Europatitan eastwoodi, a new sauropod from the lower Cretaceous of Iberia in the initial radiation of somphospondylans in Laurasia

Fidel Torcida Fernández-Baldor[1,2], José Ignacio Canudo[3,4],
Pedro Huerta[1,2,5], Miguel Moreno-Azanza[6,7] and Diego Montero[1,2]

[1] Museo de Dinosaurios, Salas de los Infantes, Burgos, Spain
[2] Colectivo Arqueológico-Paleontológico Salense, Salas de los Infantes, Burgos, Spain
[3] Paleontología, Facultad de Ciencias, Universidad de Zaragoza, Zaragoza, Spain
[4] Grupo Aragosaurus—IUCA, Universidad de Zaragoza, Zaragoza, Spain
[5] Departamento de Geología, Escuela Politécnica Superior de Ávila, Universidad de Salamanca, Salamanca, Spain
[6] GeoBioTec, Departamento de Ciências da Terra, Faculdade de Ciências e Tecnologia, Universidade NOVA de Lisboa, Caparica, Portugal
[7] Museu da Lourinhã, Lourinhã, Portugal

ABSTRACT

The sauropod of El Oterillo II is a specimen that was excavated from the Castrillo de la Reina Formation (Burgos, Spain), late Barremian–early Aptian, in the 2000s but initially remained undescribed. A tooth and elements of the axial skeleton, and the scapular and pelvic girdle, represent it. It is one of the most complete titanosauriform sauropods from the Early Cretaceous of Europe and presents an opportunity to deepen our understanding of the radiation of this clade in the Early Cretaceous and study the paleobiogeographical relationships of Iberia with Gondwana and with other parts of Laurasia. The late Barremian–early Aptian is the time interval in the Cretaceous with the greatest diversity of sauropod taxa described in Iberia: two titanosauriforms, *Tastavinsaurus* and *Europatitan*; and a rebbachisaurid, *Demandasaurus*. The new sauropod *Europatitan eastwoodi* n. gen. n. sp. presents a series of autapomorphic characters in the presacral vertebrae and scapula that distinguish it from the other sauropods of the Early Cretaceous of Iberia. Our phylogenetic study locates *Europatitan* as the basalmost member of the Somphospondyli, clearly differentiated from other clades such as Brachiosauridae and Titanosauria, and distantly related to the contemporaneous *Tastavinsaurus*. *Europatitan* could be a representative of a Eurogondwanan fauna like *Demandasaurus*, the other sauropod described from the Castrillo de la Reina Formation. The presence of a sauropod fauna with marked Gondwananan affinities in the Aptian of Iberia reinforces the idea of faunal exchanges between this continental masses during the Early Cretaceous. Further specimens and more detailed analysis are needed to elucidate if this Aptian fauna is caused by the presence of previously unnoticed Aptian land bridges, or it represents a relict fauna from an earlier dispersal event.

INTRODUCTION

The vertebrate faunas of the Early Cretaceous of the Iberian Peninsula are of particular interest on account of the special paleobiogeographical location of the Iberian microplate. The Iberian Peninsula is the Laurasian landmass situated closest to Gondwana, and there are obvious relations between certain Iberian and Gondwanan dinosaurs and other clades in the Early Cretaceous, especially in the Barremian (*Pereda-Suberbiola et al., 2003*; *Gheerbrant & Rage, 2006*; *Canudo, Royo-Torres & Cuenca-Bescós, 2008*; *Canudo et al., 2009*; *Torcida Fernández-Baldor et al., 2011*; *Carballido et al., 2012*; *Gasca, Canudo & Moreno-Azanza, 2014*). One hypothesis that explains how the faunal exchange between Africa and Europe could be developed is the so-called "trans-Tethys" route or Apulian route (*Gheerbrant & Rage, 2006*). According to this hypothesis, the existence of archipelagos separated by shallow seas of changing eustatic levels, would make possible the migratory movement of the dinosaurs between the two continental masses quoted in a bidirectional sense. The Apulian route could have facilitated these migratory movements intermittently until the Eocene (*Gheerbrant & Rage, 2006*; *Canudo et al., 2009*). Bearing this fact in mind, modern paleobiogeographical models point out that Europe and "Gondwanan" territories possessed a common *Eurogondwanan* fauna during the earliest Cretaceous, but that from the Barremian onwards dispersal took place independently in Gondwana and Laurasia, with the isolation of the European faunas (*Ezcurra & Agnolín, 2012*). To resolve this paleobiogeographical problem, new dinosaur material needs to be put in its correct phylogenetic position and its age established. This may be the only way of ascertaining whether the paleobiogeographical complexity of the Iberian Peninsula in the Early Cretaceous was the result of processes of dinosaur dispersal only at certain points in time or came about as a continuous process. A particularly interesting group for studying this question is the sauropod dinosaurs due to their broad distribution on a worldwide scale in the Cretaceous.

Sauropods are one of the groups of dinosaurs of the Spanish Cretaceous of which our knowledge has increased most substantially as a result of recent discoveries such as those of the macronarians of the end of the Jurassic and the Early Cretaceous. Accordingly, *Galvesaurus* has been described in the Tithonian (*Barco et al., 2005*; *Aurell et al., 2016*), *Aragosaurus* at the base of the Cretaceous (*Sanz et al., 1987*; *Canudo et al., 2012*; *Royo-Torres et al., 2014*), *Tastavinsaurus* and *Demandasaurus* in the Barremian–lower Aptian (*Canudo, Royo-Torres & Cuenca-Bescós, 2008*; *Royo-Torres, Alcalá & Cobos, 2012*; *Torcida Fernández-Baldor et al., 2011*), and *Lirainosaurus* and *Lohuecotitan* in the upper Campanian (*Sanz et al., 1999*; *Vila et al., 2012*; *Díez Díaz et al., 2016*). In the Cretaceous, Titanosauriformes were the dominant—indeed almost the only—sauropods in the Iberian Peninsula, as shown by the fact that the vast majority of remains found have been assigned to this clade, with the exception of the rebbachisaurid *Demandasaurus* of the upper Barremian–lower Aptian (*Torcida Fernández-Baldor et al., 2011*). The systematic

position of the macronarian *Aragosaurus*, found at the base of the Cretaceous of Teruel, Spain (*Aurell et al., 2016*), is a matter of controversy: some authors recover it as a non-titanosauriform macronarian (*Mannion et al., 2013*; *Royo-Torres et al., 2014*), whereas for others it possesses characters that suggest its inclusion in Titanosauriformes (*Canudo et al., 2012*).

Titanosauriformes is the most diverse sauropod clade in the Cretaceous, and is represented on all the continents (*D'Emic, 2012*; *Mannion et al., 2013*). More derived titanosauriforms, i.e., lithostrotian titanosaurs, are characterized by apomorphies that have made it possible to identify them relatively easily (*Salgado, Coria & Calvo, 1997*; *Wilson, 2002*; *González Riga, 2003*). However, non-titanosaurian titanosauriforms have been the subject of different interpretations in different cases (*Wilson & Upchurch, 2009*). This disagreement is due to the scarcity of complete specimens, which has made it difficult to establish synapomorphies that might allow us to distinguish different groups other than the titanosaurs; another difficulty in this sense is the existence of clade definitions that offer different diagnostic characteristics (*Salgado, Coria & Calvo, 1997*; *Wilson, 2002*; *González Riga, 2003*). Titanosauriforms are important to Cretaceous paleobiogeography because of their diversity and ubiquity, but their impact on paleobiogeography has not been fully realized owing to confusion over their phylogenetic *relationships* (*D'Emic, 2012*; *Mannion et al., 2013*; *Gorscak & O'Connor, 2016*; *Poropat et al., 2016*). Resolving the role of endemism and the details of the faunal turnover of these sauropods depends on ascertaining their lower-level phylogenetic relationships. *D'Emic (2012)* has undertaken a revision of the Titanosauriformes, proposing a new phylogenetic framework that differentiates two further clades in addition to the titanosaurians: on the one hand the brachiosaurids, with their origin in the Late Jurassic of Pangaea, and on the other hand a second clade of Asian somphospondylans, Euhelopodidae, distributed across the Early-mid Cretaceous of Asia. *Ksepka & Norell (2010)* also identify several taxa of Asian titanosauriforms as somphospondylans and they point out that there is not evidence of Asian brachiosaurids. The proposal of *D'Emic (2012)* includes a number of non-titanosaurian Laurasian and Gondwanan genera (*Tastavinsaurus*, *Sauroposeidon*, *Ligabuesaurus*) that are not accommodated within these two clades (see also *Mannion et al., 2013*). This hypothesis is not the only one that has been proposed, since *Royo-Torres, Alcalá & Cobos (2012)* have identified a clade they designate Laurasiformes containing Iberian and North American taxa from the Early Cretaceous, bringing together various earlier proposals (*Canudo & Cuenca-Bescós, 2004*). In spite of these significant contributions to what is known of the phylogenetic relations among the basal titanosauriforms, as well as their paleobiogeographical relationships (especially those relations between Gondwana and Laurasia), further specimens are required to shed new light on the problem.

A particularly prolific area when it comes to continental vertebrate fossil remains from the Early Cretaceous of Spain is the region of Salas de los Infantes (Burgos) in the north of the Iberian Peninsula (*Sanz, 1983*; *Pereda-Suberbiola et al., 2003*, *2011*; *Torcida Fernández-Baldor, 2006*; *Torcida Fernández-Baldor et al., 2005*, *2011*; *Huerta et al., 2012*). On the basis of the discoveries of the last 20 years, a project has been undertaken to bring paleontology to the public attention, its cornerstone being the Dinosaur Museum of Salas de los

Infantes, where various dinosaur tracksites have also been prepared as exhibits. In this context, the site of El Oterillo II was found in 2003 and excavated in the following years 2004–2006. The specimen in question is the semi-articulated specimen of a sauropod, from which various remains from the cranial and postcranial skeleton have been recovered. These materials were attributed to Titanosauriformes in a preliminary research on the basis of the morphology of the caudal vertebrae (*Torcida Fernández-Baldor et al., 2009*). The fossils that constitute the holotype are housed in the Dinosaur Museum of Salas de los Infantes (Burgos). The aim of the present paper is to provide a complete description of the sauropod of El Oterillo II, to ascertain its phylogenetic position in relation to the most recent proposals for Titanosauriformes, and to draw relevant paleobiogeographical conclusions.

LOCATION AND GEOLOGICAL SETTING

The site of El Oterillo II is located in the province of Burgos in northern Spain, 2.5 km to the west of the village of Barbadillo del Mercado in Salas de los Infantes (Fig. 1; Fig. S1). Geologically, El Oterillo II is located in the Cameros Basin, which was filled during the upper Jurassic–lower Cretaceous by a non-marine succession (Fig. 1). This basin is a half-graben related to the second phase of the Iberian Rift System, which accumulated around 9,000 m of sediment in its depocenter (*Salas & Casas, 1993*; *Salas et al., 2001*). The basin has classically been divided into two sectors. The eastern part is where the depocenter is located and where low-grade metamorphism occurred. It is probably for this reason that fossil bone sites are extremely rare in this area (*Canudo et al., 2010*), although there are many footprint sites (*Castanera et al., 2014*). In the western part of the basin (the "*Subcuenca Occidental de Cameros*"), vertebrate bone and track sites are abundant (*Torcida Fernández-Baldor, 2006*). It is in this part of the basin that the site of El Oterillo II is located. The sediments of the Cameros Basin have traditionally been divided into five groups: Tera, Oncala, Urbión, Enciso, and Olivan. The stratigraphy of the western part of the basin is quite complex due to the different stratigraphic proposals (*Platt, 1989*; *Martín-Closas & Alonso Millán, 1998*; *Arribas et al., 2003*; *Clemente Vidal, 2010*). The site of El Oterillo II is located in the Urbión Group (Fig. 1).

The bed-to-bed correlation based on aerial photos with stratigraphic logs previously published for the Salas de los Infantes area allows the site of El Oterillo II to be placed in the Castrillo de la Reina Fm., one of the formations included in the Urbión Group (Fig. 1). This lithostratigraphic unit is constituted by alternating sandstone layers ranging from 50 cm to 2 m in thickness with red lutite layers among which there are occasional levels with carbonate encrustations (nodular caliches). These facies are interpreted as distal alluvial plains that record prolonged periods of low clastic sedimentation. As a whole, the sequence represents a distal fluvial–alluvial system originating from the southwest. In the last 10 years, an abundant fossil fauna of dinosaurs and other vertebrates has been described in this formation (*Pereda-Suberbiola et al., 2003*; *Torcida Fernández-Baldor, 2006*; *Torcida Fernández-Baldor et al., 2005*, *2008*, *2011*, *2015*; *Pérez-García et al., 2011*). The age of the Castrillo de la Reina Fm. is upper Barremian–Aptian, as determined mainly
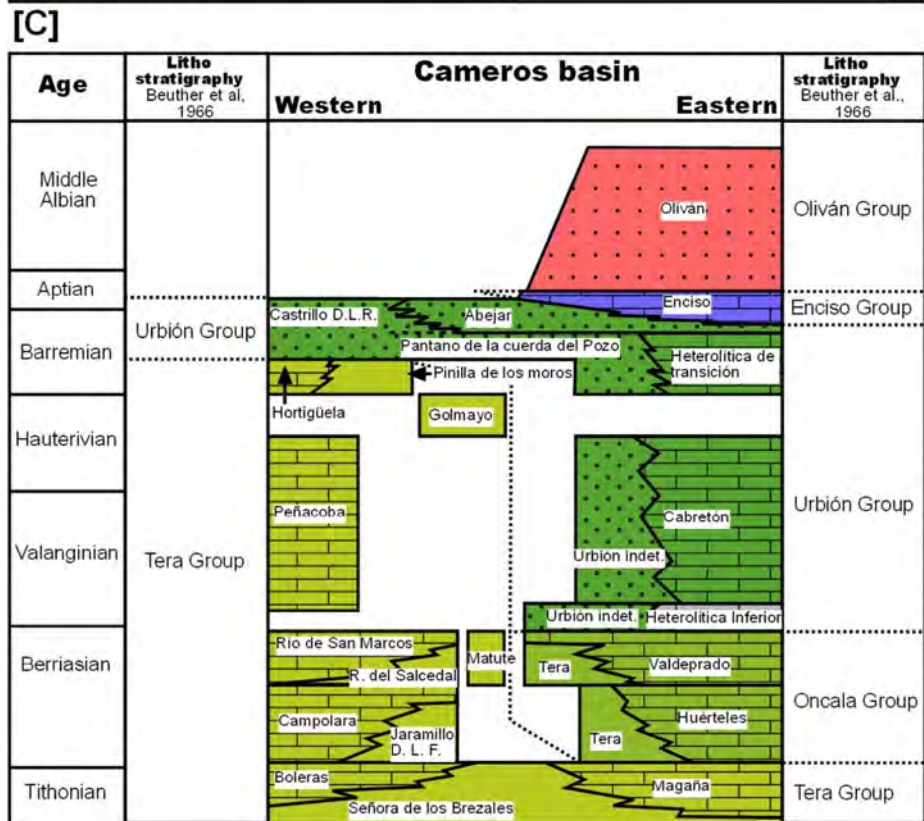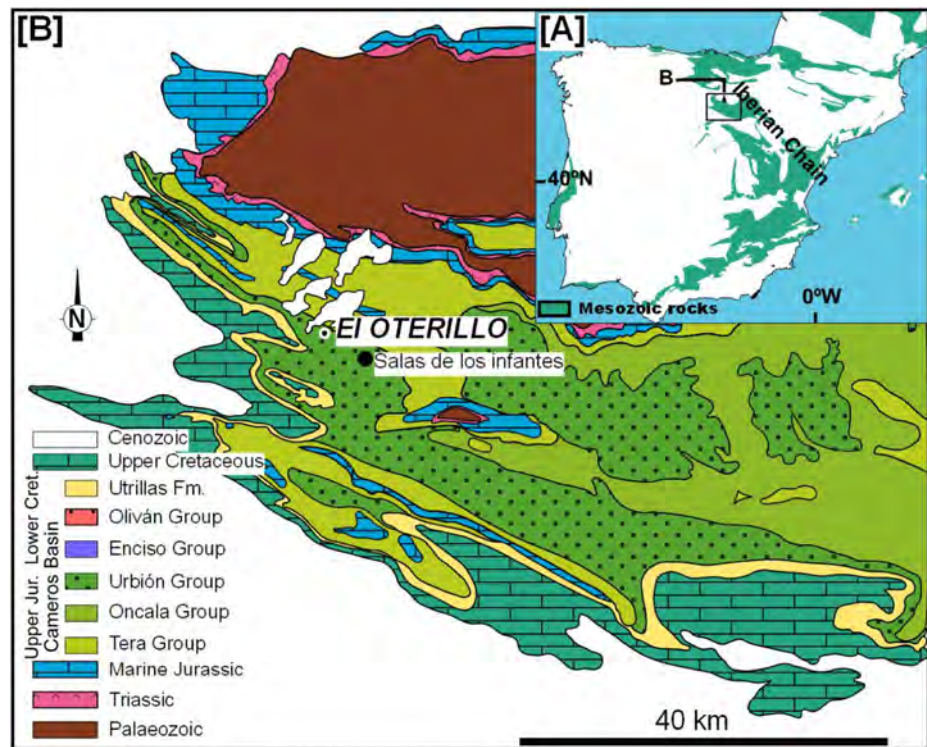
Figure 1 Geological map of the western Cameros Basin. Based on *Beuther et al. (1966)* indicating the location of El Oterillo site and stratigraphy of the basin modified from *Martín-Closas & Alonso Millán (1998).*
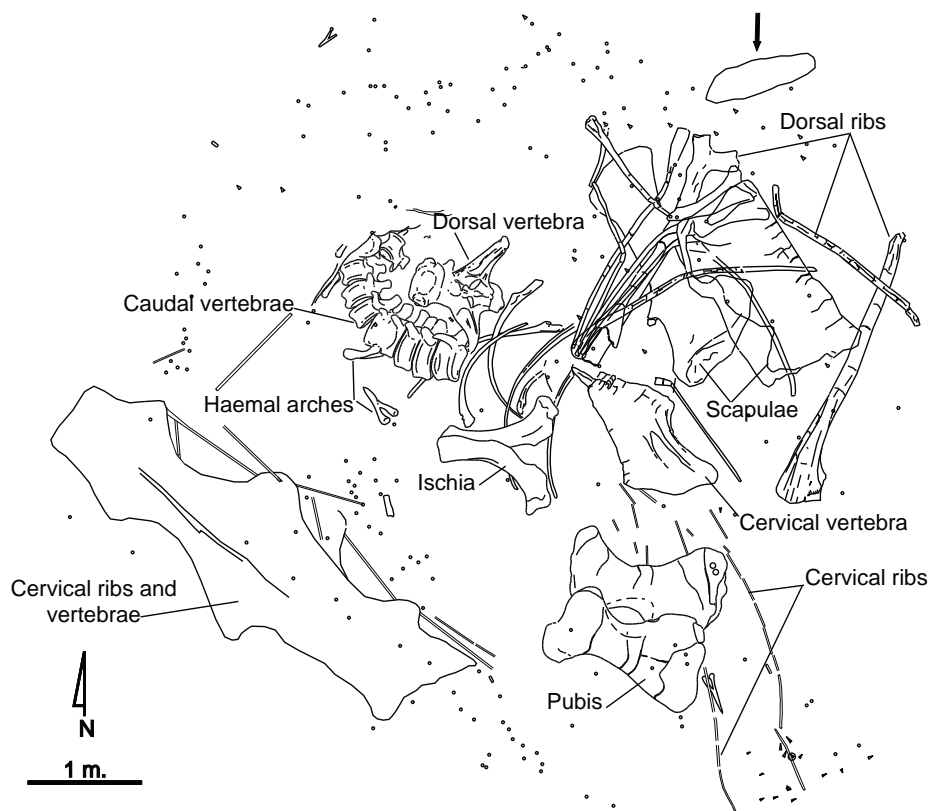
Figure 2 Quarry map of the partial skeleton of *Europatitan eastwoodi* n. gen. n. sp. from the late Barremian–early Aptian, Early Cretaceous, of El Oterillo II site, Spain. The arrow indicates an iguanodontoid ilium (*Contreras et al., 2007*). Circular symbols correspond to splinters, and triangles to isolated teeth of theropods.

on the basis of charophyte and ostracod biostratigraphy (*Martín-Closas & Alonso Millán, 1998*; *Schudack & Schudack, 2009*).

The site of El Oterillo II is located at the top of a sandstone bed with channel geometry, 50 cm thick and 8 m wide, and interbedded with red mudstones. The sandstone bed shows cross-stratification and scattered quartzite clasts. The color of the sandstone is reddish-brown and becomes grey-blue toward the top, where the dinosaur bones appear. In some parts of the site, just below or very close to the bones, a lag of quartzite clasts (1–2.5 cm diameter) with theropod and crocodyliform teeth appears. The paleocurrent measured in the channel indicates an ENE direction. Sandstone channel fills are scarce in the area; other sandstone beds have tabular geometries that are large in extension and centimeters to meters in thickness. The beds dip 15° southwards.

El Oterillo II has yielded the remains of only one sauropod individual (Fig. 2), as well as isolated theropod teeth, which tends to be the case with herbivore carcasses (*Alonso, Canudo & Torcida Fernández-Baldor, 2016*). An iguanodontian ilium was found at the site although separated from the main bone set (*Contreras et al., 2007*). A total of 350 fossils belonging to the sauropod specimen have been recovered. A major percentage of these materials are fragments of dorsal and cervical ribs, as well as fragments of vertebral laminae. The most complete material has been studied for the present paper.

From the site, a series of caudal vertebrae from the sauropod appears articulated, whereas others such as the hipbones, or the scapula and several ribs, are close to their anatomical position although slightly displaced (Fig. 2). Several bones show tooth marks (*Alonso, Canudo & Torcida Fernández-Baldor, 2016*), and some are in a poor state of preservation at their distal or proximal ends. Long bones have not been found.

The sandstone bed underlying the dinosaur remains is interpreted as a fluvial channel isolated in floodplain deposits, as is inferred from the geometry, the sedimentary structures, the paleocurrents and the fluvial origin of the Castrillo de la Reina Fm. (*Clemente & Perez-Arlucea, 1993*; *Martín-Closas & Alonso Millán, 1998*). The articulation of the sauropod caudal vertebrae and the anatomical position of other bones reveal that transport did not take place. The size of the quartzite clasts and their position below the dinosaur remains suggest that the channel flow was not strong enough to move a sauropod body and that flow occurred before the arrival of the dinosaur. The tooth marks found in some bones, and the presence of several theropod teeth, reveal the presence of carrion feeders. Some parts of the body that are well preserved and do not show tooth marks, such as the caudal vertebrae, were probably covered by water and/or sediment.

SYSTEMATIC PALEONTOLOGY

Materials and methods

El Oterillo II (OT-II) was found in 2003 during the prospection campaign carried out as part of the Paleontological Inventory of the Sierra de la Demanda (file 243/03-BU JDVR/MCP). The material described in this publication was excavated in 2004, 2005, and 2006 with the corresponding permits from the Heritage Office (*Dirección General de Patrimonio*) of the regional government of Castilla y León (dossiers 307/04-BU; 257/05-BU; 262/06-BU), which is the department responsible for the administration of the paleontological heritage of this region of Spain. Accordingly, the material complies with all the regulations of the Spanish state. All the material described in the present publication is housed in the Dinosaur Museum of Salas de los Infantes (MDS; previously MPS) (Salas de los Infantes, Burgos, Spain), where it is available for comparative study by qualified researchers. The material studied comprises one tooth, five cervical vertebrae, one dorsal vertebra, nine caudal vertebrae, 11 cervical ribs, five dorsal ribs, seven hemal arches, the two scapulae, the left coracoid, the left metacarpals I and III, the two pubes, and the two ischia. The museum numbers are MDS-OTII,1 to MDS-OTII,32.

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archived and available from the following digital repositories: PeerJ, PubMed Central and CLOCKSS.

