Demandasaurus darwini, a New Rebbachisaurid Sauropod from the Early Cretaceous of the Iberian Peninsula

Authors: Fidel Torcida Fernández-Baldor, José Ignacio Canudo, Pedro Huerta, Diego Montero, Xabier Pereda Suberbiola, et. al.
Source: Acta Palaeontologica Polonica, 56(3) : 535-552
Published By: Institute of Paleobiology, Polish Academy of Sciences
URL: https://doi.org/10.4202/app.2010.0003
**Demandasaurus darwini**, a new rebbachisaurid sauropod from the Early Cretaceous of the Iberian Peninsula

FIDEL TORCIDA FERNÁNDEZ-BALDOR, JOSÉ IGNACIO CANUDO, PEDRO HUERTA, DIEGO MONTERO, XABIER PEREDA SUBERBIOLA, and LEONARDO SALGADO


A new medium-sized rebbachisaurid sauropod from the Castrillo la Reina Formation (Upper Barremian–Lower Aptian) in Burgos Province, *Demandasaurus darwini* gen. et sp. nov., is described. It is known from an incomplete but associated skeleton that includes cranial and post-cranial remains. *Demandasaurus darwini* gen. et sp. nov. presents 9 autapomorphies in the teeth and vertebrae. *Demandasaurus* is the first diplodocoid sauropod described from the Cretaceous of the Iberian Peninsula. Its inclusion in the Rebbachisauridae is well supported by our phylogenetic hypothesis, which situates it as a sister group of *Nigersaurus* from the Aptian of Niger, with which it shares various synapomorphies. The discovery of *Demandasaurus* provides further evidence of the sporadic use of the Apulian Route by dinosaurs during the Early Cretaceous for moving between the south of Europe (Laurasia) and the north of Africa (Gondwana).

Key words: Sauropoda, Rebbachisauridae, systematic, palaeobiogeography, Early Cretaceous, Spain.

Fidel Torcida Fernández-Baldor [fideltorcida@hotmail.com], Pedro Huerta [phuerta@usal.es], and Diego Montero [monteropodo@hotmail.com], Museo de Dinosaurios de Salas de los Infantes, 09600 Salas de los Infantes, Burgos, Spain and Colectivo Arqueológico−Paleontológico Salense (CAS), Plaza Jesús Aparicio 9, 09600 Salas de los Infantes, Burgos, Spain; José Ignacio Canudo [jicanudo@unizar.es], Grupo Aragosaurus-IUCA, Paleontología, Facultad de Ciencias, Universidad de Zaragoza, Pedro Cerbuna 12, 50009 Zaragoza, Spain; Xabier Pereda Suberbiola [xabier.pereda@ehu.es], Universidad del País Vasco/EHU, Facultad de Ciencia y Tecnología, Estratigráfía y Paleontología, Apartado 644, 48080 Bilbao, Spain; Leonardo Salgado [lsalgado@uncoma.edu.ar], INIBIOMA−CONICET, Museo de Geología y Paleontología, Universidad Nacional del Comahue, Buenos Aires 1400, 8300 Neuquén, Argentina.

Received 8 January 2010, accepted 23 December 2010, available online 29 December 2010.

Introduction

The rebbachisaurids have proved to be a group of dinosaurs of great palaeobiogeographical interest in the Early Cretaceous. They form a clade of basal diplodocoid sauropods that is widely represented in sediments from the late Early Cretaceous and early Late Cretaceous of Argentina (Calvo and Salgado 1995; Gallina and Apesteguía 2005; Salgado and Bonaparte 2007), Brazil (Carvalho et al. 2003; Medeiros and Schultz 2004) and Africa (Lavocat 1954; Sereno et al. 1999, 2007). This joint presence is used as an argument supporting a connection between Africa and South America at the end of the Early Cretaceous (Calvo and Salgado 1996). One might thus consider the rebbachisaurids to be a Gondwanan taxon, but recent discoveries of remains of these diplodocoids in Europe suggest that the origin of the rebbachisaurids is in Pangaea (Dalla Vecchia 1999; Pereda Suberbiola et al. 2003; Sereno et al. 2007; Canudo et al. 2009; Mannion 2009). Thus, the presence of rebbachisaurids in the Early Cretaceous of Europe may be explained by both early dispersal or late local extinction.

Many sauropod remains have been found in the Early Cretaceous of the Iberian Peninsula in recent years. Three taxa of macronarians have been described: *Aragosaurus* from the Late Hauterivian (Sanz et al. 1987), *Galvesaurus* from the Early Berriasian (Barco et al. 2005) and *Tastavinsaurus* from the Early Aptian (Royo Torres 2005; Canudo et al. 2008). Fragmentary remains of other macronarians of uncertain position are abundant in Lower Cretaceous formations of the Iberian Peninsula (Canudo et al. 2002; Ruiz-Omeñaca et al. 2004; Ortega et al. 2006). By contrast, representatives of the other great neosauropod clade, the diplodocoids (Wilson 2002; Upchurch et al. 2004a), were unknown until recently. Diplodocoids are known from the Late Jurassic of the Iberian Peninsula (Bonaparte and Mateus 1999; Royo-Torres and Cobos 2004), but none had been found in the rich Wealden beds of Spain (Ruiz-Omeñaca et al. 2004). This changed when Pereda Suberbiola et al. (2003) described the first rebbachisaurid re-
Fig. 1. A. Location map, geological sketch of the Salas de los Infantes area (Burgos, Spain), and stratigraphic position of the fossiliferous level. B. Quarry map of the partial skeleton of *Demandasaurus darwini* gen. et sp. nov. The numbers on the skeleton correspond to the collection number given in the text. The irregular line located to the upper left corner of the map is the limit of the excavation.
mains from Spain, from the Late Barremian–Aptian of Salas de los Infantes, the specimen under study in this paper. These authors argued that this provided proof of dispersal from Gondwana to Laurasia via an intercontinental bridge cited by other authors (see palaeobiogeographical discussion). The relationship between the rebbachisaurid from Salas de los Infantes and Gondwana taxa was reinforced by the first cladistic study of this group of sauropods (Sereno et al. 2007). In their phylogenetic analysis, Sereno et al. (2007) propose that *Nigersaurus*, from the Aptian or maybe Barremian–Aptian of Niger (Le Loeuff et al. 2010), and the Spanish rebbachisaurid form a clade that is clearly differentiated from the South American taxa. The aim of this paper is to describe the rebbachisaurid from Salas de los Infantes as a new genus and species of rebbachisauriad, to ascertain its phylogenetic position, and to evaluate its palaeobiogeographical relationship with the African forms.

For vertebral laminae and for vertebral pneumatic structures we follow the nomenclature of Wilson (1999) and Wedel (2003) respectively. We use the clade Diplodocoidae in this work following the cladistic definition of Upchurch (1995). The taxon Diplodocimorpha consists of the most recent common ancestor of *Rebbachisaurus garasbae* and *Diplodocus* and all of its descendants (Calvo and Salgado 1995). Diplodocimorpha is a node-based taxon, and less inclusive than the stem-based Diplodocoidea (Taylor and Naish 2005), which is defined as “all neosauropods closer to *Diplodocus* than to *Saltasaurus*” (Wilson and Sereno 1998).

**Institutional abbreviation.**—MDS (previously MPS), Museo de Dinosaurios de Salas de los Infantes, Salas de los Infantes, Burgos, Spain.

