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

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Demandasaurus darwini, a new rebbachisaurid sauropod from the Early Cretaceous of the Iberian Peninsula

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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.

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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-

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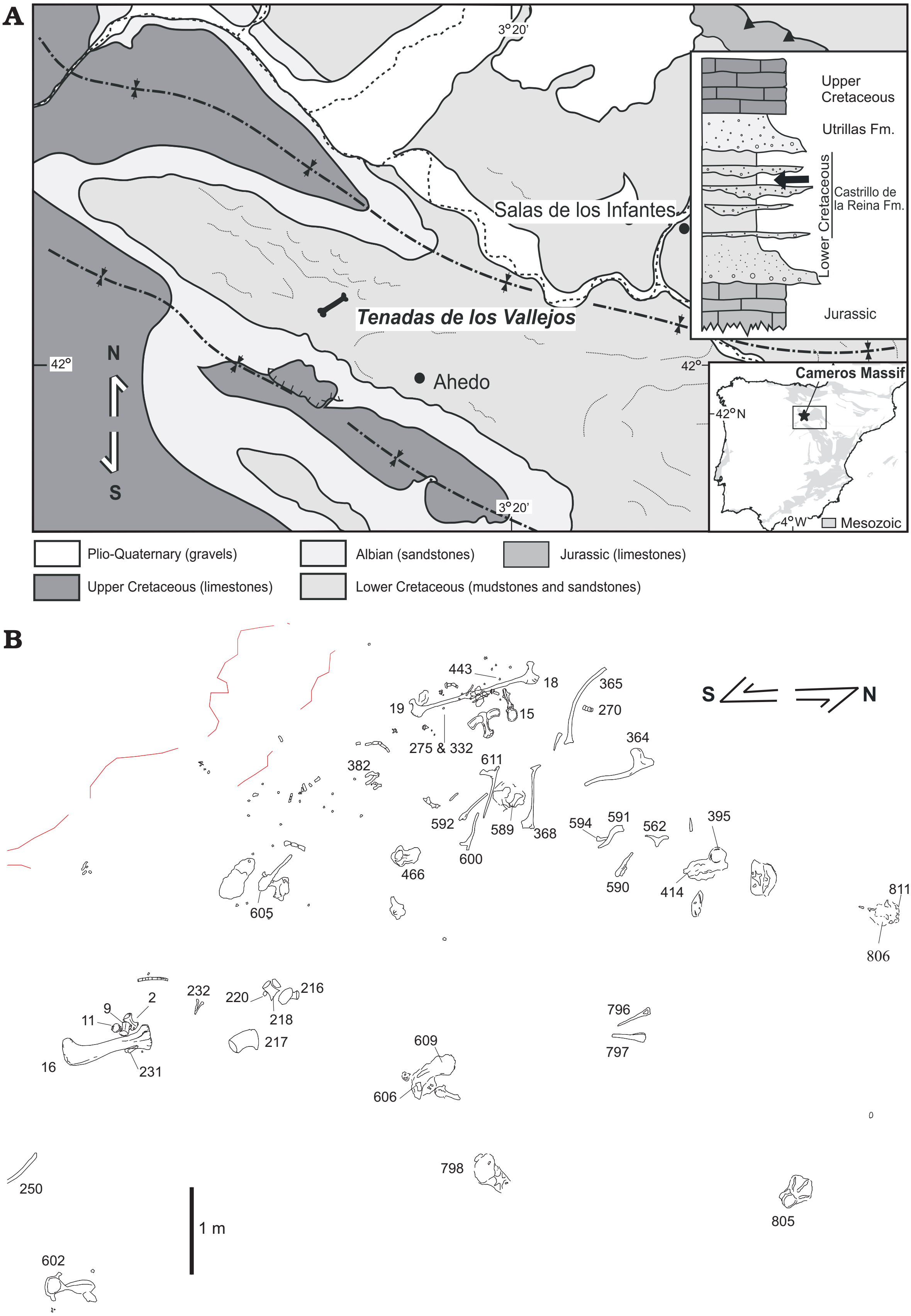

Fig. 1. **A**. Location map, geological sketch of the Salas de los Infantes area (Burgos, Spain), and stratigraphic position of the fossiliferous level. **B**. Quarry map of the partial skeleton of *Demandasaurus darwini* gen. et sp. nov. The numbers on the skeleton correspond to the collection number 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 Gondwanan 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 rebbachisaurid, 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 Diplodocoidea 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 Vallejos 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 Vallejos 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 lithostratigraphic 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-Closas and Alonso Millán 1998; Schudack and Schudack 2009).

The Tenadas de los Vallejos II site was discovered in 1999 during prospection work carried out by the Archaeological-Palaeontological Group of Salas de los Infantes (Colectivo Arqueológico-Paleontológico de 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 m^2. 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
Diplodocoidea 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 Vallejos II locality), regarded as Late Barremian to Early Aptian in age (Martín-Closas 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-

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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), prezygodiapophyseal (prdl) and spinoprezygapophyseal (sprl) 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 centrodiapophyseal laminae (pcdl) are very wide and make contact posteriorly 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 (cpol), 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 interpremaxillary 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).