Nomenclature

In general, we use the standardized anatomical nomenclature based on the *Nomina Anatomica Avium* and *Nomina Anatomica Veterinaria* (see *Harris, 2004*). The nomenclature for the vertebral laminae follows *Wilson (1999)*, with modifications (apcdl) from *Salgado, Apesteguía & Heredia (2005)* and *Wilson et al. (2011)*. The nomenclature for the vertebral pneumatic structures follows *Wedel (2003)* and *Wilson et al. (2011)*.

Order SAURISCHIA *Seeley, 1887*

Infraorder SAUROPODA *Marsh, 1878*

NEOSAUROPODA *Bonaparte, 1986*

Titanosauriformes *Salgado, Coria & Calvo, 1997*

Somphospondyli *Wilson & Sereno, 1998*

Genus *Europatitan* gen. nov.

urn:lsid:zoobank.org:act:29532C3F-4E3F-4702-845A-2D75EF3C63B

(Figs. 3–17)

Etymology: In reference to Europe, the continent where it was found, and the titans, ancient Greek deities known for their gigantic size, endowed with great power.

Type Species: *Europatitan eastwoodi* sp. nov., see below.

Diagnosis: As for the type and only known species.

    E. eastwoodi sp. nov.

    urn:lsid:zoobank.org:act:B436CCB2-6E5C-498E-80A5-4BF271AC3175.

Etymology: Dedicated to US actor Clint Eastwood, the protagonist of the film "The Good, the Bad and the Ugly," which was partially filmed near Salas de los Infantes.

Type Locality and Horizon: The site of El Oterillo II is located in the province of Burgos in northern Spain, 2.5 km to the west of the village of Barbadillo del Mercado in Salas de los Infantes (Fig. 1), Burgos Province, Spain; Urbión Group, Castrillo de la Reina Fm., lower Cretaceous, regarded as late Barremian–early Aptian in age (*Martín-Closas & Alonso Millán, 1998*).

Holotype: MDS-OTII,1 to MDS-OTII-32. The disarticulated carcass of a single specimen consisting of the following material: one tooth, five cervical vertebrae, one dorsal vertebra, nine caudal vertebrae, 11 cervical ribs, five dorsal ribs, seven hemal arches, the two scapulae, the left coracoid, the left metacarpals I and III, the two pubes, and the two ischia.

Diagnosis: A large titanosauriform sauropod diagnosed by a combination of autapomorphic and synapomorphic characters. The autapomorphies are as follows: (1) posterior cervical vertebrae with a parapophysis that presents a triradiate laminar structure in its dorsal part dividing the lateral pneumatic fossa; (2) middle and posterior dorsal vertebrae with a horizontal tpol lamina positioned dorsal to the hyposphene;

(3) middle and posterior dorsal vertebrae with centroprezygapophyseal lamina joined laterally to two accessory laminae delimiting pneumatic cavities and that partially subdivides the centroprezygapophyseal parapophyseal fossa; (4) in the middle and posterior dorsal vertebrae dorsally the centropostzygapophyseal laminae reach the lateroventral margin of the hyposphene and are forked at their ventral end, (5) middle and posterior dorsal vertebrae with posterior part of the centrodiapophyseal postzygapophyseal fossa broad and divided by various small accessory laminae situated between the posterior centrodiapophyseal and the postzygodiapophyseal laminae, giving rise to small, highly conspicuous pneumatic subfossae; (6) in the middle and posterior dorsal vertebrae there is an accessory lamina present between the anterior and posterior spinodiapophyseal laminae; this lamina divides the fossa situated between the two laminae; (7) on the anterior surface of the capitulum the posterior dorsal ribs present a crest that is sinusoidal in outline running in a proximodistal direction; (8) the dorsal area of the deltoid crest of the scapula presents a sub-elliptical process with a rugose surface, accompanied in its ventral part by a rugose flat area and a pronounced groove; (9) on the dorsal margin of the scapular blade, approximately in its middle part, there is a rugose tubercle with two projections separated by a semicircular depressed area.

The combination of synapomorphic characters is as follows: flat or slightly convex ventral surface of the cervical centra (Ch. 112:0); very reduced pleurocoels in cervical centra (Ch. 114:3) with a well-defined anterior excavation and smooth posterior fossa (Ch. 115:3); dorsal vertebrae with a strongly compressed centrum (Ch. 162:2); procoelous anterior caudal vertebrae (Ch. 193:3); lack of prespinal lamina in the neural arches of the anterior caudal vertebrae (Ch. 207:0); long chevron, hemal canal (Ch. 126:1); rounded expansion on acromial side (Ch. 232:1); well-developed acromion process (Ch. 235:1); ventromedial process of the ventral margin of the scapula well developed (Ch. 237:1); glenoid scapular orientation strongly beveled medially (Ch. 240:1); muscle scar on the proximal end of the ischium (Ch. 291:1); and lack of a ventral bulge on the transverse process of the first caudal (Ch. 358:0).

Description

Teeth: One tooth labeled as MDS-OTII,18. This tooth has a complete dental crown, which preserves the base of the pulp cavity and does not have a root (Fig. 3). The overall shape of the tooth is triangular, more spoon-shaped than pencil-shaped, with the crown slightly displaced posteriorly. It is interpreted as being a right maxillary or left mandibular tooth. It is 20 mm in height, 9 mm in mesiodistal width, and its labiolingual width is 4 mm. The approximate value of the slenderness index (SI; *Upchurch, 1998*) is 2.2. Diplodocoids and titanosaurians have very slender, peg-like teeth with SI values >4.0 and reduced lingual concavities (*Upchurch, 1998*), indicating that MDS-OTII,18 cannot be referred to either of these clades. However, the SI values are consistent with referral to a basal titanosauriform (*Barrett et al., 2002*; *Chure et al., 2010*). Its section is somewhat flattened lateromedially and oval, slightly asymmetrical and more triangular in the apical zone. The mesial and distal edges present fine carinae without denticles. It has subtle ornamentation with crenulations only visible by light microscopy; it possesses gentle crests running in a
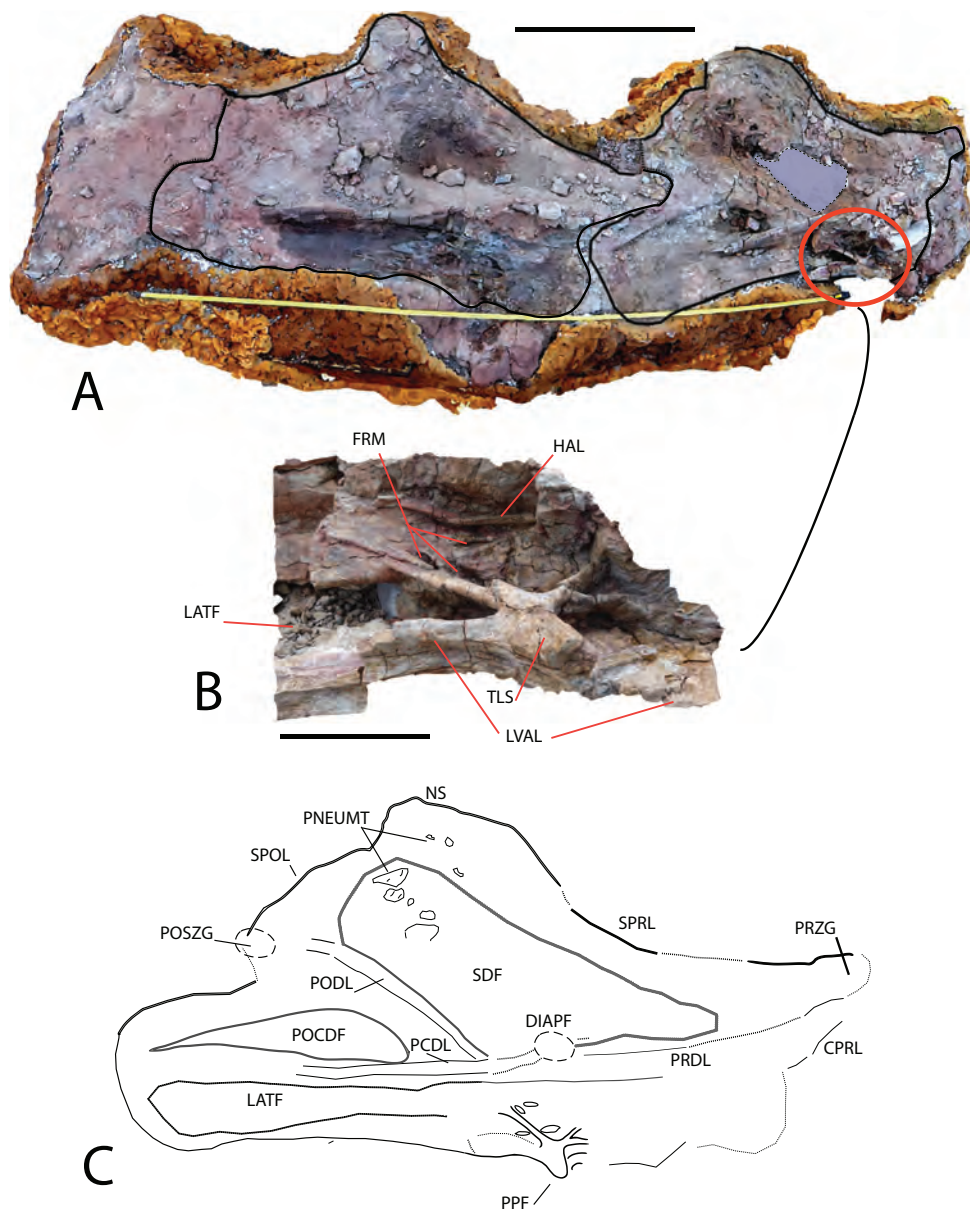
Figure 3 Tooth (MDS-OTII,18) from *Europatitan eastwoodi* n. gen. n. sp. (A) Anterior view. (B) Distal view. (C) Lingual view. (D) Mesial view. (E) Adapical view. Scale: 1 cm.
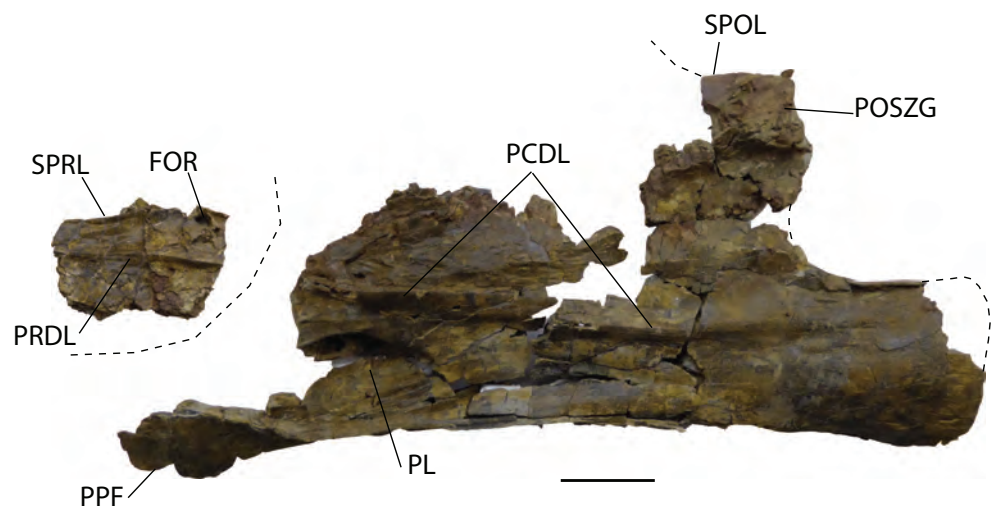
Figure 4 Cervical vertebra (MDS-OTII,32) from *Europatitan eastwoodi* n. gen. n. sp., left lateral view. FOR, foramen; PCDL, posterior centrodiapophyseal lamina; PL, pleurocel; POSZG, postzygapophyses; PPF, parapophyses; PRDL, prezygodiapophyseal lamina; SPOL, spinopostzygapophyseal lamina; SPRL, spinoprezygapophyseal lamina. Scale: 10 cm.

longitudinal direction, three on the lingual face and four on the labial face. It is a functional tooth, with an apical wear facet. This feature distinguishes it from basal macronarians such as *Camarasaurus* with a V-shaped facet. In basal titanosauriforms such as *Giraffatitan*, teeth with high-angled mesial and distal wear facets but no apical wear have been described, while others display a combination of apical wear and mesial and distal wear (*Barrett et al., 2002*). Other non-titanosaurian titanosauriforms show sharply inclined wear facets, as occurs in *Ligabuesaurus* (*Bonaparte, González Riga & Apesteguía, 2006*). The crown base lacks the cingular structure described in the putative euhelopodid of the Early Cretaceous of Spain (*Canudo et al., 2002*).

Cervical vertebrae: Five incomplete cervical vertebrae have been recovered. In the cervical series, these could be the 7th (MDS-OTII,32) and the 8th, 9th, 10th, and 11th, which are articulated (MDS-OTII,31A, B, C, D). MDS-OTII,32 preserves the posterior half of the vertebral body, as well as the left postzygapophysis, part of the right parapophysis, and an anterior fragment of the neural arch; its right side is in a very poor condition (Fig. 4).

Figure 5 **Cervical vertebrae (MDS-OTII,31 A–D) from *Europatitan eastwoodi* n. gen. n. sp.** (A) Block from the excavation containing the vertebrae; draw the contour of MDS-OTII,31B and 31C. (B) Detail of triradiated structure in the parapophysis of MS-OTII,31B. (C) Reconstruction of MS-OTII,31B. CPRL, centroprezygapophyseal lamina; DIAPF, diapophysis; FRM, foramina; HAL, horizontal accessory lamina; LATF, lateral fossa; LVAL, lateroventral accessory lamina; NS, neural spine; PCDL, posterior centrodiapophyseal lamina; PNEUMAT, pneumatic subfossae; POCDF, centrodiapophyseal post-zygapophyseal fossa; PODL, postzygodiapophyseal lamina; POSZG, postzygapophyses; PPF, para-pophyses; PRDL, prezygodiapophyseal lamina; PRZG, prezygapophyses; SDF, spinodiapophyseal fossa; SPOL, spinopostzygapophyseal lamina; SPRL, spinoprezygapophyseal lamina; TLS, trirradiated laminar structure. Scale: 50 cm (A), 10 cm (B).

Of the ?A3B2 tlsb?> articulated series, MDS-OTII,31A preserves a small posterior part of the vertebral body; MDS-OTII,31D preserves the most anterior part of the vertebral body, of the neural arch and the neural spine; MDS-OTII,31B and C are almost complete although

Table 1 Measurements of vertebrae of *Europatitan eastwoodi*.

Vertebra	TW (cm)	TH (cm)	CL (cm)	ACW (cm)	ACH (cm)	PCW (cm)	PCH (cm)	NAH (cm)	NSH (cm)	NSW (cm)	UI	WI
MDS-OTII,31B	–	76	114	–	–	–	–	56	44	–	–	–
MDS-OTII,31C	–	74	112	–	–	–	–	53	33	–	–	–
MDS-OTII,32	–	–	–	–	–	13.5[1]	17[1]	–	–	–	–	–
MDS-OTII,1	95	77[1]	24	38	23	43	25	–	–	–	0.56	0.96
MDS-OTII,2	45.5	61	14.5	26	31	29	32	32	21	11	0.5	0.45
MDS-OTII,3	39.5	57	13.5	2.5	32	26	27	30	8	11	0.52	0.5
MDS-OTII,4	35	54	15	26	29	25	27.5	27	7.5	10	0.6	0.54
MDS-OTII,6	30.5	44	15.5	25	23	23.5	23	20.5	8	7	0.66	0.67
MDS-OTII,7	26	41.5	14.5	24	23	23	22	20	9	6	0.63	0.66
MDS-OTII,8	23	37.5	15	22.5	20.5	22	20.5	19	7.5	5.5	0.68	0.73
MDS-OTII,9	17	28.5	15.5	17.5	14.5	17	15.5	13.5	8	2.5	0.91	1

Notes:
TW, total width; TH, total height; CL, centrum length; ACW, anterior centrum width; ACH, anterior centrum height; PCW, posterior centrum width; PCH, posterior centrum height; NAH, neural arch height; NSH, neural spine height; NSW, neural spine mediolateral width; UI, elongation index *sensu Upchurch (1998)*; WI, elongation index *sensu Wilson (2002)*. Measurements are in cm.
[1] Incomplete or estimate.

they have lost some laminae, the diapophysis and part of the parapophysis (Fig. 5). These articulated vertebrae form part of a rocky block in a delicate state of preservation, from which preparation work has made it possible to expose the left side of the vertebrae.

The cervical vertebrae of *Europatitan* are remarkable for their extreme pneumatization and the great anteroposterior lengthening of the vertebral centrum (Table 1), which implies an extremely long neck as displayed by some titanosauriforms, such as *Giraffatitan*, *Sauroposeidon*, and *Erketu* (*Janensch, 1950*; *Wedel, Cifelli & Sanders, 2000a*; *Ksepka & Norell, 2006*).

MDS-OTII,31B and 31C have a vertebral centrum that is anteroposteriorly lengthened and relatively low, slightly higher than wide (Fig. 4). The vertebral centrum is opisthocoelous with a very marked concavity in its posterior articular face, which is oval. The ventral surface of the centra is transversely concave in its anterior part; in MDS-OTII,32 is, flat with two short and shallow crests in the middle. The lateral surfaces are excavated almost entirely by large pneumatic fossae separated medially by a very fine bony partition. The lateral fossa is perforated by a small pleurocoel that is clearly delimited posteriorly by a sharp edge in MDS-OTII,32 and MDS-OTII,31C. The interior of the pleurocoel is complex, being divided into two parts by laminae that are in turn subdivided by other internal laminae, resulting in a total of six subcavities. Furthermore, there are foramina in each of these subcavities. The pneumatic fossa takes up approximately 80% of the vertebral body, as in *Sauroposeidon* (*Wedel, Cifelli & Sanders, 2000a*). A horizontal lamina is located dorsal to the pneumatic fossa of the vertebral centrum, delimiting it from the neural arch, like the crest presented by a middle cervical vertebra from the titanosauriform *Astrophocaudia* (*D'Emic, 2013*), Fig. 5B: HAL.

The parapophysis is located in the anterior half of the vertebral body, which anteriorly and posteriorly has accessory laminae developed on its lateroventral margin

(Fig. 5B: LVAL). *Europatitan* shares this characteristic with *Sauroposeidon* and *Giraffatitan* (*Janensch, 1929*, *1950*; *Wedel, Cifelli & Sanders, 2000a*, *2000b*; *Rose, 2007*). One of these laminae has been described as a posterior centroparapophyseal lamina (pcpl) (*Wedel, Cifelli & Sanders, 2000b*), but this may not be the homologous lamina described in the dorsal vertebrae, since in the latter the acpl and the pcpl have the neurocentral junction as a landmark, whereas in the cervical vertebrae of *Europatitan* the reference point is the lateroventral margin (*Wilson, 1999*). In MDS-OTII,31B the parapophysis supports two well-developed accessory laminae in its dorsal part, one of them oriented posteriorly and the other anteriorly. This appears forked at its origin in the wall of the lateral fossa of the vertebral body. Together they form a highly conspicuous triradiate laminar structure whose branches delimit various parts of the lateral pneumatic fossa and contain up to six foramina (Fig. 5B: TLS, FRM). Such a triradiate laminar structure has not been described in other sauropod taxa and is considered an autapomorphy of *E. eastwoodi*.

The neural arch is expanded dorsoventrally and flattened lateromedially. The neural spine is simple, greatly developed dorsoventrally and anteroposteriorly, as a result of which it occupies 80% of the length of the vertebral body. The neural arch presents a subtriangular outline in lateral view. The dorsal margin of the spine has some lateral bumps that are irregular in shape. The lateral surfaces of the neural spine are occupied by a large spinodiapophyseal fossa (sdf), which reaches its greatest depth in its ventral half. In MDS-OTII,31B this fossa presents various minor fossae that are relatively small (8 × 3 cm, 3 × 3.5 cm, 7.5 × 4.5 cm) and have well-delimited margins (Fig. 5C). These fossae are similar to those presented by *Sauroposeidon*, but without the associated development of accessory laminae shown by this taxon (*Wedel, Cifelli & Sanders, 2000b*). The neural spine also presents various foramina in its anterodorsal and lateral part. *You & Li (2009)* suggest that the neural spine with deep spinodiapophyseal fossae (sdf) could be a synapomorphy of brachiosaurids, being a character shared by *Giraffatitan*, *Sauroposeidon* and *Qiaowanlong*. However, for other authors *Qiaowanlong* is a more derived taxon, included among the somphospondylans (*Ksepka & Norell, 2010*; *Mannion et al., 2013*).

The simple neural spine is a character shared with brachiosaurids, which differentiates it from the Euhelopodidae, which have a bifid neural spine (*D'Emic, 2012*). It presents a certain simplification regarding the development of bony laminae associated with it. On the anterior surface of the spine there are two well-developed spinoprezygapophyseal laminae (sprl), which delimit the spinoprezygapophyseal fossa (sprf). There is no prespinal lamina (prsl). On the posterior surface, there are two deep spinopostzygapophyseal laminae (spol), which delimit the spinopostzygapophyseal fossa (spof). Spinodiapophyseal laminae (spdl) are absent, as in *Sauroposeidon* (*Wedel, Cifelli & Sanders, 2000a*, *2000b*).

The zygapophyses are not preserved in the vertebral series MDS-OTII,31A, B, C, D, but some observations can be made thanks to the development of the sprl. The prezygapophyses extend beyond the anterior end of the vertebral body, while the postzygapophyses do not reach the posterior limit. The prezygapophyses present deep centroprezygapophyseal laminae (cprl) and laterally they have a prezygodiapophyseal lamina (prdl) in a ventral position. Lateral to the sprl there is a foramen delimited dorsally

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by a small crest. The left postzygapophysis of MDS-OTII,32 has a subtriangular articular surface and is oriented lateroventrally. Ventral to the postzygapophyses there are centropostzygapophyseal laminae (cpol) and laterally it presents a thick postzygodiapophyseal lamina (podl).

The diapophyses are not preserved, but they can be interpreted as being located in the anterior part of the neural arch, dorsal to the parapophysis. The diapophysis presents prdl and podl, as well as a well-marked posterior centrodiapophyseal lamina (pcdl) with a foramen in its posterior part. The cervical vertebrae of *Europatitan* lack the anterior centrodiapophyseal lamina (acdl), like *Qiaowanlong* (*You & Li, 2009*). The absence of this lamina is a variable character, for it may be missing in several of the vertebrae of the cervical series (*Ksepka & Norell, 2010*). This lamina is present in other basal titanosauriforms such as *Giraffatitan* and *Sauroposeidon* (*Janensch, 1950*; *Rose, 2007*); in *Giraffatitan* it is a short lamina, and in *Sauroposeidon* it is only found in immature specimens, if *Paluxysaurus* is considered a senior synonym of *Sauroposeidon* (*D'Emic, 2013*). Finally, between the diapophysis and the podl and pcdl laminae there is a deep postzygapophyseal centrodiapophyseal fossa (pocdf).

Dorsal vertebra: One middle-posterior dorsal vertebra labeled as MDS-OTII,1. Its total height is 77 cm, and its maximum width is 95 cm. It is almost complete and is well preserved; it is only missing the dorsal end of the neural spine and some fragments of the bony laminae (Table 1; Fig. 6; Fig. S2). The vertebral centrum is flattened dorsoventrally, expanded lateromedially, opisthocoelous, wider than long, and approximately as long as it is high, as occurs in macronarians (*Wilson & Sereno, 1998*; *Salgado, Coria & Calvo, 1997*). Its articular faces are dorsoventrally compressed, oval in outline, with a greater width in the ventral half; the anterior face is convex, and the posterior concave. The lateral surfaces are anteroposteriorly concave, with a large pleurocoel in the dorsal half, oval in outline and connected to a pneumatic chamber that is deep and well developed both ventrally and anteriorly toward the anterior articular face, and less developed dorsally. Inside the pneumatic chamber there are various scarcely developed laminae. The anterior articular face has lost part of the cortex, making it possible to see its pneumatized internal structure (Fig. 6A), which is of the camellate sort characteristic of Titanosauriformes (*Wilson, 2002*). The ventral surface is anteroposteriorly concave and smooth, without the medial crest possessed by brachiosaurid titanosauriforms such as *Brachiosaurus* and *Giraffatitan* (*Upchurch, Barrett & Dodson, 2004*).