### Geological and geographic setting

The fossil bones studied in this paper were recovered in the “Tenadas de los Valles II” quarry, located 10 km southwest of the town of Salas de los Infantes (Province of Burgos, northern Spain, Fig. 1).

In geological terms, this area lies within the western Cameros Basin, which is located in the north-westernmost part of the Iberian Range, outcropping in the provinces of Burgos, Soria and La Rioja. This basin is one of the most subsident basins formed during the rift interval at the end of the Jurassic and the Early Cretaceous (Salas et al. 1991), which affected this part of the Iberian Peninsula. The sediments of the Tenadas de los Valles II quarry belong to the Castrillo de la Reina Formation and comprise red clay beds intercalated with sheet-like sandstone channel fills that are interpreted as floodplain and fluvial channel deposits respectively. The fluvial system of the Castrillo de la Reina Formation shows a braided channel pattern with well developed and drained floodplains. This lithostatigraphic unit belongs to the fifth depositional sequence of the six ones that divide the basin (Mas et al. 1993). The age of the fifth depositional sequence is Late Barremian to Early Aptian as is suggested by charophyte and ostracod biostratigraphy (Martín-Clossas and Alonso Millán 1998; Schudack and Schudack 2009).

The Tenadas de los Valles II site was discovered in 1999 during prospection work carried out by the Archaeological-Palaentontological Group of Salas de los Infantes (Colectivo Arqueológico-Paleontológico of Salas de los Infantes, CAS). Ten caudal vertebrae, a haemal arch, two ischia and a femur, as well as bone fragments were collected in the site. Excavations were carried out during the years 2002–2004, covering a surface area of some 240 m². Approximately 810 skeletal elements and bone fragments were recovered, and most of them belong to a single specimen of rebbachisaurid sauropod. The remains were found disarticulated in the same bed and in close proximity to each other. The neural arches of the vertebrae are firmly co-ossified to the centra. There are no anatomically repeated elements, and the bones correspond presumably to a single individual. The relative size of the bones suggests a medium-sized individual whose total length was approximately 10–12 m. In addition, several vertebral centra and femur fragments from a small ornithopod, two spinosaurid theropod vertebrae and a crocodile tooth were recovered from the site.

### Systematic palaeontology

**Saurischia Seeley, 1887**

**Sauropodomorpha von Huene, 1932**

**Sauropoda Marsh, 1878**

**Neosauropoda Bonaparte, 1986**

**Diplodocoididae Marsh, 1878 sensu Upchurch, 1995**

**Diplodocimorpha Calvo and Salgado, 1995**

**Rebbachisauridae Bonaparte, 1997**

**Genus Demandasaurus nov.**

**Etymology:** In reference to the Sierra de la Demanda, the mountain chain where the type specimen was found and from Greek *sauros*, lizard, reptile.

**Type species:** Demandasaurus darwini sp. nov.; see below.

**Diagnosis.**—As for the type and only known species.

**Demandasaurus darwini** sp. nov.

**Figs. 2–13.**

**Etymology:** In honour of the naturalist Charles R. Darwin (1809–1882).

**Type locality and age:** Upper section of the Castrillo de la Reina Formation (Tenadas de los Valles II locality), regarded as Late Barremian to Early Aptian in age (Martín-Clossas and Alonso Millán 1998).

**Holotype:** A partial skeleton represented by the right (MDS-RVII.275) and left (MDS-RVII.332) premaxillae, left dentary (MDS-RVII.443), six isolated teeth (MDS-RVII.340; MDS-RVII.436; MDS-RVII.437; MDS-RVII.438; MDS-RVII.440; MDS-RVII.441), three cervical vertebrae (MDS-RVII.589; MDS-RVII.606 [axis]; MDS-RVII.806), five cervical ribs (MDS-RVII.379; MDS-RVII.458; MDS-RVII.466; MDS-RVII.587; MDS-RVII.811), two dorsal vertebrae (MDS-RVII.242; MDS-RVII.798), nine dorsal ribs (MDS-RVII.14; MDS-RVII.301; MDS-RVII.364; MDS-RVII.365; MDS-RVII.368; MDS-
RVII,382; MDS-RVII,592; MDS-RVII,600; MDS-RVII,611), nineteen caudal vertebrae (MDS-RVII,2; MDS-RVII,3; MDS-RVII,4; MDS-RVII,9; MDS-RVII,10; MDS-RVII,11; MDS-RVII,12; MDS-RVII,15; MDS-RVII,101; MDS-RVII,216; MDS-RVII,217; MDS-RVII,218; MDS-RVII,470; MDS-RVII,602; MDS-RVII,605; MDS-RVII,609; MDS-RVII,610; MDS-RVII,629 and MDS-RVII,805), nine haemal arches (MDS-RVII,23; MDS-RVII,99; MDS-RVII,231; MDS-RVII,232; MDS-RVII,590; MDS-RVII,591; MDS-RVII,594; MDS-RVII,796; MDS-RVII,797), left (MDS-RVII,18) and right (MDS-RVII,19) ischia, and left femur (MDS-RVII,16).

**Diagnosis.**—*Demandasaurus darwini* gen. et sp. nov. is characterised by 9 autapomorphic characters: (1) the teeth are ornamented with longitudinal crests on the labial and lingual faces of the crown, and bear mesial and distal carinae; (2) the posterior cervical vertebrae have an infraprezygapophyseal chamber with a forked vertical accessory lamina; (3) the posterior cervical vertebrae have a rhombic accessory structure where the centroprezygapophyseal (cprl), prezygodiaphyseal (pddl) and spinoprezygapophyseal (spprl) laminae are connected, dorsally to the prezygapophyses; (4) the centroprezygapophyseal laminae (cprl) are divided in the cervical and dorsal vertebrae; (5) presence in the mid dorsals of two large neural arch pneumatic foramina that pass all the way through the neural arch anteroposteriorly; (6) presence of two large, deep pneumatic cavities, divided by accessory laminae, in the transverse processes of the anterior caudals; (7) in the anterior caudal vertebrae the anterior centroparapophyseal (acpl), posterior centroparapophyseal (pcpl) and posterior centrodiaaphyseal laminae (pddl) are very wide and make contact posteri- orly and ventrally with the diapophysis; (8) presence of two parallel laminae running in an anteroposterior direction, an upper one from the prezygapophysis to the base of the centropostzygapophyseal (copol), and a lower one from the base of the prezygapophysis to the dorsal surface of the anterior caudal centra; (9) presence of two parallel crests running anteroposteriorly on the lateral faces of the middle-posterior caudal vertebral centra.

**Description**

**Premaxillae** (Fig. 2).—Two premaxillae have been preserved (MDS-RVII,275, right premaxilla, and MDS-RVII,332, left premaxilla). Both lack the nasal and maxillary processes. The general shape is subrectangular (taller than wide), similar to that of *Nigersaurus* (Sereno et al. 2007). In medial view they are thickest in their tooth-bearing portion. The anterior surface is somewhat weathered, but shows a rugose ornamentation comprising irregularly alternating crests and valleys (Fig. 2A, D). The anterior side is gently convex, and the posterior side is convex-concave. Medially the premaxillae present a flat and smooth surface for the intermaxillary symphysis (Fig. 2C). The contact with the maxilla is sinuous. The surface for the articulation with the maxilla is smaller than that of the symphyseal area. The anterior premaxillary margin is non-stepped (almost straight), similar to that displayed by the other diplodocoids (Wilson 2002; Rauhut et al. 2005). The premaxilla has four dental positions. The right premaxilla presents the most mesial teeth inside (Fig. 2A, C). The disposition of these teeth and the alveoli indicates that the functional teeth of the premaxillae are procumbent, a character present in other diplodocoids, such as *Diplodocus* (see Wilson and Sereno 1998: fig. 6).