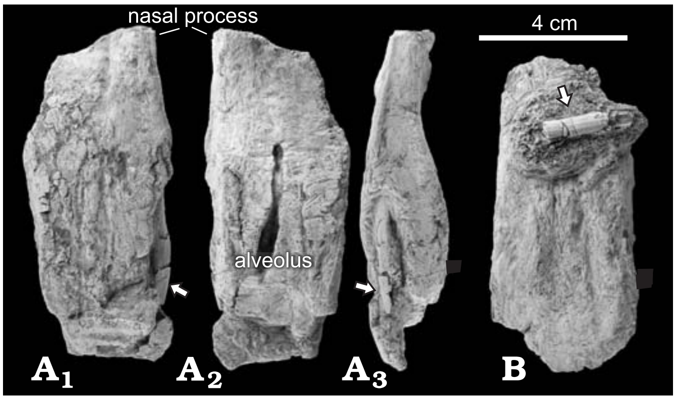

Fig. 2. Premaxilla of rebbachisaurid sauropod *Demandasaurus darwini* gen. et sp. nov. from Late Barremian–Early Aptian, Early Cretaceous of Tenadas de los Vallejos II, Spain. **A**. Right premaxilla MDS-RVII,275, in anterior (A_1), posterior (A_2) and medial (A_3) views. **B**. Left premaxila MDS-RVII, 322, in anterior view. The arrow in A_1 and A_3 indicate a premaxillary tooth in anatomical position, and the arrow in B indicate the tooth MDS-RVII,436 attached to the rostral face of the left premaxila.

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 dorsoventraly 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

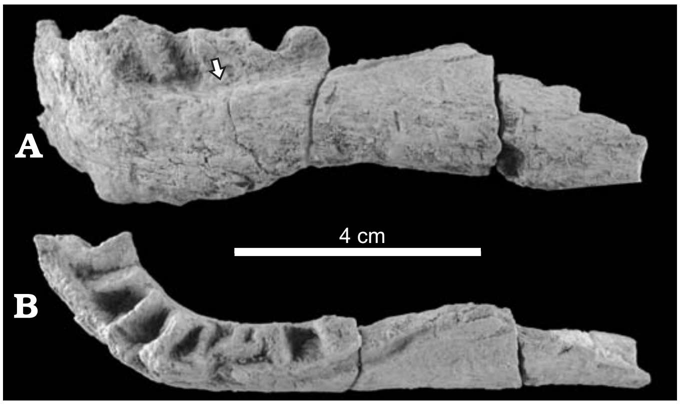

Fig. 3. Left dentary of rebbachisaurid sauropod *Demandasaurus darwini* gen. et sp. nov. from Late Barremian–Early Aptian, Early Cretaceous of Tenadas de los Vallejos II, Spain, MDS-RVII,443, in lateral (**A**) and dorsal (**B**) views. The arrow indicates a depressed area in a dorsolateral position.

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; WLaLi, labiolingual width; WMeDi, mesiodistal width. Estimated measurements are in brackets.

Teeth	H	WLaLi	WMeDi	Longitudinal crests
MDS-RVII,436	(2.60)	–	0.60	
MDS-RVII,340	(1.50)	0.35	0.55	
MDS-RVII,437	1.85	0.35	0.55	
MDS-RVII,438	1.55	0.4	0.55	4 in labial, 3 in lingual
MDS-RVII,440	1.45	0.35	0.60	4 in labial
MDS-RVII,441	1.20	–	0.50	5 in labial, 1 in lingual

(Fig. 3B); the mandibular ramus turns medially to form an angle of 57° with its anteroposterior axis . Six alveoli are preserved, 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 the rostral face of the premaxilla MDS-RVII, 332 (Fig. 2D); all these show the same morphological characters. The teeth of *Demandasaurus* are fairly unique and morphologically well-differentiated from those of other rebbachisaurids (Calvo and Salgado 1995; Salgado et al. 2004; Apesteguía 2007; Sereno et al. 2007). They are elongated and slender (pencil-type), almost straight, with a slight curve in a lingual direction, labiolingually compressed (Fig. 4A); they have an elliptical cross-sectional shape at mid-crown (Fig. 4B), and are somewhat more circular toward the base of the crown. The teeth that preserve the apex lack a wear facet, their end is narrow and sharp, and as such they were possibly not functional (Fig. 4A). In teeth attributed to *Nigersaurus* two wear facets have been described on opposite faces of the crown, forming very different angles with the surface of these faces (Sereno and Wilson 2005). The mesial and distal edges of the teeth of *Demandasaurus* display carinae without denticles (Fig. 4A, C) that gradually disappear towards the base. The presence of carinae in pencil-type teeth has also been described in derived South American titanosaurs such as *Rinconsaurus caudamirus* (Calvo and Gonzalez Riga 2003) and *Muyelensaurus pecheni* (Calvo et al. 2007). The *Demandasaurus* teeth exhibit enamel thickness differentiation (as in *Nigersaurus*; Sereno et al. 1999), the enamel being thicker on the labial face (Fig. 4B), unlike *Limaysaurus*, which has undifferentiated enamel (Salgado et al. 2004). The enamel of *Demandasaurus* is practically smooth to the naked eye. The labial side usually has 4–5 very scarcely developed longitudinal crests, which fade away toward the apex; on the lingual face there are up to 3 crests, which are also scarcely marked (Fig. 4A, C; Table 1). On the tooth MACN PV N101 (Apesteguía 2007) and in *Nigersaurus* (Sereno and Wilson 2005) there are faint crests and valleys, developed only on one face of the tooth, and *Limaysaurus* has smooth enamel (Calvo and Salgado 1995). No attrition surfaces are visible on the teeth of *Demandasaurus*, suggesting that there was no contact between them. The combination of teeth ornamented with longitudinal crests on the labial and lingual faces of the crown, and the presence of mesial and distal carinae constitutes an autapomorphy of *Demandasaurus*.