The neural arch is dorsoventrally elongated, and greatly expanded lateromedially; it is situated in an anterior position on the vertebral centrum. The prezygapophyses are large and thick, reach the anterior margin of the anterior articular face, and are connected to one another by a weak, horizontally developed intraprezygapophyseal lamina (tprl), as occurs in anterior dorsal vertebrae (Figs. 6A and 7A). The presence of this lamina in *Europatitan* is significant in that it tends to disappear with the development of the hyposphene (*Wilson, 2002*). The articular surface of the prezygapophyses is subrectangular and is slightly inclined ventromedially. Ventrally, the prezygapophyses form a large hypantrum delimited by thick centroprezygapophyseal laminae (cprl). These laminae fork ventrally (Fig. 8A). The right cprl in turn laterally receives two accessory laminae with
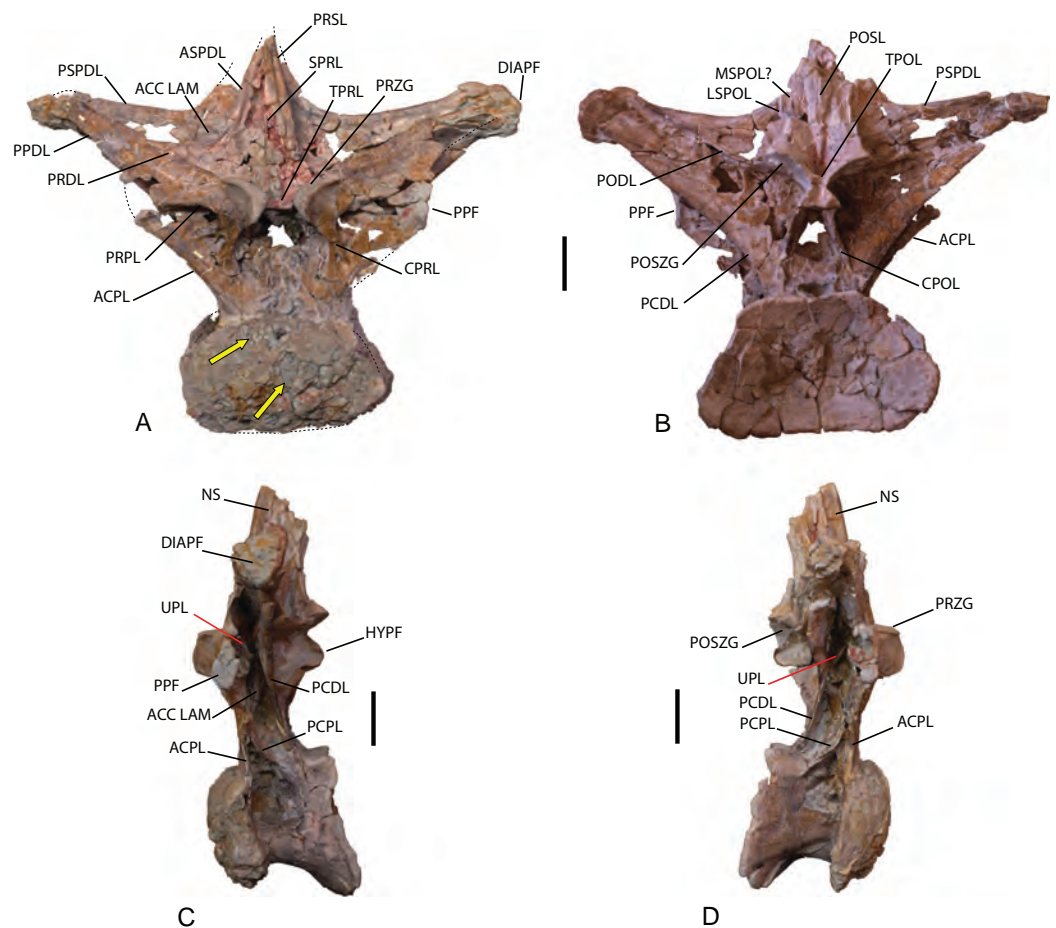
Figure 6 Dorsal vertebra (MDS-OTII,1) from *Europatitan eastwoodi* n. gen. n. sp. (A) Anterior view. (B) Posterior view. (C) Left lateral view. (D) Right lateral view. The arrows in (A) show the pneumatized camellate structure. ACC LAM, accesory lamina; ACPL, anterior centroparapophyseal lamina; ASPDL, anterior spinodiapophyseal lamina; CPOL, centropostzygapophyseal lamina; CPRL, centroprezygapophyseal lamina; DIAPF, diapophysis; HYPF, hyposphenum; LSPOL, lateral spino-postzygapophyseal lamina; MSPOL?, medial spinopostzygapophyseal lamina?; NS, neural spine; PCDL, posterior centrodiapophyseal lamina; PCPL, posterior centroparapophyseal lamina; POSL, postespinal lamina; PODL, postzygodiapophyseal lamina; POSZG, postzygapophyses; PPDL, pre-zygaparadiapophyseal lamina; PPF, parapophyses; PRDL, prezygodiapophyseal lamina; PRPL, pre-zygaparapophyseal lamina; PRSL, prespinal lamina; PRZG, prezygapophyses; PSPDL, posterior spinodiapophyseal lamina; SPRL, spinoprezygapophyseal lamina; TPOL, intrapostzigapophyseal lamina; TPRL, intraprezygapophyseal lamina; UPL, unnamed parapophyseal lamina. Scale: 10 cm.

pneumatic cavities between them, which partially subdivide the centroprezygapophyseal parapophyseal fossa (pacprf). The prezygoparapophyseal laminae (prpl) are horizontal and short. The prezygodiapophyseal lamina (prdl) is a thick, poorly developed ridge that does not reach the diapophysis.

The postzygapophyses are situated at the base of the neural spine and are ventromedially oriented. They are subrectangular and are joined to one another by a short, inconspicuous, horizontal intrapostzygapophyseal lamina (tpol), which is situated dorsal to the hyposphene (Figs. 6B and 7B). The presence of a horizontal tpol lamina in posterior dorsal vertebrae with a hyposphene has been cited in *Sauroposeidon*, if
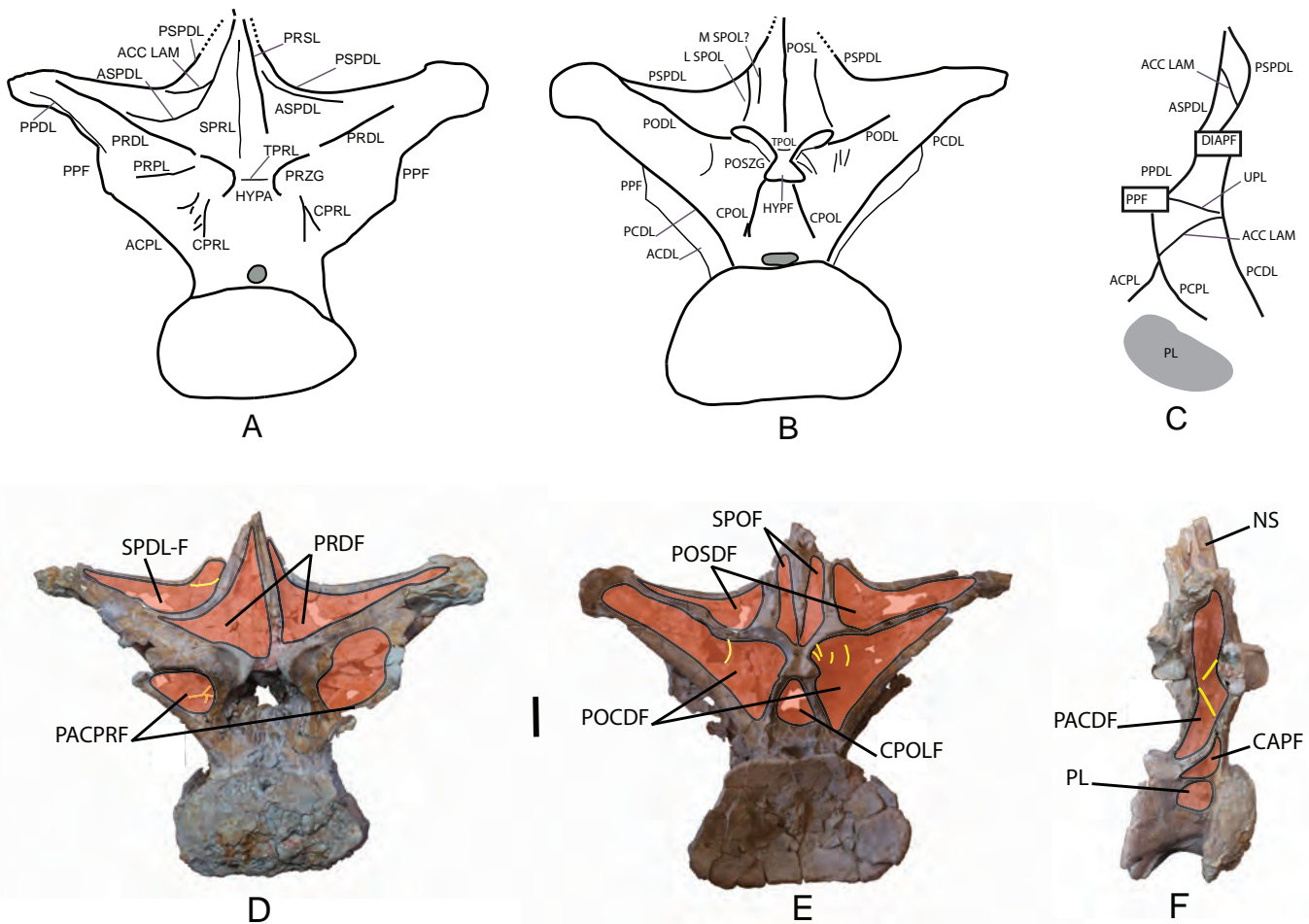
Figure 7 Pneumaticity and lamination of dorsal vertebra MDS-OTII,1 from *Europatitan eastwoodi* n. gen. n. sp. (A–C) Scheme of the laminae. (A) Anterior view. (B) Posterior view. (C) Left lateral view. (D–F) Pneumaticity. (D) Anterior view. (E) Posterior view. (F) Right lateral view. The yellow lines mark the laminae that subdivide the main fossae. ACC LAM, accessory lamina; ACPL, anterior centroparapophyseal lamina; ASPDL, anterior spinodiapophyseal lamina; CAPF, centroparapophyseal fossa; CPOL, centropostzygapophyseal lamina; CPOLF, centropostzygapophyseal fossa; CPRL, centroprezygapophyseal lamina; DIAPF, diapophysis; HYPA, hypantrum; HYPF, hyposphenum; LSPOL, lateral spinopostzygapophyseal lamina; MSPOL?, medial spinopostzygapophyseal lamina?; NS, neural spine; PACDF, centrodiapophyseal parapophyseal fossa; PACPRF, centroprezygapophyseal parapophyseal fossa; PCDL, posterior centrodiapophyseal lamina; PCPL, posterior centroparapophyseal lamina; PL, pleurocelo; POCDF, centrodiapophyseal postzygapophyseal fossa; PODL, postzygodiapophyseal lamina; POSDF, postzygapophyseal spinodiapophyseal fossa; POSL, postespinal lamina; POSZG, postzygapophyses; PPDL, prezygaparadiapophyseal lamina; PPF, parapophyses; PRDL, prezygodiapophyseal lamina; PRDF, prezygapophyseal spinodiapophyseal fossa; PRSL, prespinal lamina; PRZG, prezygapophyses; PSPDL, posterior spinodiapophyseal lamina; SPDL-F, spinodiapophyseal laminae fossa; SPOF, spinopostzygapophyseal fossa; SPRL, spinoprezygapophyseal lamina; TPOL, intrapostzigapophyseal lamina; TPRL, intraprezygapophyseal lamina; UPL, unnamed parapophyseal lamina. Scale: 10 cm.

Paluxysaurus is considered a senior synonym of *Sauroposeidon* (*Rose, 2007*; *D'Emic, 2013*), although other authors do not identify it with this taxon (*D'Emic & Foreman, 2012*). The development of the hyposphene in middle and posterior dorsal vertebrae tends to be associated with the development of the tpol ventrally to a hyposphene connecting with the neural canal, or with the absence of the tpol (*Apesteguía, 2005a*; *Wilson, 1999*).

The hyposphene has a triangular outline in posterior view and a vertical fossa in its central part. Dorsally, the centropostzygapophyseal laminae (cpol) reach the lateroventral
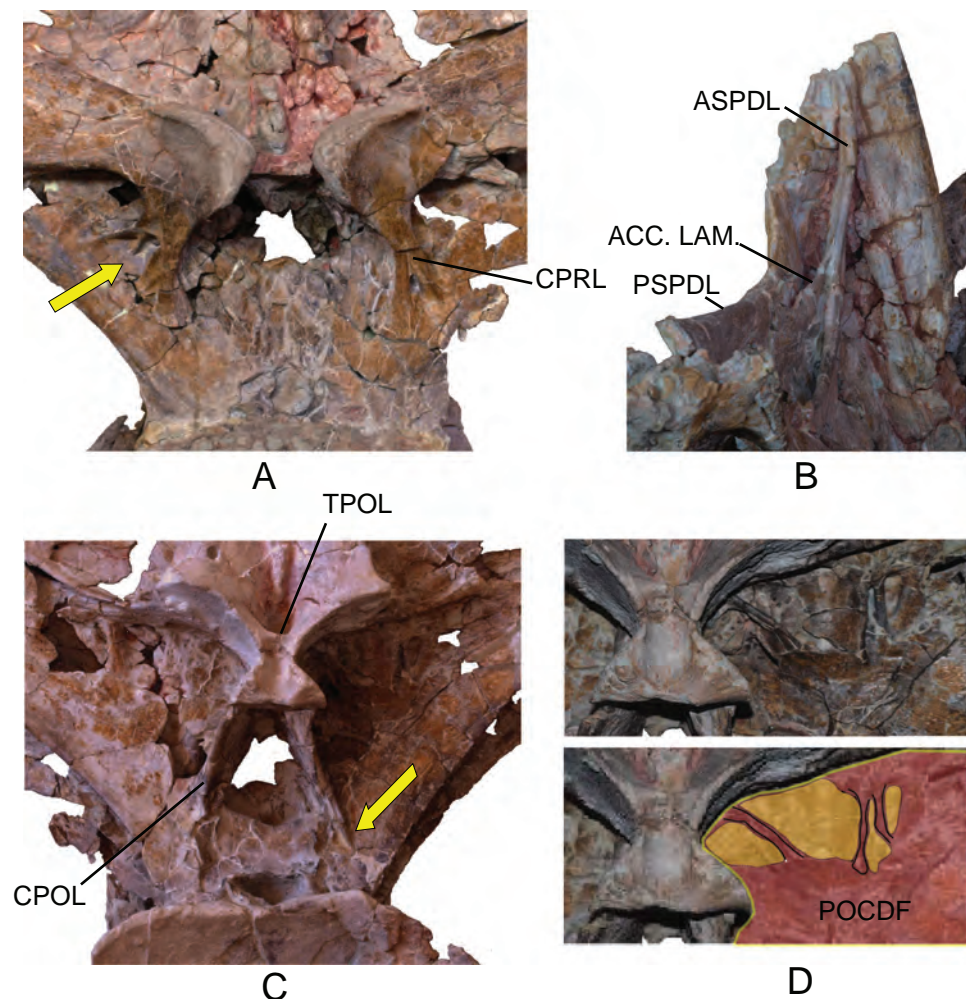
Figure 8 **Autapomorphies of *Europatitan eastwoodi* n. gen. n. sp. in the dorsal vertebra MDS-OTII,1.** (A) Anterior view, accessory laminae to cprl (arrow). (B) Anterolateral view, accessory lamina between aspdl and pspdl laminae. (C) Posterior view, branched cpol lamina, horizontal tpol lamina. (D) Posterior view (photography and interpretive image), laminae and pneumatic subfossae (yellow colored areas) in the pocdf (red colored area). ASPDL, anterior spinodiapophyseal lamina; CPOL, centropostzygapophyseal lamina; CPRL, centroprezygapophyseal lamina; POCDF, centrodiapophyseal postzygapophyseal fossa; PSPDL, posterior spinodiapophyseal lamina; TPOL, intrapostzigapophyseal lamina.

margin of the hyposphene and are forked at their ventral end (Fig. 8C). The postzygodiapophyseal lamina (podl) joins the pspdl before it reaches the diapophysis. Ventral to the hyposphene there is a deep centropostzygapophyseal fossa (cpolf). In posterior view the centrodiapophyseal postzygapophyseal fossa (pocdf) is large and is subdivided by various accessory laminae, as many as six on the right side, which are arranged between the pcdl and the podl, giving rise to small but conspicuous pneumatic subfossae. This character is not described in other sauropods (Fig. 8D). In *Sauroposeidon* anterior dorsal vertebrae have been documented with laminae in a similar position to what is described in *Europatitan*, but in the posterior dorsal vertebrae of *Sauroposeidon* there is only one lamina that joins the pcdl and podl laminae, dividing the pocdf fossa into two clearly differentiated subfossae (*D'Emic & Foreman, 2012*, Figs. 3.2, 4, 6.2).

The neural spine seems to be short. There is a prominent, thick and rugose prespinal lamina (prsl) on its anterior surface, with striations and grooves running dorsoventrally (Fig. 7); the spinoprezygapophyseal laminae (sprl) follow a trajectory parallel to the prsl on the neural spine, until they disappear dorsally, as occurs in *Trigonosaurus* and *Rapetosaurus* and other titanosauriforms (*Powell, 1987*; *Martínez et al., 2004*; *Campos et al., 2005*; *Curry Rogers, 2009*). There are anterior and posterior spinodiapophyseal laminae (aspdl and pspdl) crossing the lateral surface of the neural spine (Figs. 6 and 7) and delimit an interlaminar fossa that we propose to be named spdl-f, Fig. 7D. These two laminae are present in the dicraeosaurid *Brachytrachelopan* and in titanosaurians (*González Riga, 2003*; *Martínez et al., 2004*; *Rauhut et al., 2005*; *Salgado & Coria, 2009*; *Salgado & Powell, 2010*). The right aspdl and pspdl laminae are in contact with one another by means of an accessory lamina that divides the fossa situated between the two spinodiapophyseal laminae (spdl), (Figs. 6C, 7A, 7C and 8B). The posterior surface of the neural spine preserves in its most ventral part a thick, rugose structure that would correspond to a postspinal structure, situated inside a deep spinopostzygapophyseal fossa (spof). The lateral spinopostzygapophyseal lamina (lspol) starts from the postzygapophysis and joins the pspdl to form a compound lateral lamina of the neural spine, as occurs in *Argentinosaurus* and *Epachthosaurus* (*Salgado & Powell, 2010*). At the base of the neural spine, in an intermediate position between the lspol and the postspinal structure, there are some scarcely developed crests that run toward the lateral lamina or toward the postspinal structure. It is difficult to identify them: they may correspond to medial spinopostzygapophyseal laminae (mspol). There have been citations of lspol laminae in some diplodocimorphs and in Brachiosauridae. *Salgado et al. (2004)* point out that the lspol join at the neural spine to form a posterior medial lamina (posl).

The diapophyses are oriented almost horizontally. The parapophyses are situated at the height of the prezygapophyses, and join the diapophyses via the paradiapophyseal lamina (ppdl). In lateral view, the posterior centrodiapophyseal lamina (pcdl) is very prominent, and it is wide in posterior view; it runs parallel to the anterior centroparapophyseal lamina (acpl), and between them there is an extensive centrodiapophyseal parapophyseal fossa (pacdf). Two accessory laminae divide the pacdf. One of the laminae is parallel and situated dorsal to the centroparapophyseal lamina (pcpl), between the parapophysis and the pcdl. A similar lamina has been described in *Neuquensaurus* as upl (*D'Emic & Foreman, 2012*), and it is present in other titanosaurians such as *Rocasaurus*, *Saltasaurus*, *Rapetosaurus*, and *Opisthocoelicaudia* (*Salgado, Apesteguía & Heredia, 2005*). The other accessory lamina, ventral to the upl and located within the pacdf fossa, runs between the acpl lamina and the pcdl lamina, and is the same lamina as that possessed by the ninth dorsal vertebra of *Neuquensaurus* (*Salgado, Apesteguía & Heredia, 2005*, Fig. 4C). Ventral to the pacdf fossa is the centroparapophyseal fossa (cpaf), delimited dorsally by the pcpl lamina (posterior centroparapophyseal), which is scarcely developed and joins the acpl in its middle part (Fig. 7F).

Cervical and dorsal ribs: Forty-six ribs (several fragments included) as MDS-OTII,19-24 and MDS-OTII,33-72. Their posterior process represents most of the cervical ribs. MDS-OTII,24 is from a left cervical rib. Between capitulum and tuberculum there is a
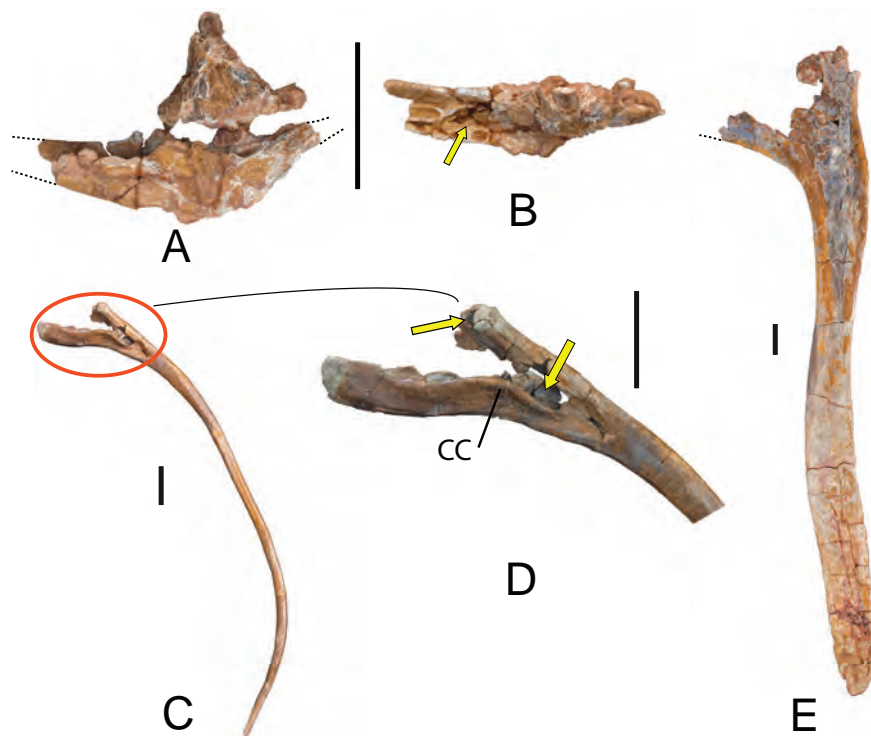
Figure 9 Cervical and dorsal ribs of *Europatitan eastwoodi* n. gen. n. sp. Cervical rib MDS-OTII,24 in (A) medial view and (B) dorsal view; arrow in (B) indicates the pneumatic fossa in the shaft. (C) Dorsal posterior rib MDS-OTII, 20 in (D) posterior view and detail of crested capitulum (cc) and pneumatopores (arrows). (E) Anterior rib (MDS-OTII,21), anterior view. Scale: 10 cm.

deep pneumatic fossa that extends through the dorsal part of the posterior process (Figs. 9A and 9B). The posterior process of MDS-OTII,24 is incomplete, reaching a length of 120 cm. Numerous fragments of the posterior process have also been found; these fossils are biconvex or circular in section and elongated, which seems to suggest that the cervical ribs were very long. MDS-OTII,33 is a rib that articulated with the cervical vertebra MDS-OTII,32, and does not preserve its proximal part. It would be greater than 185 cm in length. The articulated series of cervical vertebrae MDS-OTII,31A, B, C, D is associated with various cervical ribs that at a minimum exceed the length of the vertebral centrum to which they are joined, at least partially reaching the following vertebral centrum.