**Dentary** (Fig. 3).—A fragment of the left dentary (MDS-RVII,443), lacking its distal end, the dentary symphysis and the functional teeth, is preserved (Fig. 3A, B). Anteriorly, the dentary becomes more robust and dorsoventrally expanded (Fig. 3A). The anteroventral margin is rounded, and is well distinguished from the more derived diplodocoids, which have a sharply projecting triangular process (Wilson 2002; Harris 2006). The preserved part lacks a mandibular fenestra. Dorsally it has an elongated depressed area which runs along the dorsolateral part of the mandibular ramus. This structure could be equivalent to the vascular canal displayed by *Nigersaurus* (Sereno et al. 2007), though much more developed. Distally this depressed area becomes a groove that ends up as a continuation of the alveoli. In dorsal view, it is U-shaped
(Fig. 3B); the mandibular ramus turns medially to form an angle of 57°/176° with its anteroposterior axis. Six alveoli are pre−
erved, and one more is sectioned. This reduced number of
dental positions distinguishes Demandasaurus from other
rebbachisaurids such as Nigersaurus, which have more than
30 teeth in the dentary (Sereno et al. 1999). The more mesial
alveoli are rectangular and larger than the posterior ones,
which are subsquare. The teeth are situated in the most
mesial part of the main mandibular body and in the most
mesial part of the mandibular ramus.

Teeth (Fig. 4).—The preserved teeth (MDS−RVII,340; MDS−
RVII,436; MDS−RVII,437; MDS−RVII,438; MDS−RVII,440;
MDS−RVII,441) are not complete (the roots are lacking from
all specimens). In addition to these individual teeth, there are
others situated within the premaxillae (MDS−RVII,275 and
MDS−RVII,332), and the tooth MDS−RVII,436 is attached to
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all these show the same morphological characters. The teeth of
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Table 1. Measurements (in mm) of the teeth of Demandasaurus darwini
gen. et sp. nov., Castrillo de la Reina Formation (Late Barremian−Early
Aptian), Burgos, Spain. Abbreviations: H, dental crown height; WLalLi,
labiolingual width; WMeDi, mesiodistal width. Estimated measure−
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<td>–</td>
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<td>1.50</td>
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<tr>
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<tr>
<td>MDS−RVII,438</td>
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<td>0.4</td>
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<td>4 in labial, 3 in lingual</td>
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The arrows indicate the mesial and distal carinae. Scale bars 5 mm.

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Fig. 4. Tooth of rebbachisaurid sauropod Demandasaurus darwini gen. et sp.
nov. from Late Barremian−Earl Aptian, Early Cretaceous of Tenadas de los
Vallejos II, Spain. A. MDS−RVII,438, in lingual (A1) and basal (A2) views. B. Detail of the ornamentation of the tooth MDS−RVII,437, in lingual view.
The arrows indicate the mesial and distal carinae. Scale bars 5 mm.

doi:10.4202/app.2010.0003
of the neural spine. Moreover, attached to it is a fragment of the prezygapophysis of the third vertebra. The axis exhibits an opisthocoelous vertebral centrum, longer than wide. The ventral side is spindle-shaped, with anterior and posterior widening and a keel that connects the two parts. The anterior articular face is divided into two parts; the upper portion corresponds to the odontoid process. The posterior articular face is oval. The lateral face is taken up by a deep pleurocoel, the anterior part of which displays a subcircular fossa. The diapophysis is best preserved on the right side and forms a process positioned just dorsal to the neurocentral junction. The diapophyses project laterally. The prezygapophyses are short, rounded in outline, and with articular facets oriented laterodorsally. The laminae observed are the centroprezygapophyseal, centropostzygapophyseal, prezygodiapophyseal, postzygodiapophyseal, and anterior and posterior centrodiapophyseal. The neural spine has a V-shaped section and is inclined roughly 50° posterodorsally (Fig. 5).

Anterior-middle vertebra (Fig. 6).—MDS−RVII,589 is almost complete, lacking only the end of the neural spine. The left side is flattened, which has caused a displacement of some of the vertebral laminae. The height of the cervical vertebra is less than the length of the centrum (Table 2). This is opisthocoelous, with a well-developed sub-hemispherical anterior articulation and a concave posterior articulation (Fig. 6A, D). The anterior articulation is asymmetrical in lateral view, with its apex positioned dorsally. The ventral side has a prominent sagittal keel. The anteroventral part of the centrum is concave, and the posterior part is convex. The centrum is short, and the anteroposterior length / height ratio of the posterior face is 2.84. The articular faces are slightly taller than they are wide (Fig. 6D). A large, deep oval pleurocoel takes up the lateral face of the centrum. This pleurocoel is complex, being more deeply excavated in its anterior and posterior parts, which are separated by a pleurocentral lamina (Fig. 6B). Furthermore, there are small laminae delimiting smaller depressions in the posterior part of the pleurocoel. The parapophyses are short,
situated in the ventrolateral half of the centrum (Fig. 6B), and lack a pneumatic cavity in their dorsal surface. The prezygapophyses are long and directed dorsally and anteriorly. The postzygapophyses are fractured, and the articular facets are not preserved. The neural spine is broken and only its base is preserved, yet from this it can be observed to be simple. The vertebra MDS-RVII,589 possesses a well-developed system of laminae, as is characteristic of Eusauropoda (Wilson 2002). These include: centroprezygapophyseal (divided), centropostzygapophyseal, anterior centrodiaophyseal, posterior centrodiaophyseal, spinoprezygapophyseal, spinopostzygapophyseal, prezygodiapophyseal and postzygodiapophyseal. There is also an accessory lamina situated between the postzygodiapophyseal and spinoprezygapophyseal laminae (Fig. 6B), which Sereno et al. (2007) call the epipophyseal-prezygapophyseal lamina. This accessory lamina is present, more or less developed, in rebbachisaurids such as *Limaysaurus* (Calvo and Salgado 1995), *Cathartesaura* (Gallina and Apesteguia 2005), *Zapalasaurus*, and *Nigersaurus* (Sereno et al. 2007). A similar lamina can be seen in macronarians such as *Galvansaurus*, *Camarasaurus*, and *Euhelopus* (Barco et al. 2006; Wilson and Upchurch 2009), or in dicraeosaurids such as *Amargasaurus*. The homology of this structure is difficult to establish at present.

**Posterior cervical vertebra** (Fig. 7).—The posterior cervical vertebra (MDS-RVII,806) is incomplete but well preserved. It is different from the anterior-middle cervical and represents the transition to the dorsal vertebrae, which have a high neural arch. Unlike other sauropods, the parapophysis and diapophysis are located posteriorly.

