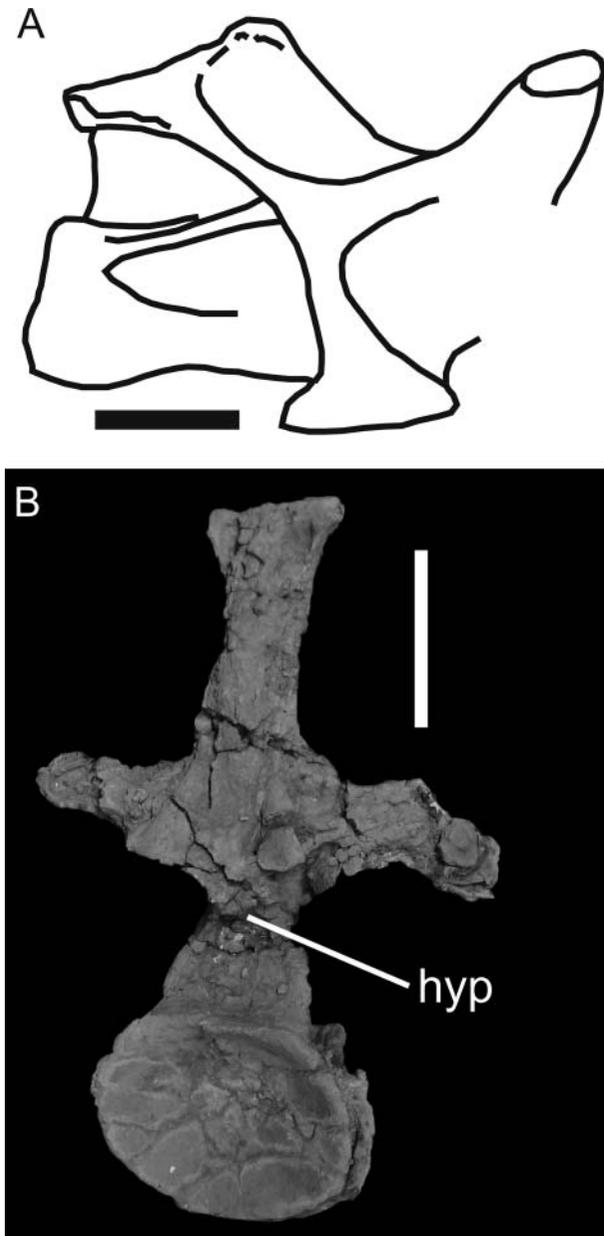


Figure 9. Diplodocidae indet. (ML 418): **A**, cervical vertebra in right lateral view (line drawing); and **B**, dorsal vertebra in posterior view (photograph). Abbreviation: hyp, hyposphene. Scale bars = 200 mm. Part A after Antunes and Mateus (2003).

(Fig. 9B), contrasting with the dorsolaterally projecting processes of *Dinheirosaurus*. The neural spine has a similar morphology to *Dinheirosaurus*, including the posterior pits, dorsolateral expansion, midline cleft and possibly the bulbous process on the dorsal surface (Fig. 9B). In general, the vertebra displays a remarkable similarity to Dv5–6 of *Apatosaurus* (Gilmore 1936, pl. 25), although it lacks any autapomorphies of that taxon (Wilson 2002; Upchurch *et al.* 2004a, b). The combination of a neural spine twice the height of the centrum (a diplodocoid synapomorphy;

Upchurch *et al.* 2004a; Whitlock 2011), along with laterally projecting diapophyses (absent in basal diplodocoids and dicraeosaurids: see above) indicates diplodocid affinities for this specimen. However, the orientation of the diapophyses distinguishes it from *Dinheirosaurus* and, although non-diagnostic, it indicates the presence of a second diplodocid taxon in the Late Jurassic of Portugal.

Diplodocoid intrarelationships and the phylogenetic position of *Dinheirosaurus*

Outgroup choice, terminal taxa and characters

Our cladistic analysis is based on a modified version of the analysis presented by Whitlock (2011). The latter study incorporated 189 characters for 22 ingroup putative diplodocoid taxa; we have modified this in several ways:

1. Addition of 30 characters denoted by either '[added]' or '[new]' after the character number. 'Added' characters come from lists presented in previous studies, whereas 'new' characters have not, to our knowledge, been recognized previously. The original Whitlock (2011) character numbers are tracked as '[Wxxx]' after each revised character number used in the current list (see Online Supplementary Material: Appendix A).
2. Modification of the wording or construction of some characters (denoted by '[modified]' after the character number), in order to clarify state boundaries or avoid problematic gaps between plesiomorphic and derived states. For example, character W165 (Whitlock 2011), scores variation in the ratio of the length of the longest metacarpal (usually Mc. III) to radius length, such that the derived state is defined as a value over 0.45 and the plesiomorphic state is defined as a ratio close to 0.3. However, there are several taxa, e.g. *Apatosaurus* (Mc. III: radius length ratio = 0.40–0.43; Gilmore 1936; Upchurch *et al.* 2004b), that do not fall unambiguously into either of the available states, making them difficult to score without an arbitrary decision by the researcher. When such problems occur, we have adjusted the state definitions to remove such 'gaps'.
3. Deletion of 21 of Whitlock's (2011) characters (see 'Deleted characters' in Online Supplementary Material: Appendix B) because they are autapomorphic, parsimony uninformative (e.g. character W20 has scores solely comprising '?'s and '1's), or likely to be non-independent relative to certain other characters. Bryant (1995) has argued that autapomorphies should not be included in data matrices because they contribute no phylogenetically informative data, while artificially inflating measures of support such as the Consistency Index and Retention Index.

Over-splitting of characters can also over-weight some of the phylogenetically informative information and may bias the results of cladistic analyses. Identification of characters that are non-independent is a difficult issue, although some strategies have been proposed (Wilkinson 1995; Upchurch 1999; O’Keefe & Wagner 2001; Pol & Gasparini 2009). Here, we have argued that certain characters (e.g. W31 and W34) are non-independent because the two characters duplicate the same codings (as represented by ‘0’s and ‘1’s in the matrix) and because it can be argued that there exists a causal relationship between them.

4. Reductive coding is used here, rather than the absence coding used by Whitlock (2011). Although Whitlock (2011) noted some difficulties created by the use of reductive coding, simulation studies (Strong & Lipscomb 1999) indicate that this approach is preferable to absence coding. In practice, this means that the ‘9’s in Whitlock’s (2011) data matrix have been replaced by ‘?’s in our matrix, and some characters have been constructed differently.
5. Insertion of author citations in order to identify the original sources of characters.
6. Rescoring of the character states for several taxa (i.e. *Amazonsaurus*, *Demandasaurus* (= ‘Spanish rebbachisaurid’), *Dinheirosaurus*, *Limaysaurus*, *Losillasaurus*, *Supersaurus* and *Zapalasauros*) on the basis of personal observations of the material by PDM and PU, as well as additional information relating to *Supersaurus* and *Tornieria* in Lovelace *et al.* (2008) and Remes (2007), respectively. Note that the coding of *Demandasaurus* was based only on the material described by Pereda-Suberbiola *et al.* (2003), i.e. prior to the description of additional material by Torcida Fernández-Baldor *et al.* (2011). Whitlock (2011) included codings for scapula characters for *Amphicoelias*; however, the referral of a scapula by Osborn & Mook (1921) was arbitrary (McIntosh 1990) and thus we have rescored these characters as ‘?’s. A full list of altered character state scores (111 changes) is presented in the Online Supplementary Data (Appendix C).
7. Addition of the Chinese Middle Jurassic basal eusauropod *Shunosaurus* as an outgroup taxon. Character state scores for this genus are based on Zhang (1988), Zheng (1991) and personal observations by PU. We added this outgroup in order to clarify, or strengthen, the polarity determinations for certain characters. This enabled the conversion of some parsimony uninformative characters (e.g. W77 that was originally scored entirely as ‘1’s and ‘?’s) into potentially informative ones.

The result of these various changes is a data matrix comprising 198 characters, scored for five outgroup taxa and

22 ingroup putative diplodocoid sauropods (see Online Supplementary Material: Appendix D).