The dorsal ribs MDS-OTII,19 and MDS-OTII,21 are elongated; they are greater than 200 cm in proximodistal length (Fig. 9E). The shaft is subtriangular. Distally it becomes progressively more flattened anteroposteriorly and greatly expanded in a lateromedial direction, such that its overall shape in anterior view is rectangular. MDS-OTII,19 and MDS-OTII, 21 are two anterior ribs, with the capitulum and tuberculum apparently well developed, and the flattened shaft typical of Titanosauriformes (*Wilson, 2002*). On the articular head the anterior surface is convex and the posterior concave, a character that is found in *Haplocanthosaurus*, *Camarasaurus*, and rebbachisaurids and is considered a synapomorphy of Neosauropoda (*Wilson & Sereno, 1998*).

MDS-OTII, 22 has its capitulum and tuberculum clearly separated from one another, and the tuberculum is scarcely developed. These characteristics place it in the middle-posterior part of the dorsal series (*Upchurch, Barrett & Dodson, 2004*). The ribs MDS-OTII,20 and MDS-OTII,23 would be located in the posterior part of the dorsal series. They present intense pneumatization in their proximal part, with a pneumatic depression in the anterior face at the beginning of the shaft, between capitulum and tuberculum. Further, they possess pneumatopores that give access to pneumatic cavities both in the capitulum and the tuberculum (Figs. 9C and 9D). On MDS-OTII,20 there is a crest that is sinusoidal in outline running proximodistally on the anterior surface of the capitulum, delimiting the pneumatic cavity of the capitulum, a character that is considered autapomorphic for *Europatitan*. The pneumaticity of dorsal ribs is a character described for Titanosauriformes that is also shared by diplodocids and rebbachisaurids, although in titanosauriforms the cavities open by means of pleurocoels on the articular head (*Gilmore, 1936*; *Wilson & Sereno, 1998*; *Lovelace, Hartman & Wahl, 2007*; *Mannion et al., 2012*; *Torcida Fernández-Baldor, 2012*).

Caudal vertebrae: Eight anterior caudal vertebrae labeled as MDS-OTII,2, 3, 4, 5, 6, 7, 8, one middle caudal vertebra (MDS-OTII,9); see Fig. S2. The most anterior vertebra of the caudal series is MDS-OTII,2 (Fig. 10). The vertebral centrum is amphicoelous. The lateral faces are slightly plano-convex dorsoventrally, and concave anteroposteriorly. The ventral surface is concave anteroposteriorly. The neural arch is located in the anterior part of the centrum, as occurs in Titanosauriformes (*Salgado, Coria & Calvo, 1997*; *Wilson, 2002*). The transverse processes are laterally projected; they are horizontal and triangular in anterior view (Fig. 10). Between the diapophysis and the vertebral centrum runs the acdl, clearly marked in lateral view. The surfaces of the transverse process present shallow, extensive fossae: in the anterior surface, two centrodiapophyseal prezygapophyseal fossae (prcdf); in the posterior surface, two centrodiapophyseal postzygapophyseal fossae (pocdf). Ventral to the transverse process there is a shallow subcircular fossa. The prezygapophyses are laminar in shape; ventrally they receive the cprl, and dorsally the sprl. The postzygapophyses are reduced; in their dorsal part, they present spol laminae that are very close to one another, delimiting a small but deep spinopostzygapophyseal fossa (spof). There is no hyposphene as presented by derived somphospondylans (*Upchurch, 1998*; *Mannion et al., 2013*). The neural spine is posteriorly inclined; its distal end is globular, wide and rugose, with abundant crests and grooves. The section of the spine is subrectangular, and on its lateral faces there are weakly marked spdl laminae, which do not reach the end of the spine.
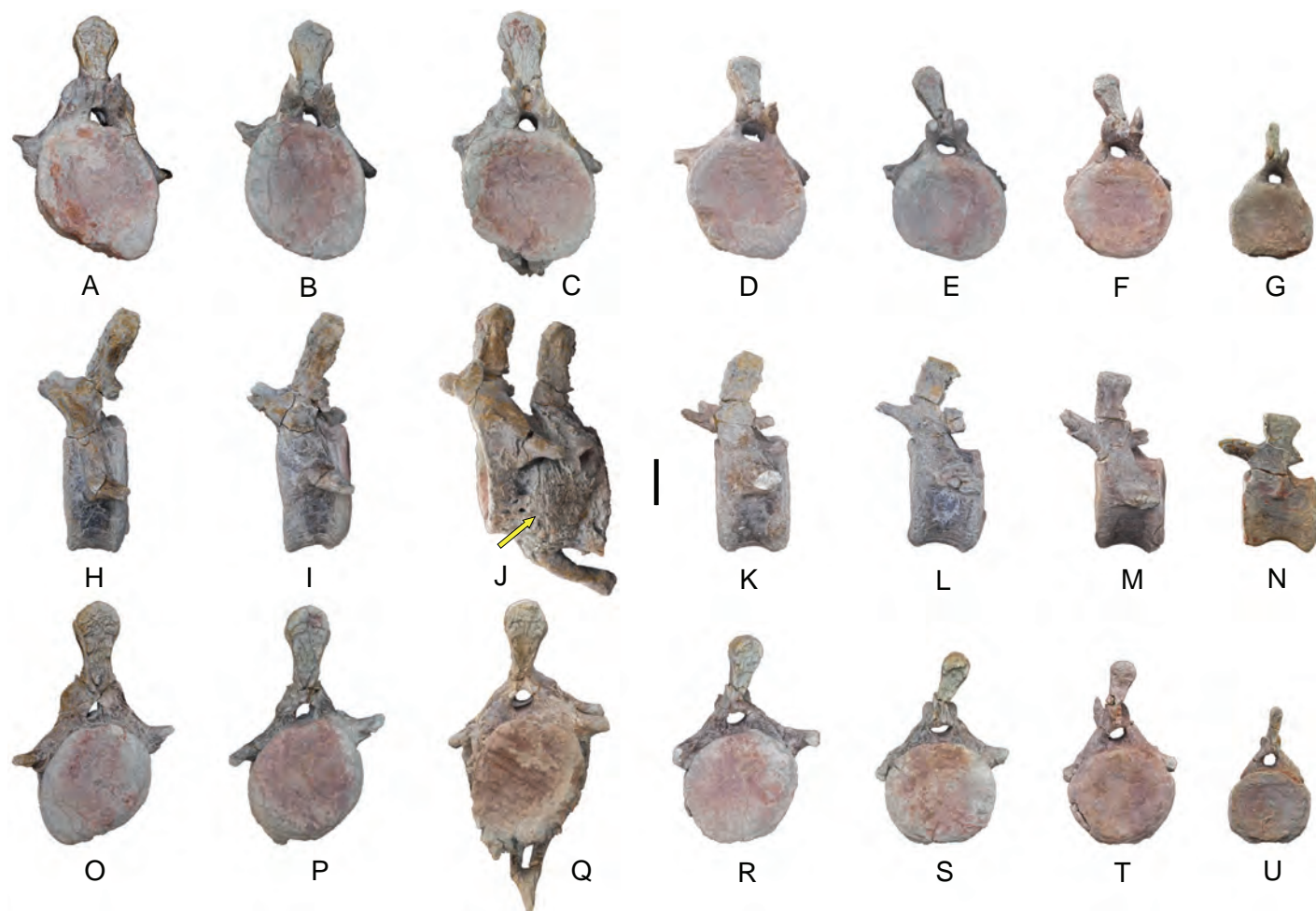
The rest of the anterior caudal vertebrae of *Europatitan* have an anterior articular face that is concave, in some cases deeply so (Fig. 11). The posterior articular face varies from being slightly convex to presenting a concave central part and a convex periphery. This character has been described in Titanosauriformes not included in Titanosauria such as *Venenosaurus* and *Tastavinsaurus* (*Tidwell, Carpenter & Meyer, 2001*; *Canudo, Royo-Torres & Cuenca-Bescós, 2008*). Such morphology could represent an incipient procoely in the anterior caudal vertebrae, a primitive state in relation to the procoely of Titanosauria, which show a deep proximal concavity and a highly pronounced distal convexity in the shape of a

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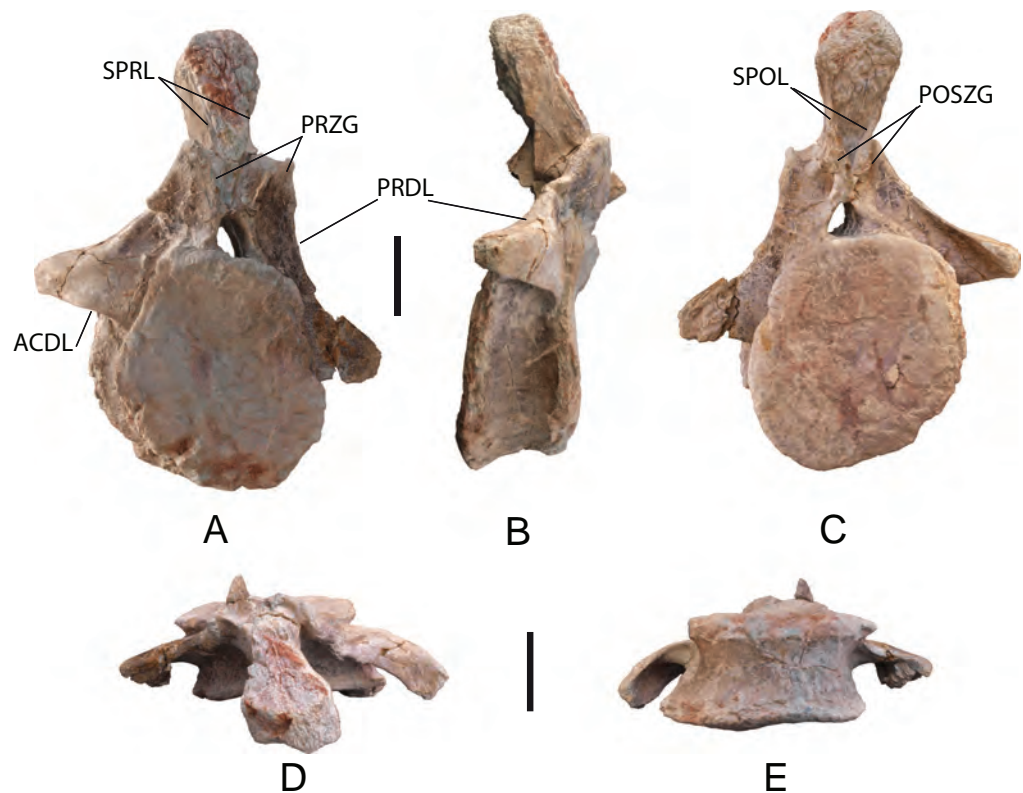
Figure 10 First caudal vertebra (MDS-OTII,2) of *Europatitan eastwoodi* n. gen. n. sp. (A) Anterior view. (B) Right lateral view. (C) Posterior view. (D) Dorsal view. (E) Ventral view. ACDL, anterior centrodiapophyseal lamina; POSZG, postzygapophyses; PRDL, prezygodiapophyseal lamina; PRZG, prezygapophyses; SPOL, spinopostzygapophyseal lamina; SPRL, spinoprezygapophyseal lamina. Scale: 10 cm.

ball (*Salgado, Coria & Calvo, 1997*; *Canudo, Royo-Torres & Cuenca-Bescós, 2008*). Starting from the third caudal vertebra, there appear articular facets for the hemal arches. The neural arch is situated in an anterior position on the vertebral centrum (Figs. 11H–11N). The prcdf, pocdf, and spof fossae decrease in extent and depth until they disappear in the fourth vertebra. The fossae ventral to the transverse processes are very shallow and disappear toward the more posterior vertebrae in the series. The postzygapophyses become increasingly prominent in the course of the series, and in all these vertebrae they receive the cpol laminae. The sprl and spol disappear from the seventh caudal vertebra on. These vertebrae lack a hyposphene, as occurs in Titanosauria (*Upchurch, Barrett & Dodson, 2004*); this contrasts with the reduced, crest-shaped hyposphene present in some somphospondylans (*Mannion et al., 2012*; *D'Emic, 2012*). The neural spines are simple, straight, and posteriorly inclined; they have a club-like dorsal extremity that exhibits conspicuous rugosities on its anterior and posterior faces, like the neural spines described in other macronarians of the Early Cretaceous of Iberia such as *Aragosaurus* and *Tastavinsaurus* (*Canudo, Royo-Torres & Cuenca-Bescós, 2008*; *Royo-Torres et al., 2014*).

The middle caudal vertebra of *Europatitan* (MDS-OTII,9) has a spool-shaped centrum that is relatively short and amphicoelous, as in *Tastavinsaurus* and unlike the vertebral

Figure 11 Caudal vertebrae of *Europatitan eastwoodi* n. gen. n. sp. Anterior caudal vertebrae: MDS-OTII,3 (A, H, O), MDS-OTII,4 (B, I, P), MDS-OTII,5 (C, J, Q), MDS-OTII,6 (D, K, R), MDS-OTII,7 (E, L, S), MDS-OTII,8 (F, M, T). Middle caudal vertebra: MDS-OTII,9 (G, N, U), anterior view (A–G), left lateral view (H–N), and posterior view (O–U). The arrow indicates an irregular surface of pathological origin. Scale: 10 cm.

centra present in titanosaurians such as *Alamosaurus* and *Saltasaurus* (*Powell, Sanz & Buscalioni, 1992*; *Lehman & Coulson, 2002*). The lateral faces of the centrum are concave and smooth; the ventral surface is also concave anteroposteriorly. The neural arch is in an anterior position. It presents reduced sprl laminae, between which a sprf fossa is present. The postzygapophyses are very reduced, presenting spol laminae that delimit a spof fossa. The neural spine is straight, lateromedially compressed, and rugose on its anterior and posterior faces and its dorsal margin (Figs. 11G, 11N and 11U).

Hemal arches: Seven hemal arches labeled as 04.17 OT-II,25, 26, 27, 28, 29, and 30; one hemal is fused to MDS-OTII,5 (Fig. 12). The hemal arches are open at the proximal end, a synapomorphy of Neosauropoda (*Wilson, 2002*). The proximal "crus" bridging the superior margin of the hemal canal is present in some basal sauropods, many flagelicaudatans, and some macronarians, but this character can vary through the caudal series, as in the rebbachisaurid diplodocimorphs (*Pereda-Suberbiola et al., 2011*; *Salgado et al., 2012*; *Otero et al., 2012*). The first hemal arch of the series, MDS-OTII,27

Figure 12 Hemal arches of *Europatitan eastwoodi* n. gen. n. sp. (A) MDS-OTII,27, first hemal arch in anterior view and (B) posterior view. (C) MDS-OTII,25, hemal arch in anterior view, (D) left lateral view, (E) posterior view. (F) MDS-OTII,26, hemal arch in anterior view, (G) left lateral view, (H) posterior view, (I) right lateral view, (J) proximal view. Scale: 10 cm.

(Figs. 12A and 12B) is articulated with the third and fourth caudal vertebrae, as in *Tastavinsaurus* (*Canudo, Royo-Torres & Cuenca-Bescós, 2008*). In lateral view the hemal arches are straight, and their proximal end has a double articulation, with a convex anterior surface and a flat posterior surface (Fig. 12J). The surface is smooth and without ornamentation. The first hemal arch is Y-shaped, with dorsal and ventral branches that are similar in length and the ventral branch compressed anteroposteriorly. The separation between the branches is greater than in the rest of the hemal arches (Fig. 12). In all the other hemal arches the ventral branch is lateromedially compressed and is longer than the dorsal branch. The hemal canal (except the first) is roughly 40% of the total length of the hemal arch, similar to *Aragosaurus* and *Tastavinsaurus* (*Canudo, Royo-Torres & Cuenca-Bescós, 2008*; *Royo-Torres et al., 2014*); this differentiates them from titanosaurs, which reach values of 50% (*Wilson, 2002*).

Scapulae: The two scapulae labeled as MDS-OTII,14, left scapula in connection with part of the left coracoid, MDS-OTII,15; MDS-OTII,16, right scapula. The two scapulae are almost complete The left scapula is larger in size than the right one. A description has been made of MDS-OTII,14 (Fig. S3), which has the axis of the scapular blade arranged horizontally. MDS-OTII,14 lacks part of the proximal, proximodorsal and dorsodistal margins of the proximal lamina, as well as part of the distal margin of the scapular blade (Fig. 13). Its general shape is similar to that of Brachiosauridae such as *Giraffatitan*
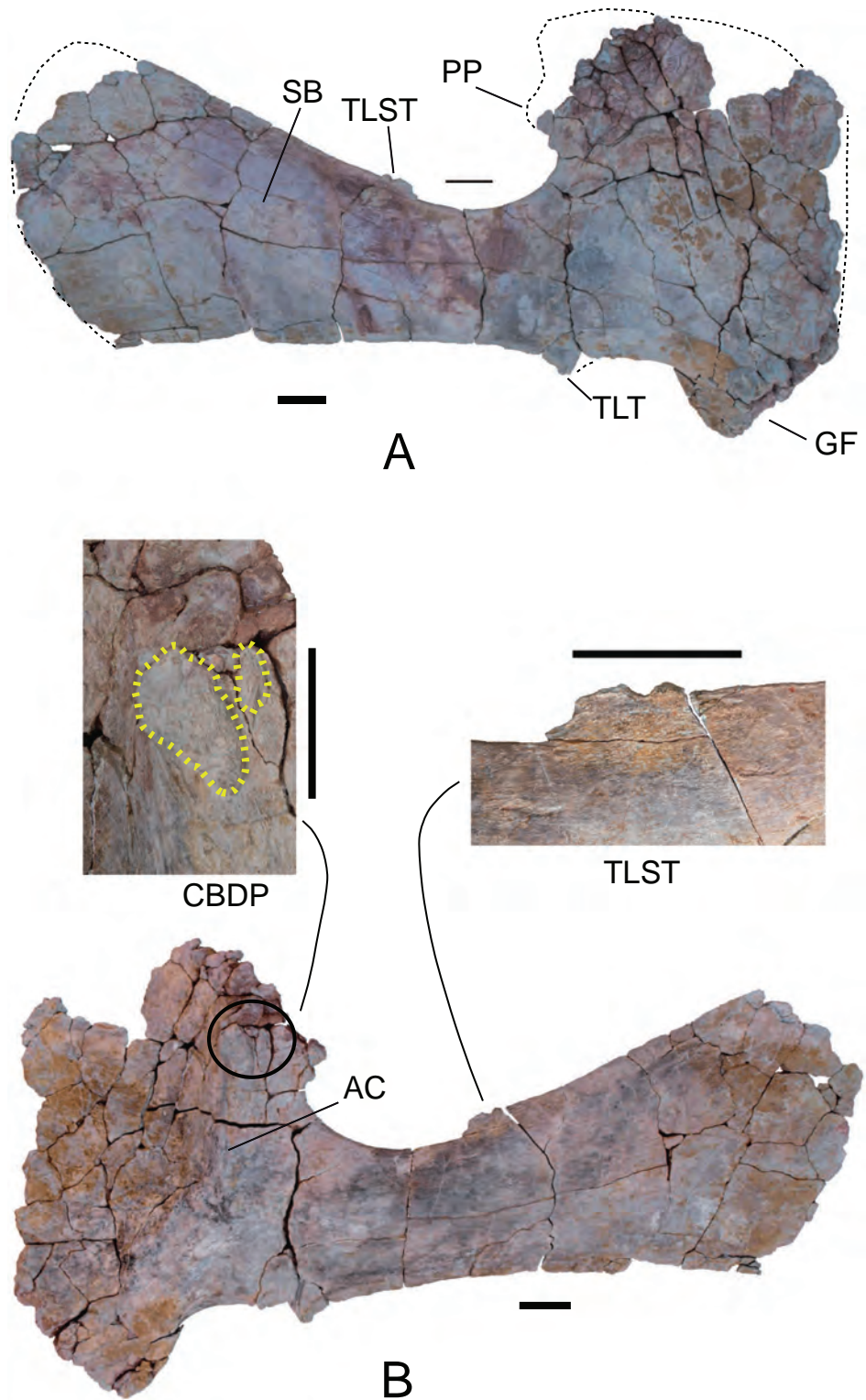
Figure 13 Left scapula (MDS-OTII,14) of *Europatitan eastwoodi* n. gen. n. sp. (A) Medial view. (B) Lateral view with details of two autapomorphic characters detailed in the text. AC, acromial/deltoid crest; CBDP, *coracobrachialis brevis dorsalis* process; GF, glenoid fossa; PP, postacromial process; SB, scapular blade; TLST, *trapezius* and *levator scapulae* tubercle; TLT, *triceps longus* process. Scale: 10 cm.

(*Janensch, 1950*; *Curtice, Stadtman & Curtice, 1996*) and basal somphospondylans such as *Ligabuesaurus* (*Bonaparte, González Riga & Apesteguía, 2006*) and *Phuwiangosaurus* (*Martin, Suteethorn & Buffetaut, 1999*). It differs clearly from the racquet-shaped scapula of Rebbachisauridae (*Carballido et al., 2010*). The maximum length is 165 cm and as such more than six times the minimum dorsoventral width of the scapular blade, as occurs in many eusauropods and in contrast with basal forms of sauropod such as *Cetiosaurus* (*Upchurch & Martin, 2003*) and with derived titanosaurians such as *Saltasaurus* (*Powell, Sanz & Buscalioni, 1992*). The proximal lamina is wide, and the scapular lamina is elongated, with a more pronounced distal expansion on the acromial margin, as shown by certain basal forms of camarasauromorph, where the acromial margin of the scapular blade presents a marked expansion and rounding, as in *Camarasaurus* (*Ostrom & McIntosh, 1966*) and *Giraffatitan brancai* (*Janensch, 1961*).

The proximal lamina is up to 150% wider dorsoventrally than the minimum width of the scapular lamina (*Harris, 2006*) and this ratio reaches a value of 3.5. Values for this character of less than 5.5 are broadly distributed among non-macronarian sauropodomorphs such as *Barapasaurus* (*Jain et al., 1979*), whereas values greater than 5.5 are seen mainly in the non-titanosaurian macronarians (*Borsuk-Bialynicka, 1977*; *Tidwell, Carpenter & Meyer, 2001*; *Bonaparte, González Riga & Apesteguía, 2006*; *Li et al., 2014*). Among titanosaurians values below 5.5 are generally observed (*Powell, Sanz & Buscalioni, 1992*).

In the distal margin of the proximal lamina, part of the postacromial process is preserved (Fig. 13A), which is possessed by various taxa within Titanosauriformes (*Bonaparte, González Riga & Apesteguía, 2006*; *You et al., 2008*; *Li et al., 2014*). The scapulocoracoid articulation ends before the dorsal margin of the acromion, such that the dorsal margin of the coracoid does not reach the dorsal margin of the scapula; *D'Emic (2012)* includes as a synapomorphy of Saltasauridae a scapulocoracoid suture extends to dorsal margin of acromion and coracoid. The articular face of the glenoid is oriented medially, as in *Apatosaurus* and in somphospondylans (*Wilson & Sereno, 1998*; *Upchurch, Barrett & Dodson, 2004*). The acromial or deltoid crest is robust and wide; it forms an angle of 75° with the longitudinal axis of the scapular blade and divides the acromion into two fossae, the anterior of which is wider than the posterior, which has a low lateromedial width. In comparison with other taxa within Macronaria (*Harris, 2006*, character 207), the dorsalmost point of the acromion is closer to the midpoint of the scapula than to the glenoid.