The centrum is opisthocoelous, but it is proportionally shorter and lower than the centrum of the anterior-middle cervical MDS-RVII, 589. The lateral faces of the centrum possess a large, oval pleurocoel that is not divided by laminae; in its interior there are vertical and horizontal sheets of bone. The neural spine is not preserved. In anterior view, above the neural canal there is a deep infraprezygapophyseal chamber (Fig. 7A), which is delimited by the centroprezygapophyseal lamina and the prezygapophysis; inside this chamber there is a forked vertical accessory lamina; this structure is absent in other sauropods, and we consider it to be an autapomorphy of *Demandasaurus*. The diapophysis, as well as the whole of the neural arch, is positioned quite high in relation to the centrum. The postzygodiapophyseal lamina and two accessory laminae delimit a subtriangular surface that extends dorsally (Fig. 7B). A forked centroprezygapophyseal lamina reaches the prezygapophysis. The prezygapophyses are developed vertically and extend far from the vertebral centrum. Dorsal to the prezygapophyses, the vertebra has conspicuous rhombic structures where the centroprezygapophyseal, prezygodiapophyseal, and spinoprezygapophyseal laminae are connected (Fig. 7A); this character constitutes another autapomorphy of *Demandasaurus*. The postzygapophyses are not preserved. Part of the accessory lamina that connects the spinoprezygapophyseal and postzygodiapophyseal laminae is preserved. Between these three laminae a subtriangular pneumatic depression is located medially.

**Cervical ribs** (Fig. 8).—Six cervical ribs are preserved, three of which are fragmentary. The most complete cervical rib is MDS-RVII,811, which is shorter than the centrum in length, a feature displayed by diplodocoids (Sereno et al. 2007). The ribs are gracile with pneumatic cavities that vary in position between the capitulum and the tuberculum. On the anterior ramus, they display pneumatic cavities in a dorsal (MDS-RVII,379) or in a medial position (MDS-RVII,562). The angle

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**Fig. 6.** Anterior-middle cervical vertebra of rebbachisaurid sauropod *Demandasaurus darwini* gen. et sp. nov. from Late Barremian–Early Aptian, Early Cretaceous of Tenadas de los Vallejos II, Spain, MDS-RVII,589, in anterior (**A**), right lateral (**B**), dorsal (**C**), and posterior (**D**) views. Scale bars 10 cm.

**Fig. 7.** Posterior cervical vertebra of rebbachisaurid sauropod *Demandasaurus darwini* gen. et sp. nov. from Late Barremian–Early Aptian, Early Cretaceous of Tenadas de los Vallejos II, Spain, MDS-RVII,380, in anterior (**A**) and left lateral (**B**) views. The arrow indicates a subtriangular surface located dorsally to the diapophysis.

doi:10.4202/app.2010.0003
between the tuberculum and the capitulum is less than 90°, except for the most posterior rib (MDS−RVII,811), where the angle is near 90°. MDS−RVII,811 was found in association with the posterior cervical MDS−RVII,806. The tuberculum and the capitulum are well flattened mediolaterally, giving them a laminar appearance. MDS−RVII,379 presents an anterior process (spine, sp of Sereno et al. 2007). This anterior process is strongly developed, even in MDS−RVII,562, more so than the rib. The shape of this anterior process varies from mediolaterally flattened (MDS−RVII,562) to dorsoventrally flattened in the most posterior, MDS−RVII,811 (Fig. 8A, C). The general shape of the rib varies from subtriangular in MDS−RVII,242; MDS−RVII,798, to oval in MDS−RVII,562.

Dorsal region.—The dorsal region is represented by two incomplete dorsal vertebrae and ten ribs.

Dorsal vertebrae (Fig. 9).—Two mid-posterior, probably consecutive dorsal vertebrae (MDS−RVII,242; MDS−RVII,798) are partially preserved. The preserved parts are in excellent condition, but they both lack the neural spine and a good part of the transverse processes (Fig. 9). The interior of the vertebrae exhibits normal spongy osseous tissue, without pneumatic cavities. The vertebral centra are opisthocoelous, with an anterior articular face that is slightly convex and a posterior one that is slightly concave. By contrast, Rebbachisaurus has amphicoelous dorsal centra (Wilson 2002). The vertebral centrum of Demandasaurus is subcircular in section. The articular faces are subhexagonal and slightly higher than wide (Fig. 9A, C). The centrum is scarcely elongated anteroposteriorly (the Elongation Index EI sensu Upchurch 1998, is less than 1). In ventral view, it has a broad, gentle ventral groove. The dorsal centra have large, deep, clearly-edged pleurocoels (Fig. 9B). These pleurocoels are oval and dorsoventrally asymmetrical, and taper to points on the anterior and posterior side. The inner part of the pleurocoels lacks internal divisions, as in diplodocoids and other rebbachisaurids, such as Rebbachisaurus garasbae, Limaysaurus, and Amazonsaurus (Lavocat 1954; Calvo and Salgado 1995; Carvalho et al. 2003).

The neural arch is seemingly vertical and is in a slightly posterior position in relation to the centrum (Fig. 9B). It is deeply excavated anteriorly, in the sense of Upchurch et al. (2004a) and Harris (2006). The transverse processes run dorsolaterally at approximately 45° to the horizontal, as in other rebbachisaurids, such as Limaysaurus, Nigersaurus, and Histriasaurus (Dalla Vecchia 1999; Salgado et al. 2004; Sereno et al. 2007). The neural spine is simple. The parapophysis and the diapophysis are positioned very high in relation to the vertebral centrum, such that the parapophysis is above the prezygapophysis. The transverse processes lie posterior to the parapophyses. The prezygapophyses and postzygapophyses have large articular surfaces that are subtriangular and rectangular respectively. They incline at roughly 45°, joining at their medial part. The dorsal vertebrae display very deep, semi-oval infraprezzygapophyseal and infrapostzygapophyseal cavities, with two large pneumatic foramina that pass all the way through the neural arch anteroposteriorly (Fig. 9A, C). These pneumatic foramina are delimited by the ceiling of the neural canal (ventrally) and by the centroprezygapophyseal and centropostzygapophyseal laminae (laterally). In the dorsal part of the infraprezzygapophyseal lamina cavity there is also an opening laterally. This type of pneumatisation is present in theropods, such as Majungatholus and Aves (O’Connor and Claessens 2005).
but has not been described in sauropods and is an autapomorphic character of *Demandasaurus*. There is a reduced, laminar hypophene, the medial edges of which join the postzygapophyses (Fig. 9C). There are only two other rebbachisaurids in which the hypophene-hypanthrum articulation is developed: *Histriasaurus* and *Nopcsaspondylus* (Apesteguía 2007).

The pedicle is distinctively wide mediolaterally in anterior view, due to the fact that it is composed of the centroprezygaphyseal lamina and the anterior centroparapophyseal lamina. The centroprezygaphyseal laminae are forked, as occurs in the cervical vertebrae, which is considered an autapomorphy of *Demandasaurus*. There is no prezygodiaphyseal lamina, an absence shared with *Haplocanthosaurus* and *Dicraeosaurus* (Upchurch 1998). There are some very narrow spinoprezygapophyseal laminae, which run very close to one another, separated by a rugose area. Close to the contact with the prezygapophyses, they finally fuse. The prezygapophyseal laminae are very well developed, and together with the spinoprezygapophyseal laminae (sppl) they delimit deep subtriangular cavities (Fig. 9A). Through these cavities an accessory lamina runs parallel to the prezygapophyseal laminae, yet without making contact with the spinopostzygapophyseal laminae. The presence of the prezygapophyseal laminae distinguishes our specimen from other rebbachisaurids such as *Limaysaurus* and *Nigersaurus*, which lack this lamina (Salgado et al. 2004; Sereno et al. 2007). The spinopostzygapophyseal laminae are well developed, forked at their contact with the postzygapophyses, fusing at the base of the neural spine. The centropostzygapophyseal laminae are well developed, forking at their dorsal end to form a median centropostzygapophyseal lamina.