Analytical protocols

The data matrix presented in Appendix D (Online Supplementary Material) was analysed using TNT 1.1 (Goloboff *et al.* 2008). All analyses were run over two stages: (1) an initial phase in which the New Technology Search was used to find a selection of most parsimonious trees (MPTs) via stabilization of the consensus five times; and (2) a second analysis in which the MPTs found during stage 1 were used as the starting topologies for a traditional heuristic search. Both stages 1 and 2 implemented tree bisection-reconstruction (TBR) branch swapping. This two-stage protocol was implemented because the stabilized consensus analysis searches efficiently for a wide range of MPT topologies, but often collects only a small subset of the total number of possible MPTs. The stabilised consensus searches have the advantage that they are more likely to find representative MPTs from each of a number of ‘islands’ of maximum parsimony than the traditional heuristic search (even with TBR branch-swapping). However, the traditional heuristic search collects more of the MPTs once an island of maximum parsimony has been located. Thus, by combining the stabilized consensus search with a traditional heuristic search, we increase the probability that TNT will first discover all or most of the islands of maximum parsimony, and then find all or most of the MPTs within each island. We believe this to be the most effective means of searching tree space when analysing large morphological datasets with TNT.

As noted in Appendix A (Online Supplementary Material), characters 73 and 104 (numbers of cervical and dorsal vertebrae, respectively) are scored as multistate characters that can be treated as unordered or ordered. Here we have examined the consequences of both of these assumptions in Analyses 1 (unordered) and 2 (ordered) (see below).

The ‘pruned trees’ option in TNT was used to identify the least stable taxa in the MPTs. Selected unstable taxa have then been deleted from the MPTs in order to generate strict reduced consensus cladograms (for details of this approach, see Wilkinson 1994).

The support for the phylogenetic relationships was assessed using both Bremer support and bootstrapping (based on 5000 replicates and the Traditional Search) as implemented in TNT. Constrained searches were carried out using TNT, with the resulting MPTs imported into PAUP 4.10b (Swofford 2002) in order to run Templeton’s tests.

Character state mapping has been carried out using TNT and MacClade v.4.08 (Maddison & Maddison 2005).

Analyses and results

Analysis 1 (characters 73 and 104 unordered) yielded a total of eight MPTs of 336 steps in length. The strict consensus tree of these eight MPTs is shown in Fig. 10, and a strict reduced consensus cladogram (produced via the a

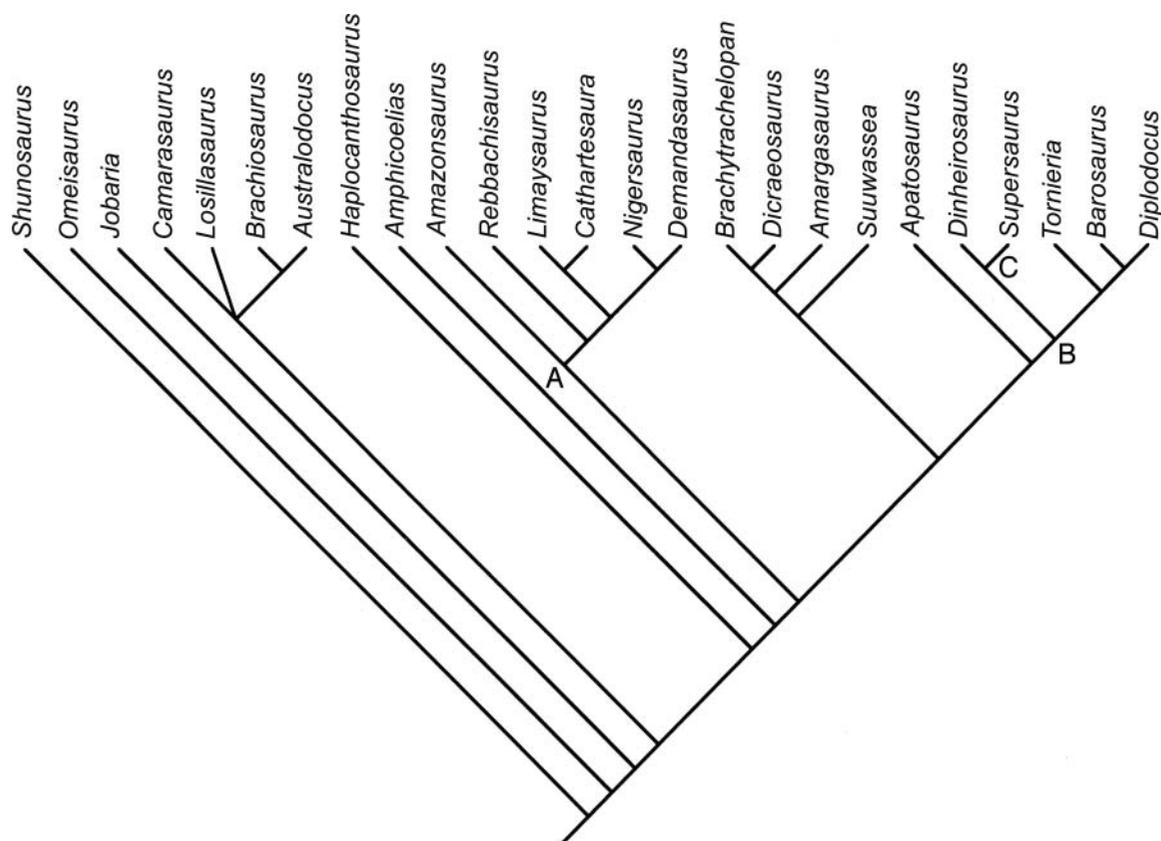


Figure 11. Strict reduced consensus cladogram generated via the a posteriori deletion of *Histriasaurus* and *Zapalasaurus* from the eight MPTs recovered by analysis 1. The synapomorphies for nodes A–C are discussed in the main text.

20 MPTs of 340 steps (i.e. four steps longer than the unconstrained MPTs). In all of the constrained topologies, *Dinheirosaurus* is the sister taxon to Flagellicaudata, and the relationships within the latter clade are identical to those shown in Fig. 10. Application of a Templeton's test yields p -values of 0.16–0.64, indicating that these constrained topologies are not statistically significantly worse explanations of the data than the unconstrained MPTs. When the constraint is applied and characters 73 and 104 are ordered, TNT recovers 80 MPTs of 345 steps (i.e. four steps longer than the original unconstrained MPTs). *Dinheirosaurus* again forms the sister taxon to Flagellicaudata in all of these 80 MPTs, and the altered position of *Dinheirosaurus* does not affect the relationships within the latter clade. Application of a Templeton's test produced p -values of 0.25–0.51, indicating that the constrained MPTs are not a statistically significantly worse explanation of the data than the unconstrained MPTs.

Character state mapping

We have restricted our detailed consideration of character state mapping to those parts of the MPTs which depart most radically from the results obtained by Whitlock (2011) (i.e. the placement of *Amazonsaurus* as a

basal rebbachisaurid) and those that are directly relevant to the relationships of *Dinheirosaurus*. We therefore focus on three nodes in the cladograms shown in Figs 10–13: Node A (*Amazonsaurus* + other rebbachisaurids); Node B (*Dinheirosaurus* + *Supersaurus* + other diplodocines); and Node C (*Dinheirosaurus* + *Supersaurus*). We have also used character state mapping to identify the local autapomorphies that characterize *Dinheirosaurus* (see also 'Description and Comparisons'). Unless stated otherwise, all of the characters mentioned below provide unequivocal support to the specified node: that is, their states have the same distribution under both accelerated and delayed transformation optimization (ACCTRAN and DELTRAN), and they have individual consistency indices of 1.0.