The dorsal area of the deltoid crest exhibits a sub-elliptical process with a rugose surface, which in its ventral part is accompanied by a rugose flat area and a pronounced groove (Fig. 13B). This process could correspond to the insertion for the *coracobrachialis brevis dorsalis* muscle (*Meers, 2003*). Two other, very gentle crests with smooth surfaces delimited by grooves lateral to them are present on the deltoid crest in its middle part and would correspond to the insertion for the *scapulohumeralis anterior* muscle (*Borsuk-Bialynicka, 1977*). Other muscular insertion marks are preserved on the medial surface of the scapular lamina, such as crests and grooves perpendicular to the proximal margin.

The scapular blade expands anterodistally in a uniform manner from its narrowest part toward the distalmost area of the blade. The lateral surface of the scapular blade is convex dorsoventrally, and the medial surface is slightly concave, endowing the scapular blade with a D-shaped cross-section, which becomes weaker distally due to lateromedial flattening. The D-shaped profile is a synapomorphy for the group of *Jobaria* and more derived sauropods, which is present in basal somphospondylans such as *Chubutisaurus* (*Carballido et al., 2011*). The medial surface of the scapular blade presents a somewhat rugose circular depression in its ventral part where the expansion of the proximal lamina begins, which corresponds to the insertion mark for the *subcoraculoscapularis* muscle in *Opisthocoelicaudia* (*Borsuk-Bialynicka, 1977*), described as an "eminence" in *Suuwassea* (*Harris, 2006*).

In the junction between the acromion and the scapular blade there is a triangular process with a rugose surface accompanied by long shallow grooves both on its lateral and medial surfaces (Fig. 13A); these marks would correspond to the insertion for the *triceps longus* muscle (*Meers, 2003*; *Li et al., 2014*). It is very prominent, as is the case in the basal somphospondylans *Ligabuesaurus* and *Daxiatitan* (*Bonaparte, González Riga & Apesteguía, 2006*; *You et al., 2008*). This process has been described in basal and derived titanosauriforms (*Janensch, 1961*; *Martin, Suteethorn & Buffetaut, 1999*; *Bonaparte, González Riga & Apesteguía, 2006*; *Harris, 2007*; *Carballido et al., 2011*; *D'Emic, 2012*). On the dorsal margin of the scapular blade, approximately in its middle part, there is a rugose tubercle with two projections separated by a semicircular depression (Fig. 13), which could correspond to the insertion for the *trapezius* and *levator scapulae* muscles (*Meers, 2003*). A similar tubercle has been figured in diplodocoids, where it is a gentle enlargement of the margin of the scapular blade; in basal macronarians such as *Camarasaurus*, where it is very prominent; and in titanosauriforms such as *Giraffatitan* (*Janensch, 1950*; *Curtice, Stadtman & Curtice, 1996*; *Hocknull et al., 2009*). In *Europatitan* the tubercle is divided, which distinguishes it from the rest of the sauropods in which this structure has been cited or figured. Furthermore, its position is more distal in *Europatitan*, except in relation to *Euhelopus* (*Young, 1935*), where it occupies an intermediate position, similar to *Europatitan*. The insertion marks for the *levator scapulae* muscle extend along the dorsal margin of the medial surface. On the ventral margin of the scapular blade there are insertion marks for the *serratus* muscle, and there are other marks on the distal margin that could correspond to insertions for the *suprascapular* ligament (*Borsuk-Bialynicka, 1977*; *Meers, 2003*).

Coracoid: A left coracoid (MDS-OTII,15), articulated with the left scapula. MDS-OTII,14 is in a poor state of preservation; it is deformed and fractured (Fig. 14). The articulations with the scapula and the dorsoproximal margin are incomplete. It is a quadrangular, equidimensional bone, with a proximodistal length of 52 cm and a dorsoventral length of 59 cm. Its maximum length corresponds to one-third the length of the scapula, and is greater than the scapulocoracoid articulation, a character described in derived titanosaurians (*Wilson, 2002*; *Upchurch, Barrett & Dodson, 2004*). The proximal margin is convex and rounded in outline, as occurs in other titanosauriforms such as *Euhelopus, Brachiosaurus, Paluxysaurus, Daxiatitan*, and *Yongjinglong* (*Young, 1935*;
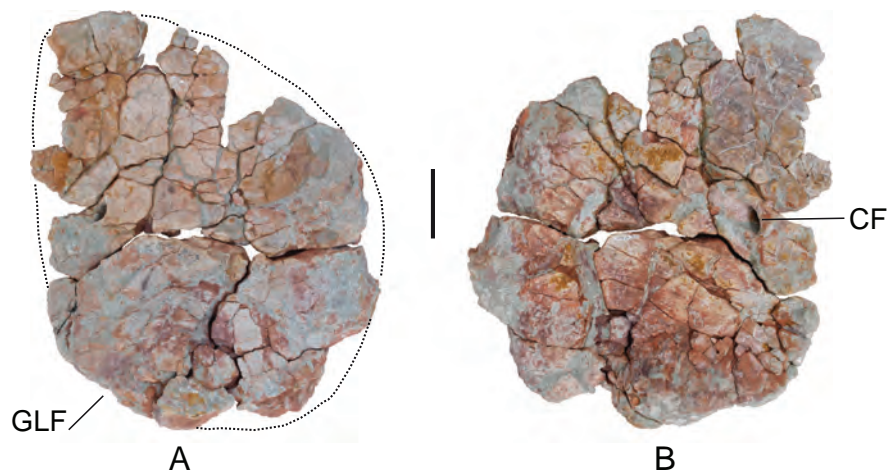
Figure 14 Left coracoid (MDS-OTII,15) of *Europatitan eastwoodi* n. gen. n. sp. (A) Medial view. (B) Lateral view. CF, coracoid foramen; GLF, glenoid fossa. Scale: 10 cm.

Curtice, Stadtman & Curtice, 1996; *Rose, 2007*; *You et al., 2008*; *Li et al., 2014*). The distal and ventrodistal margins are enlarged, especially the latter, where the enlargement is projected laterally. The coracoid foramen is located close to the distal margin and is closed. The scapulocoracoid articulation forms an angle of roughly 90° with the longitudinal axis of the scapular blade, similar to *Brachiosaurus* (*Curtice, Stadtman & Curtice, 1996*). An angle of 45° would be a synapomorphy of Nemegtosauridae and more derived titanosaurians (*Wilson, 2002*), although in a phylogenetic study of *Chubutisaurus* it has also been proposed that it is a synapomorphic character of somphospondylans (*Carballido et al., 2011*). The medial surface preserves parts with striated areas that correspond to the origin of various muscles: the *triceps longus caudalis* in the glenoid area, and the *supracoracoideus longus* in the dorsodistal area. Likewise, there are marks for the insertion of the *costocoracoideus profundus* muscle near the proximal margin (*Meers, 2003*).

Metacarpals: Two proximal fragments of left metacarpals I and III have been recovered (MDS-OTII,118 and MDS-OTII,17, respectively), and part of the diaphysis of metacarpal III (Fig. 15). For the anatomical description it has been taken into account that in proximal view the metacarpals of most sauropods form a semicircle, in such a way that Mc I and V are very close together in the posterior part of the manus (*Wilson & Sereno, 1998*).

Mc I is robust (Figs. 15A–15E). Its maximum proximodistal length is 20 cm. The proximal articular surface is flat and rugose (Fig. 15E). In proximal view it is oval and D-shaped, being anteroposteriorly expanded (with a width of 19.5 cm); the area of articulation with Mc II is slightly concave. The D-shaped proximal outline of Mc I can be cited in various clades of neosauropods, both primitive and derived, including *Camarasaurus*, *Giraffatitan*, *Aragosaurus*, *Opisthocoelicaudia*, and *Wintonotitan* (*Gilmore, 1936*; *Janensch, 1961*; *Ostrom & McIntosh, 1966*; *Borsuk-Bialynicka, 1977*; *Royo-Torres et al., 2014*; *Poropat et al., 2015a*). The D-shaped proximal outline of MDS-OTII,118 is fairly similar to that of *Opisthocoelicaudia* (*Borsuk-Bialynicka, 1977*).
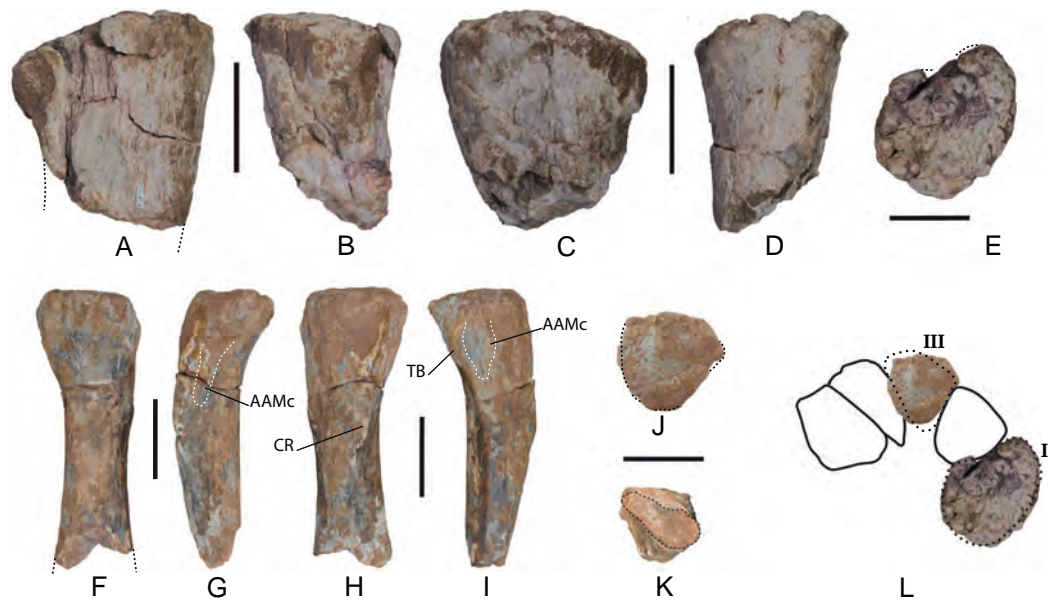
Figure 15 Left metacarpals of *Europatitan eastwoodi* n. gen. n. sp. (1) (A–E) Metacarpal I (MDS-OTII,118). (A) Anterior view. (B) Medial view. (C) Posterior view. (D) Lateral view. (E) Proximal view. (F–K) Metacarpal III (MDS-OTII,17). (F) Anterior view. (G) Medial view. (H) Posterior view. (I) Lateral view. (J) Proximal view. (K) Distal view cross-section of the shaft. (L) Proposed hypothetical reconstruction in proximal view of the set of left metacarpals of *Europatitan*, based on drawing of *Opisthocoelicaudia* (*Borsuk-Bialynicka, 1977*). AAMc, articular area with metacarpal; CR, crest; TB, tubercle. Scale: 10 cm.

This characteristic clearly distinguishes it from the compressed morphology presented by other titanosaurians such as *Andesaurus* and *Argyrosaurus* (*Apesteguía, 2005b*; *Mannion & Otero, 2012*).

The proximal anterior surface of MDS-OTII,118 is concave, forming a shallow fossa, delimited by two more protruding areas from the medial and lateral surfaces (Fig. 15A). This anterior surface presents grooves and crests that correspond to articulation marks with Mc II and that are prolonged ventrally. More distally, the anterior surface is flat, and it also possesses crests and grooves in its most medial part. The proximal posterior surface is flattened and is slightly convex.

MDS-OTII,17 is the proximal half of the left Mc III (Figs. 15F–15K). Its maximum proximodistal length is 35 cm. In proximal view, it is subtriangular, with its anterior margin wider and its posterior margin narrower. The proximal surface is flat and rugose. It has an anteroposterior width of 12 cm and a lateromedial width of 13 cm. The shaft is twisted in a proximodistal direction and presents one surface oriented anteriorly, another laterally, and another posteromedially, giving rise to a subtriangular cross-section in its proximal part and becoming more oval distally. In anterior view, MDS-OTII,17 is lateromedially wide in the proximal area, becoming thinner distally. Close to the proximal margin there are various short grooves perpendicular to this margin. In lateral view MDS-OTII,17 curves proximally and shows a crest that crosses the surface in a proximodistal direction; it forms a thick, prominent tubercle proximally (Fig. 15I: TB), becoming weaker

and sharper distally, as occurs in other titanosauriforms (*Apesteguía, 2005b*; *Hocknull et al., 2009*; *Poropat et al., 2015a*; *2015b*). Posterior to the tubercle there is a subtriangular area that corresponds to the articulation with Mc IV (Fig. 15I: AAMc); its surface displays many grooves and crests that give it a rugose appearance. These irregularities develop proximodistally over the whole surface, the development being greater in the proximal half. The medial surface of MDS-OTII,17 also possesses irregularities in its proximal half, which correspond to its articulation with Mc II (Fig. 15G: AAMc). In posterior view, MDS-OTII,17 presents a thick crest in its proximal half (Fig. 15H: CR). The long intermetacarpal articular surfaces shown by *Europatitan* are characteristic of Neosauropoda and are present in diplodocoids, *Camarasaurus* and Titanosauriformes (*Wilson & Sereno, 1998*) although *Apesteguía (2005b)* points out that basal titanosauriforms display a reduced dorsal articular contact.

Mc I and Mc III of *Europatitan* differ significantly in their dimensions: the former has an anteroposterior width of 19.5 cm; the latter of 12 cm, 39% less. This ratio is similar to that shown by the metacarpals of *Giraffatitan* and *Wintonotitan* (*Janensch, 1961*; *Poropat et al., 2015a*) and almost identical to that of *Opisthocoelicaudia* (*Borsuk-Bialynicka, 1977*), (Fig. 15L). The relative dimensions of the proximal extremity in other titanosauriforms are variable, and either of the first two metacarpals may be the larger (*Bonnan, 2003*; *Apesteguía, 2005b*; (*Poropat et al., 2015a*; *2015b*).

Pubis: Two pubes labeled as MDS-OTII,10 (rigth) and MDS-OTII,11 (left). The left pubis is more complete, although in both cases the anteroproximal corner of the iliac peduncle and a large part of the ischial peduncle are missing, as is the whole of the obturator foramen (Fig. 16). The pubes have a dorsoventral length of 104 cm. They are longer than the ischia (83 cm, 1.3 times longer, Table 2), as in Titanosauriformes (*Upchurch, 1998*; *Calvo & Salgado, 1995*); this ratio reaches its highest level in titanosaurids such as *Opisthocoelicaudia* and *Rapetosaurus* (*Curry Rogers & Forster, 2001*). The relative proportions of ischium and pubis in *Europatitan* are very similar to those obtained for the euhelopodid *Tangvayosaurus* (*Allain et al., 1999*). The pubes have a robust overall appearance, like the pubis of *Camarasaurus* (*Ostrom & McIntosh, 1966*), *Giraffatitan* (*Janensch, 1961*), and somphospondylans (*Martin, Suteethorn & Buffetaut, 1999*; *Salgado & Azpilicueta, 2000*; *Canudo, Royo-Torres & Cuenca-Bescós, 2008*; *D'Emic et al., 2013*). In posterior view, they are sinuous. The area of the acetabulum is large, and it is slightly concave anteroposteriorly. The lateral surface of this extremity has an area that is slightly concave in its middle part, unlike the medial surface, which is very convex. The obturator foramen is situated ventral to the acetabulum, in the proximal part of the ischial peduncle.

The ischial peduncle is well expanded posteriorly and proximodistally. Its lateral surface is convex, and its medial surface concave. Its estimated expansion for *Europatitan* is 0.4, similar to that of basal titanosauriforms and titanosaurians, where the greatest expansion is attained (*Royo-Torres, 2009*, character C136). *Europatitan* presents a greater expansion of the ischial peduncle than basal eusauropods and diplodocoids. The length of the ischial ramus of the pubis of *Europatitan* is relatively long and similar to that of other primitive titanosauriforms (*Royo-Torres, 2009*), by contrast with titanosaurids, which
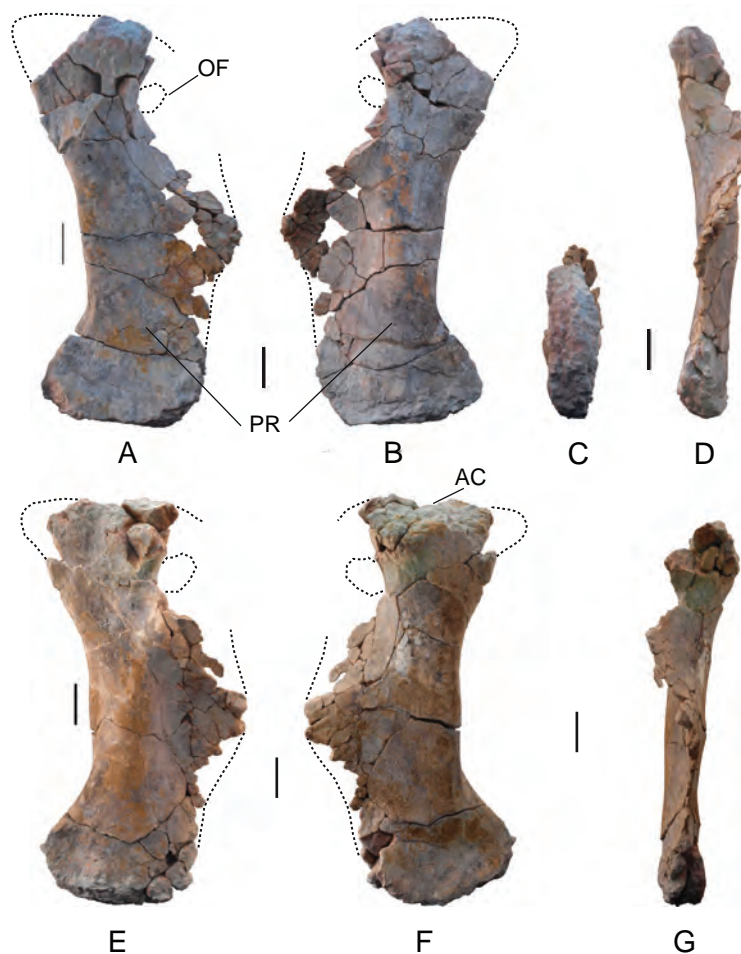
Figure 16 Pubes of *Europatitan eastwoodi* n. gen. n. sp. (A) Right pubis, MDS-OTII,10, in medial view (A), lateral view (B), distal view (C), and posterior view (D). Left pubis, MDS-OTII,11, in lateral view (E), medial view (F), and posterior view (G). AC, acetabulum; OF, obtutator foramen; PR, pubic ramus. Scale: 10 cm.

Table 2 Measurements of pubes of *Europatitan eastwoodi*.

Pubis	MDS-OTII,10 (Left)	MDS-OTII,11 (Right)
PL (cm)	104.5	104
DEIP (cm)	70	62[1]
APW (cm)	42	40[1]
IPL (cm)	45–50[1]	45–50[1]
APWIP (cm)	–	38
MWPS (cm)	27	28
MWDE (cm)	42	40[1]

Notes:
PL, proximodistal length; DEIP, distance from distal end to base of ischial peduncle; APW, anteroposterior width (measured at the base of ischial peduncle); IPL, ischial peduncle length; APWIP, anteroposterior width of ischial peduncle; MWPS, anteroposterior minimum width of pubic shaft; MWDE, anteroposterior maximum width distal end. Measurements are in cm.
[1] Incomplete or estimate.

present a short ischial ramus (*Salgado, Coria & Calvo, 1997*). The ratio between the length of the ischial articular surface and the total length of the pubes of *Europatitan* shows values between 0.43 and 0.48, values similar to the ratios displayed by *Giraffatitan* and *Andesaurus* (*Ostrom & McIntosh, 1966*; *Calvo & Bonaparte, 1991*). Derived titanosaurids have lower values, i.e., they have a short ischial symphysis (*Mannion et al., 2013*). *Tastavinsaurus* also displays lower values of around 0.37, the same as *Aragosaurus* (*Canudo, Royo-Torres & Cuenca-Bescós, 2008*; *Royo-Torres, Alcalá & Cobos, 2012*; *Royo-Torres et al., 2014*). The symphysis extends proximally to leave a series of grooves close to the anterior margin of the ischial ramus, occupying almost the whole of it. This character is considered derived and appears in other titanosauriforms (*Upchurch, 1998*; *Wilson, 2002*).

The pubic ramus is robust, well-expanded lateromedially and compressed anteroposteriorly, except at its distal end, where it becomes thicker (Fig. 16). The lateral side of the ramus is convex and the medial side straight. The ratio between the anteroposterior width of the ramus in its narrowest part and its distal extremity is 0.48, which indicates a scarcely expanded distal end. This value varies among Titanosauriformes, with values similar to *Europatitan* in *Brachiosaurus;* in the titanosaurians reaches higher values (i.e., relatively low distal expansion) and a weak distal expansion of the pubic ramus. *Tastavinsaurus* is an exception, with a value of 0.36, which corresponds to a distal extremity that is well expanded anteroposteriorly (*Canudo, Royo-Torres & Cuenca-Bescós, 2008*).

The outline of the distal end in lateral view is slightly convex, with the anterior and posterior margins rounded, the anterior margin somewhat more protruding. This feature distinguishes it from the pubis of *Camarasaurus*, *Aragosaurus*, and *Tastavinsaurus*, which have a very marked projection (*Ostrom & McIntosh, 1966*; *Canudo, Royo-Torres & Cuenca-Bescós, 2008*; *Royo-Torres, Alcalá & Cobos, 2012*; *Royo-Torres et al., 2014*). In the posteromedial part of the distal end there is a somewhat irregular expansion. The distal articular surface has an ellipsoidal outline, with its major axis running in an anteroposterior direction; it is convex, and in the course of it there emerges a crest.