The postzygodiaphyseal lamina is well-developed and exhibits an accessory lamina at its contact with the postzygapophyses. In lateral view there is an undivided, narrow, vertical posterior centroparapophyseal lamina. The anterior centroparapophyseal lamina and the posterior centroparapophyseal laminae join to form a gentle depression. The lateral lamina would be formed by a spinodiaphyseal lamina, which distinguishes our specimen from more derived diplodocoids, where the lateral lamina is a result of the union of the lateral spinopostzygapophyseal laminae and the spinodiaphyseal lamina (Wilson 2002).

**Dorsal ribs.**—Ten dorsal ribs are preserved, one of which (MDS-RVII,364) is complete. The ribs are gracile. The capitulum is oval and has a concave articular surface. The tuberculum is more robust, with a sub-oval section and a concave articular surface. The tuberculum is oval and has a concave articular surface. The tuberculum is more robust, with a sub-oval section and a concave

**Caudal region.**—There are eight anterior caudals (MDS-RVII,15; MDS-RVII,470; MDS-RVII,602; MDS-RVII,605; MDS-RVII,609; MDS-RVII,610; MDS-RVII,629 and MDS-RVII,805), four middle caudals (MDS-RVII,2; MDS-RVII,3; MDS-RVII,9 and MDS-RVII,11), and seven middle-posterior caudals (MDS-RVII,4; MDS-RVII,10; MDS-RVII,12; MDS-RVII,101; MDS-RVII,216; MDS-RVII,217 and MDS-RVII,218) preserved. The vertebrae MDS-RVII,605 and MDS-RVII,609 lack the articular facets for the haemal arches, and thus they could be regarded as the first two caudals. The distal caudal vertebrae are not represented. Nine disarticulated haemal arches were found.

**First caudal vertebra** (Fig. 10).—MDS-RVII,605 is nearly complete, lacking part of the vertebral centrum, the diaphyses, the lateral ends of the transverse processes, and the greater part of the neural laminae. The inside of the bone exhibits normal spongy tissue. The vertebral centrum is slightly opisthocoelous. The anterior articular face is flat, somewhat oval, its major axis running in a dorsoventral direction, and its surface is irregular because it could have been fused to the last sacral vertebra (Fig. 10A). The posterior articular face is concave and probably subcircular (it lacks the left half; Fig. 10B). The vertebral centrum is slightly higher than long, and longer anteroposteriorly than wide mediolaterally (Table 2). It lacks pleurocoels. The neural spine is very high: 2.7 times the height of the centrum (Table 2). It is curved posteriorly, the curvature being greater in the dorsal half. The neural canal is large, elliptical, with a greater dorsoventral development anteriorly, and subcircular in posterior view.

MDS-RVII,605 presents a complex system of laminae.
The probable position of the diapophyses has been inferred on the basis of the confluence of the anterior centrodiapophyseal and the prezygodiapophyseal laminae. They would be in an anterior position with respect to the parapophyses. Ventral to the diapophyses and confluent with the anterior centrodiapophyseal lamina is the paradiapophyseal lamina. The spinodiapophyseal lamina is very prominent. The postzygodiapophyseal lamina is subhorizontal, and runs anteriorly to join the spinodiapophyseal lamina, in such a way that it would not have made contact with the diapophyses. Between the anterior centrodiapophyseal lamina and the prezygodiapophyseal lamina there is a triangular depressed area. In lateral view the anterior centrodiapophyseal lamina can be seen to fork at its dorsal end.

The bases of the prezygapophyses are preserved, which project in front of the vertebral centrum. In contact with the prezygapophyses are the spinoprezygapophyseal and centro-prezygapophyseal laminae and an intraprezygapophyseal lamina. The postzygapophyses are situated at the base of the neural spine; they make contact with one another medially. Their articular surfaces are subelliptical and directed lateroventrally. They project far enough to reach the plane of the posterior articular face of MDS−RVII,605 there is (right lateral) a broad and deep pneumatic cavity, oval in shape (with its major axis running in an anteroposterior direction) and with an accessory lamina that divides it into two subequal halves. The anterior side of the transverse process is reached by a lamina from the anterodorsal edge of the vertebral centrum, which could be the anterior centroparapophyseal lamina.

The neural spine is rectangular in lateral view and posteriorly recumbent, above all in the dorsal half. The dorsal end of the neural spine is very wide in anterior view, with two lateral hanging processes (Fig. 10A); this is where the spinoprezygapophyseal laminae end. This dorsal end has the shape of a helmet, with pneumatic cavities situated in a ventrolateral position. In cross section the neural spine is cruciform. It is formed by the spinodiapophyseal lamina and by very prominent prespinal and postspinal laminae (Fig. 10). These robust laminae comprise the spinoprezygapophyseal laminae (anterior) and the spinopostzygapophyseal laminae (posterior), which run very close together (though separately) and between which there is a rugose area that links them. The prespinal structure becomes wider at the dorsal end. Between the spinoprezygapophyseal laminae it presents a scarcely marked prespinal lamina, which dorsally ends up joining the right spinoprezygapophyseal lamina. There is also an accessory lamina that dorsally links the prezygapophyses with the ventrolateral part of the neural spine (it is scarcely developed, and visible on the right side of the spine). The spinodiapophyseal lamina is somewhat sinusoidal in outline. In posterior view the postspinal structure is wider at the dorsal end; in the lateral surfaces of the posterior part of the neural spine there are shallow pneumatic depressions.

Fig. 11. Anterior caudal vertebra of rebbachisaurid sauropod *Demandasaurus darwini* gen. et sp. nov. from Late Barremian–Early Aptian, Early Cretaceous of Tenadas de los Vallejos II, Spain, MDS−RVII,610, in anterior (A), lateral (B), and posterior (C) views. The neural spine is incomplete.
Anterior and middle caudal vertebrae (Figs. 11, 12).—Internally, the caudal vertebrae are spongy without large internal cells. The anterior caudals possess amphicoelous vertebral centra (Fig. 11), which distinguish them from the weakly procopcoelous vertebrae of derived diplodocoids such as Barosaurus, Diplodocus, Dicraeosaurus, and Amargasaurus (Salgado et al. 2004), with articular faces that are subhexagonal-subsquare in outline, as displayed with variations in all the caudals. The anterior caudal centra are flattened antero-posteriorly, and the middle-posterior centra are flattened dorsoventrally (Figs. 11, 12). All the caudals except the anteriormost present a very deep ventral groove. The articular facets for the haemal arches are very well developed in the posterior part of the centrum in all the vertebrae, except in the first ones, where the articular facets are absent. The ventral side is concave in lateral view. The centra of the anterior caudals are relatively short and vary little in length antero-posteriorly, whereas the middle-posterior ones are longer (Table 2). The vertebral centra lack pleurocoels. The middle and middle-posterior caudals (Fig. 12) exhibit two parallel laminar crests running in an anteroposterior direction, an upper one from the prezygapophysis to the base of the centropostzygapophyseal, and a lower one from the base of the prezygapophysis and the dorsal surface of the anterior caudal centra (Fig. 12A, C). Further, they present two crests running antero-posteriorly on their lateral face (in Limaysaurus there is a similar crest; Salgado et al. 2004). This combination of laminar crests on the middle and posterior caudal vertebrae is unique among the sauropods, and we interpret it as autapomorphic in Demandasaurus. In all the caudals the neural canal is well developed and is excavated in the vertebral centrum, as a result of which the dorsal edge of the centrum is concave.