Cervical region.—The axis (MDS-RVII,606), one anterior to middle cervical vertebra (MDS-RVII,589) and one posterior cervical vertebra (MDS-RVII,806) have been preserved (Table 2). The vertebrae lack the camellate pneumatic structure that is characteristic of titanosauriform sauropods (Wilson and Sereno 1998; Wedel et al. 2000). Eleven cervical ribs are also known.

Axis (Fig. 5).—MDS-RVII,606 is complete, though poorly preserved. It is lacking part of the laminae on both sides, part of the anterior articular face, the postzygapophyses, and part

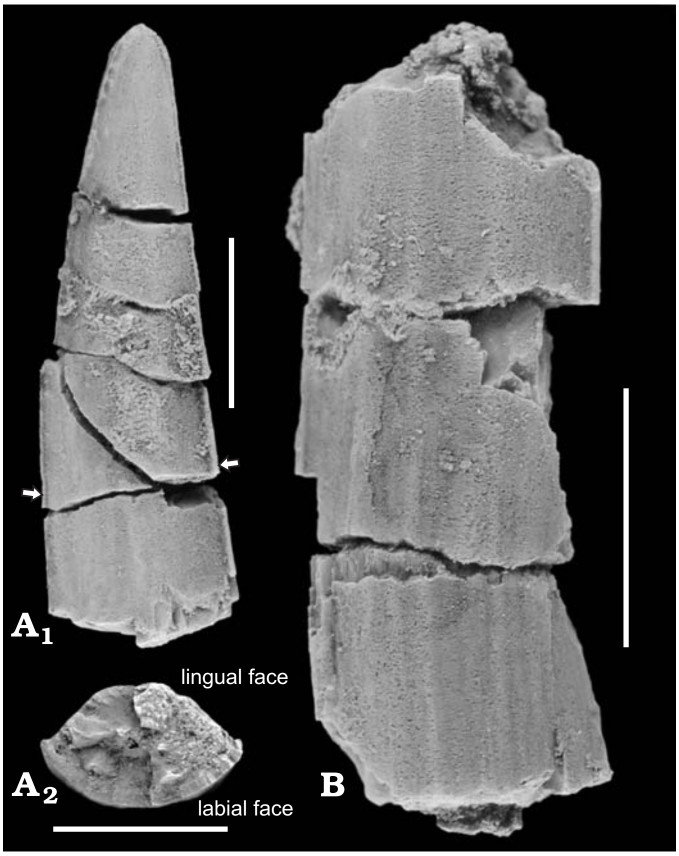

Fig. 4. Tooth of rebbachisaurid sauropod *Demandasaurus darwini* gen. et sp. nov. from Late Barremian–Early Aptian, Early Cretaceous of Tenadas de los Vallejos II, Spain. **A**. MDS-RVII,438, in lingual (A_1) and basal (A_2) views. **B**. Detail of the ornamentation of the tooth MDS-RVII,437, in lingual view. The arrows indicate the mesial and distal carinae. Scale bars 5 mm.

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Table 2. Measurements (in mm) of the vertebrae of *Demandasaurus darwini* gen. et sp. nov., Castrillo de la Reina Formation (Late Barremian–Early Aptian), Burgos, Spain. Estimated measurements are in brackets. Abbreviations: cadvW, dorsoventral width of the anterior articular surface of the vertebral centra; camlW, mediolateral width of the anterior articular surface of the vertebral centra; cL, centrum length; cpdvW, dorsoventral width of the posterior articular surface of the vertebral centra; cpmlW, mediolateral width of the posterior articular surface of the vertebral centra; dvW, dorsoventral width; nadvW, dorsoventral width of the neural arch; neA, angle between the neural spine and the centra vertebra (in degrees).

Vertebrae	Number	cL	dvW	cadvW	cpdvW	camlW	cpmlW	nadvW	neA
axis	MDS-RVII,606	100	180	42	(38)	(38)	34	(140)	50
anterior-middle cervical	MDS-RVII,589	270	(200)	90	95	70	85	–	–
posterior cervical	MDS-RVII,806	–	(258)	70	–	65	–	–	–
middle-posterior dorsal	MDS-RVII,602	150	290	140	145	145	(145)	–	–
middle-posterior dorsal	MDS-RVII,798	150	460	145	160	140	150	–	–
first caudal	MDS-RVII,605	145	620	160	170	(135)	–	460	78
anterior (second?) caudal	MDS-RVII,609	92	(222)	(155)	175	184	(154)	–	–
anterior caudal	MDS-RVII,15	98	390	125	135	115	135	250	73
anterior caudal	MDS-RVII,805	100	(315)	165	143	161	150	–	43
middle caudal	MDS-RVII,3	150	(185)	–	135	–	135	–	–
middle-posterior caudal	MDS-RVII,4	165	140	110	95	130	125	(40)	–
middle-posterior caudal	MDS-RVII,10	165	115	105	100	120	(11)	–	–
middle-posterior caudal	MDS-RVII,216	185	135	80	70	110	105	(65)	–
middle-posterior caudal	MDS-RVII,217	175	140	85	80	–	110	65	–
middle-posterior caudal	MDS-RVII,218	175	190	105	115	130	125	89	–

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).