Ischium: Two ischia labeled MDS-OTII,12 (right) and MDS-OTII,13 (left). The ischia are reasonably complete, lacking part of the pubic peduncle (Fig. 17). The ischium of *Europatitan* is smaller in size than the pubis: its dorsoventral length is 83 cm (Table 3). The iliac ramus is clearly differentiated, projecting posteriorly. It has a conic outline in posterior view, with the proximal part the widest. In posterior view, it is rugose, with crests and grooves and many nutrition foramina throughout the proximal part. The lateral surface of the iliac ramus has a crest close to the posterior margin (Fig. 17G: CR), which is associated with a gentle depression in its posterior part corresponding to the insertion for the *flexor tibialis internus* muscle (*Borsuk-Bialynicka, 1977*). A similar crest has been documented in *Haplocanthosaurus* (*Hatcher, 1903*) and in rebbachisaurids such as *Demandasaurus* and *Zapalasaurus* (*Salgado, García & Daza, 2006*; *Torcida Fernández-Baldor, 2012*). It has also been described in *Aragosaurus* (*Sanz et al., 1987*), in the somphospondylans *Huabeisaurus* and *Wintonotitan* (*D'Emic et al., 2013*; *Poropat et al., 2015a*) and in titanosaurians (*Curry Rogers, 2009*; *Otero, 2010*; *D'Emic et al., 2013*;
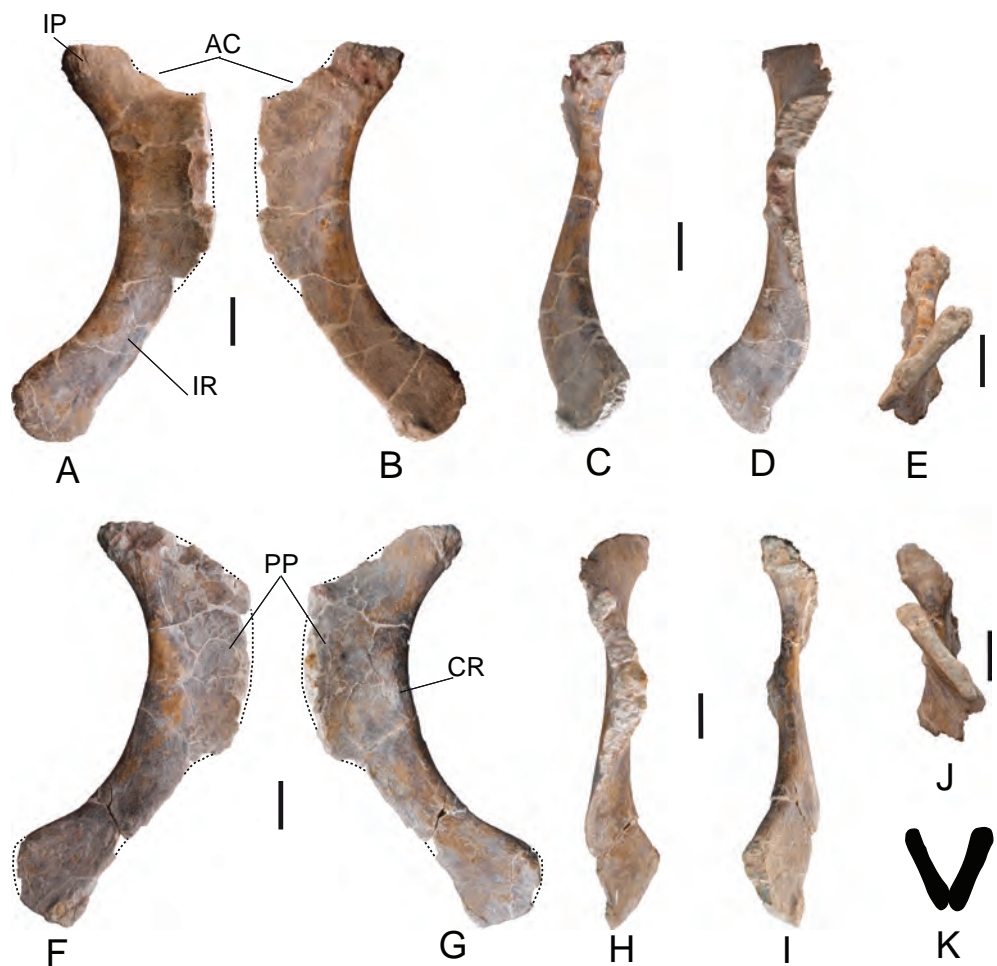
Figure 17 Ischia of *Europatitan eastwoodi* n. gen. n. sp. (A–E) Right ischium, MDS-OTII,12. (F–J) Left ischium, MDS-OTII,13. (A, G) Lateral view. (B, F) Medial view. (C, I) Posterior view. (D, H) Anterior view. (E, J) Posteroventral view. (K) Distal profile of ischia in posterior view. AC, acetabulum; CR, crest; IP, iliac peduncle; IR, ischial ramus; PP, pubis peduncle. Scale: 10 cm.

Table 3 Measurements of ischia of *Europatitan eastwoodi*.

Ischium	MDS-OTII,12 (Right)	MDS-OTII,13 (Left)
PL (cm)	83	83
PPL (cm)	41[1]	37[1]
APWIP (cm)	15	–
MWIS (cm)	15	14
MWDE (cm)	20	21

Notes:
  PL, proximodistal length; PPL, pubic peduncle length; APWIP, anteroposterior width of iliac peduncle; MWIS, anteroposterior minimum width of ischial shaft; MWDE, anteroposterior maximum width distal end. Measurements are in cm.
  [1] Incomplete or estimate.

Gallina & Apesteguía, 2015). The acetabulum has a slightly concave outline, with a very narrow margin in proximal view; it continuously links the iliac and pubic peduncles. Its lateral surface is concave. The contribution of the ischium to the acetabulum is notably,

as occurs in most sauropods except *Giraffatitan* and *Tastavinsaurus* (*Wilson, 2002*; *Canudo, Royo-Torres & Cuenca-Bescós, 2008*). The pubic ramus in its anatomical position is arranged vertically; it is lateromedially compressed, developed in an anterior direction, and expanded dorsoventrally. Its medial surface is concave, and its lateral surface is convex. Close to the anterior margin, the lateral surface is rugose, with abundant crests and grooves. In anterior view, the pubic symphysis is rugose, thicker in its proximal part and becoming thinner distally.

The ischial ramus of *Europatitan* is long. It is lateromedially compressed and progressively expands anteroposteriorly as it develops proximodistally, which gives rise to a rectangular shape in medial view; the ramus expands anteroposteriorly (or dorsoventrally in anatomical position) at the distal end, with a greater expansion in its posterior part, creating a convex margin and as a whole resulting in a distal end with a semicircular outline. The ischial ramus is directed posteroventrally and forms an angle of 48°–50° with the horizontal, a value that falls within the range of variability observed for most sauropods (*Royo-Torres, 2009*) except *Camarasaurus* and *Lourinhasaurus*, which have a rather horizontal ramus (*Ostrom & McIntosh, 1966*; *Dantas et al., 1998*). The distal end has the same lateromedial width as the rest of the ischial ramus. The anterior margin is sharp, and the posterior margin rounded and wider. The ischial symphysis lies in the distal part of the medial surface of the ischial ramus, at its anteroventral end; it is small, rugose, and level in the left ischium, projecting in the right one. The symphysis extends proximally to leave a series of grooves close to the anterior margin of the ischial ramus, occupying almost all of it, as is seen in MDS-OTII,12. An ischial symphyseal joint that extends beyond the distal extremity of the ischial ramus is a derived character present convergently in *Apatosaurus* and in Titanosauria such as *Alamosaurus* and *Opisthocoelicaudia* (*Gilmore, 1936*; *Borsuk-Bialynicka, 1977*), where the ischia join together proximally. *Europatitan* possesses ischia that are only fused at their distal end, a primitive character shared with basal macronarians such as *Camarasaurus* (*McIntosh et al., 1996*) and somphospondylans such as *Tangvayosaurus* and *Tastavinsaurus* (*Royo-Torres, 2009*; *Royo-Torres, Alcalá & Cobos, 2012*; *D'Emic, 2012*). On the posterior margin of the distal part of the ischial ramus there are various grooves and crests that extend very close to the distal end in a very irregular surface; these marks could correspond to the cartilaginous covering of this part of the bone (*Borsuk-Bialynicka, 1977*).

PHYLOGENETIC ANALYSIS

To assess the phylogenetic position of *Europatitan* within Eusauropoda, we coded this new taxon in the matrix published by *Carballido et al. (2015)*, a dataset focused on studying the relations among titanosauriforms. The resulting dataset included 75 terminal taxa coded for 370 characters, 20 of which were treated as ordered (12, 21, 58, 95, 96, 106, 108, 115, 116, 120, 145, 152, 163, 213, 216, 232, 233, 234, 252, 256, 299, and 301), and all of them were equally weighted. The resulting matrix (see Data S1 for *Europatitan* codings) was analyzed with TNT 1.1 (*Goloboff, Farris & Nixon, 2008*). The most-parsimonious trees were sought using a heuristic search, with Wagner starting trees and 1,000 random addition sequences, saving up to 10 trees per replication. Bremer support and bootstrap

values after 1,000 replicates were calculated for each branch to assess its robustness. To test the hypothesis of the monophyly of the Spanish stem Somphospondyli, constrained analyses were carried out using TNT (see Data S2 for the exact constrains applied). The resulting trees were subjected to Templeton's test (*Templeton, 1983*) using the TNT script by Schmidt-Lebuhn (original script can be downloaded at http://www.anbg.gov.au/cpbr/tools/templetontest.tnt).

Five most-parsimonious trees of 1,101 steps (consistency index = 0.40, retention index = 0.72, rescaled consistency index = 0.29) were recovered (Fig. 18) in 114 of the 1,000 replicates. Further searches using tree bisection reconnection on the existing trees failed to find new most-parsimonious trees. The overall topology of the consensus tree is similar to the tree published by *Carballido et al. (2015)*. *Europatitan* is recovered as a basal member of Somphospondyli (Fig. 18), as it fulfils the definition provided by *Wilson & Sereno (1998)*: "Neosauropods more closely related to *Saltasaurus loricatus* than to *Brachiosaurus altithorax*." *Europatitan* is recovered in a trichotomy with *Tendaguria* and the clade formed by *Sauroposeidon* and all its descendants. Nevertheless, it is worth noting that, although better resolved, the support for these topologies is as low as in previous analyses. The monophyly of Somphospondyli is supported by a single synapomorphy: the lack of a middle single fossa projected through the midline of the neural spine of the dorsal vertebrae (ch. 144, 0 → 1).

The high diversity of sauropod dinosaurs during the Late Jurassic and Early Cretaceous in Iberia peninsula raises the non-trivial question of the existence of an endemic Iberian clade of Titanosauriformes sauropods. The existence of this clade, either restricted to Iberia or with a slightly wider distribution has been postulated in the past. *Royo-Torres (2009)* and *Royo-Torres, Alcalá & Cobos (2012)* recovered a clade of mainly European forms, which they named Laurasiformes. This clade originally included *Aragosaurus, Galvesaurus, Phuwiangosaurus, Venenosaurus, Cedarosaurus, Tehuelchesaurus, Sonorasaurus*, and *Tastavinsaurus*, although its composition and position within Macronaria has varied (*Barco, 2010*; *Carballido et al., 2011*) and most recent analysis failed to recover this clade as such (*D'Emic, 2012*; *Upchurch, Mannion & Taylor, 2015*; *Mocho, Royo-Torres & Ortega, 2016*).

To test the existence of this clade, a second version of the dataset was built, this time including the late Berriasian Spanish sauropod *Aragosaurus*. This taxon was coded based in a combination of direct observations of the holotype by one of us (JIC), with the addition of new data based in the new material reported by *Royo-Torres et al. (2014)*. At the time of this study we were not able to perform direct observations on the newly reported material, with this the reason for which we did not include this taxon in our first analysis.

The inclusion of *Aragosaurus* resulted in a total of 76 MPTs of 1,112 steps. The strict consensus is poorly resolved, with the collapse of Brachiosauridae at the base of Macronaria. *Europatitan* is recovered in this polytomy. A posteriori deletion of *Lusotitan, Tendaguria*, and *Padillasaurus*, identified as wildcard taxa with the pruned trees option of TNT, resulted in a better-resolved reduced strict consensus. Here, *Europatitan* is recovered in a polytomy with Brachiosauridae and Somphospondyli (Fig. 19A). Its position in the
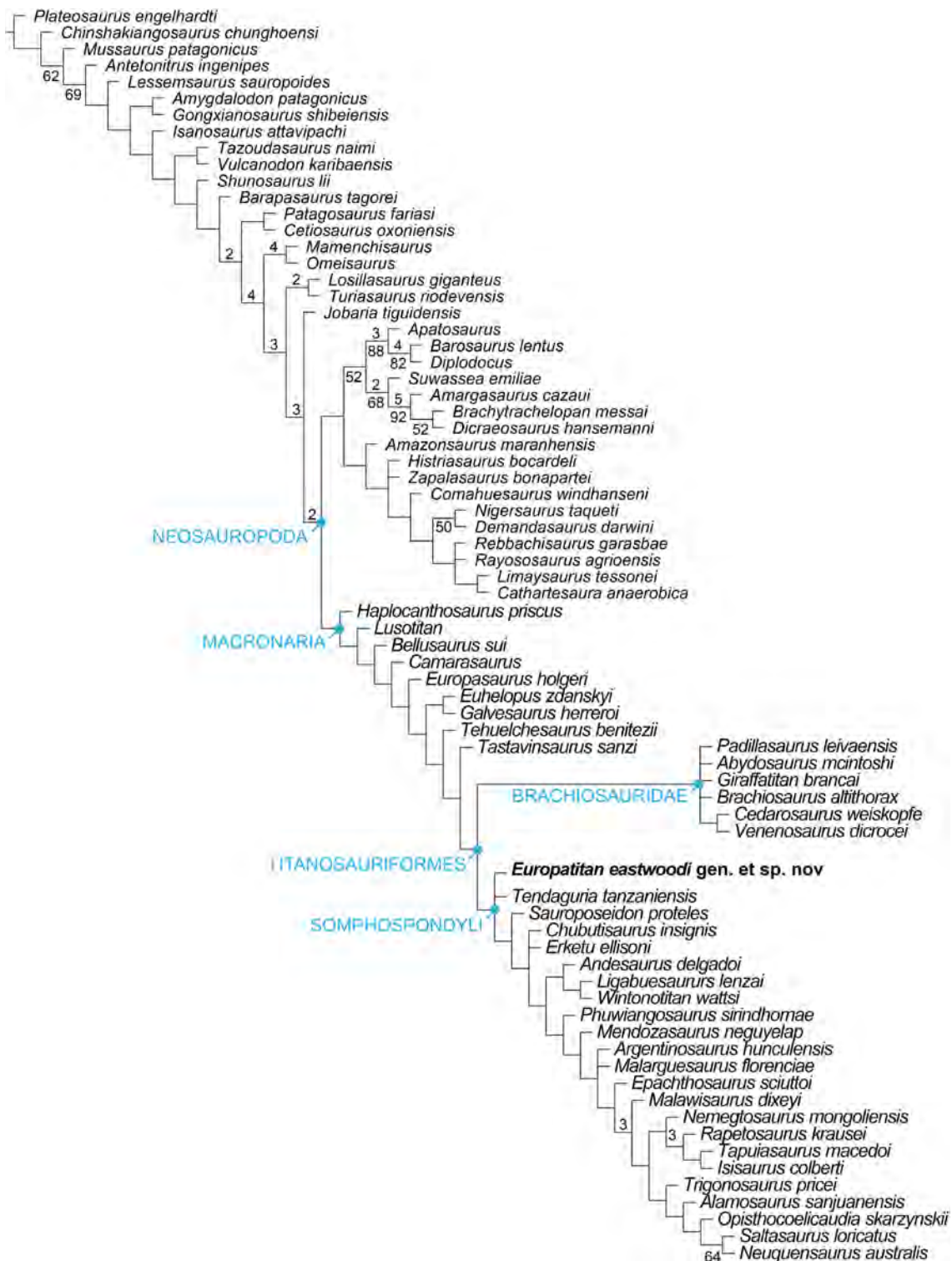
Figure 18 Strict consensus tree showing the phylogenetic relations of *Europatitan eastwoodi* gen. et. sp. nov. within Sauropoda using the matrix of *Carballido et al. (2015)* (See Appendix 4 for *Europatitan* scores). Strict consensus of five most-parsimonious trees of 1,101 steps. *Europatitan* is recovered as a basal somphospondylan, and more derived than the contemporaneous *Tastavinsaurus*, which is recovered as a non-titanosauriform camarasauromorph. Numbers over nodes represent Bremer support values over 2. Numbers below nodes represent bootstrap values over 50. The topology is better resolved than in previous analyses, but the general support is still low.

different MPTs varies between a basal Somphospondyli and a sister taxon of Titanosauriformes, with its position highly influenced by the location of *Lusotitan* in each tree. Interestingly, *Europatitan* is always recovered closer to the Jurassic *Lusotitan* than to the contemporaneous *Tastavinsaurus*. To further explore the relation between the Iberian taxa, two additional constrained analyzes were performed: one enforcing the monophyly of *Tastavinsaurus* + *Europatitan*, and another enforcing the monophyly of a wider Iberian clade, formed by *Tastavinsaurus*, *Europatitan*, *Aragosaurus*, *Galvesaurus*, and *Lusotitan*.

The first constrained analysis (Fig. 19B) resulted in 20 trees of 1,113 steps. The strict consensus places the *Tastavinsaurus* + *Europatitan* clade as the sister taxa of Titanosauriformes (Brachiosauridae + Somphospondyli). Templeton's test does not allow rejecting this topology, as it is only one step longer than the most parsimonious trees. Nevertheless, the *Tastavinsaurus* + *Europatitan* is supported by only two synapomorphies, (ch. 199, 0 → 1; ch. 213, 2 → 1). Both characters, especially ch. 199, 0 → 1 are widely distributed through Neosauropoda, with multiple reversions and convergences occurring.

The second constrained search resulted in ten trees of 1,115 steps, three steps longer than the most parsimonious trees (Fig. 19C). The resulting consensus is poorly resolved, with the Iberian clade recovered in a polytomy with *Tendaguria*, Brachiosauridae and Somphospondyli. Again, Templeton's test failed to reject this topology at any confident level, but in this occasion the Iberian clade is not supported by any synapomorphies. The topology of this clade is also odd, with the Berriasian *Aragosaurus* as the basalmost member of the clade, and with *Europatitan* closer to *Lusotitan* and *Tastavinsaurus* closer to *Galvesaurus*.

To summarize, the current dataset fails to find evidence supporting or against the existence of an Iberian clade of basal Titanosauriformes. The general lack of support for the clades recovered in our analysis, mainly caused by the fragmentary condition of most of the specimens included, results in that many different topologies can be obtained when trees with few steps more than the MPTs are considered. This is a common problem in dinosaur phylogenetic analysis (*Butler, Upchurch & Norman, 2008*; *McDonald, 2012*) and is even more severe in sauropod datasets (*Mannion et al., 2013*; Upchurch, Mannion & Taylor, 2015) where the rule is that the strict consensus is very poorly resolved, recovering only a few clades with relatively good support, with Macronaria a particularly low supported clade in all the analysis. Adding new, relatively complete specimens, such as the holotype of *Europatitan* to future datasets, together with the revision of scorings of previously known specimens will help to improve our knowledge of this hotspot of sauropod evolution.

DISCUSSION AND CONCLUSION

For the first time, all known material of the sauropod from the site of El Oterillo II in the Castrillo de la Reina Formation (upper Barremian–lower Aptian) of Burgos (Spain) is described with the name *E. eastwoodi*. The holotype of this new sauropod presents a series of autapomorphic characters in the posterior cervical vertebrae, the middle-posterior dorsal vertebra, the posterior dorsal ribs, and the scapula, indicating that *E. eastwoodi* is a previously undescribed taxon clearly distinct from other sauropods of the Early
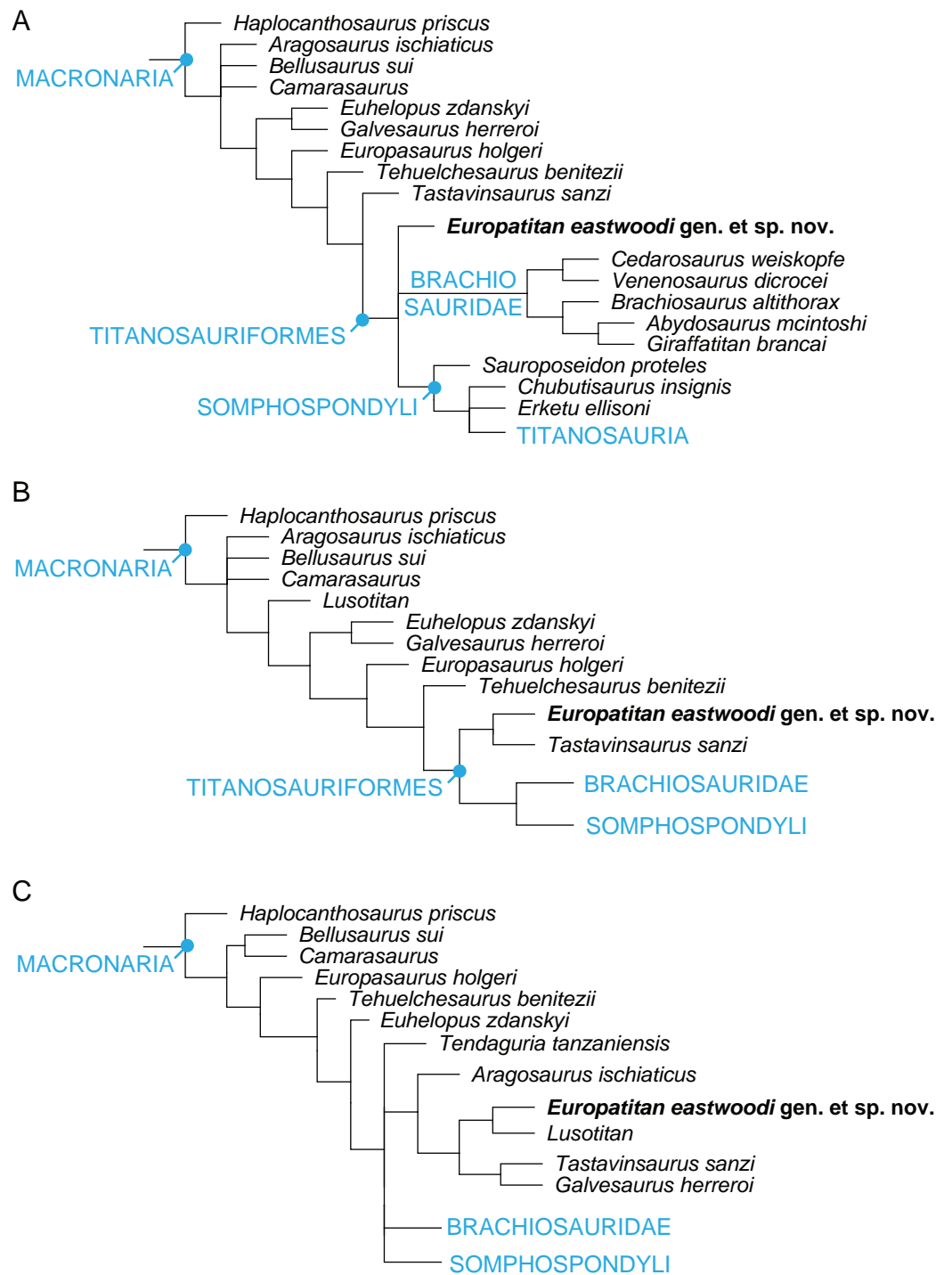
Figure 19 **(A) Reduced strict consensus (RSC) tree showing the phylogenetic relations of *Europatitan eastwoodi* within Sauropoda using the matrix of Carballido et al. (2014), with a deletion of *Lusotitan, Tendaguria, and Padillasaurus.*** Here, *Europatitan* is recovered in a polytomy with Brachiosauridae and Somphospondyli. (B) First additional constrained analysis enforcing the monophyly of *Tastavinsaurus + Europatitan*. The strict consensus places the *Tastavinsaurus + Europatitan* clade as the sister taxa of Titanosauriformes (Brachiosauridae + Somphospondyli). (C) Second additional constrained search enforcing the monophyly of *Lusotitan + Europatitan*. The strict consensus is poorly resolved, with the Iberian clade recovered in a polytomy with *Tendaguria*, Brachiosauridae and Somphospondyli.
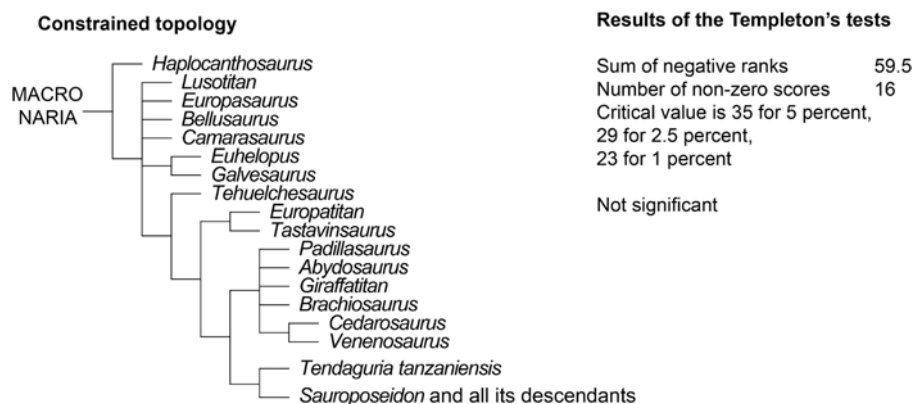
Figure 20 Topology of the subtree including all macronarians after enforcing the monophyly of *Tastavinsaurus* + *Europatitan*. Consensus of the 40 trees of 1,103 steps obtained after a constrained search enforcing the monophyly of the clade *Tastavinsaurus* + *Europatitan*, and results of Templeton's test comparing the first most-parsimonious trees with the first constrained tree.