In the anterior caudals, the neural spine is on the middle of the centrum, whereas in the middle-posterior caudals it is in an anterior position. The anterior position of the neural arch is convergent in Titanosauriformes (Salgado et al. 1997) and in some rebbachisaurids (Salgado et al. 2004). The neural spine of the anterior caudals is more than twice as high as the vertebral centrum, as in Diplodocoidea (Calvo and Salgado 1995; Harris 2006). The neural spine is distinctly inclined posteriorly in the anterior caudals (Fig. 11A2), becoming practically vertical in the middle ones (Pereda Suberbiola et al. 2003). In the posterior caudals the neural spine is straight and is located on the posterior part of the vertebral centrum. The neural spine of the anterior caudals exhibits triangular lateral projections near its dorsal end (Pereda Suberbiola et al. 2003), very similar to those observed in Nigerosaurus (Sereno et al. 2007).

The anterior caudals are morphologically similar to the dorsals, with a broad and complex system of laminae, some of which are present on the middle caudals. The lateral face of the neural spine in the anterior caudals runs along the spinodiapophyseal laminae; on the anterior face of the neural spine there is a slanting accessory lamina that links the spinoprezygapophyseal lamina with the spinodiapophyseal lamina (spdl). The neural spine has a petal-shaped transverse section, a synapomorphy of Rebbachisauridae (Wilson 2002). The anterior caudals have a robust and complex prespinal lamina to which the spinoprezygapophyseal laminae contribute and which contains a much-reduced “prespinal lamina”; a postspinal structure is formed in a similar way by the spinopostzygapophyseal lamina. There is a lamina parallel to the spinopostzygapophyseal lamina only on the right side, which runs next to the postzygapophyses (accessory to the spinopostzygapophyseal lamina). The course of the spinoprezygapophyseal laminae is “festooned” as in Nigersaurus (Sereno et al. 2007), in such a way that in some parts they almost touch one another, while in other parts they diverge, as happens at the dorsal end. The first caudals have anterior centrodiaophyseal and posterior centrodiaophyseal laminae that are very wide and undivided. The anterior caudals have a transverse process (actp of Gallina and Otero 2009) that is rectangular in shape and occupies part of the vertebral centrum (Fig. 11). These transverse processes are complex and are formed by the spinodiapophyseal and prezygodiapophyseal laminae (dorsally), by anterior centroparapophyseal plus posterior centroparapophyseal laminae (ventrally) and the posterior centrodiaophyseal lamina (posteriorly). These laminae define two large, oval pneumatic depressions (one on each side), inside which are accessory laminae distributed irregularly (Fig. 11A). The transverse processes are deeply excavated below the prezygodiapophyseal lamina in the medial margin. In posterior view, the transverse processes display small depressions separated by a thick ridge. This transverse process combines two autapomorphies: the laminar complex that is associated with the diapophysis and the deep pneumatic cavities with accessory laminae in their interior. The middle-posterior caudals are not pneumatized.

The anterior caudals have a small hypophene in the form of a crest. The prezygapophyses are small and project clearly anteriorly, in such a way that they go beyond the anterior face.
of the vertebral centrum in the anterior caudals. The post−zygapophyses are also small and present an almost vertical articular face.

**Haemal arches (Fig. 13).**—Nine haemal arches are preserved (MDS−RVII,23; MDS−RVII,99; MDS−RVII,231; MDS−RVII,232; MDS−RVII,590; MDS−RVII,591; MDS−RVII,594; MDS−RVII,796; MDS−RVII,797). These have a Y shape in anterior view. The most anterior ones in the series have a haemal canal that is closed (“cross−bridged”, Fig. 13A−D), but this becomes open in the posterior ones (MDS−RVII,23, MDS−RVII,232, and MDS−RVII,594, see Pereda Suberbiola et al. 2003: fig. 2F), as occurs in Diplodocus and Apatosaurus (Marsh 1896; Osborn 1899). The closed haemal canal is the primitive stage of the character displayed by basal sauropods and by Flagellicaudata (Wilson and Sereno 1998; Wilson 2002; Harris 2006). The presence of a closed haemal canal in the anterior caudals distinguishes *Demandasaurus* from all other rebbachisaurids, in which it is open (Calvo and Salgado 1995; Sereno et al. 1999; Carvalho et al. 2003; Salgado et al. 2004). The chevron haemal canal is short (23–27% chevron length) in the anterior ones (Table 3). These values are similar to those of diplodocoids and basal sauropods, differentiating it from the representatives of Titanosauriformes, which display values greater than 30%.

The ventral ramus in the anterior chevrons is fairly straight, forming an angle of 150° with respect to the proximal end (Fig. 13). The ventral ramus is flattened mediolaterally. Its anterior and posterior edges run parallel to one another, lacking the distal expansion (in lateral view) presented by *Tastavinsaurus* (Canudo et al. 2008). The distal end of the ventral ramus in lateral view is sharply pointed. This distal end is slightly widened mediolaterally in the anterior haemal arches (MDS−RVII,591). The most posterior haemal arch (MDS−RVII,594) lacks distal fusion of the ventral ramus (Fig. 13E), as well as lacking the anterior projection displayed by more derived diplodocoids such as *Dicraeosaurus*, Diplodocus, and Barosaurus (Upchurch et al. 2004a).

**Appendicular skeleton.**—The appendicular skeleton of *Demandasaurus darwini* gen. et sp. nov. is only known for the two ischia and the left femur.

**Ischium.**—The two ischia (MDS−RVII,18, left; MDS−RVII,19, right) are preserved and were figured in Pereda Suberbiola et al. (2003). The three constituent parts are clearly made out: the pubic peduncle, the iliac peduncle and the ischial branch. The ischium makes a significant contribution to the acetabulum. The iliac peduncle is well developed and is more prominent than the pubic one. The outline of the articulation with the ilium is trapezoidal. The posteroventral end of the iliac peduncle displays a small notch similar to the one shown by *Haplocanthosaurus priscus* Hatcher, 1903. The pubic peduncle has a well−marked neck. The outline of the articulation with the pubis is triangular and is very short in comparison with the total length of the ischium (15%), which makes it one of the shortest in the sauropod record. There is an elongated and well−developed tuberosity on the lateral surface of the proximal end. The right ischium displays

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![Fig. 13. Haemal arches of rebbachisaurid sauropod Demandasaurus darwini gen. et sp. nov. from Late Barremian–Early Aptian, Early Cretaceous of Tenadas de los Vallejos II, Spain.](image-url)
plays a large nutritive foramen in a medial position on the pu-
bic peduncle.

