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New contributions to the phylogenetic position of the sauropod *Galvesaurus herreroi* from the late Kimmeridgian-early Tithonian (Jurassic) of Teruel (Spain)

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ABSTRACT

Galvesaurus herreroi is a sauropod from the Villar del Arzobispo Formation (late Kimmeridgian-early Tithonian), from the municipality of Galve (Teruel). Its phylogenetic relations have been long debated, so we carried out a phylogenetic analysis, using a new data matrix recently published by Carballido *et al.* (2017). The characters of *Galvesaurus* were coded on the basis of the redescription of the published remains and the description of two unpublished fossils: a right coracoid and a fragment of the right pubis. The results of the analysis suggest the inclusion of *Galvesaurus* in the clade Titanosauriformes, as a sister taxon to *Lusotitan*, these two taxa form part of the Brachiosauridae clade. Likewise, a stratigraphic study was undertaken, placing the *Galvesaurus* site in the lower part of the Villar del Arzobispo Formation, thus assigning the sauropod a late Kimmeridgian-early Tithonian age.

Keywords: Brachiosauridae, cladistics, Iberian Range, Kimmeridgian, sauropods.

Nuevas aportaciones a la posición filogenética del saurópodo **Galvesaurus herreroi** *del Kimmeridgiense superior-Titoniense inferior (Jurásico) de Teruel (España)*

RESUMEN

Galvesaurus herreroi *es un saurópodo recuperado en la Formación Villar del Arzobispo (Kimmeridgiense superior-Titoniense inferior), del término municipal de Galve (Teruel). Sus relaciones filogenéticas han sido largamente discutidas, para dar solución a este problema se ha llevado a cabo un análisis filogenético, con nuevos datos y usando una moderna propuesta filogenética (Carballido* et al.*, 2017). Los caracteres de* Galvesaurus *se han codificado basándose en la redescripción de los restos publicados y en la descripción de dos fósiles inéditos: el coracoides derecho y un fragmento del pubis derecho. Los resultados del análisis inducen a proponer la inclusión de* Galvesaurus *en el clado Titanosauriformes, como taxón hermano de* Lusotitan, *y siendo incluidos ambos dentro de Brachiosauridae. Así mismo, se ha realizado un estudio estratigráfico que sitúa el yacimiento de* Galvesaurus *en la parte baja de la Formación Villar del Arzobispo, asignándole al saurópodo una edad Kimmeridgiense superior-Titoniense inferior.*

Palabras clave: Brachiosauridae, cladística, Cordillera Ibérica, Kimmeridgiense, Sauropoda.

Introduction and background

The continental Jurassic-Cretaceous boundary is characterized by a faunal turnover in the vertebrate fossil record, especially among large-sized terrestrial vertebrates such as dinosaurs (Bakker, 1998; Barret *et al.*, 2009; Tennant *et al.*, 2017). This interval of transition led to a renewal of dinosaur faunas, resulting in the emergence of the main groups of dinosaurs that characterized the Cretaceous. However, there are still many gaps in what is known about this question, so every new discovery sheds light on the issue.

The Iberian Range is one of the places in the world where the transition between the Jurassic and the Cretaceous is exemplified by the associated vertebrate remains (Aurell *et al.*, 2016). In this area, vast outcrops of transitional-continental formations can be found, traditionally representing the deposits of the uppermost Jurassic and the transition to the Lower Cretaceous (Aurell *et al.*, 1994; Mas *et al.*, 2004). These formations are rich in vertebrate fossils and dinosaur tracks, with remains of ornithopods, thyreophorans, sauropods and theropods. Amongst the discoveries, a few stand out, such as the stegosaur *Dacentrurus* (Cobos *et al.*, 2010), theropods (Canudo *et al.*, 2006), and the sauropods *Losillasaurus*, *Turiasaurus* and *Galvesaurus* (Casanovas *et al.*, 2001; Royo-Torres *et al.*, 2006; Barco *et al.*, 2005). These findings are complemented by a rich record of dinosaur tracks, including tracks belonging to ornithopods (Castanera *et al.*, 2013), thyreophorans (Cobos *et al.*, 2010) sauropods (Castanera *et al.*, 2011) and theropods (Cobos *et al.*, 2014).