In both Analyses 1 and 2, Node A (*Amazonsaurus* + other rebbachisaurids) is supported by characters 142 (hyposphenal ridge on anterior caudal vertebrae is absent [reversed in *Demandasaurus*]) and 154 (middle caudal centra have subtriangular articular faces that are widest along their ventral margins [reversed in *Demandasaurus*]). In Analysis 2, character 163 (absence of the bridge of bone over the haemal canal in most or all chevrons) also supports Node A under DELTRAN only, but this could be the retention of a plesiomorphic state: interpretation of the

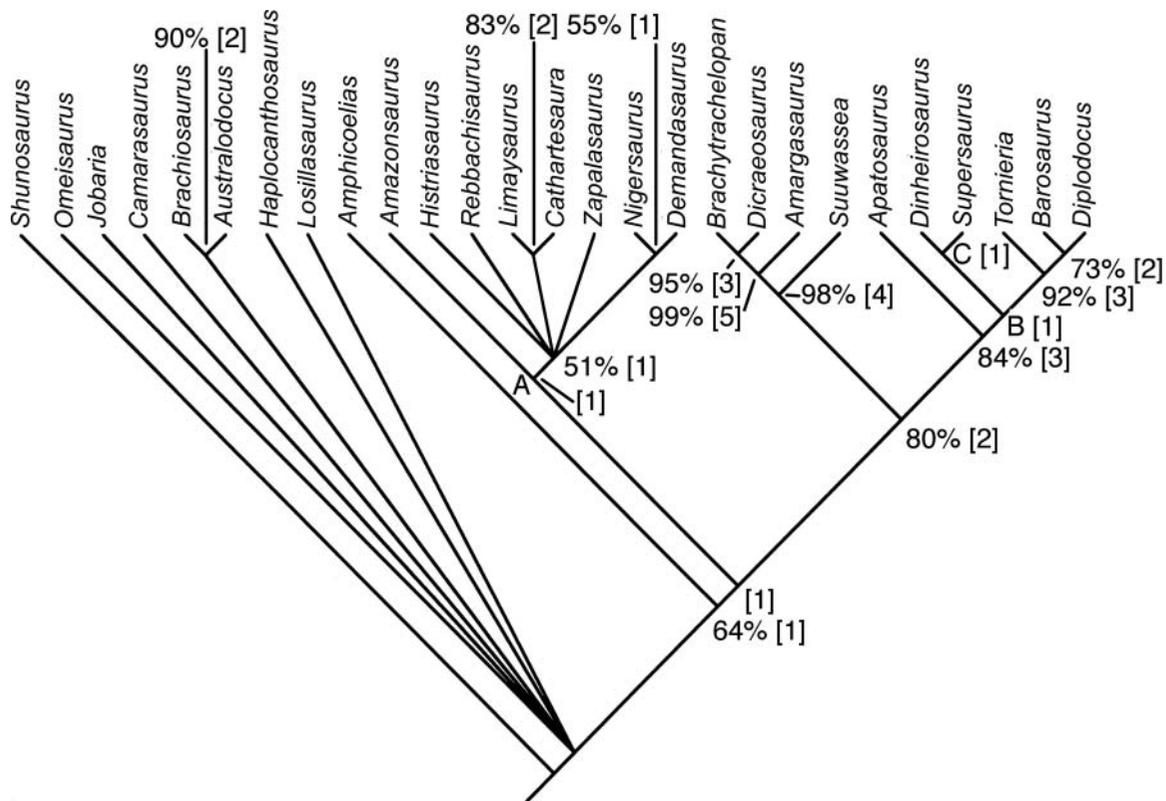


Figure 12. Strict consensus cladogram generated from the 52 MPTs recovered by analysis 2 (see main text for details). Bootstrap values are shown as percentages (nodes lacking percentages have bootstrap values of less than 50%). Bremer supports are shown in square brackets. The synapomorphies for nodes A–C are discussed in the main text.

evolution of this character depends on whether *Haplocanthosaurus* is the most basal diplodocoid or is placed within the outgroups.

Support for Node B (*Dinheirosaurus* + *Supersaurus* + other diplodocines) depends on the treatment of characters 73 and 104. In Analysis 1, only character 99 (dorsoventrally elongate coel on the lateral surfaces of the neural spines of posterior cervicals) unequivocally supports this node, and character 139 (deep pneumatopores in the lateral surfaces of anterior caudal centra) supports it under DELTRAN only. The same character state distributions occur in the MPTs produced by Analysis 2, except that character 110 (ventral keel on anterior dorsal vertebrae) also provides unequivocal support for Node B.

Node C (*Dinheirosaurus* + *Supersaurus*) is supported by characters 115 (pneumatic foramina [= ‘pleurocoels’] in middle and posterior dorsal vertebrae are divided by a vertical rod-like strut) and 116 (accessory lamina links the PCDL and PCPL in middle and posterior dorsal vertebrae) in both Analyses 1 and 2.

In Analyses 1 and 2, the local autapomorphies of *Dinheirosaurus* are reconstructed as characters 95 (subvertical lamina links the PCDL and PODL in posterior cervicals [DELTRAN only]), 97 (posterior cervical neural spines

are unbifurcated), and 108 (dorsal transverse processes directed dorsolaterally [DELTRAN only]). Because these are local autapomorphies, all three of these characters have individual CIs of 0.5 or lower. For example, as noted above, the unbifurcated posterior cervical neural spines and dorsolaterally directed dorsal transverse processes are widespread among basal diplodocoids such as *Haplocanthosaurus* and rebbachisaurids, and therefore represent reversals in *Dinheirosaurus*.

Discussion

The phylogenetic relationships of *Dinheirosaurus*

The two previous phylogenetic analyses that have included *Dinheirosaurus* (Rauhut *et al.* 2005; Whitlock 2011) have placed this genus within the Diplodocidae, closer to Diplodocinae than *Apatosaurus*. The precise relationships of *Dinheirosaurus*, however, have remained unclear: it typically forms a polytomy with *Tornieria* and the *Barosaurus* + *Diplodocus* lineage. Here, however, revision of character scores and addition of some new characters (particularly

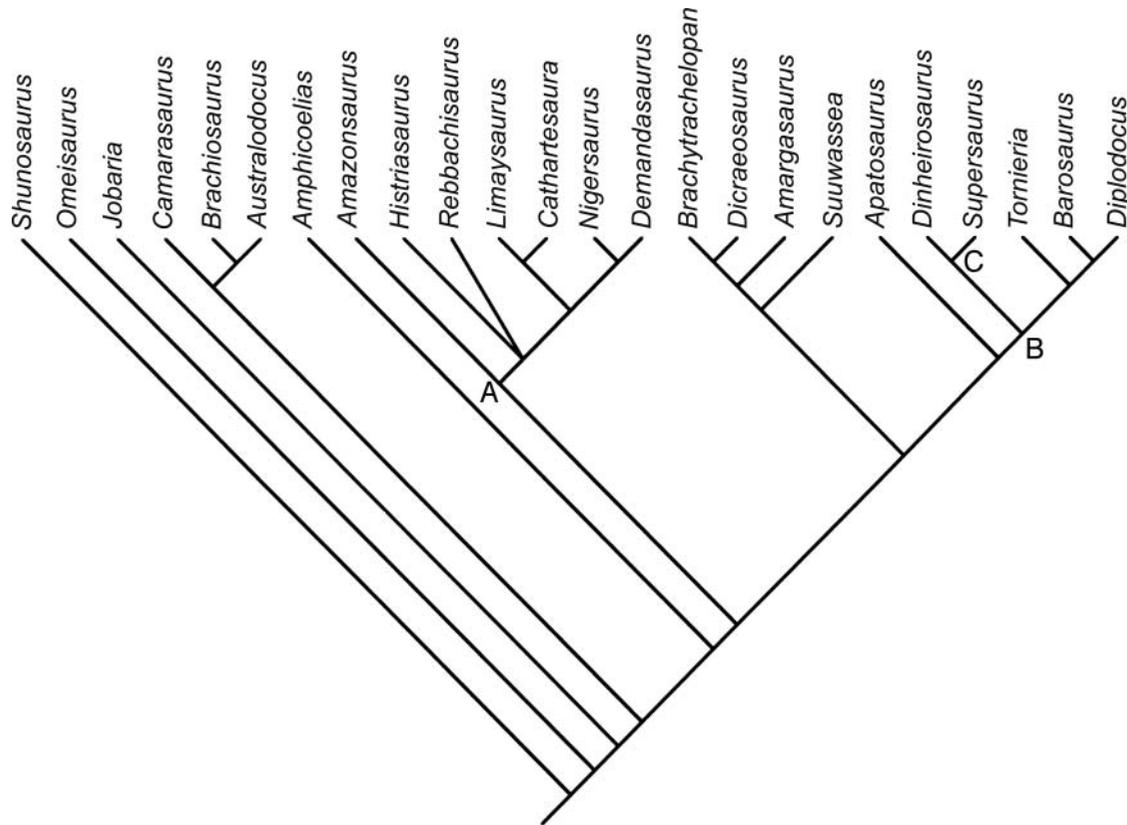


Figure 13. Strict reduced consensus cladogram generated via the a posteriori deletion of *Haplocanthosaurus*, *Histriasaurus* and *Losiliasaurus* from the 52 MPTs recovered by analysis 2. The synapomorphies for nodes A–C are discussed in the main text.