The ischial branch is distinctively straight, elongated (ap-
proximately 80% of the length of the ischium) and gracile, like that of *Haplocanthosaurus priscus*. The ischial branch is
perpendicular to the iliac peduncle, which means that it pro-
jects posteriorly, as occurs in *Camarasaurus* (Ostrom and
McIntosh 1966). The section of the ischial branch at its mid-
point is subtriangular. The ischiadic shaft is slightly twisted
and much smaller than in sauropods such as *Camarasaurus*
or *Tastavinsaurus* (Canudo et al. 2008). The distal end of the
ischium shows little lateral expansion in relation to the main
shaft. The section of the distal end is blade-like. The dorso-
distal end of the ischia presents an elongated-triangular,
rugose, symphyseal area, which occupies a sixth of the total
length (condition described as emarginate distal to pubic
peduncle by Wilson 2002). In their anatomical position, the
ischia form a nearly coplanar structure in cross-section
(Pereda Suberbiola et al. 2003).

The absence of a significant distal expansion and the
narrow ischiadic shaft clearly distinguish the ischium of
*Demandasaurus* from that of more derived diplodocoids such
as *Apatosaurus* (Upchurch et al. 2004b). Its overall gracility
and its well-developed iliac peduncle distinguish it from basal
macronarians such as *Camarasaurus* (Ostrom and McIntosh
1966) and derived ones such as titanosaurids (Salgado et al.
1997). Among the rebbachisaurids, the ischium of *Lamia-
saurus tessonei* differs from that of *Demandasaurus* in having
a somewhat curved shaft (Calvo and Salgado 1995) and in
lacking the marked neck of the iliac peduncle as seen in
*Demandasaurus*.

**Femur.—** MDS-RVII,16 is the left femur, preserved virtually
complete (Table 4). The femur is well figured in Pereda
Suberbiola et al. (2003). It has a diaphysis that is slightly
curved and distinctively gracile (slenderness index: 0.12); the
section of the diaphysis is subelliptic in outline, with the major
axis in a mediolateral direction. The proximal and distal ends
are aligned medially and display the same mediolateral expan-
sion. The distal end is twisted roughly 30° medially with re-
spect to the lateromedial axis of the diaphysis. The femoral
head is well individualised and is located almost perpendicular
to the longitudinal axis of the diaphysis, with a small elevation
above the greater trochanter. The articular head is oval in
proximal view. It lacks an anterior trochanter, a character it
shares with other eusauropods (Wilson 2002). It displays a
well-developed pilaster on the posterolateral side of the prox-
imal third, beneath the area of the greater trochanter.

The diaphysis is curved on its medial side and practi-
cally straight on the lateral side. Its interior presents a central
cavity described in basal sauropods such as *Shunosaurus*
(Zhang et al. 1984). The diaphysis is compressed antero-
posteriorly with an eccentricity close to 0.5 (Table 4). It dis-
plays a scarcely developed proximolateral bulge below the
greater trochanter, similar to that of other rebbachisaurids
(Calvo and Salgado 1995) and much less developed than that
shown by Titanosauriformes (Salgado et al. 1997). The lat-
eral bulge is located in a rather low position, and does not
reach the proximolateral corner of the femur. The fourth
trochanter is situated on the posterior face of the femur, with-
out occupying any part of the medial side of the diaphysis. It
is closer to the proximal end (one third of the total way
along). It consists of a small bulge, similar in its development
to that of other rebbachisaurids (Salgado et al. 2004). The
scarc development of the fourth trochanter is convergent in
certain titanosaurians (Sanz et al. 1999). Situated medially in
relation to the fourth trochanter is a depressed area parallel to
it. The lateromedial width of the diaphysis decreases distally.

The distal end is expanded both mediolaterally and antero-
posteriorly. The condyles are well developed; the tibial is
larger than the fibular, and they are separated from one another
by a deep intercondylar groove. The distal surface of the distal
end of the femur presents a bulge coinciding with the fibular
condyle. The epicondyle is well developed and is separated
from the fibular condyle by a groove. The tibial condyle is
situated in the middle part of the distal end of the femur; it has
a proximal projection at its posterior end, and is slightly project-
ing on its anterior side.

**Discussion**

Bonaparte (1996) was the first to recognise the existence of a
monophyletic group of diplodocoids by the family name of
Rebbachisauridae from the Early Cretaceous and the base of

![Table 4. Measurements (in mm) of the femur (MDS-RVII,16) of *Demandasaurus darwini* gen. et sp. nov., Castrillo de la Reina Formation (Late Barremian–Early Aptian), Burgos, Spain. The proximal length to the 4th trochanter is taken at the point where it is most prominent.](https://bioone.org/journals/Acta-Palaeontologica-Polonica)
the Late Cretaceous of Africa and South America. This name has generally been used (Sereno et al. 1999; Wilson 2002; Pereda Suberbiola et al. 2003; Harris and Dodson 2004; Mannion 2009), although it is not formally defined. Upchurch et al. (2004a: 303) point out that Sereno et al. (1999) use it as a “stem-based taxon defined as Diplodocoidea more closely related to *Rebbachisauridae* than to *Diplodocidae*”. It would be a sister group of the rest of the rebbachisaurids except *Rebbachisaurus*, which is situated as the most basal taxon. In fewer trees it is. These authors took the polarities on the basis of the paper published (Pereda Suberbiola et al. 2003) with the description of the anterior and middle caudal vertebrae, a chevron, ischia and femur. Now the cranial characters have been added (dental, premaxillae, teeth), as well as those of the cervical vertebrae, dorsal vertebrae, anterior and middle-posterior caudals, ribs and haemal arches, prepared over the last few years. A total of 21 new polarities have been added, and 7 have been changed from the coding of Sereno et al. (2007) for *Demandasaurus* (Appendix 1).

For the phylogenetic study, the PAUP program was used (Swofford 2001); 102 unordered characters were analysed. Following the heuristic search procedure, 35 equally parsimonious trees were obtained. The tree length is 160, with a consistency index (CI) of 0.69, a rescaled consistency index (RC) of 0.52, and a homoplasy index (HI) of 0.31. The strict and semistrict consensus (equal), 50% majority-rule consensus and Adams consensus cladograms were obtained (Fig. 14). The topologies of the cladograms are fairly similar to the strict consensus tree of Sereno et al. (2007), although there are some differences in the relationships among the rebbachisaurids.

In our strict consensus tree there is a polytomy of all the rebbachisaurids except *Histriasaurus*, which is situated as the sister group to the remainder of the rebbachisaurids, and *Nigersaurus* and *Demandasaurus* share an exclusive common ancestor (Fig. 14A). However, the 50% majority-rule consensus and Adams consensus trees (Fig. 14B, C) differentiate the Argentinean rebbachisaurids more clearly on a separate node, as displayed by the strict consensus tree of Sereno et al. (2007). These differences are due to the scarcity of fossil remains in rebbachisaurids, which is particularly significant in the case of *Rebbachisaurus* and *Histriasaurus*. This means that the phylogenetic proposal for the relations between rebbachisaurids is poorly supported, and a few changes in polarities can produce major changes. Nonetheless, it should be stressed that in all the trees obtained in our study the rebbachisaurids are consistently shown to be monophyletic. Furthermore, in all the trees obtained, even the most parsimonious, *Nigersaurus* and *Demandasaurus* are situated in the same clade (Fig. 14). Thus, in many of the trees this is found as the sister group to the rest of the rebbachisaurids except *Histriasaurus*, which is always the most basal taxon. In fewer trees it
appears as the sister group to the Argentinean rebbachisaurids or together with Rebbachisaurus forming a separate clade also with Rebbachisaurus, Cathartesaurus, Limaysaurus, and Zapalassaurus. As such, it is notable that with the character-taxon matrix of Sereno et al. (2007) used in this paper, Demandasaurus is closely related to the African rebbachisaurids, more than to the South American members of this clade.