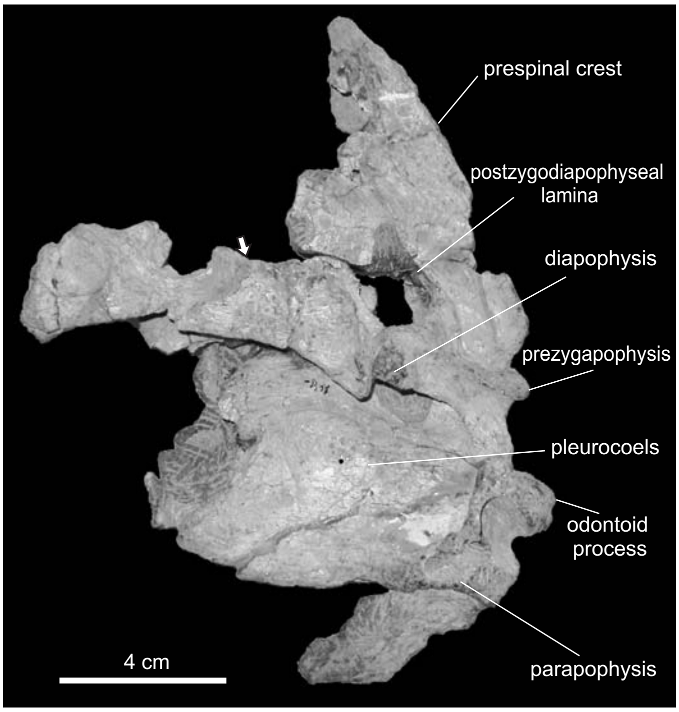

Fig. 5. Axis of rebbachisaurid sauropod *Demandasaurus darwini* gen. et sp. nov. from Late Barremian–Early Aptian, Early Cretaceous of Tenadas de los Vallejos II, Spain, MDS-RVII,606, in lateral view. The arrow indicates a structure in the third cervical vertebra.

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 centrodiapophyseal, posterior centrodiapophyseal, 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 *Galvesaurus*, *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.

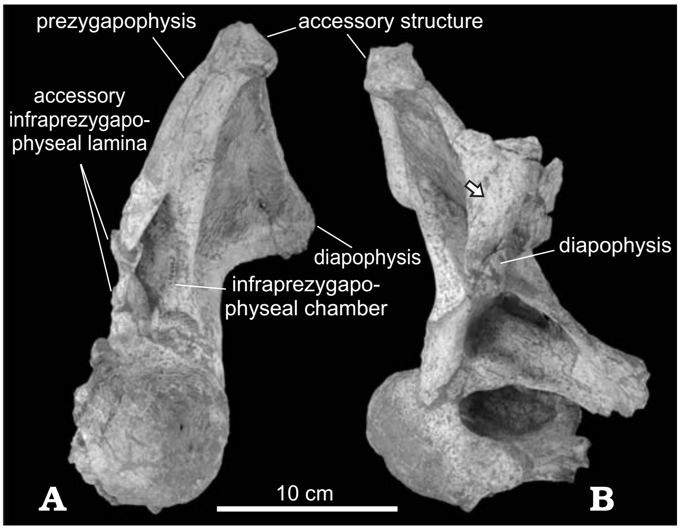

Fig. 7. Posterior cervical vertebra of rebbachisaurid sauropod *Demandasaurus darwini* gen. et sp. nov. from Late Barremian–Early Aptian, Early Cretaceous of Tenadas de los Vallejos II, Spain, MDS-RVII,806, in anterior (**A**) and left lateral (**B**) views. The arrow indicates a subtriangular surface located dorsally to the diapophysis.

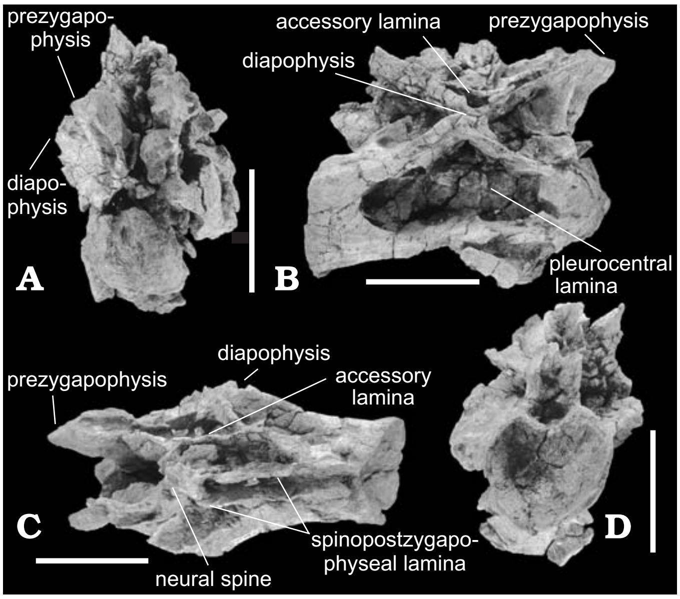

Fig. 6. Anterior-middle cervical vertebra of rebbachisaurid sauropod *Demandasaurus darwini* gen. et sp. nov. from Late Barremian–Early Aptian, Early Cretaceous of Tenadas de los Vallejos II, Spain, MDS-RVII,589, in anterior (**A**), right lateral (**B**), dorsal (**C**), and posterior (**D**) views.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