The sauropod *Galvesaurus* in itself raises a number of questions. Beyond its problematic definition with different names (for further references see Barco *et al.*, 2012), this sauropod has had an unstable phylogenetic position within the clade Sauropoda. *Galvesaurus* has been located both inside and outside the clade Neosauropoda in different research. Barco (2005, 2009, 2010), Carballido *et al.* (2011) Barco and Canudo (2012) classify *Galvesaurus* as a macronarian neosauropod, whereas Sánchez-Hernández (2005) included it in Cetiosauridae (as a non-neosauropod eusauropod). Furthermore, Royo-Torres *et al.* (2006) classify it as Turiasauria, meanwhile D'Emic (2012) considers *Galvesaurus* as a putative titanosauriform, with possible brachiosaurid affinities. Finally, Mocho *et al.*, (2017) also recovered *Galvesaurus* as putative brachiosaurid, and consider it to be particularly difficult to distinguish *Galvesaurus* from *Lusotitan*, and they do not exclude the possibility of *Galvesaurus herreroi* being a junior synonymous of *Lusotitan atalaiensis.* The phylogenetic position of *Galvesaurus* has shown a high degree of uncertainty, since the skeleton was not complete and the area of the cladogram where *Galvesaurus* is situated has been characterized by low stability due to the scarcity of basal neosauropods. During the last decade, important advances have been made in what is known of the basal neosauropods as a result of the study of new taxa, which has allowed the resolution in this part of the cladogram to be improved (e.g. *Europasaurus,* Sander *et al.*, 2006; *Lourinhasaurus*, Mocho *et al.*, 2014; *Padillasaurus*; Carbadillo *et al.*, 2015). We have also studied unpublished material from the type specimen of *Galvesaurus*, which has helped us to fill some of the gaps in the matrix of characters.

Moreover, the age of *Galvesaurus* has been too unstable, due to the fact that that the stratigraphic position of its type locality has never been located with enough resolution (Barco, 2009; Royo-Torres *et al.,* 2009), and the age of Villar del Arzobispo Fm. has been widely discussed (Aurell *et al.*, 2016; Campos-Soto *et al.*, 2017; Val *et al.*, 2018). Therefore, a detailed stratigraphic study was needed in order to fix the stratigraphic position of *Galvesaurus* in the most recent chronostratigraphic proposal (Val *et al.*, 2018). For all these reasons, the main objective of this study was to carry out a new phylogenetic analysis for *Galvesaurus herreroi* with an updated matrix (Carballido *et al.*, 2017), in order to clarify its phylogenetic relationships and unearth its palaeobiogeographic implications.

Geographical and geological setting

The holotype of *Galvesaurus herreroi* was found in the area around the village of Galve, in the central part of the province of Teruel, NE Spain (Fig. 1A). The site where the *Galvesaurus* fossils were discovered, "Cuesta Lonsal-1" (CL), is located around half a kilometre west of Galve (Fig. 1B). Geologically, the Cuesta Lonsal-1 site is located in the western limb of the Galve syncline, a N-S oriented fold, made up of marine, transitional and continental deposits from the Late Jurassic to Early Cretaceous (Díaz-Molina and Yébenes, 1987; Soria, 1997; Aurell *et al.*, 2016). This syncline is part of the Galve sub-basin, and is situated in its northwest area (Fig. 2A). Along with six other sub-basins, this sub-basin makes up the Mesozoic Maestrazgo Basin (Salas *et al.*, 2001).

The 'Cuesta Lonsal-1' site is included within the Villar del Arzobispo Fm. (Aurell *et al.*, 2016), which, along with the overlying Aguilar del Alfambra Fm.,