Demandasaurus and Nigersaurus share the following synapomorphies: centropostzygapophyseal lamina divided in the middle and posterior dorsal neural arches; anterior caudal neural spines flared distally, with pendant triangular lateral processes; presence of triangular lateral processes in the caudal neural spines; presence of an elongated muscle scar on the proximal end of the ischium and the presence of a pronounced ridge on the posterior surface between the greater trochanter and the articular head of the femur. Demandasaurus differs from Nigersaurus in that it displays much less specialisation in the mandible. Demandasaurus thus has a much smaller number of teeth in the mandible, a smaller number of dental positions, and it also presents teeth on the lateral side of the mandible. The teeth of Demandasaurus are flattened, and further display ornamentation based on longitudinal striations and carinae, which distinguishes them from the smooth enamel presented by the teeth of Nigersaurus (Sereno et al. 2007).

Palaeobiogeographical implications

The rebbachisaurids are a group of sauropods frequently cited in the latest Early Cretaceous and the early Late Cretaceous of Africa and South America (Calvo and Salgado 1995; Salgado et al. 2004; Gallina and Apesteguía 2005; Sereno et al. 2007; Carballido et al. 2010). At the end of the Early Cretaceous, the separation of Africa and South America took place, with the definitive opening of the South Atlantic. The presence of rebbachisaurids on both continents has been interpreted in terms of a persisting land connection at the end of the Early Cretaceous (Calvo and Salgado 1996). The abundance of rebbachisaurids in Gondwana and their significant absence in Laurasia has resulted in these sauropods being traditionally considered Gondwanan. In this scenario, the presence of Demandasaurus on the Iberian Peninsula can be interpreted as a process of dispersal (Pereda Suberbiola et al. 2003; Canudo et al. 2009). However, the members of Rebbachisauridae are of clearly Pangaean origin; indeed, it is a clade of diplodocoids more primitive than Diplodocus (Sereno et al. 2007), a taxon that stems from the Late Jurassic of North America. As such, the presence of Demandasaurus in the Barremian–Aptian transition of the Iberian Peninsula might also be explained as a product of vicariance.

The sauropod record in the Late Jurassic and Early Cretaceous of the Iberian Peninsula, though fragmentary, is sufficiently informative to ascertain the absence of either rebbachisaurids or basal diplodocoids other than Demandasaurus (see the update by Ortega et al. 2006). Moreover, the rebbachisaurid closest to Demandasaurus is Nigersaurus, which situates the divergence of the clade formed by these two taxa in the middle part of the Early Cretaceous (Sereno et al. 2007) and as such later in time than the separation of Gondwana and Laurasia at the end of the Jurassic. In the context of the fossil record of the Iberian sauropods, the presence of Demandasaurus in Iberia tallies better with a rebbachisaurid dispersal event during the Barremian (Pereda Suberbiola et al. 2003) than with vicariance. Moreover, there are other taxa common to both southern Europe and Africa, such as the spinosaurid theropods (Buffetaut 1989; Sereno et al. 1998; Canudo et al. 2009), lending further weight to the hypothesis of a sporadic connection between these two emerged areas.

In recent years, a great effort has been made to establish the most suitable area for this intercontinental bridge (Raspini 1998; Polcyn et al. 1999; Bosellini 2002; Gheerbrant and Rage 2006). The root of the problem is that palaeogeographical models locate an ocean between Europe and Africa that would have been impossible to cross for continental tetrapods such as dinosaurs. The first key to identifying this bridge was the description of the rebbachisaurid Histriasaurus on the marine platform of the Hauterivian of the Italian Peninsula (Dalla Vecchia 1999). In fact, Histriasaurus represents an example of dispersal by a mechanism that has been termed “Noah’s Ark” (McKenna 1973), since part of what is today known as Italy (the Apulian Plate) was a fragment of Gondwana that split off and finally collided with the south of Europe, thus becoming part of Laurasia. This migration by the Apulian Plate was possibly the starting-point for what is known as the “Apulian Route,” well documented at the end of the Cretaceous and beginning of the Eocene (Gheerbrant and Rage 2006), but which may have also been used during the Early Cretaceous (Dalla Vecchia 2002; Canudo et al. 2009). The Apulian Route linking the continents of the northern and southern hemispheres may never have amounted to a continuous land corridor, but the islands that presumably constituted it appear to have been sufficiently close to one another for certain terrestrial tetrapods to be able to move between them, as may have been the case with Demandasaurus or a proximal ancestor. In support of the existence of the Apulian Route in the Early Cretaceous there are abundant papers demonstrating the presence of dinosaur ichnites in shallow marine sediments of the Apulian Plate (Dalla Vecchia 2002; Bosellini 2002; Nicosia et al. 2007), which shows that dinosaurs were present.

Conclusions

Demandasaurus darwini gen. et sp. nov. is the first diplodocoid sauropod to be described from the Cretaceous of the Iberian Peninsula. This is based on the remains of a single specimen that was found in a disarticulated condition in fluvial sediments of the Castrillo de la Reina Formation (Barremian–
Aptian transition) near Salas de los Infantes (Burgos, Spain). Among the material recovered are fragmentary cranial remains (premaxillae, dentary, teeth), cervical, dorsal, and caudal vertebrae; cervical and dorsal ribs, and haemal arches. Of the appendicular skeleton, the femur and the ischia are known. Nine autapomorphies have been recognised in the teeth and the vertebrae. Inclusion of *Demandasaurus* in the Rebbachisauridae is well supported by phylogenetic analyses (Sereno et al. 2007; and this work). *Demandasaurus darwini* is hypothesised to be a sister taxon to *Nigersaurus* from the Aptian of Niger. The close phylogenetic relationships of the two sauropods corroborate the existence of the Apulian Route and its use by dinosaurs during the Early Cretaceous for moving between the south of Europe (Laurasia) and the north of Africa (Gondwana).

Acknowledgements

We thank all collaborators for their participation in the excavations from 2002 to 2004. Alberto Bengoechea Molinero (Colectivo Arqueológico-Paleontológico Salense, Salas de los Infantes, Burgos, Spain) informed us of the discovery. We thank Jesús Rodríguez and Rubén Contreras (both MDS) for the fossil preparation. We appreciate the facilities provided by the MDS for the study of the material. Rupert Glasgow translated and edited the text in English. The field works of 2003 and 2004 were financed by the “Dirección General de Patrimonio de la Junta de Castilla y León”. This work forms a part of the project CGL2007-64629 (“Ministerio de Educación y Ciencia” of Spain and ERDF funds) and the Government of Aragon (“Financiación de Grupos Consolidados”). Financial support of XPS was provided by the projects CGL2007-64061/BTE and CGL2010-18851/BTE (MICINN) and the research group GIC07/14-361 and IT-320-10 (Basque Government).

References


Appendix 1

Character score for *Demandasaurus darwini* gen. et sp. nov. For character-taxon matrix see Sereno et al. (2007).

\[
\begin{array}{cccccccccccc}
1 & 0 & 0 & 1 & 1 & 1 & 1 & 1 & 1 & 0 & 1 & 0 \\
1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
1 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
\end{array}
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