those relating to similarities shared by *Dinheirosaurus* and *Supersaurus*), have produced a fully resolved set of relationships for Diplodocidae. According to these results (see Figs 10–13), *Dinheirosaurus* is the sister taxon to *Supersaurus*, and this clade in turn forms the sister taxon to other diplodocines (*Tornieria* + *Barosaurus* + *Diplodocus*). This interpretation of the relationships of *Dinheirosaurus*, however, should be regarded as provisional. *Dinheirosaurus* is relatively incomplete (13% complete based on the character completeness metrics of Mannion & Upchurch 2010), as are *Supersaurus* (35%) and to a lesser extent *Tornieria* (51%). These large proportions of missing data contribute to the relatively low Bremer supports and bootstrap values for Nodes B and C in Figs 10 and 12. Moreover, the current position for *Dinheirosaurus* necessitates a number of character state reversals and convergences, some of which might be unlikely given our current knowledge of sauropod evolution. For example, if the placement of *Dinheirosaurus* within Flagellicaudata is correct, then this provides the only clear example of the loss of bifurcation of posterior cervical neural spines. The single cervical and dorsal neural spines, lack of anteroposterior shortening in centra along the dorsal sequence, and dorsolaterally directed transverse processes of dorsal vertebrae, are consistent with a

more basal position for *Dinheirosaurus* within Diplodocidae; however, these character states are currently outnumbered by those which support the diplodocine interpretation. Nevertheless, only four additional steps are required to place *Dinheirosaurus* outside of Flagellicaudata, and this decrease in parsimony is not statistically significant according to Templeton's tests. The discovery of more complete specimens of *Dinheirosaurus* will play a key role in testing its current relationships, and there are grounds for suspecting that such new data will result in this taxon shifting to a different position within the Diplodocoidea.

The phylogenetic relationships of other diplodocoids

Although *Dinheirosaurus* forms the focus of the current study, it is clear that our results have implications for the wider phylogenetic relationships of diplodocoids. In general, our dataset produces less well-resolved results than those obtained by Whitlock (2011): the latter recovered just three MPTs, whereas our analyses recovered eight (ordered) and 52 (unordered) MPTs. This increased number of MPTs is largely caused by the destabilization of *Haplocanthosaurus* in Analysis 2, and poorer resolution of

rebbachisaurid relationships. However, in terms of flagellicaudatan relationships our MPTs are more highly resolved than those found by Whitlock (2011) and all other previous analyses.

Haplocanthosaurus has proved to be a problematic taxon throughout most of the history of the application of cladistic analysis to sauropod phylogeny. To date, this genus has been recovered variously as a non-neosauropod eusauropod (Upchurch 1998; Rauhut *et al.* 2005; Harris 2006), a macronarian (Upchurch 1995; Wilson & Sereno 1998; Casanovas *et al.* 2001; Upchurch *et al.* 2004a) and a basal diplodocoid (Calvo & Salgado 1995; Wilson 2002; Salgado *et al.* 2004, 2006; Barco *et al.* 2006; Remes 2006; Sereno *et al.* 2007; Lovelace *et al.* 2008; Whitlock 2011). Our analyses demonstrate that the position of *Haplocanthosaurus* is highly sensitive to the treatment of the multi-state characters that score for numbers of cervical and dorsal vertebrae. When these characters (numbers 73 and 104) are treated as unordered, *Haplocanthosaurus* is the most basal diplodocoid, as proposed by several previous authors (see above). However, ordering of these characters results in *Haplocanthosaurus* taking up a number of different positions within the outgroups in the majority of MPTs (see above). In some MPTs, *Haplocanthosaurus* is the most basal diplodocoid, in others it is a macronarian, and in still others it is a relatively basal eusauropod (being placed as the sister taxon to *Omeisaurus* + all other taxa except *Shunosaurus*). The relationships of *Haplocanthosaurus* require further examination in the context of a more general analysis of sauropod phylogeny. It is worth noting, however, that one of the potential problems with this taxon is that its character state scores usually incorporate information from two species, *H. priscus* (the type species: Hatcher 1903) and *H. delfsi* (McIntosh & Williams 1988). If these two species are not congeneric (see analyses by Calvo & Salgado 1995; Gallina & Apesteguía 2005), then the character data for '*Haplocanthosaurus*' may be chimeric. Furthermore, new material of a *Haplocanthosaurus*-like animal (Bilbey *et al.* 2000) includes many parts of the postcranial skeleton that are currently unknown in the type species and referred specimens, and may eventually shed light on both the congeneric status of the two existing species and their wider phylogenetic relationships. Future analyses should consider tackling such problems through species or specimen-level analyses (e.g. Upchurch *et al.* 2004b). For the present, however, the results of Analysis 2 indicate that the recognition of *Haplocanthosaurus* as the most basal diplodocoid should be treated with caution.

Amazonsaurus was found to be a basal flagellicaudatan by Salgado *et al.* (2004), a macronarian by Rauhut *et al.* (2005), a rebbachisaurid by Salgado *et al.* (2006) and Carballido *et al.* (2010b), and a basal diplodocoid by Whitlock (2011). Here, however, our cladistic analysis finds it to be the most basal rebbachisaurid, supported by two characters pertaining to caudal vertebrae (numbers 142

and 154; see above). *Amazonsaurus* is extremely incomplete (completeness score = 11% according to Mannion & Upchurch 2010), which contributes to the relatively weak Bremer support and bootstrap values for Node A (Rebbachisauridae) in Figs 10 and 12.

The relationships among the Rebbachisauridae are poorly resolved in the strict consensus cladograms (Figs 10 and 12). However, application of reduced consensus methods indicates that there is more agreement among the topologies than implied by the strict consensus cladograms. In all MPTs, *Nigersaurus* is the sister taxon to *Demandasaurus* (forming the Nigersaurinae of Whitlock 2011), *Limaysaurus* is the sister taxon to *Cathartesaura* (forming the Limaysaurinae of Whitlock 2011), and the Limaysaurinae and Nigersaurinae are sister taxa (see the reduced strict consensus cladograms in Figs 11 and 13). Moreover, *Rebbachisaurus* is consistently placed as the sister taxon to the Limaysaurinae + Nigersaurinae clade. The poor topological resolution is caused by the instability of *Histriasaurus* and *Zapalasaurus*. Inspection of the original MPTs indicates that *Histriasaurus* always lies outside of the Limaysaurinae + Nigersaurinae clade, whereas *Zapalasaurus* lies outside of this clade in most MPTs, but occasionally clusters with the Nigersaurinae. The placement of *Histriasaurus* is consistent with all previous analyses to have included it (Sereno *et al.* 2007; Carballido *et al.* 2010b; Whitlock 2011). *Zapalasaurus* has proven to be an unstable taxon: Salgado *et al.* (2006) recovered it as a basal diplodocoid, whereas it was placed at the base of Limaysaurinae by Sereno *et al.* (2007) and Carballido *et al.* (2010b), and as the basal-most member of the Nigersaurinae in Whitlock (2011). As with *Amazonsaurus*, the fluctuating position of *Zapalasaurus* most likely relates to its incompleteness (completeness score = 17% according to Mannion & Upchurch 2010) and poor preservation.

Some authors (Sereno *et al.* 2007; Carballido *et al.* 2010b; Whitlock 2011) have commented on the potential biogeographic significance of the existence of a South American Limaysaurinae and Afro-European Nigersaurinae forming sister clades: the initial division between Limaysaurinae and Nigersaurinae may reflect vicariance between South America and Africa, and the occurrence of *Demandasaurus* may indicate dispersal from Africa to Europe in the Early Cretaceous. However, our results are inconsistent with the vicariance component of this biogeographic scenario for two reasons. Firstly, the South American *Zapalasaurus* does not cluster with Limaysaurinae, but instead lies either outside of the Limaysaurinae + Nigersaurinae clade or clusters with the Nigersaurinae (see also Whitlock 2011). Secondly, the South American *Amazonsaurus* and African *Rebbachisaurus* consistently lie outside of the Limaysaurinae + Nigersaurinae clade. Additionally, the main dispersal direction between Europe and Africa may have been southward (see also Gheerbrant & Rage 2006), on the basis that the oldest currently known

rebbachisaurid occurrences are from Europe (Dalla Vecchia 1998; Sereno & Wilson 2005; Mannion 2009) and that *Histriasaurus* is consistently recovered in a more basal position than African rebbachisaurids. These results suggest that the palaeobiogeographic history of rebbachisaurids may have been more complex than previously proposed. Once again, however, caution is required when interpreting evolutionary history based on the current relationships of rebbachisaurids. Many of the taxa are highly incomplete (e.g. *Amazonsaurus* and *Zapalasauros*; see also Turner *et al.* (2009) for issues pertaining to missing data in biogeographic analysis), there is a 30 million year ghost lineage extending back from the Hauterivian to the Late Jurassic (Upchurch & Barrett 2005; Sereno *et al.* 2007), and there are also some curious instances of character state reversals and convergence implied by the MPTs (e.g. the apparent re-invention of the caudal hyposphenal ridge, and reversion to subcircular articular faces in middle caudal centra, in *Demandasaurus*). Fortunately, at least some forms, such as *Rebbachisaurus* and *Demandasaurus*, are known from more material than has been described in the literature to date (Lavocat 1954; Pereda-Suberbiola *et al.* 2003; see Torcida Fernández-Baldor *et al.* 2011); thus, there is some

hope that the resolution of rebbachisaurid intrarelationships will improve in the near future.