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

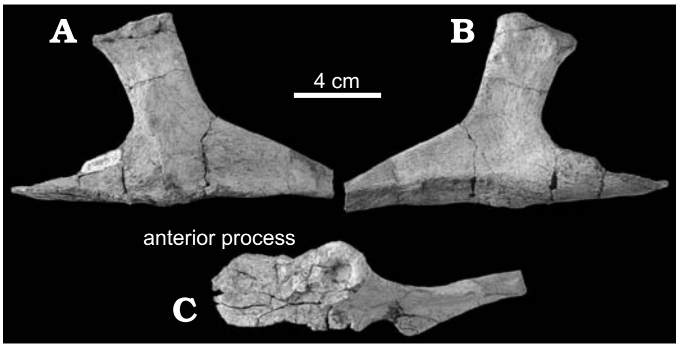

Fig. 8. Posterior cervical rib of rebbachisaurid sauropod *Demandasaurus darwini* gen. et sp. nov. from Late Barremian–Early Aptian, Early Cretaceous of Tenadas de los Vallejos II, Spain, MDS-RVII,811 (associated to the cervical vertebra MDS-RVII,806), in dorsal (**A**), ventral (**B**), and medial (**C**) views.

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,811 (Fig. 8A, B) 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 subrectangular respectively. They incline at roughly 45°, joining at their medial part. The dorsal vertebrae display very deep, semi-oval infraprezygapophyseal 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 infraprezygapophyseal 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),

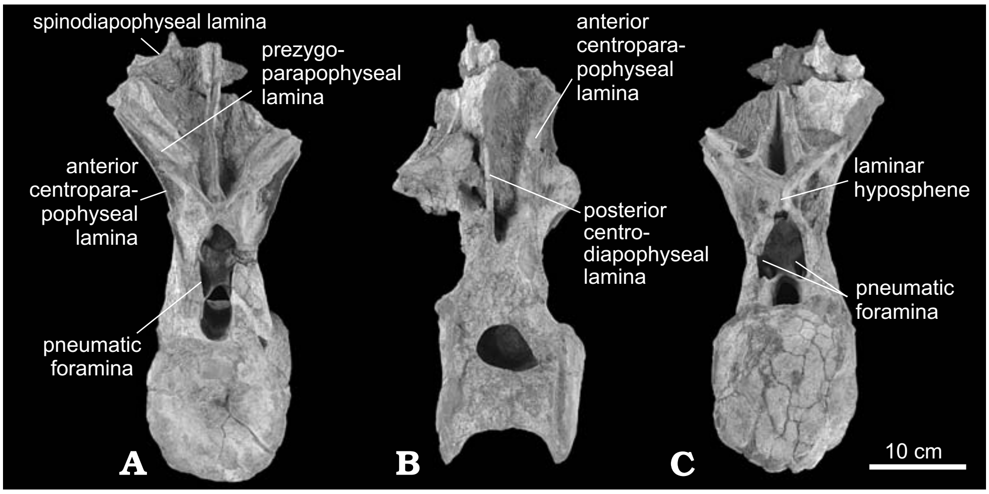

Fig. 9. Dorsal vertebra of rebbachisaurid sauropod *Demandasaurus darwini* gen. et sp. nov. from Late Barremian–Early Aptian, Early Cretaceous of Tenadas de los Vallejos II, Spain, MDS-RVII,798, in anterior (**A**), lateral (**B**), and posterior (**C**) views.

but has not been described in sauropods and is an autapomorphic character of *Demandasaurus*. There is a reduced, laminar hyposphene, the medial edges of which join the postzygapophyses (Fig. 9C). There are only two other rebbachisaurids in which the hyposphene-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 centroprezygapophyseal lamina and the anterior centroparapophyseal lamina. The centroprezygapophyseal laminae are forked, as occurs in the cervical vertebrae, which is considered an autapomorphy of *Demandasaurus*. There is no prezygodiapophyseal 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 prezygoparapophyseal laminae are very well developed, and together with the spinoprezygapophyseal laminae (sprl) they delimit deep subtriangular cavities (Fig. 9A). Through these cavities an accessory lamina runs parallel to the prezygoparapophyseal laminae, yet without making contact with the spinopostzygapophyseal laminae. The presence of the prezygoparapophyseal 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 medial centropostzygapophyseal lamina.

The postzygodiapophyseal 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 centrodiapophyseal lamina. The anterior centroparapophyseal lamina and the posterior centroparapophyseal laminae join to form a gentle depression. The lateral lamina would be formed by a spinodiapophyseal 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 spinodiapophyseal 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 and the capitulum are joined by a lamina of fine bone that presents an excavated pneumatic area. The ribs lack pneumatopores, and the interior of the bone displays a normal spongy structure.

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.