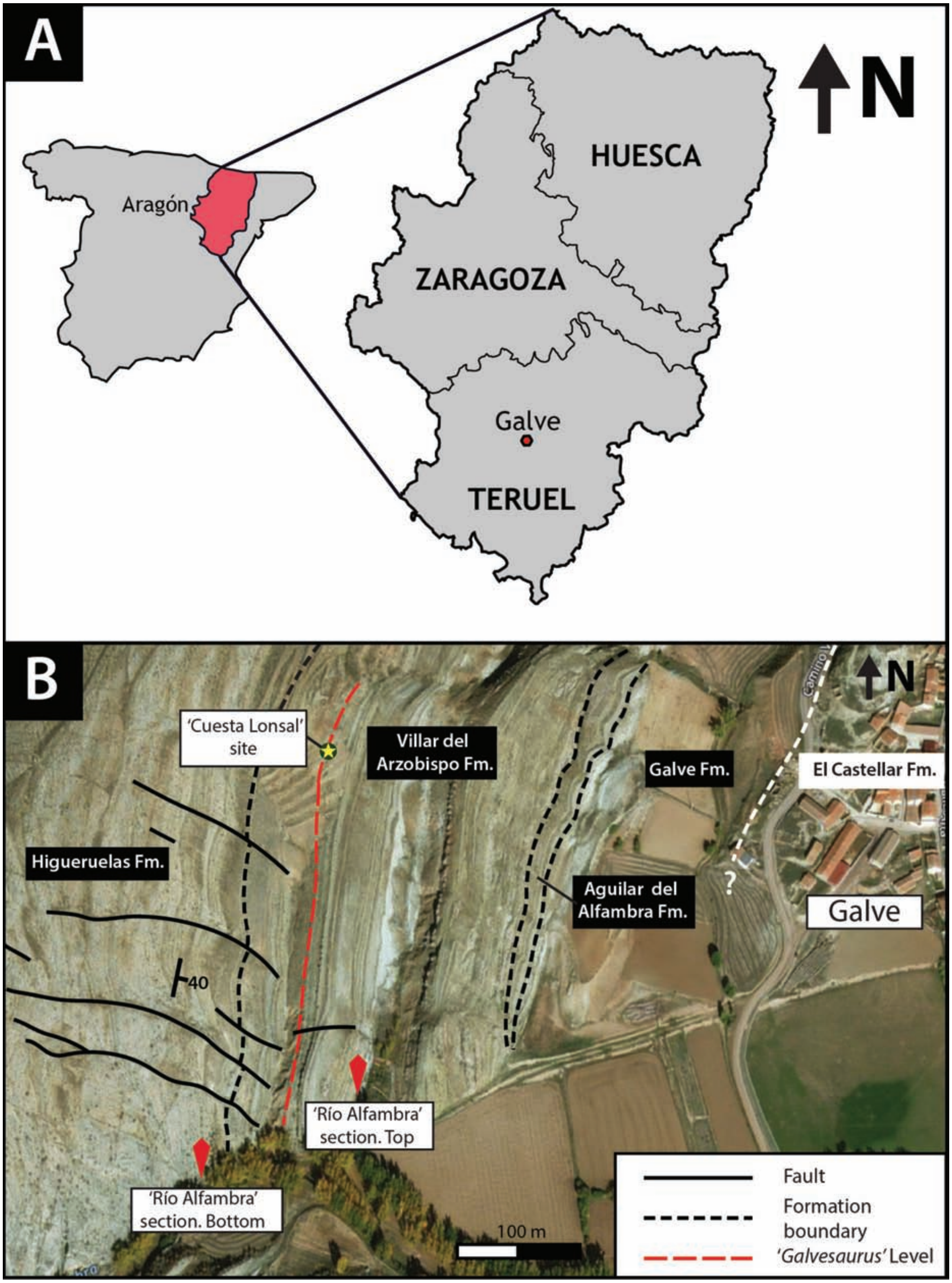


Figure 1. A) Geographic location of Galve (Teruel). B) Detailed aerial photo of the outcrops situated WSW of Galve, where the fossils were found (available in https://www.bing.com/maps).

Figura 1. *Situación geográfica de Galve (Teruel). B) Foto aérea detallada de los afloramientos situados al OSO de Galve, donde fueron hallados los fósiles (disponible en https://www.bing.com/maps).*