Review of the European diplodocoid fossil record

Below we outline and discuss all putative diplodocoid occurrences from Europe, beginning with the earliest known examples from the UK. We also attempt to determine the taxonomic status of each individual based on the phylogenetic information content of their anatomical characters. Table 3 provides a summary of these specimens and their taxonomic affinities. Figure 14 shows the distribution of genuine diplodocoid occurrences.

United Kingdom. The oldest remains ascribed to diplodocoids come from the Middle Jurassic of England. '*Cetiosaurus glymptonensis* was named by Phillips (1871) based on nine middle-posterior caudal vertebrae (OUMNH J13750-13758) from the late Bathonian of Oxfordshire. Upchurch & Martin (2003) noted that these caudal centra have higher length:height ratios than most sauropods, but comparable to the lowest values seen in diplodocoids. These authors also highlighted the presence of two

Table 3. Summary of all putative European diplodocoids, including geographical and stratigraphical ranges (based on updates to Mannion, Upchurch, Carrano *et al.* 2011), as well as taxonomic affinities. Diplodocoids are highlighted in bold. Abbreviations: MJ = Middle Jurassic; LJ = Late Jurassic; EK = Early Cretaceous. References are provided where there may be some ambiguity as to which specimen is being referred to.

Specimen	Country	Stratigraphic range	Taxonomic affinity
' <i>Cetiosaurus glymptonensis</i>	UK	Late Bathonian (MJ)	Eusauropoda
<i>Cetiosauriscus stewarti</i>	UK	Callovian (MJ)	Eusauropoda
NHMUK R.1967	UK	Callovian (MJ)	Neosauropoda
Bexhill metacarpal	UK	Valanginian–Barremian (EK)	Sauropoda
MIWG 6544 and teeth	UK	Barremian (EK)	Rebbachisauridae
MIWG 5384	UK	Barremian (EK)	Rebbachisauridae
NHMUK R.8924	UK	Barremian (EK)	Eusauropoda
NHMUK R.9224	UK	Barremian (EK)	Titanosauriformes
NHMUK R.11187	UK	Barremian (EK)?	Eusauropoda
MIWG 6593	UK	Barremian (EK)	Sauropoda
NHMUK R.10141	UK	Barremian (EK)	Sauropoda
NHMUK unnumbered (Blows 1998)	UK	Barremian (EK)	Titanosauriformes
Caudal centrum (Gabunia <i>et al.</i> 1998)	Georgia	Middle Oxfordian (LJ)	Diplodocinae
' <i>Cetiosauriscus greppini</i>	Switzerland	Early Kimmeridgian (LJ)	Eusauropoda
Teeth (Malafaia <i>et al.</i> 2006)	Portugal	Late Kimmeridgian–early Tithonian (LJ)	Diplodocoidea
<i>Dinheirosaurus</i>	Portugal	Late Kimmeridgian–early Tithonian (LJ)	Diplodocidae
ML 418	Portugal	Late Kimmeridgian–early Tithonian (LJ)	Diplodocidae
Tooth (Martínez <i>et al.</i> 2000)	Spain	Kimmeridgian–Tithonian (LJ)	Neosauropoda
Caudal centrum (Ruiz-Omeñaca <i>et al.</i> 2008)	Spain	Kimmeridgian–Tithonian (LJ)	Diplodocidae
MCNV unnumbered ('La Serranía sauropod')	Spain	Oxfordian–Tithonian (LJ)	Sauropoda
Ilium (Royo-Torres & Cobos 2004)	Spain	Middle Tithonian–early Berriasian (LJ–EK)	Sauropoda
Caudal centrum (Royo-Torres <i>et al.</i> 2009)	Spain	Middle Tithonian–early Berriasian (LJ–EK)	Diplodocinae
Tooth (Canudo <i>et al.</i> 2005)	Spain	Middle Tithonian–early Berriasian (LJ–EK)	Neosauropoda
<i>Losillasaurus</i>	Spain	Middle Tithonian–early Berriasian (LJ–EK)	Eusauropoda
<i>Demandasaurus</i>	Spain	Late Barremian–early Aptian (EK)	Rebbachisauridae
<i>Histriasaurus</i>	Croatia	Late Hauterivian–early Barremian (EK)	Rebbachisauridae

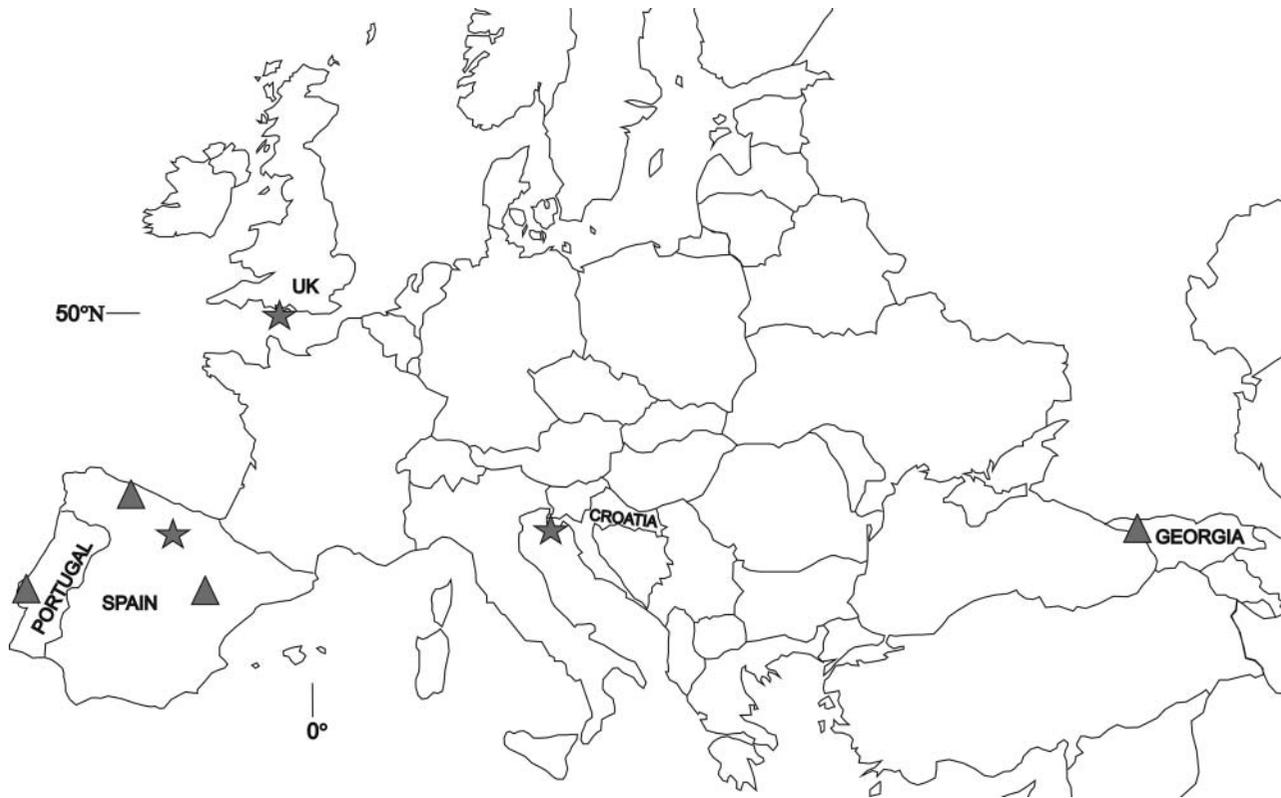


Figure 14. Map of Europe showing distribution of diplodocoid specimens. Symbols: star = rebbachisaurid; triangle = diplodocid.

horizontal ridges on the lateral surfaces of the centra; a similar pattern of ridges is present on the middle caudal vertebrae of *Demandasaurus* (Pereda-Suberbiola *et al.* 2003; see below). Thus, based on these features, it is possible that '*Cetiosaurus*' *glymptonensis* represents the earliest known diplodocoid (Upchurch & Martin 2003; Upchurch *et al.* 2004a), but more complete material is required to confirm this (see also Whitlock 2011).