Cretaceous of Spain. The phylogenetic study based on the proposal by *Carballido et al. (2015)* allows it to be located among the somphospondylan titanosauriforms, clearly differentiated from sauropods of the other clades of Titanosauriformes such as Brachiosauridae, Euhelopodidae and Titanosauria. According to our phylogenetic hypothesis, *Europatitan* would be one of the basalmost somphospondylans, in a position close to other basal somphospondylans such as *Tendaguria* and *Sauroposeidon*.

Our analysis shows an unexpectedly distant relation between *Europatitan* and *Tastavinsaurus sanzi*, a sauropod described in a geological level of similar age in Spain, initially considered a basal somphospondylan (*Canudo, Royo-Torres & Cuenca-Bescós, 2008*), although its position varies with the author (*D'Emic, 2012*; *Royo-Torres, Alcalá & Cobos, 2012*; *Carballido et al., 2015*) between a sister group to Titanosauriformes and a basal form of somphospondylan. This discussion lies beyond the scope of the present paper, but bearing in mind the phylogenetic, geographical, and chronological proximity of *Tastavinsaurus* and *Europatitan*, it seems relevant to demonstrate clearly that they are indeed distinct taxa. In the phylogenetic proposal used in this paper, *Tastavinsaurus* is recovered as the sister taxon of Titanosauriformes. To further test the hypothesis of the sister–taxon relationship between the two Spanish taxa, a constrained search was carried out, enforcing the monophyly of the *Tastavinsaurus* + *Europatitan* clade, otherwise maintaining all the settings used in the first analysis. Only two steps more were required to satisfy this constraint, resulting in 40 trees of 1,103 steps (see topology of the area of interest in Fig. 20). The resulting consensus is similar to the consensus of the MPTs. Templeton's test indicates that there is no significant difference between the constrained MPTs and the unconstrained topology, thus making it impossible to reject the hypothesis of a sister–taxon relationship between *Tastavinsaurus* and *Europatitan* solely based on the cladistic analysis. Nevertheless, *Europatitan* can be clearly differentiated from *Tastavinsaurus* by the bones that they share. Some of these differences are found in the dorsal vertebra and the hip bones (Fig. 21). The laminae present in *Europatitan* and their arrangement in the dorsal vertebrae are different from in *Tastavinsaurus*. *Europatitan*
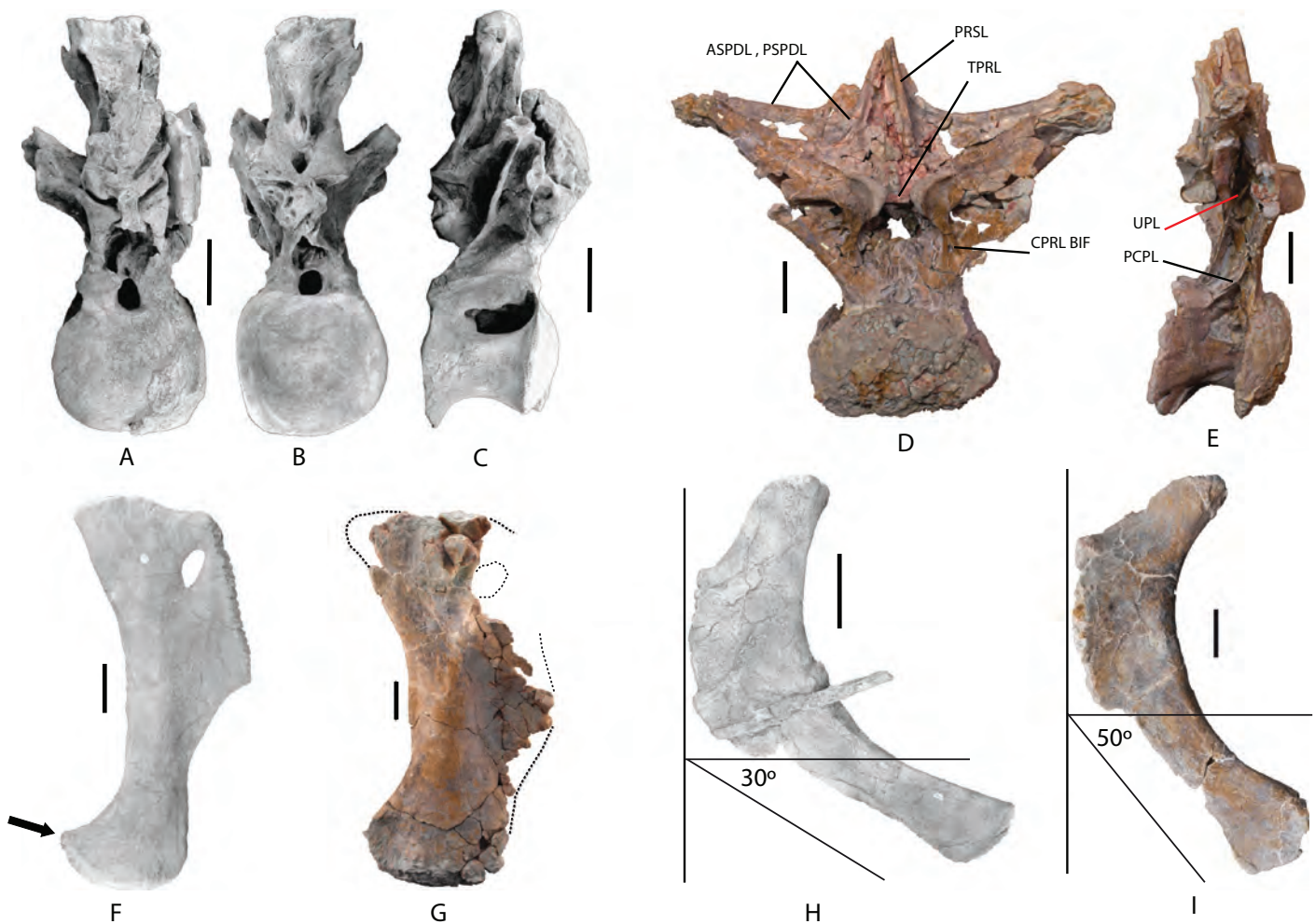
Figure 21 Comparison of selected anatomical characters of *Tastavinsaurus* (A, B, C, F, H) with *Europatitan* (D, E, G, I). Dorsal posterior vertebra Ars1-98 of *Tastavinsaurus* in anterior (A), posterior (B), and right lateral (C) views. *Europatitan* shows several laminae in its mid-posterior dorsal vertebra MDS-OTII,1 in anterior (D) and right lateral (I) views that do not have *Tastavinsaurus*. The pubis Ars1-16 of *Tastavinsaurus* (F, lateral view) has an anteroventral corner of the distal extremity acute (black arrow), directed anteroposteriorly. The pubis MDS-OTII,11 of *Europatitan* has this distal corner rounded (G, lateral view). In the Ischia Ars1-24 of *Tastavinsaurus* (H, medial view) the ischial ramus forms an angle of 30° respects the horizontal. In the ischium MDS-OTII,13 of *Europatitan* (I, medial view) this angle has a value of 50° (less posteroventral orientation). ASPDL, anterior spinodiapophyseal lamina; CPRL BF, bifurcated centroprezygapophyseal lamina; PCPL, posterior centroparapophyseal lamina; PRSL, prespinal lamina; PSPDL, posterior spinodiapophyseal lamina; TPRL, intraprezygapophyseal lamina; UPL, unnamed parapophyseal lamina. Scale: 10 cm.

possesses anterior and posterior spdl laminae and a prsl lamina; the cprl lamina is forked at its base; and the tprl lamina links the prezygapophyses. These characters of the laminae are not present in *Tastavinsaurus*. Moreover, the spdl joins the spol, and the pcpl joins the acpl, junctions that are not present in the dorsal vertebrae of *Tastavinsaurus* (Figs. 21D and 21E). The cranioventral corner of the distal extremity of the pubis is acute in *Tastavinsaurus* (autapomorphy) and rounded in *Europatitan* (Figs. 21F and 21G). The distal extremity of the pubis of *Europatitan* is much wider than in *Tastavinsaurus*. The pubic ramus of the ischium is at an angle of 45°–50° in relation to the horizontal in *Europatitan* and 30° in *Tastavinsaurus* (*Canudo, Royo-Torres & Cuenca-Bescós, 2008*), Figs. 21H and 21I.

Europatitan provides us with new information on the initial radiation of the somphospondylans in the lower Cretaceous of Laurasia, which could have taken place in Europe. The phylogenetic proposal used in this paper separates *Europatitan* from the brachiosaurids that represent an early radiation of Titanosauriformes at the end of the Jurassic. *Europatitan* would be a representative of the Eurogondwanan fauna (*Ezcurra & Agnolín, 2012*), like *Demandasaurus*, the other sauropod described from the Castrillo de la Reina Formation. These authors suggest that an exchange of vertebrate faunas between Gondwana and Laurasia took place at the beginning of the Early Cretaceous, whereas in the post-Barremian period the processes of dispersal occurred independently in Laurasia and Gondwana. However, other authors have argued based on the theropod record that there was a process of dispersal between Gondwana and Laurasia at the end of the Barremian (*Gasca, Canudo & Moreno-Azanza, 2014*). The sauropods of the Castrillo de la Reina Formation (*Europatitan* and *Demandasaurus*), as well as the new interpretations of the sauropod *Rebbachisaurus* (*Wilson & Allain, 2015*), also seem to indicate that the dispersal did not break off in the Barremian.

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ADDITIONAL INFORMATION AND DECLARATIONS

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Competing Interests

The authors declare that they have no competing interests.

Author Contributions

- Fidel Torcida Fernández-Baldor conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
- José Ignacio Canudo conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, wrote the paper, reviewed drafts of the paper.
- Pedro Huerta conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
- Miguel Moreno-Azanza conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
- Diego Montero performed the experiments, contributed reagents/materials/analysis tools, prepared figures and/or tables, reviewed drafts of the paper.

Data Availability

The following information was supplied regarding data availability:

The raw data has been supplied as Supplemental Dataset Files.

New Species Registration

The following information was supplied regarding the registration of a newly described species:

Publication LSID: urn:lsid:zoobank.org:pub:E76E9C58-CB53-4CBE-8CF5-87561A5365A1.

Genus name: urn:lsid:zoobank.org:act:29532C3F-4E3F-4702-845A-2D75EF3C63B.

Species name: urn:lsid:zoobank.org:act:B436CCB2-6E5C-498E-80A5-4BF271AC3175.

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REFERENCES

Allain R, Taquet P, Battail B, Dejax J, Richir P, Véran M. 1999. Un nouveau genre de dinosaure sauropode de la formation des Grès supérieurs (Aptien-Albien) du Laos. *Comptes Rendus de l'Académie des Sciences—Series IIA—Earth and Planetary Science* **329**:609–616 DOI 10.1016/S1251-8050(00)87218-3.

Alonso A, Canudo JI, Torcida Fernández-Baldor F. 2016. Isolated theropod teeth associated with sauropod remains from El Oterillo II (Early Cretaceous) site of Salas de los Infantes (Burgos, Spain). In: Torcida Fernández-Baldor F, Canudo JI, Huerta P, Pereda X, eds. *Actas de las VII Jornadas Internacionales Sobre Paleontología de Dinosaurios y su Entorno.* Salas de los Infantes: Colectivo Arqueológico y Paleontológico de Salas, 39–41.

Apesteguía S. 2005a. Evolution of the hyposphene–hypantrum complex within sauropoda. In: Tidwell V, Carpenter K, eds. *Thunder-Lizards: The Sauropodomorph Dinosaurs.* Bloomington: Indiana University Press, 248–267.

Apesteguía S. 2005b. Evolution of the titanosaur metacarpus. In: Tidwell V, Carpenter K, eds. *Thunder-Lizards: The Sauropodomorph Dinosaurs.* Bloomington: Indiana University Press, 321–345.

Arribas J, Alonso A, Mas R, Tortosa A, Rodas M, Barrenechea JF, Alonso-Azcarate J, Artigas R. 2003. Sandstone petrography of continental depositional sequences of an intraplate rift basin: western Cameros Basin (North Spain). *Journal Sedimentary Research* **73**:309–327 DOI 10.1306/082602730309.

Aurell M, Bádenas B, Gasca JM, Canudo JI, Liesa C, Soria AR, Moreno-Azanza M, Najes L. 2016. Stratigraphy and evolution of the Galve sub-basin (Spain) in the middle Tithonian-early Barremian: implications for the setting and age of some dinosaur fossil sites. *Cretaceous Research* **65**:138–162 DOI 10.1016/j.cretres.2016.04.020.

Barco JL, Canudo JI, Cuenca-Bescos G, Ruiz-Omeñaca JI. 2005. Un nuevo dinosaurio saurópodo *Galvesaurus herreroi* gen. nov., sp. nov., del tránsito Jurásico-Cretácico en Galve (Teruel, NE de España). *Naturaleza Aragonesa* **15**:4–17.

Barco JL. 2010. Implicaciones filogenéticas y paleobiogeográficas del saurópodo *Galvesaurus herreroi* Barco, Canudo, Cuenca-Bescós y Ruiz-Omeñaca 2005. In: Huerta P, Torcida Fernández-Baldor F, eds. *V Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno. Libro de Resúmenes/Abstract Book.* Salas de los Infantes: Colectivo Arqueológico y Paleontológico de Salas, 3–6.

Barrett PM, Hasegawa Y, Manabe M, Isaji S, Matsuoka H. 2002. Sauropod dinosaurs from the lower Cretaceous of eastern Asia: taxonomic and biogeographical implications. *Palaeontology* **45**:1197–1217 DOI 10.1111/1475-4983.00282.

Beuther A, Dahm H, Kneuper-Haack F, Mensik H, Tischer G, Brinkmann R, Dupuy de Lôme, Herbert L. 1966. Der Jura und Wealden in Nordost Spanien. *Beiheftezum Geologischen Jahrbuch* **44**:1–224.

Bonaparte JF. 1986. Los dinosaures (Carnosaures, Allosauridés, Sauropodes, Cétiosauridés) du Jurassique moyen de Cerro Cóndor (Chubut, Argentina). *Annales de Paléontologie* **72**:247–289.

Bonaparte JF, González Riga BJ, Apesteguía S. 2006. *Ligabuesaurus leanzai* gen. et sp. nov. (Dinosauria, Sauropoda), a new titanosaur from the Lohan Cura Formation (Aptian, lower Cretaceous) of Neuquén, Patagonia, Argentina. *Cretaceous Research* **27**:364–376 DOI 10.1016/j.cretres.2005.07.004.

Bonnan MF. 2003. The evolution of manus shape in sauropod dinosaurs: implications for functional morphology, forelimb orientation, and phylogeny. *Journal of Vertebrate Paleontology* **23**:595–613 DOI 10.1671/A1108.

Borsuk-Bialynicka M. 1977. A new camarasaurid sauropod *Opisthocoelicaudia skarzynskii* gen. n., sp. n. from the upper Cretaceous of Mongolia. *Palaeontologia Polonica* **37**:5–64.

Butler RJ, Upchurch P, Norman DB. 2008. The phylogeny of the ornithischian dinosaurs. *Journal of Systematics Palaeontology* **6(1)**:1–40 DOI 10.1017/S1477201907002271.

Calvo JO, Bonaparte JF. 1991. *Andesaurus delgadoi* gen. et. sp. nov. (Saurischia-Sauropoda), dinosaurio Titanosauridae de la Formacion Rio Limay (Albiano-Cenomaniano), Neuquén, Argentina. *Ameghiniana* **28**:303–310.

Calvo JO, Salgado L. 1995. *Rebbachisaurus tessonei* sp. nov. a new sauropoda from the Albian-Cenomanian of Argentina; new evidence of the origin of the Diplodocidae. *Gaia* **11**:13–33.

Campos DA, Kellner AWA, Bertini RJ, Santucci RM. 2005. On a titanosaurid (Dinosauria, Sauropoda) vertebral column from the Bauru Group, Late Cretaceous of Brazil. *Arquivos do Museu Nacional* **63(3)**:565–593.

Canudo JI, Barco JL, Castanera D, Torcida Fernández-Baldor F. 2010. New record of a sauropod in the Jurassic–Cretaceous transition of the Iberian Peninsular (Spain): palaeobiogeographical implications. *Paläontologische Zeitschrift* **84**:427–435 DOI 10.1007/s12542-010-0057-x.

Canudo JI, Barco JL, Pereda-Suberbiola X, Ruiz-Omeñaca JI, Salgado L, Torcida Fernández-Baldor F, Gasulla JM. 2009. What Iberian dinosaurs reveal about the bridge said to exist between Gondwana and Laurasia in the Early Cretaceous. *Bulletin de la Societe Geologique de France* **180**:5–11 DOI 10.2113/gssgfbull.180.1.5.

Canudo JI, Cuenca-Bescós G. 2004. Morphometric approach to Titanosauriformes (Sauropoda, Dinosauria) femora: implications to the paleobiogeographic analysis. In: Elewa A, ed. *Morphometrics. Application Morphometric Analysis.* Berlin, Heidelberg: Springer-Verlag, 143–156.

Canudo JI, Gasca JM, Moreno-Azanza M, Aurell M. 2012. New information about the stratigraphic position and age of the sauropod *Aragosaurus ischiaticus* from the Early Cretaceous of the Iberian Peninsula. *Geological Magazine* **149**:252–263 DOI 10.1017/S0016756811000732.

Canudo JI, Royo-Torres R, Cuenca-Bescós G. 2008. A new sauropod: *Tastavinsaurus sanzi* Gen. et sp. nov. from the Early Cretaceous (Aptian) of Spain. *Journal of Vertebrate Paleontology* **28**:712–731 DOI 10.1671/0272-4634(2008)28[712:ANSTSG]2.0.CO;2.

Canudo JI, Ruiz-Omeñaca JI, Barco JL, Royo-Torres R. 2002. ¿Saurópodos asiáticos en el Barremiense inferior (Cretácico inferior) de España? *Ameghiniana* **39**:443–452.

Carballido JL, Garrido AC, Canudo JI, Salgado L. 2010. Redescription of *Rayososaurus agrioensis* Bonaparte (Sauropoda, Diplodocoidea), a rebbachisaurid from the Early Late Cretaceous of Neuquén. *Geobios* **43**:493–502 DOI 10.1016/j.geobios.2010.01.004.

Carballido JL, Pol D, Cerda I, Salgado L. 2011. The osteology of *Chubutisaurus insignis* del Corro, 1975 (Dinosauria: Neosauropoda) from the "middle" Cretaceous of central Patagonia, Argentina. *Journal of Vertebrate Paleontology* **31**:93–110 DOI 10.1080/02724634.2011.539651.

Carballido JL, Pol D, Parra Ruge ML, Padilla Bernal S, Páramo-Fonseca ME, Etayo-Serna F. 2015. A new Early Cretaceous brachiosaurid (Dinosauria, Neosauropoda) from northwestern Gondwana (Villa de Leiva, Colombia). *Journal of Vertebrate Paleontology* **35**:e980505 DOI 10.1080/02724634.2015.980505.

Carballido JL, Salgado L, Pol D, Canudo JI, Garrido A. 2012. A new basal rebbachisaurid (Sauropoda, Diplodocoidea) from the Early Cretaceous of the Neuquén Basin; evolution and biogeography of the group. *Historical Biology* **24**:631–654 DOI 10.1080/08912963.2012.672416.

Castanera D, Vila B, Razzolini NL, Santos VF, Pascual C, Canudo JI. 2014. Sauropod trackways of the Iberian Peninsula: palaeoetological and palaeoenvironmental implications. *Journal of Iberian Geology* **40**:49–59 DOI 10.5209/rev_JIGE.2014.v40.n1.44087.

Chure D, Britt BB, Whitlock JA, Wilson JA. 2010. First complete sauropod dinosaur skull from the Cretaceous of the Americas and the evolution of sauropod dentition. *Naturwissenschaften* **97**:379–391 DOI 10.1007/s00114-010-0650-6.

Clemente P, Perez-Arlucea M. 1993. Depositional architecture of the Cuerda del Pozo Formation, lower Cretaceous of the extensional Cameros Basin, north-central Spain. *Journal of Sedimentary Research* **63**:437–452 DOI 10.1306/D4267B1D-2B26-11D7-8648000102C1865D.

Clemente Vidal MP. 2010. Review of the upper Jurassic-lower Cretaceous stratigraphy in western Cameros Basin, Northern Spain. *Revista de la Sociedad Geológica de España* **23**:101–143.

Contreras R, Cruzado-Caballero P, Torcida Fernández-Baldor F, Huerta P, Izquierdo LA, Montero Huerta D. 2007. Descripción de un ilion de un dinosaurio "iguanodontido" procedente del Cretácico Inferior de Burgos (España). *IV Jornadas Internacionales Sobre Dinosaurios y su Entorno*. Libro de Resúmenes: Salas de los Infantes, 53–54.

Curry Rogers K. 2009. The postcranial osteology of *Rapetosaurus krausei* (Sauropoda: Titanosauria) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology* **29(4)**:1046–1086 DOI 10.1671/039.029.0432.

Curry Rogers K, Forster CA. 2001. The last of the dinosaur titans: a new sauropod from Madagascar. *Nature* **412**:530–534 DOI 10.1038/35087566.

Curtice B, Stadtman K, Curtice L. 1996. A reassessment of *Ultrasaurus macintoshi* (Jensen, 1985). *Museum of Northern Arizona Bulletin* **60**:87–96.

D'Emic MD. 2012. The early evolution of titanosauriform sauropod dinosaurs. *Zoological Journal of Linnean Society* **166**:624–671 DOI 10.1111/j.1096-3642.2012.00853.x.

D'Emic MD. 2013. Revision of the sauropod dinosaurs of the lower Cretaceous Trinity Group, southern USA, with the description of a new genus. *Journal of Systematic Palaeontology* **11(6)**:707–726 DOI 10.1080/14772019.2012.667446.

D'Emic MD, Foreman BZ. 2012. The beginning of the sauropod dinosaur hiatus in North America: insights from the lower Cretaceous Cloverly Formation of Wyoming. *Journal of Vertebrate Paleontology* **32**:883–902 DOI 10.1080/02724634.2012.671204.

D'Emic MD, Mannion PD, Upchurch P, Benson RBJ, Pang Q, Zhengwu C. 2013. Osteology of *Huabeisaurus allocotus* (Sauropoda: Titanosauriformes) from the upper Cretaceous of China. *PLoS ONE* **8**:e69375 DOI 10.1371/journal.pone.0069375.

Dantas P, Sanz JL, Marques da Silva C, Ortega F, Santos V, Cachão M. 1998. *Lourinhasaurus* n. gen. Novo dinossáurio saurópode do Jurássico superior (Kimeridgiano superior-Titoniano inferior) de Portugal. *Actas Do V Congresso Nacional de Geologia*. Comunicações do Instituto Geológico e Mineiro, 91–94.

Díez Díaz V, Mocho P, Páramo A, Escaso F, Marcos-Fernández F, Sanz JL, Ortega F. 2016. A new titanosaur (Dinosauria, Sauropoda) from the upper Cretaceous of Lo Hueco (Cuenca, Spain). *Cretaceous Research* **68**:49–60 DOI 10.1016/j.cretres.2016.08.001.

Ezcurra MD, Agnolín FL. 2012. A new global palaeobiogeographical model for the late Mesozoic and early Tertiary. *Systematic Biology* **61**:553–566 DOI 10.1093/sysbio/syr115.

Gallina PA, Apesteguía S. 2015. Postcranial anatomy of *Bonitosaura salgadoi* (Sauropoda, Titanosauria) from the Late Cretaceous of Patagonia. *Journal of Vertebrate Paleontology* **35(3)**: DOI 10.1080/02724634.2014.924957.

Gasca JM, Canudo JI, Moreno-Azanza M. 2014. A large-bodied theropod (Tetanurae: Carcharodontosauria) from the Mirambel Formation (Barremian) of Spain. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **273**:13–23 DOI 10.1127/0077-7749/2014/0413.

Gheerbrant E, Rage JC. 2006. Paleobiogeography of Africa: how distinct from Gondwana and Laurasia? *Palaeogeography, Palaeoclimatology, Palaeoecology* **241**:224–246 DOI 10.1016/j.palaeo.2006.03.016.