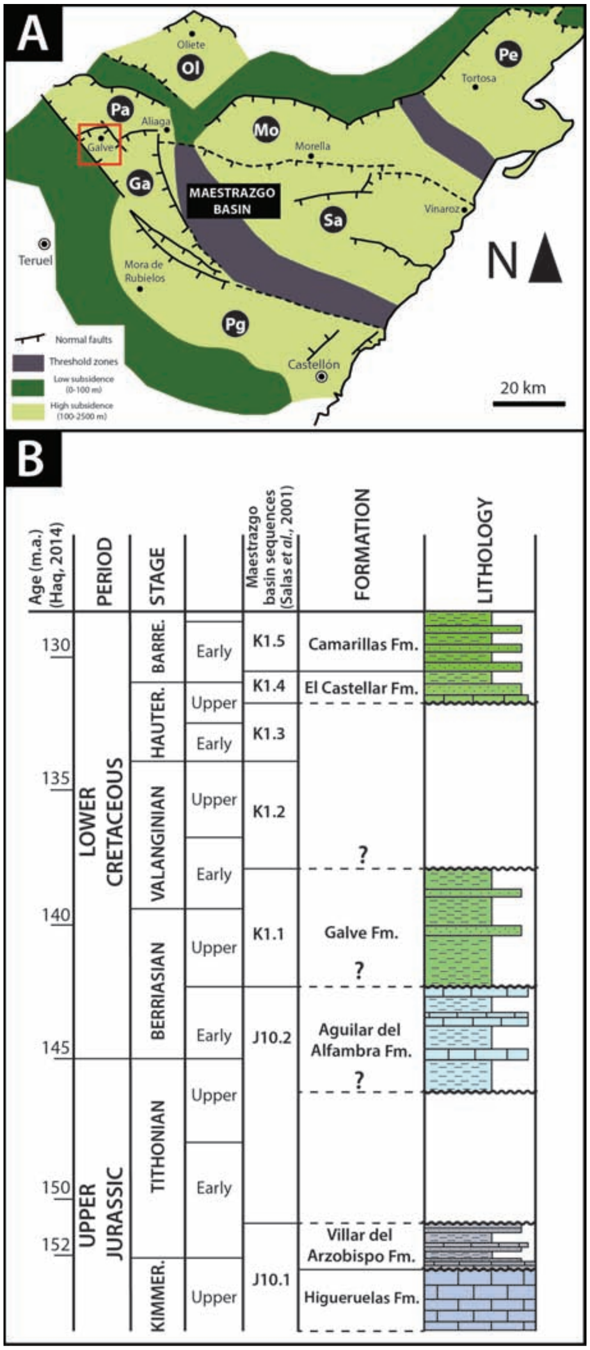


Figure 2. A) Palaeogeography of Maestrazgo sedimentary basin and its main sub-basins during the Lower Cretaceous (Ga, Galve; Mo, Morella; Ol, Oliete; Pa, Las Parras; Pe, Perelló; Pg, Peñagolosa; Sa, Salzedella). Modified from Salas *et al.* (2001) and Aurell *et al.* (2016). B) Synthetic stratigraphy of the Jurassic-Cretaceous boundary succession recorded in the depocentral areas of the Galve sub-basin. Adapted from Aurell *et al.* (2016).

Figura 2. *A) Paleogeografía de la cuenca sedimentaria del Maestrazgo y sus principales subcuencas durante el Cretácico Inferior (Ga, Galve; Mo, Morella; Ol, Oliete; Pa, Las Parras; Pe, Perelló; Pg, Peñagolosa; Sa, Salzedella). Modificado de Salas* et al. *(2001) y Aurell* et al. *(2016). B) Estratigrafía sintética de la sucesión del límite Jurásico-Cretácico registrada en los depocentros de la subcuenca de Galve. Adaptado de Aurell* et al. *(2016).*

corresponds to the *Purbeck* facies, which represent the Tithonian-Berriasian sequence (J10) of the basin (Salas *et al.*, 2001) (Fig. 2B). The Villar del Arzobispo Fm. is constituted by an alternation of carbonate, sandy and muddy levels, representing a wide set of transitional depositional environments (Díaz-Molina *et al.*, 1984; Aurell *et al.*, 1994). The limestone is both peloidal and grain-supported, corresponding to lagoon and carbonate tidal-flat deposits (Díaz-Molina and Yébenes, 1987; Aurell *et al.*, 2016), whereas the terrigenous deposits represent delta and delta-plain environments with a marked fluvial influence (Díaz-Molina and Yébenes, 1987; Barco, 2009). In Galve, the Villar del Arzobispo Fm. is limited by two low-angle erosive unconformities as its lower and upper boundaries (Canudo *et al.*, 2012; Aurell *et al.*, 2016), being situated between the Jurassic marine Higueruelas Fm. and the transitional Early Cretaceous Aguilar del Alfambra Fm. (Fig. 2B).

Material and methods

Institutional abbreviations

The fossils studied in this paper are housed in the Museo Paleontológico de Galve (CL, CLH), in the Museo de Ciencias Naturales de la Universidad de Zaragoza (MPZ, see Canudo, 2018) and in the Gobierno de Aragón (GAL).

Anatomical nomenclature

For the description of the bones, 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 *et al.* (2005) and Wilson *et al.* (2011). The nomenclature for the vertebral pneumatic structures follows Wedel (2003) and Wilson *et al.* (2011).

For this study, the existing *Galvesaurus* remains were re-examined. A broad description of these bones is to be found in various articles (Barco, 2005; Barco *et al.*, 2005, 2006; Barco and Canudo, 2012) and especially in the doctoral thesis of Barco (2009). In this study, these descriptions were reviewed and updated, noting those aspects that were relevant for the phylogenetic analysis. In addition, some *Galvesaurus* bones were studied for the first time: the right coracoid (CL-CBC-908) and a distal part of the right pubis (GAL01/CL/150).