Cetiosauriscus stewarti (NHMUK R.3078), from the Callovian (Middle Jurassic) of Cambridgeshire, England (Woodward 1905; von Huene 1927; Charig 1993), has been considered a diplodocoid by a number of authors (Charig 1980; Berman & McIntosh 1978; McIntosh 1990; Upchurch 1995; Upchurch *et al.* 2004a). However, the only studies to have included *Cetiosauriscus* in a phylogeny recovered it as a non-neosauropod eusauropod (Heathcote & Upchurch 2003; Rauhut *et al.* 2005), a position agreed upon here. Woodward (1905) also assigned a series of 10 elongate, biconvex distal caudal vertebrae (NHMUK R.1967) from the same deposits to *Cetiosauriscus*, but there is no recorded association and no anatomical overlap; thus there is no basis for this referral (Upchurch *et al.* 2004a; Naish & Martill 2007). A biconvex morphology is present in the distal caudal vertebrae of both diplodocoids and saltasaurid titanosaurs (Calvo & Salgado 1995; Upchurch 1995; Wilson *et al.* 1999). However, the length:height ratio

of the caudal vertebrae of NHMUK R.1967 is lower than in diplodocoids (see also Whitlock 2011) and closer to the condition found in saltasaurids (Wilson *et al.* 1999), whereas the central position of the neural arches differs from the anteriorly positioned arches found in titanosauriforms, but is comparable to diplodocoids. Although it is possible that it represents a basal diplodocoid (see also Harris 2006), NHMUK R.1967 should be considered an indeterminate neosauropod, with the combination of moderately elongate distal caudal vertebrae and a centrally positioned neural arch being plesiomorphic for this clade.

An isolated metacarpal from Valanginian–Barremian deposits of Bexhill, East Sussex, has previously been considered to represent a diplodocid (Naish & Martill 2007, p. 499); however, this specimen cannot even be referred to the less exclusive Diplodocoidea, and should be regarded as an indeterminate sauropod (Upchurch & Mannion 2009, p. 1204).

Numerous remains from the Barremian (Early Cretaceous) of the Isle of Wight, England, have been referred to the Diplodocoidea. Sereno & Wilson (2005, p. 170) suggested that teeth (figured by Naish & Martill 2001, pl. 36) were referable to Rebbachisauridae, and this assignment is tentatively followed here. Definitive rebbachisaurid remains are known from the UK, with an incomplete

scapula (MIWG 6544) from a nearby locality and the same stratigraphical level as that of the aforementioned teeth (Mannion 2009). Upchurch (1995, p. 382) suggested an anterior caudal vertebra (MIWG 5384) may have flagellicaudatan affinities, although the specimen represents a rebbachisaurid, with close affinities to the Nigersaurinae (Mannion, Upchurch, & Hutt 2011).

Several other specimens from the Barremian of the Isle of Wight have also been referred to the Diplodocoidea. Charig (1980) assigned an isolated skid-like chevron (NHMUK R.8924) to the Diplodocidae; however, this referral cannot be substantiated, as this morphology is also present in dicraeosaurids, as well as a number of basal eusauropods (Upchurch & Mannion 2009, pp. 1204–1205). Additionally, Charig (1980, p. 238) briefly mentioned a middle-posterior caudal centrum (NHMUK R.9224) that he noted shared similarities with *Diplodocus*. The centrum is mildly amphicoelous and the preserved base of the neural arch is situated anteriorly; this combination is frequently observed in titanosauriforms (Calvo & Salgado 1995; Upchurch 1995, 1998) and NHMUK R.9224 should thus be provisionally considered an indeterminate member of that clade. Upchurch (1995, p. 382) listed a large right metatarsal I (NHMUK R.11187) with putative flagellicaudatan affinities. There is some suggestion that the metatarsal may actually be from the Late Jurassic Oxford Clay of Bedfordshire, rather than the Early Cretaceous of the Isle of Wight. This element is robust, with a D-shaped proximal outline, and possesses a laterodistal process. The latter is a feature of diplodocoids (Berman & McIntosh 1978), but is also present in brachiosaurids and some Chinese eusauropods (Upchurch 1998). The only proposed diplodocid synapomorphy pertaining to metatarsal I (presence of a rugosity on the dorsolateral surface of the distal end; Upchurch *et al.* 2004a) is absent in NHMUK R.11187; thus, this element should be considered an indeterminate eusauropod. A fragmentary portion of ischium (MIWG 6593) was also tentatively suggested to belong to a diplodocid (Naish & Martill 2001, p. 234), but shows no synapomorphies of that clade and should be regarded as an indeterminate sauropod. Lastly, Blows (1998, p. 34) mentioned an additional ‘metatarsal’ (NHMUK R.10141) and a tooth (NHMUK unnumbered), which he regarded as indeterminate diplodocids. The former is missing its proximal end but actually appears to be a metacarpal and probably Mc. IV, based on the prominent ridges along the lateral and medial margins (Apesteguía 2005); however, no diplodocid synapomorphies are currently known for metacarpals (Upchurch & Mannion 2009, p. 1204) and NHMUK R.10141 should thus be considered an indeterminate sauropod. Only the crown of the tooth is preserved. This element lacks labial grooves or a lingual concavity, is curved lingually and has a strongly convex labial surface, indicating neosauropod affinities (Upchurch 1998). As preserved, it has a Slenderness Index

(SI) of 3 (crown length divided by maximum mesiodistal width), which is considerably lower than in titanosaurs and diplodocoids (Upchurch 1998). Overall, the tooth most closely resembles those of titanosauriforms; this position is consistent with the SI and thus we regard this element as belonging to an indeterminate member of that clade.

Georgia. Gabunia *et al.* (1998) described an isolated anterior-middle caudal centrum from the middle Oxfordian (Late Jurassic) of Abkhazia, western Georgia. These authors considered it to represent a diplodocine, based on its mild procoely and the presence of a lateral fossa. The anterior caudal vertebrae of some non-diplodocid taxa also possess shallow lateral fossae, but these tend to disappear early on in the sequence (e.g. the titanosauriform *Cedarosaurus* only possesses shallow fossae in Cd1–5; Tidwell *et al.* 1999). Some saltasaurids retain shallow lateral fossae in their middle caudal vertebrae (NHMUK R.2359; Upchurch & Mannion 2009), but these vertebrae are prominently procoelous. The Georgian specimen has similar dimensions to Cd13 of *Apatosaurus* (NSMT-PV 20375; Upchurch *et al.* 2004b, pl. 6), which is consistent with its placement as an anterior-middle caudal vertebra; this, combined with the absence of prominent procoely, thereby supports its diplodocid affinities. Furthermore, the caudal vertebra displays one feature comparable to the diplodocine *Tornieria*, in that the lateral fossa is restricted to the dorsal third of the centrum (Remes 2006). The vertebra lacks the ventral excavations of *Tornieria* but it is possible that it belongs to a clade of *Tornieria*-like diplodocines; thus, the specimen is here considered an indeterminate putative diplodocine and represents the earliest known diplodocid. This provides support for the view that the three diplodocid clades originated at least at the start of the Late Jurassic, and probably in the Middle Jurassic (Upchurch & Martin 2003; Upchurch & Barrett 2005; Harris 2006; Remes 2006, 2007; Whitlock 2011), rather than towards the end of the Late Jurassic (Carballido *et al.* 2010b).

Switzerland. ‘*Cetiosauriscus*’ *greppini* is known from the disarticulated remains of at least three individuals from the early Kimmeridgian (Late Jurassic) of north-western Switzerland (Schwarz *et al.* 2007b). Originally described by von Huene (1922) as ‘*Ornithopsis*’ *greppini*, these remains were then referred to *Cetiosauriscus* (von Huene 1927), which, as discussed above, has been incorrectly considered a diplodocid by some workers. However, ‘*Cetiosauriscus*’ *greppini* is distinct from *Cetiosauriscus stewarti* and is here considered a non-neosauropod eusauropod, deserving a new generic name (Schwarz *et al.* 2007b).