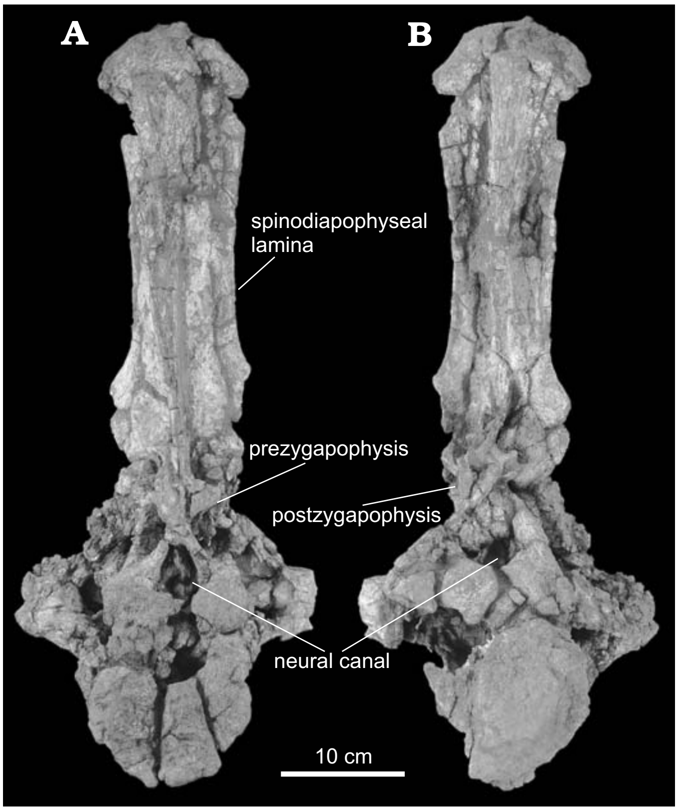

Fig. 10. First caudal vertebra of rebbachisaurid sauropod *Demandasaurus darwini* gen. et sp. nov. from Late Barremian–Early Aptian, Early Cretaceous of Tenadas de los Vallejos II, Spain, MDS-RVII,605, in anterior (**A**) and posterior (**B**) views.

First caudal vertebra (Fig. 10).—MDS-RVII,605 is nearly complete, lacking part of the vertebral centrum, the diapophyses, 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.

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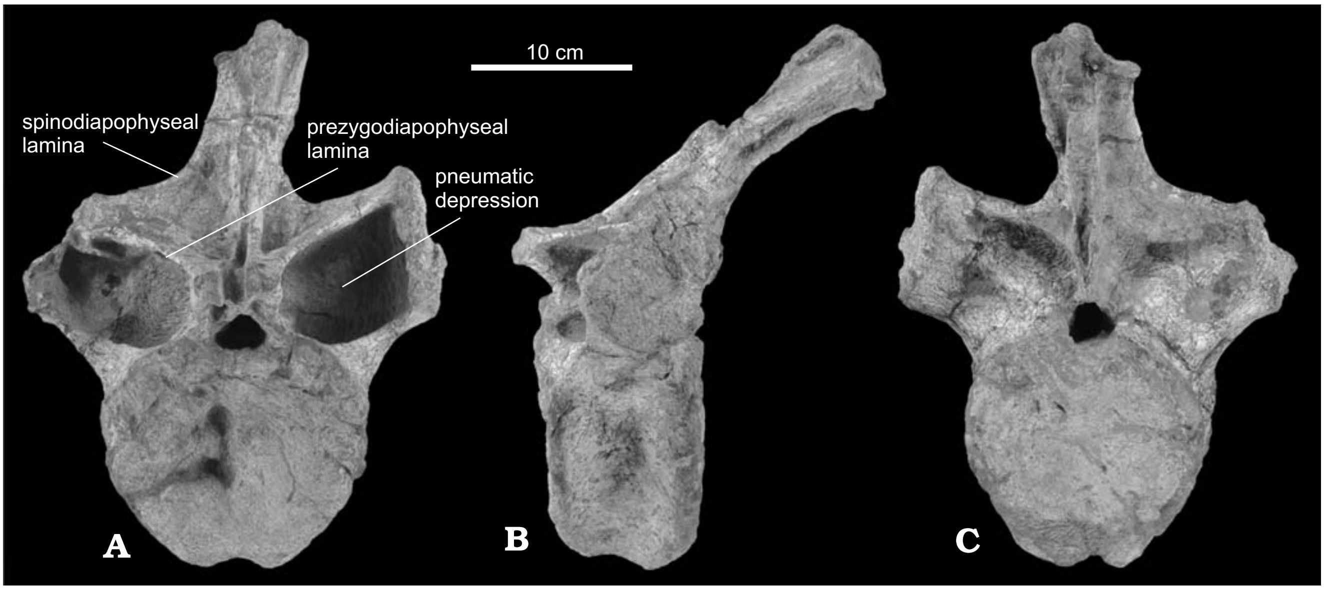

Fig. 11. Anterior caudal vertebra of rebbachisaurid sauropod *Demandasaurus darwini* gen. et sp. nov. from Late Barremian–Early Aptian, Early Cretaceous of Tenadas de los Vallejos II, Spain, MDS-RVII,610, in anterior (**A**), lateral (**B**), and posterior (**C**) views. The neural spine is incomplete.

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 (in left lateral view) 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 centroprezygapophyseal 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 the vertebral centrum. The postzygapophyses connect ventrally with thick centropostzygapophyseal laminae, which delimit a triangular area (scarcely depressed) between the neural canal and the postzygapophyses. Laterally our specimen presents postzygodiapophyseal laminae and dorsally the well-developed spinopostzygapophyseal laminae.

In lateral view, in the dorsal and middle-posterior parts of the vertebral centrum are the poorly-preserved transverse processes. They are very tall dorsoventrally and seem to display an anterior pneumatic cavity similar to that exhibited by the rest of the anterior vertebrae of the caudal series of *Demandasaurus*. Between the anterior part of the transverse process and the edge of the anterior 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.

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 procoelous 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 anteroposteriorly, 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 anteroposteriorly, 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 anteroposteriorly 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. 11A_2), 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 *Nigersaurus* (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 centrodiapophyseal and posterior centrodiapophyseal 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 centrodiapophyseal lamina (posteriorly). These laminae delimit two large, oval pneumatic depressions (one on each side), inside which there 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.