Gilmore CW. 1936. Osteology of *Apatosaurus*, with special reference to specimens in the Carnegie Museum. *Memoirs of the Carnegie Museum* **11**:175–300.

Goloboff PA, Farris JS, Nixon KC. 2008. TNT, a free program for phylogenetic analysis. *Cladistics* **24**:774–786 DOI 10.1111/j.1096-0031.2008.00217.x.

González Riga BJ. 2003. A new titanosaur (Dinosauria, Sauropoda) from the upper Cretaceous (Cerro Lisandro formation) of Mendoza Province, Argentina. *Ameghiniana* **51**:3–25 DOI 10.5710/AMEGH.26.12.1013.1889.

Gorscak E, O'Connor PM. 2016. Time-calibrated models support congruency between Cretaceous continental rifting and titanosaurian evolutionary history. *Biology Letters* **12**:20151047.

Harris JD. 2004. Confusing dinosaurs with mammals: tetrapod phylogenetics and anatomical terminology in the world of homology. *Anatomical Record Part A* **281**:1240–1246 DOI 10.1002/ar.a.20078.

Harris JD. 2006. The significance of *Suuwassea emilieae* (Dinosauria: Sauropoda) for flagellicaudatan intrarelationships and evolution. *Journal of Systematic Palaeontology* **4**:185–198 DOI 10.1017/S1477201906001805.

Harris JD. 2007. The appendicular skeleton of *Suuwassea emilieae* (Sauropoda: Flagellicaudata) from the upper Jurassic Morrison Formation of Montana (USA). *Geobios* **40**:501–522 DOI 10.1016/j.geobios.2006.02.002.

Hatcher JB. 1903. Osteology of *Haplocanthosaurus* with description of a new species, and remarks on the probable habits of the Sauropoda, and the age and origin of the *Atlantosaurus* beds. *Memoirs of the Carnegie Museum* **2**:1–72.

Hocknull SA, White MA, Tischler TR, Cook AG, Calleja ND, Sloan T, Elliott DA. 2009. New mid-Cretaceous (latest Albian) dinosaurs from Winton, Queensland, Australia. *PLoS ONE* **4**:e6190 DOI 10.1371/journal.pone.0006190.

Huerta P, Torcida Fernández-Baldor F, Farlow JO, Montero D. 2012. Exceptional preservation processes of 3D dinosaur footprint casts in Costalomo (lower Cretaceous, Cameros Basin, Spain). *Terra Nova* **12**:136–141 DOI 10.1111/j.1365-3121.2011.01047.x.

Jain SL, Kutty TS, Roy-Chwdhury TK, Chatterjee S. 1979. Some characteristics of *Barapasaurus tagorei*, a sauropod dinosaur from the lower Jurassic of Deccan, India. *Proceedings of IV International Gondwana Symposium* **1**:204–216.

Janensch W. 1929. Material und Formengehalt der Sauropoden in der Ausbeute der Tendaguru-Expedition. *Palaeontographica* **2(Suppl 7)**:2–34.

Janensch W. 1950. Die Wirbelsäule von *Brachiosaurus brancai*. *Palaeontographica* **7**:27–93.

Janensch W. 1961. Die Gliedmaszen und Gliedmaszengürtel der Sauropoden der Tendaguru-Schichten. *Palaeontographica* **7(Suppl. 2)**:177–235.

Ksepka DT, Norell M. 2006. *Erketu ellisoni*, a long-necked sauropod from Bor Guvé (Dornogov Aimag, Mongolia). *American Museum Novitates* **3508**:1–16 DOI 10.1206/0003-0082(2006)3508[1:eealsf]2.0.co;2.

Ksepka DT, Norell MA. 2010. The illusory evidence for Asian Brachiosauridae: new material of Erketu ellisoni and a phylogenetic reappraisal of basal Titanosauriformes. *American Museum Novitates* **3700**:1–27.

Lehman TM, Coulson AB. 2002. A juvenile specimen of the sauropod dinosaur *Alamosaurus sanjuanensis* from the upper Cretaceous of Big Bend National Park, Texas. *Journal of Paleontology* **76**:156–172.

Li L-G, Li D-Q, You H-L, Dodson P. 2014. A new titanosaurian sauropod from the Hekou Group (lower Cretaceous) of the Lanzhou-Minhe Basin, Gansu Province, China. *PLoS ONE* **9**:e85979 DOI 10.1371/journal.pone.0085979.

Lovelace DM, Hartman SA, Wahl WR. 2007. Morphology of a specimen of *Supersaurus* (Dinosauria, Sauropoda) from the Morrison Formation of Wyoming, and a re-evalutation of diplodocid phylogeny. *Arquivos do Museu Nacional* **65**:527–544.

McDonald AT. 2012. The status of *Dollodon* and other basal iguanodonts (Dinosauria: Ornithischia) from the Lower Cretaceous of Europe. *Cretaceous Research* **33**:1–6.

Mannion PD, Otero A. 2012. A reappraisal of the Late Cretaceous Argentinean sauropod dinosaur *Argyrosaurus superbus*, with a description of a new titanosaur genus. *Journal of Vertebrate Paleontology* **32(3)**:614–638 DOI 10.1080/02724634.2012.660898.

Mannion PD, Upchurch P, Barnes RN, Mateus O. 2013. Osteology of the Late Jurassic Portuguese sauropod dinosaur *Lusotitan atalaiensis* (Macronaria) and the evolutionary history of basal titanosauriforms: *Lusotitan* and titanosauriform evolution. *Zoological Journal of Linnean Society* **168**:98–206 DOI 10.1111/zoj.12029.

Mannion PD, Upchurch P, Mateus O, Barnes RN, Jones MEH. 2012. New information on the anatomy and systematic position of *Dinheirosaurus lourinhanensis* (Sauropoda: Diplodocoidea) from the Late Jurassic of Portugal, with a review of European diplodocoids. *Journal of Systematic Palaeontology* **10**:521–551 DOI 10.1080/14772019.2011.595432.

Marsh OC. 1878. Principal characters of American Jurassic dinosaurs. Part I. *American Journal of Science* **3**:411–416.

Martin V, Suteethorn V, Buffetaut E. 1999. Description of the type and referred material of *Phuwiangosaurus sirindhornae*, a sauropod from the lower Cretaceous of Thailand. *Oryctos* **2**:39–91.

Martín-Closas C, Alonso Millán A. 1998. Estratigrafía y bioestratigrafía (Charophyta) del Cretácico Inferior en el sector occidental de la Cuenca de Cameros (Cordillera Ibérica). *Revista de la Sociedad Geológica de España* **11**:253–269.

Martínez RD, Giménez O, Rodríguez J, Luna M, Lamanna MC. 2004. An articulated specimen of the basal titanosaurian (dinosauria: sauropoda) *Epachthosaurus sciuttoi* from the early late Cretaceous Bajo Barreal formation of Chubut province, Argentina. *Journal of Vertebrate Paleontology* **24**:107–120 DOI 10.1671/9.1.

McIntosh J, Miller W, Stadtman K, Gillette D. 1996. The osteology of *Camarasaurus lewisi* (Jensen, 1988). *Brigham Young University Geological Study* **41**:73–95.

Meers MB. 2003. Crocodylian forelimb musculature and its relevance to Archosauria. *Anatomical Record* **274**:891–916 DOI 10.1002/ar.a.10097.

Mocho P, Royo-Torres R, Ortega F. 2016. New data of the Portuguese brachiosaurid *Lusotitan atalaiensis* (Sobral Formation, Upper Jurassic). *Historical Biology* **168(1)**:98–206 DOI 10.1080/08912963.2016.1247447.

Ostrom JH, McIntosh J. 1966. *Marsh's Dinosaurs: The Collections from Como Bluff.* New Haven: Yale University Press.

Otero A. 2010. The appendicular skeleton of *Neuquensaurus*, a Late Cretaceous saltasaurine sauropod from Patagonia, Argentina. *Acta Palaeontologica Polonica* **55**:399–426 DOI 10.4202/app.2009.0099.

Otero A, Gallina PA, Canale JI, Haluza A. 2012. Sauropod haemal arches: morphotypes, new classification and phylogenetic aspects. *Historical Biology* **24(3)**:243–256.

Pereda-Suberbiola X, Ruiz-Omeñaca JI, Torcida Fernández-Baldor F, Maisch MW, Huerta P, Contreras R. 2011. A tall-spined ornithopod dinosaur from the Early

Cretaceous of Salas de los Infantes (Burgos, Spain). *Comptes Rendus Palevol* **10**:551–558 DOI 10.1016/j.crpv.2011.04.003.

Pereda-Suberbiola X, Torcida F, Izquierdo LA, Huerta P, Montero D, Pérez G. 2003. First rebbachisaurid dinosaur (Sauropoda, Diplodocoidea) from the early Cretaceous of Spain: palaeobiogeographical implications. *Bulletin de la Societé Géologique de France* **174**:471–479 DOI 10.2113/174.5.471.

Pérez-García A, Murelaga X, Huerta P, Torcida Fernández-Baldor F. 2011. Turtles from the lower Cretaceous of the Cameros Basin (Iberian Range, Spain). *Cretaceous Research* **33**:146–158 DOI 10.1016/j.cretres.2011.09.011.

Platt NH. 1989. Continental sedimentation in an evolving rift basin: the lower Cretaceous of the western Cameros Basin (northern Spain). *Sedimentary Geology* **64**:91–109 DOI 10.1016/0037-0738(89)90086-9.

Poropat SF, Mannion PD, Upchurch P, Hocknull SA, Kear BP, Elliot DA. 2015a. Reassessment of the non-titanosaurian somphospondylian *Wintonotitan wattsi* (Dinosauria: Sauropoda: Titanosauriformes) from the mid-Cretaceous Winton Formation, Queensaland, Australia. *Papers in Palaeontology* **1**:59–106 DOI 10.1002/spp2.1004.

Poropat SF, Mannion PD, Upchurch P, Hocknull SA, Kear BP, Kundrát M, Tischler TT, Sloan T, Sinapius GHK, Elliott JA, Elliott DA. 2016. New Australian sauropods shed light on Cretaceous dinosaur palaeobiogeography. *Scientific Reports* **6**:34467 DOI 10.1038/srep34467.

Poropat SF, Upchurch P, Mannion PD, Hocknull SA, Kear BP, Sloan T, Sinapius GHK, Elliott DA. 2015b. Revision of the sauropod dinosaur *Diamantinasaurus matildae* Hocknull et al. 2009 from the mid-Cretaceous of Australia: implications for Gondwanan titanosauriform dispersal. *Gondwana Research* **27**:995–1033 DOI 10.1016/j.gr.2014.03.014.

Powell JE. 1987. Morfología del esqueleto axial de los dinosaurios titanosáuridos (Saurischia, Sauropoda) del estado de Minas Gerais, Brasil. *Annais do X Congreso Brasileiro de Paleontologia* 55–171.

Powell JE, Sanz JL, Buscalioni A. 1992. Osteología de *Saltasaurus loricatus* (Sauropoda-Titanosauridae) del Cretácico Superior del Noroeste argentino. *Actas del Segundo Curso de Paleontología en Cuenca Los Dinosaurios y su Entorno Biótico* 166–230.

Rauhut OWM, Remes K, Fechner R, Cladera G, Puerta P. 2005. Discovery of a short-necked sauropod dinosaur from the Late Jurassic period of Patagonia. *Nature* **435**:670–672 DOI 10.1038/nature03623.

Rose PJ. 2007. A new titanosauriform sauropod (Dinosauria: Saurischia) from the Early Cretaceous of central Texas and its phylogenetic relationships. *Palaeontologia Electronica* **10**:8A.

Royo-Torres R. 2009. *El Saurópodo de Peñarroya de Tastavins*. Teruel: Instituto de Estudios Turolenses and Conjunto Paleontológico de Teruel-Dinópolis.

Royo-Torres R, Alcalá L, Cobos A. 2012. A new specimen of the Cretaceous sauropod *Tastavinsaurus sanzi* from El Castellar (Teruel, Spain), and a phylogenetic analysis of the Laurasiformes. *Cretaceous Research* **34**:61–83 DOI 10.1016/j.cretres.2011.10.005.

Royo-Torres R, Upchurch P, Mannion PD, Mas R, Cobos A, Gascó F. 2014. The anatomy, phylogenetic relationships, and stratigraphic position of the Tithonian–Berriasian Spanish sauropod dinosaur *Aragosaurus ischiaticus*. *Zoological Journal of the Linnean Society* **171**:623–655 DOI 10.1111/zoj.12144.

Salas R, Casas A. 1993. Mesozoic extensional tectonics, stratigraphy and crustal evolution during the Alpine cycle of the eastern Iberian basin. *Tectonophysics* **228**:33–55 DOI 10.1016/0040-1951(93)90213-4.

Salas R, Guimerà J, Mas R, Martín-Closas C, Meléndez A, Alonso A. 2001. Evolution of the Mesozoic central Iberian Rift System and its Cainozoic inversion (Iberian chain). *Mémoires du Muséum National d'Histoire Naturelle, Peri-Tethys Memories* **6**:145–185.

Salgado L, Apesteguía S, Heredia SE. 2005. A new specimen of *Neuquensaurus australis*, a Late Cretaceous saltasaurine titanosaur from North Patagonia. *Journal of Vertebrate Paleontology* **25**:623–634 DOI 10.1671/0272-4634(2005)025[0623:ansona]2.0.co;2.

Salgado L, Azpilicueta C. 2000. Un nuevo saltasaurino (Sauropoda, Titanosauridae) de la provincia de Río Negro (Formacion Allen, Cretácico superior), Patagonia, Argentina. *Ameghiniana* **37(3)**:259–264.

Salgado L, Canudo JI, Garrido AC, Carballido JL. 2012. Evidence of gregariousness in rebbachisaurids (Dinosauria, Sauropoda, Diplodocoidea) from the Early Cretaceous of Neuquén (Rayoso Formation), Patagonia, Argentina. *Journal of Vertebrate Paleontology* **32**:603–613 DOI 10.1080/02724634.2012.661004.

Salgado L, Coria RA. 2009. *Barrosasaurus casamiquelai* gen. et sp. nov., a new titanosaur (Dinosauria, Sauropoda) from the Anacleto Formation (Late Cretaceous: early Campanian) of Sierra Barrosa (Neuquén, Argentina). *Zootaxa* **2222**:e16 DOI 10.5281/zenodo.190129.

Salgado L, Coria RA, Calvo JO. 1997. Evolution of titanosaurid sauropods. 1: Phylogenetic analysis based on the postcranial evidence. *Ameghiniana* **34**:3–32.

Salgado L, García R, Daza J. 2006. Consideraciones sobre las láminas neurales de los dinosaurios saurópodos y su significado morfofuncional. *Revista del Museo Argentino de Ciencias Naturales, Nueva Serie* **8**:69–79 DOI 10.22179/revmacn.8.360.

Salgado L, Garrido A, Cocca SE, Cocca JR. 2004. Lower Cretaceous rebbachisaurid sauropods from Cerro Aguada del León (Lohan Cura Formation), Neuquén Province, northwestern Patagonia, Argentina. *Journal of Vertebrate Paleontology* **24**:903–912 DOI 10.1671/0272-4634(2004)024[0903:LCRSFC]2.0.CO;2.

Salgado L, Powell JE. 2010. Reassessment of the vertebral laminae in some South American titanosaurian sauropods. *Journal of Vertebrate Paleontology* **30**:1760–1772 DOI 10.1080/02724634.2010.520783.

Sanz JL. 1983. A nodosaurid ankylosaur from the lower Cretaceous of Salas de los Infantes (Province of Burgos, Spain). *Geobios* **16**:615–621 DOI 10.1016/S0016-6995(83)80038-2.

Sanz JL, Buscalioni AD, Casanovas ML, Santafé JV. 1987. Dinosaurios del Cretácico inferior de Galve (Teruel, España). *Estudios Geológicos* **43**:45–64 DOI 10.3989/egeol.8743Extra62.

Sanz JL, Powell JE, Le Loeuff J, Martínez R, Pereda-Suberbiola X. 1999. Sauropod remains from the upper Cretaceous of Laño (Northcentral Spain). Titanosaur phylogenetic relationships. *Estudios del Museo de Ciencias Naturales de Alava* **14**:235–255.

Schudack U, Schudack M. 2009. Ostracod biostratigraphy in the lower Cretaceous of the Iberian chain (eastern Spain). *Journal of Iberian Geology* **35**:141–168.

Seeley HG. 1887. On the classification of the fossil animals commonly named Dinosauria. *Proceedings of the Royal Society of London* **43**:165–171.

Templeton AR. 1983. Phylogenetic inference from restriction endonuclease cleavage site maps with particular reference to the evolution of humans and the apes. *Evolution* **37**:221–244 DOI 10.2307/2408332.

Tidwell V, Carpenter K, Meyer S. 2001. New titanosauriform (Sauropoda) from the poison strip member of the cedar mountain formation (lower Cretaceous), Utah. In: Tanke DH, Carpenter K, eds. *Mesozoic Vertebrate Life*. Bloomington: Indiana University Press, 137–165.

Torcida Fernández-Baldor F. 2006. Restos directos de dinosaurios en Burgos (Sistema Ibérico): un balance provisional. In: Torcida Fernández-Baldor F, Huerta P coord, eds. *Actas de las III Jornadas Internacionales Sobre Paleontología de Dinosaurios y su Entorno*. Salas de los Infantes: Colectivo Arqueológico y Paleontológico de Salas, 105–128.

Torcida Fernández-Baldor F. 2012. *Sistemática, Filogenia y Análisis Paleobiogeográfico de Demandasaurus darwini (Sauropoda, Rebbachisauridae) del Barremiense Superior-Aptiense de Burgos (España)*. Salas de los Infantes: Museo de Dinosaurios de Salas de los Infantes.

Torcida Fernández-Baldor F, Canudo JI, Huerta P, Izquierdo Montero LA, Montero Huerta D, Contreras Izquierdo R, Pérez Martínez G, Urién Montero V. 2009. Primeros datos sobre las vértebras caudales del saurópodo de El Oterillo II (Formación Castrillo de la Reina, Barremiense superior-Aptiense, Cretácico Inferior, Salas de los Infantes, España). In: Torcida Fernández-Baldor F, Huerta P, eds. *Actas de las IV Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno*. Salas de los Infantes: Colectivo Arqueológico y Paleontológico de Salas, 311–319.

Torcida Fernández-Baldor F, Canudo JI, Huerta P, Montero D, Suberbiola XP, Salgado L. 2011. *Demandasaurus darwini*, a new rebbachisaurid sauropod from the Early Cretaceous of the Iberian Peninsula. *Acta Palaeontologica Polonica* **56**:535–552 DOI 10.4202/app.2010.0003.

Torcida Fernández-Baldor F, Contreras-Izquierdo R, Huerta P, Montero Huerta D, Pérez-Martínez G, Urién Montero V. 2008. Un dinosaurio ornitópodo de gran talla en el tránsito Jurásico-Cretácico de Burgos (España). *Studia Geologica Salmanticensia* **8**:85–94.

Torcida Fernández-Baldor F, Díaz-Martínez I, Contreras R, Huerta P, Montero D, Urién V. 2015. Unusual sauropod tracks in the Jurassic–Cretaceous transition. Cameros Basin (Burgos, Spain). *Journal of Iberian Geology* **41**:141–154 DOI 10.5209/rev_JIGE.2015.v41.n1.48660.

Torcida Fernández-Baldor F, Ruiz-Omeñaca JI, Izquierdo Montero L, Montero Huerta D, Huerta Hurtado P, Urién Montero V. 2005. Dientes de un enigmático dinosaurio ornitópodo en el Cretácico Inferior de Burgos (España). *Revista Española de Paleontología* **10**:73–81.

Upchurch P. 1998. The phylogenetic relationships of sauropod dinosaurs. *Zoological Journal of Linnean Society* **124**:43–103 DOI 10.1111/j.1096-3642.1998.tb00569.x.

Upchurch P, Barrett PM, Dodson P. 2004. Sauropoda. In: Weishampel DB, Dodson P, Osmolska H, eds. *The Dinosauria*. Second Edition. Berkeley: University of California Press, 259–322.

Upchurch P, Martin J. 2003. The anatomy and taxonomy of *Cetiosaurus* (Saurischia, Sauropoda) from the Middle Jurassic of England. *Journal of Vertebrate Paleontology* **23**:208–231 DOI 10.1671/0272-4634(2003)23[208:TAATOC]2.0.CO;2.

Upchurch P, Mannion PD, Taylor MP. 2015. The Anatomy and Phylogenetic Relationships of "*Pelorosaurus*" *becklesii* (Neosauropoda, Macronaria) from the Early Cretaceous of England. *PLoS ONE* **10(6)**:e0125819 DOI 10.1371/journal.pone.0125819.

Vila B, Galobart À, Canudo JI, Le Loeuff J, Dinarès-Turell J, Riera V, Oms O, Tortosa T, Gaete R. 2012. The diversity of sauropod dinosaurs and their first taxonomic succession from the latest Cretaceous of southwestern Europe: clues to demise and extinction. *Palaeogeography Palaeoclimatology Palaeoecology* **350**:19–38 DOI 10.1016/j.palaeo.2012.06.008.

Wedel MJ. 2003. Vertebral pneumaticity, air sacs, and the physiology of sauropod dinosaurs. *Paleobiology* **29**:243–255 DOI 10.1017/s0094837300018091.

Wedel MJ, Cifelli R, Sanders K. 2000a. *Sauroposeidon proteles*, a new sauropod from the Early Cretaceous of Oklahoma. *Journal of Vertebrate Paleontology* **20**:109–114 DOI 10.1671/0272-4634(2000)020[0109:spansf]2.0.co;2.

Wedel MJ, Cifelli R, Sanders K. 2000b. Osteology, paleobiology, and relationships of the sauropod dinosaur *Sauroposeidon. Acta Palaeontologica Polonica* **45**:343–388.

Wilson JA. 1999. A nomenclature for vertebral laminae in sauropods and other saurischian dinosaurs. *Journal of Vertebrate Paleontology* **19**:639–653 DOI 10.1080/02724634.1999.10011178.

Wilson JA. 2002. Sauropod dinosaur phylogeny: critique and cladistic analysis. *Zoological Journal of Linnean Society* **136**:215–275 DOI 10.1046/j.1096-3642.2002.00029.

Wilson JA, Allain R. 2015. Osteology of *Rebbachisaurus garasbae* Lavocat, 1954, a diplodocoid (Dinosauria, Sauropoda) from the Early Late Cretaceous-aged Kem Kem beds of southeastern Morocco. *Journal of Vertebrate Paleontology* **35**:e1000701 DOI 10.1080/02724634.2014.1000701.

Wilson JA, D'Emic MD, Ikejiri T, Moacdieh E, Whitlock JA. 2011. A nomenclature for vertebral fossae in sauropods and other saurischian dinosaurs. *PLoS ONE* **6**:e17114 DOI 10.1371/journal.pone.0017114.

Wilson JA, Sereno PC. 1998. Early evolution and higher-level phylogeny of sauropod dinosaurs. *Journal of Vertebrate Paleontology* **18**:1–79 DOI 10.1080/02724634.1998.10011115.

Wilson JA, Upchurch P. 2009. Redescription and reassessment of the phylogenetic affinities of *Euhelopus zdanskyi* (Dinosauria: Sauropoda) from the Early Cretaceous of China. *Journal of Systematic Palaeontology* **7**:199–239 DOI 10.1017/S1477201908002691.

You HL, Li DQ. 2009. The first well-preserved Early Cretaceous brachiosaurid dinosaur in Asia. *Proceedings of the Royal Society B* **276(1065)**:4077–4082 DOI 10.1098/rspb.2009.1278.

You H, Li D, Zhou L, Ji Q. 2008. *Daxiatitan binglingi*: a giant sauropod dinosaur from the Early Cretaceous of China. *Gansu Geology* **17**:1–10.

Young CC. 1935. Dinosaurian remains from Mengyin, Shantung. *Bulletin of Geological Society of China* **14**:519–534 DOI 10.1111/j.1755-6724.1935.mp14004004.x.

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