Portugal. In addition to *Dinheirosaurus* and remains previously attributed to it (see above), Malafaia *et al.* (2006) listed the presence of diplodocid teeth from late

Table 4. Ratios of the transverse width divided by the anteroposterior length of humeral mid-shaft cross sections for a range of sauropods. Museum accession numbers denote those specimens examined by the authors firsthand, or where there may be some ambiguity as to which specimen is being referred to. Rebbachisaurids, including the putative Late Jurassic form ('La Serranía sauropod'), are highlighted in bold.

Taxon	Ratio	Reference
'El Chocón rebbachisaurid' (MMCH-PV 49)	1.54	PDM pers. obs. (2009)
<i>'Eobrontosaurus'</i> (PALEON 001)	1.39	PDM pers. obs. (2008)
'La Serranía sauropod' (MCNV)	1.01	This study
<i>'Pelorosaurus' becklesii</i> (NHMUK R1868)	1.49	PDM pers. obs. (2010)
<i>Agustinia</i> (MCF-PVPH-110)	1.29	PDM pers. obs. (2009)
<i>Amargasaurus</i> (MACN-PV N15)	1.88	PDM pers. obs. (2009)
<i>Apatosaurus</i> (CM 3018)	1.28	Gilmore (1936)
<i>Aragosaurus</i> (MPG)	1.68	PU pers. obs. (2009)
<i>Argyrosaurus</i> (MLP 77-V-29-1)	2.64	PDM pers. obs. (2009)
<i>Bonatitan</i> (MACN-PV RN821)	1.23	RNB pers. obs. (2009)
<i>Camarasaurus</i>	1.26	Ostrom & McIntosh (1966)
<i>Cetiosauriscus</i> (NHMUK R.3078)	1.55	PDM pers. obs. (2010)
<i>Cetiosaurus</i> (OUMNH J13612)	1.97	PDM pers. obs. (2009)
<i>Diamantinasaurus</i>	1.48	Hocknull <i>et al.</i> (2009)
<i>Dicraeosaurus</i>	1.38	Janensch (1961)
<i>Diplodocus</i> (AMNH 5855)	1.41	PU pers. obs. (1991)
<i>Duriatitan</i> (NHMUK R.44635)	1.20	PDM pers. obs. (2010)
<i>Euhelopus</i>	1.79	Young (1935)
<i>Europasaurus</i> (DFMMh)	1.24	PDM pers. obs. (2008)
<i>Ferganasaurus</i>	1.28	Alifanov & Averianov (2003)
<i>Galveosaurus</i>	2.09	Barco (2009)
<i>Giraffatitan</i>	1.40	Janensch (1961)
<i>Gondwanatitan</i> (MN 4111-V)	2.26	PDM pers. obs. (2009)
<i>Jainosaurus</i>	1.87	Wilson <i>et al.</i> (2009)
<i>Janenschia</i>	1.22	Janensch (1961)
<i>Jobaria</i> (MNN-TIG)	1.31	PDM pers. obs. (2010)
<i>Ligabuesaurus</i> (MCF-PHV-233)	1.20	PDM pers. obs. (2009)
<i>Limaysaurus</i> (MUCPv-205)	1.83	PDM pers. obs. (2009)
<i>Limaysaurus</i> sp. (Pv-6762-MOZ)	1.80	PDM pers. obs. (2009)
<i>Lirainosaurus</i> (MCNA 7465)	2.46	PDM pers. obs. (2009)
<i>Losillasaurus</i> (MCNV Lo-7)	1.83	PDM pers. obs. (2009)
<i>Lourinhasaurus</i> (MIGM)	1.21	PU pers. obs. (2009)
<i>Lusotitan</i> (MIGM)	1.66	PU pers. obs. (2009)
<i>Magyarosaurus</i> (NHMUK R3857)	1.39	PDM pers. obs. (2010)
<i>Maxakalisaurus</i> (MN 5013-V)	1.76	PDM pers. obs. (2009)
<i>Neuquensaurus</i> (MLP CS)	1.66	RNB pers. obs. (2009)
<i>Nigersaurus</i> (MNN GAD)	1.25	PDM pers. obs. (2010)
<i>Omeisaurus</i>	1.64	Young (1939)
<i>Opisthocoelicaudia</i>	1.58	Borsuk-Bialynicka (1977)
<i>Paluxysaurus</i>	1.42	Rose (2007)
<i>Paralititan</i> (CM cast)	1.47	PDM pers. obs. (2008)
<i>Pelorosaurus</i> (NHMUK R.28626)	1.35	PDM pers. obs. (2010)
<i>Qingxiusaurus</i>	1.47	Mo <i>et al.</i> (2008)
<i>Rapetosaurus</i>	1.50	Curry Rogers (2009)
<i>Saltasaurus</i>	1.72	Powell (2003)
<i>Suuwassea</i>	1.27	Harris (2007)
<i>Tazoudasaurus</i>	1.72	Allain & Aquesbi (2008)
<i>Tornieria</i>	1.39	Janensch (1961)
<i>Turiasaurus</i> (CPT-1195-1210)	1.99	PU pers. obs. (2009)

Kimmeridgian–early Tithonian (Late Jurassic) deposits in Estremadura, western Portugal. These authors did not provide any further details, although this referral is not unreasonable given the taxonomic affinity of *Dinheirosaurus*.

Spain. Two possible diplodocoid occurrences have been described from the Kimmeridgian–Tithonian (Late Jurassic) of Asturias, north-western Spain. Martínez *et al.* (2000) briefly described a tooth as pertaining to either a diplodocoid or titanosaur; this is therefore considered an

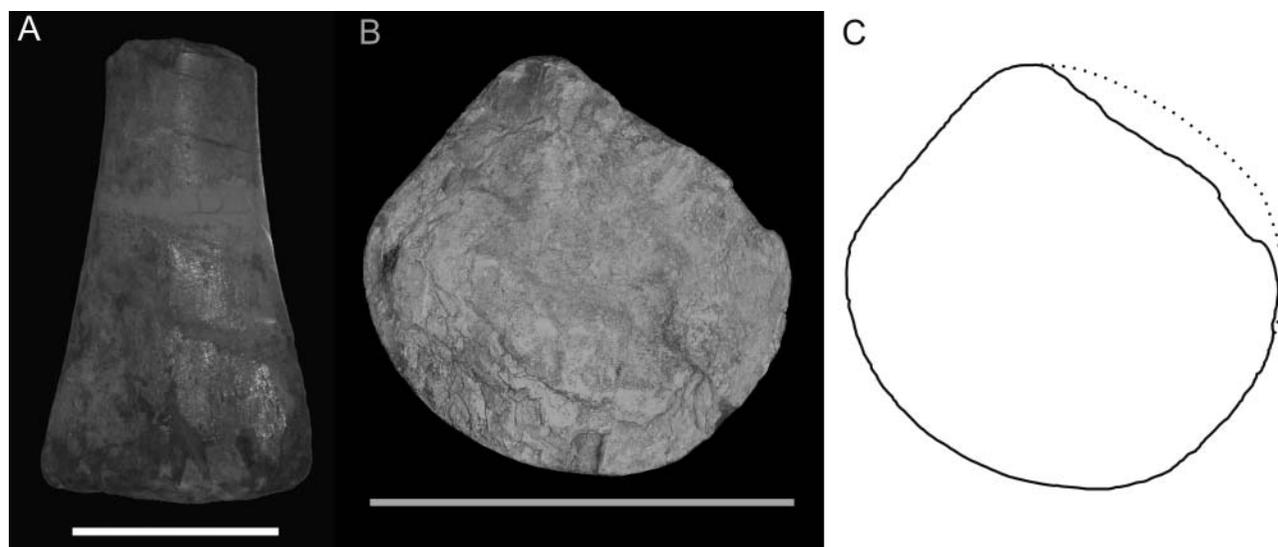


Figure 15. Sauropoda indet. ('La Serranía sauropod'; MCNV) distal half of humerus in: **A**, anterior (photo); **B**, proximal end (photograph); and **C**, proximal end (line drawing) view. Anterior surface at top of image in B and C. Dotted line in C indicates estimated outline prior to breakage. Scale bar = 100 mm (A) and 150 mm (B and C).

indeterminate neosauropod pending further study. An anterior caudal centrum was described as a diplodocine by Ruiz-Omeñaca *et al.* (2008), who noted similarities to *Tornieria*. However, these authors did not figure this vertebra and thus we refer it to the less exclusive clade Diplodocidae based on the possession of a prominent lateral pneumatic foramen.