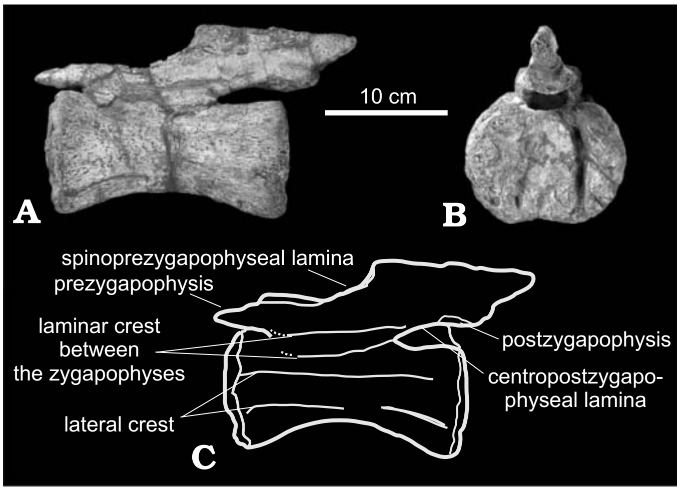

Fig. 12. Mid-posterior caudal vertebra of rebbachisaurid sauropod *Demandasaurus darwini* gen. et sp. nov. from Late Barremian–Early Aptian, Early Cretaceous of Tenadas de los Vallejos II, Spain, MDS-RVII,217, in left lateral (**A**), posterior (**B**), and schematic (**C**) views.

The anterior caudals have a small hyposphene 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

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Table 3. Measurements (in mm) of the haemal arches of *Demandasaurus darwini* gen. et sp. nov., Castrillo de la Reina Formation (Late Barremian–Early Aptian), Burgos, Spain. Abbreviations: brA, angle between the dorsal branches (in degrees); dbL, anteroposterior length of distal branch; dvdbW, dorsoventral width of the distal branch; dvhcW, dorsoventral width of the haemal canal; dvW, dorsoventral width; mldeW, mediolateral width of the distal end; mlhcW, mediolateral width of the haemal canal; mlpeW, mediolateral width of the proximal end.

Haemal arch	dvW	dvdbW	mlpeW	dbL	mldeW	brA	dvhcW	mlhcW	Position
MDS-RVII,590	315	240	90	17	26	35	84	32	anterior
MDS-RVII,591	355	245	80	(25)	25	30	92	30	anterior
MDS-RVII,797	370	260	80	27	20	30	85	30	anterior
MDS-RVII,796	340	235	77	35	24	30	81	26	anterior
MDS-RVII, 99	(135)	(25)	–	–	–	40	81	–	middle
MDS-RVII,231	205	(95)	76	–	23	27	76	23	middle
MDS-RVII,232	150	52	74	26	11	40	(67)	32	middle-posterior
MDS-RVII, 23	131	(37)	82	(24)	13	40	(65)	29	middle-posterior
MDS-RVII,594	130	–	33	–	–	–	–	–	posterior

of the vertebral centrum in the anterior caudals. The postzygapophyses 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 dis-

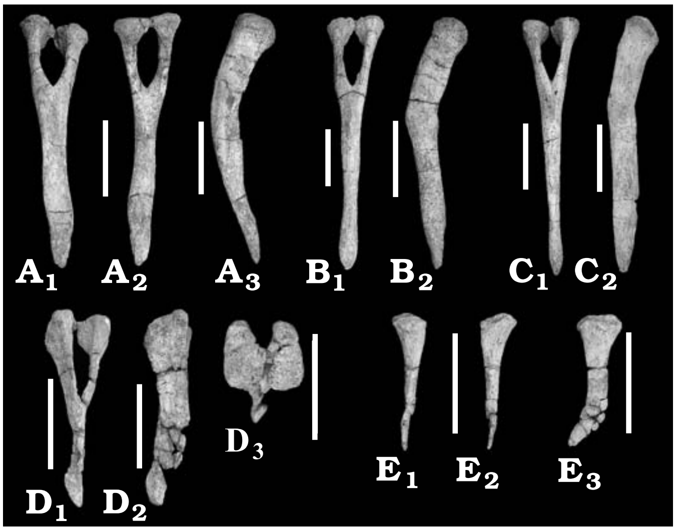

Fig. 13. Haemal arches of rebbachisaurid sauropod *Demandasaurus darwini* gen. et sp. nov. from Late Barremian–Early Aptian, Early Cretaceous of Tenadas de los Vallejos II, Spain. **A**. MDS-RVII,590, in anterior (A_1), posterior (A_2), and lateral (A_3) views. **B**. MDS-RVII,591, in anterior (B_1) and lateral (B_2) views. **C**. MDS-RVII,797, in anterior (C_1) and lateral (C_2) views. **D**. MDS-RVII,231, in anterior (D_1), lateral (D_2), and proximal (D_3) views. **E**. MDS-RVII,594, in anterior (E_1), posterior (E_2), and lateral (E_3) views. Scale bars 10 cm.

plays a large nutritive foramen in a medial position on the pubic peduncle.

The ischial branch is distinctively straight, elongated (approximately 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 projects posteriorly, as occurs in *Camarasaurus* (Ostrom and McIntosh 1966). The section of the ischial branch at its midpoint 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 dorsodistal 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 titanosaurs (Salgado et al. 1997). Among the rebbachisaurids, the ischium of *Limaysaurus 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*.

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.

Femur measurements	mm
Total length	1080
Proximal mediolateral width	320
Anteroposterior width of femur articular head	130
Anteroposterior width of greater trochanter	120
Proximal length to 4th trochanter	390
Length of 4th trochanter	120
Proximal length to minimum shaft mediolateral width	610
Shaft minimum anteroposterior width	65
Shaft minimum lateromedial width	135
Distal mediolateral width	310
Proximal mediolateral width / total length	0.30
Proximal length to minimum shaft mediolateral width / total length	0.56
Shaft minimum lateromedial width / total length (Slenderness Index)	0.12
Distal mediolateral width / total length	0.29
Proximal length to 4th trochanter / total length	0.36
Shaft minimum anteroposterior width / lateromedial width (Eccentricity)	0.48

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 expansion. The distal end is twisted roughly 30° medially with respect 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 proximal third, beneath the area of the greater trochanter.

The diapohysis is curved on its medial side and practically 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 anteroposteriorly with an eccentricity close to 0.5 (Table 4). It displays 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 lateral 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, without 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 scarce 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 anteroposteriorly. 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 projecting 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

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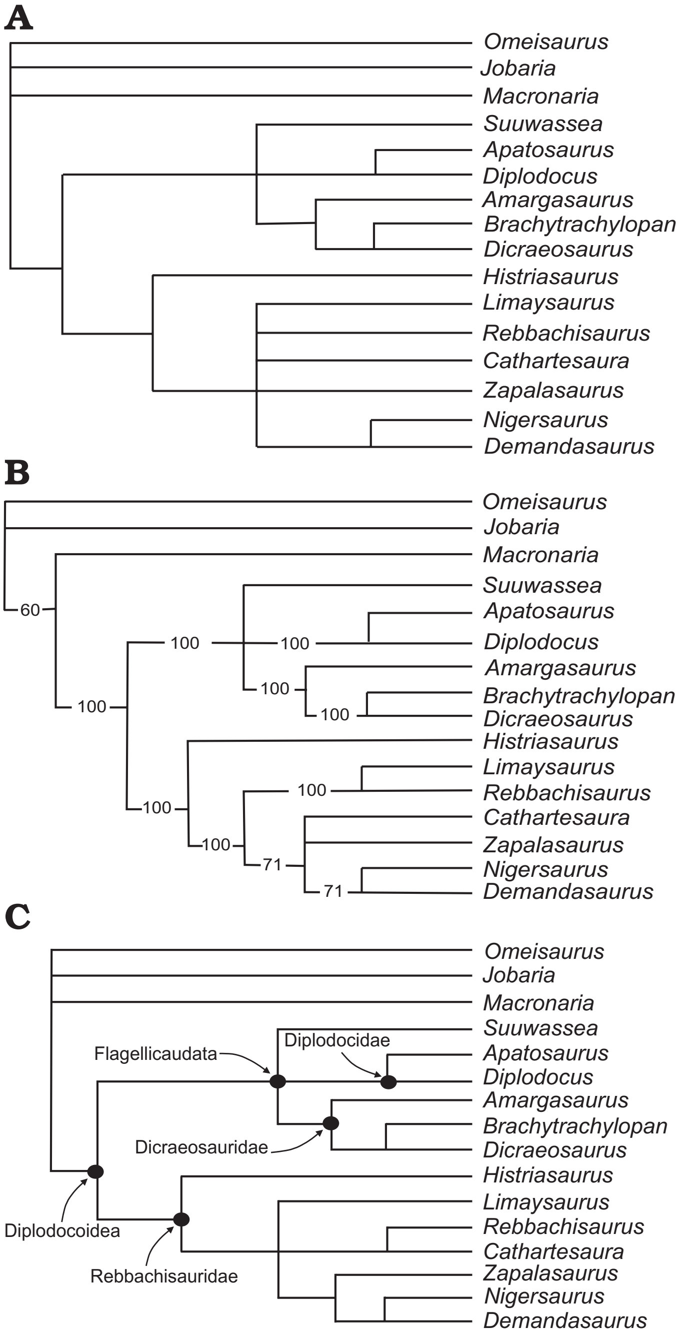

Fig. 14. Cladograms showing the phylogenetic position of *Demandasaurus darwini* gen. et sp. nov., strict consensus (**A**), 50% majority-rule consensus (**B**), and Adams consensus (**C**) of 35 equally parsimonious trees using 16 taxa and 102 unordered characters (see Sereno et al. 2007 and Appendix 1).

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 *Rebbachisaurus* than to *Diplodocus*". It would be a basal clade of diplodocoids, and this is how it has been used by the various authors (Wilson 2002; Salgado et al. 2004; Upchurch et al. 2004a; Sereno et al. 2007). Upchurch et al. (2004a: 303) cite as its autapomorphy the unique shape of the scapular blade: "a paddle-like outline in lateral view".

In order to study the phylogenetic relations of *Demandasaurus*, a cladistic analysis of the diplodocoids was carried out using the matrix of 102 characters of Sereno et al. (2007), and adding this new species. We choose the matrix of Sereno et al. (2007) because it included most other rebbachisaurids. Certain taxa known from fragmentary material are not included in the analysis of Sereno et al. (2007): taxa such as *Rayososaurus agrioensis* Bonaparte, 1996, which presents the typical scapula of this clade (Bonaparte 1997; Mannion 2009). In the proposal put forward by Sereno et al. (2007), the taxon "Spanish rebbachisaurid" is used, which is precisely what *Demandasaurus* 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 (dentary, 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 *Zapalasaurus*. 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

Demandasarus 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).

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Appendix 1

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

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?0?????????????????????????????0????001?111??00011?10000????99?1?111110?10110?00
10???10????????011101?
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