There is a previously undescribed specimen from the Late Jurassic Sinarcas site of La Serranía, Valencia (MCNV unnumbered; PDM & PU pers. obs. 2009). Only the distal half of a humerus is preserved (Fig. 15) but the transverse cross-section (at approximately midshaft) is subcircular, which has been considered a rebbachisaurid synapomorphy (Wilson 2002; Sereno *et al.* 2007; Whitlock 2011). Table 4 lists ratios of humeral midshaft transverse:anteroposterior widths for a wide array of sauropod taxa, including most European eusauropods. Contrary to previous publications, no rebbachisaurid humerus (with the possible exception of *Rebbachisaurus*: Wilson 2002) possesses a subcircular cross-section (see also Salgado *et al.* 2004). Furthermore, several basal titanosauriform humeri have low midshaft ratios (e.g. *Duriatitan* (Barrett *et al.* 2010) and *Ligabuesaurus*: Table 4), and the transverse section of the humerus of the Japanese titanosauriform *Fukuititan* is apparently "almost circular" (Azuma & Shibata 2010, p. 457). Thus, although it is possible that this Spanish specimen represents the earliest known member of Rebbachisauridae, the sole character to support this is only potentially known in one definite member of this clade (i.e. *Rebbachisaurus*: Wilson 2002) and so we consider the La Serranía specimen an indeterminate sauropod.

Specimens from several sites dated as middle Tithonian–early Berriasian (Late Jurassic–Early Creta-

ceous) around Teruel, eastern Spain, have been referred to the Diplodocoidea (Royo-Torres *et al.* 2009). An incomplete ilium was described as an indeterminate diplodocid by Royo-Torres & Cobos (2004). However, based on its incomplete preservation and the extremely subtle features used to refer it to Diplodocidae, Upchurch & Mannion (2009, p. 1204) concluded that the ilium should be considered an indeterminate sauropod. Material from a second Teruel locality includes an anterior caudal centrum considered to have diplodocine affinities (Royo-Torres *et al.* 2009, pp. 1016–1017). This centrum is mildly procoelous and possesses a deep lateral pneumatic foramen (again positioned in the dorsal third of the centrum), as well as a concavity on the ventral surface. Thus, its diplodocine affinities are supported here, and it may belong to a clade of *Tornieria*-like diplodocines (see above). Canudo *et al.* (2005, p. 41) described a pencil-shaped and slightly curved tooth which they considered may belong to a basal diplodocoid. However, titanosaur teeth also possess a similar morphology (Upchurch 1995, 1998; Wilson & Sereno 1998) and so this specimen should be considered an indeterminate neosauropod pending further study.

Losillasaurus was described by Casanovas *et al.* (2001) from the middle Tithonian–early Berriasian (Late Jurassic–Early Cretaceous) of Valencia, eastern Spain. These authors recovered it as a basal diplodocoid; however, this animal (MCNV Lo-1-26) represents a non-neosauropod eusauropod (although some of our phylogenetic trees recover it as a macronarian), a position supported by subsequent phylogenetic analyses (Rauhut *et al.* 2005; Barco *et al.* 2006; Harris 2006; Royo-Torres *et al.* 2006;

Lovelace *et al.* 2008; Whitlock 2011; Royo-Torres & Upchurch in press).

Lastly, Pereda-Suberbiola *et al.* (2003) described a rebbachisaurid (the ‘Spanish rebbachisaurid’) from the late Barremian–early Aptian (Early Cretaceous) of Burgos, northern Spain. Its rebbachisaurid affinities have also been supported by four previous phylogenetic analyses (Gallina & Apesteguía 2005; Sereno *et al.* 2007; Carballido *et al.* 2010b; Whitlock 2011), as well as the current study, and the material has now been named *Demandasaurus darwini* (Torcida Fernández-Baldor *et al.* 2011).

Croatia. A nearly complete posterior dorsal vertebra was described by Dalla Vecchia (1998) from the late Hauterivian–early Barremian (Early Cretaceous) of southwestern Istria. Dalla Vecchia (1998) coined the name *Histriasaurus boscarollii* for this vertebra and noted several similarities with *Limaysaurus*. This comparison received further support from the phylogenetic analyses of Sereno *et al.* (2007), Carballido *et al.* (2010b) and Whitlock (2011), which recovered *Histriasaurus* as the most basal rebbachisaurid known. Our analysis also found *Histriasaurus* to be a basal rebbachisaurid, although more derived than *Amazonsaurus* (see above).

Overview of European diplodocoids. Currently, only three valid diplodocoid taxa are known from Europe (*Demandasaurus darwini*, *Dinheirosaurus lourinhanensis* and *Histriasaurus boscarollii*). Additional non-diagnostic remains indicate a greater diversity (Fig. 14). European diplodocoids have a stratigraphic range spanning the middle Oxfordian (early Late Jurassic) through to the early Aptian (late Early Cretaceous), although it is possible that ‘*Cetiosaurus glymptonensis*’ extends this record back into the late Bathonian (Middle Jurassic). Numerous Late Jurassic (and possibly earliest Cretaceous) European diplodocoid remains are known from Spain, Portugal and Georgia (Fig. 14), including the earliest known member of this clade (Gabunia *et al.* 1998). Rebbachisaurids are also represented in the Early Cretaceous, with specimens known from the UK, Spain and Croatia (Fig. 14), including the earliest known and one of the most basal members of this clade (Dalla Vecchia 1998). Dicraeosaurids are yet to be discovered in Europe, and are currently known only from the Americas and Africa (Janensch 1929; Salgado & Bonaparte 1991; Rauhut *et al.* 2005; Salgado *et al.* 2006; Whitlock 2011). In total, at least four distinct diplodocoids are known from Europe: two diplodocids (*Dinheirosaurus* and at least one additional taxon) and two rebbachisaurids (*Demandasaurus* and *Histriasaurus*).

Conclusions

Redescription of the Late Jurassic Portuguese sauropod dinosaur *Dinheirosaurus lourinhanensis* demonstrates its validity on the basis of three autapomorphies as

well as a unique character combination. Incorporation of *Dinheirosaurus* into a modified version of a recent data matrix confirms its diplodocid affinities and recovers it as the sister taxon to the contemporaneous North American genus *Supersaurus*, with *Dinheirosaurus* + *Supersaurus* the sister taxon to other diplodocines. However, some caution is required: *Dinheirosaurus* displays several plesiomorphic features absent in other diplodocids, and only four additional steps are required to force it into a position outside Flagellicaudata.

Our cladistic analysis also indicates that *Amazonsaurus* is the basal-most rebbachisaurid and finds *Zapalasaurus* in a position outside the South American Limaysaurinae. Along with the placement of *Rebbachisaurus* outside Limaysaurinae + Nigersaurinae, as well as the occurrence in Europe of the oldest known rebbachisaurids, these results complicate the simplified view that the division of Limaysaurinae and Nigersaurinae reflects vicariance between South America and Africa, and that the occurrence of European rebbachisaurids necessarily indicates Early Cretaceous dispersal from Africa to Europe.

A review of the European record shows that definite diplodocoids were present in the Late Jurassic and Early Cretaceous, but older claims are impossible to substantiate because of the scant material that they are based upon. Dicraeosaurids are yet to be discovered in Europe, but diplodocids were present in the Late Jurassic (including the earliest known representative of this clade, from Georgia). Only one valid genus of European diplodocid is known (*Dinheirosaurus*), although an indeterminate Portuguese specimen indicates the presence of at least one additional diplodocid taxon. Both Portuguese specimens display strong similarities to contemporaneous North American taxa, providing further support for a palaeobiogeographic link between Europe and North America in the Late Jurassic (e.g. Escaso *et al.* 2007; Benson 2008). Rebbachisaurids occur in the Early Cretaceous, with at least two taxa known (*Demandasaurus* and *Histriasaurus*). The presence of rebbachisaurids in the Late Jurassic is predicted by phylogenetic analyses (Upchurch & Barrett 2005), which have consistently recovered them as a clade of basal diplodocoids (Calvo & Salgado 1995; Wilson 2002; Upchurch *et al.* 2004a; Salgado *et al.* 2004, 2006; Gallina & Apesteguía 2005; Rauhut *et al.* 2005; Sereno *et al.* 2007; Carballido *et al.* 2010b; Whitlock 2011). Although a highly incomplete specimen from the Late Jurassic of Spain may represent the oldest known rebbachisaurid occurrence, the feature used to support this assignment has been demonstrated to be extremely weak and better material will be needed to enable recognition of pre-Cretaceous members of this enigmatic clade.

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Supplementary material

Supplementary material can be viewed online: 10.1080/14772019.2011.595432

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