The phylogenetic position of *Galvesaurus* was analysed using the data matrix of Carballido *et al.* (2017) with modifications from Canudo *et al.* (2018). The data matrix was constructed using Mesquite V. 3.31 (Maddison and Maddison, 2017). This matrix has 412 characters coded for 90 sauropod taxa. For *Galvesaurus,* 153 characters were coded, 37% of the total. We also recoded *Lusotitan atalaiensis*, taking into account the new description and recently published data (Mannion *et al.*, 2013; Mocho *et al.*, 2017). Information on the data matrix and the modifications in the characters of *Lusotitan* are included in Appendix 1.

An equally weighted parsimony analysis was carried out using TNT v.1.5 (Goloboff and Catalano, 2016), a heuristic tree search was performed, starting from 1000 replicates of Wagner trees followed by TBR branch swapping and holding 10 trees per replication. This was followed with an additional round of tree bisection and reconnection (TBR) and Branch support was assessed with Bremer decay index and a 1000 replicates of standard bootstrap analysis.

A stratigraphic section ('Río Alfambra' section, RA) was studied (Fig. 1B, Fig. 3) in order to fix the position of the *Galvesaurus* site and other fossil vertebrate sites within the Villar del Arzobispo Fm. Thus, the age of these sites was calibrated with the new chronostratigraphic frame proposed by Aurell *et al.* (2016).

Results

Detailed stratigraphy

The 'Río Alfambra'(RA) log encompasses a stratigraphic section of approximately 65 m (Fig. 3). This stratigraphic section encompasses the last levels of the Higueruelas Fm. and the lower part of the Villar del Arzobispo Fm. (Fig. 1B and 3). Log bottom coordinates are UTM 30T 0678370 4502169 and top coordinates are 30T 0678491 4502218, with WGS84 datum. The layers show a general strike and dip of 035, 40 SE (Fig. 1B).

The RA section is characterized by an alternation of carbonate and terrigenous beds. The top of the Higueruelas Fm. consists of several peloidal-bioclastic limestones, with occasional quartz grains. On at least two of these levels, dinosaur tracks have been recognized. The tracks situated in the uppermost level of the formation (Fig. 3) correspond to the site 'Ríos Bajos' studied by Pérez-Lorente and Romero-Molina (2001), who identify them as being produced by theropod dinosaurs.

The Villar del Arzobispo Fm. begins with an alternation of fine-grained limestone, marls and ochre mudstones, which is culminated by a bioturbated sandstone bed with cross-bedding. Above this bed, a set of peloidal-bioclastic limestone can be recognized, with several beds bearing vertebrate bones (Fig. 3). The limestone is followed by a detritic section of about 14 m, constituted by a thick succession of reddish and greenish mudstones, with several sandstone levels intercalating. The uppermost sandstone level (Fig. 3), has a channelized base and shows trough cross-bedding, microconglomerate lags and bioturbation. At the base of this level, large sauropod tracks have been described (Castanera *et al.*, 2010). Furthermore, the type locality (CL) of *Galvesaurus*, situated between the top of the sandstone level and the overlying grey mudstone, with fossils having been recovered from both levels (Barco, 2009). This level corresponds to the top of sequence S1 of the Villar del Arzobispo *sensu* Val *et al.* (2018, Fig. 3).

The succession continues with another carbonated interval of peloidal limestone and marls with occasional microconglomerate levels, and mudstone and marl beds with root bioturbations (Fig. 3). Occasionally, isolated tracks can be observed in some of the limestone levels. A short detritic interval overlies the above-mentioned carbonated levels, comprising a thick sandstone bed with cross-bedding, and a much thinner mudstone and sandstone alternation. These are overlaid by a new set of limestone, bearing several vertebrate remains, including bones and tracks. The last level of this succession of fine-grained limestone corresponds to the level of 'El Cantalar', where sauropod and theropod tracks were described by Pérez-Lorente and Herrero-Gascón (2007).

Palaeontological study

Systematic paleontology
DINOSAURIA Owen, 1842
SAURISCHIA Seeley, 1887
SAUROPODOMORPHA Huene, 1932
SAUROPODA Marsh, 1878
NEOSAUROPODA Bonaparte 1986
TITANOSAURIFORMES Salgado *et al.*, *1997*
BRACHIOSAURIDAE Riggs, 1904

Genus *Galvesaurus* Barco, Canudo, Cuenca-Bescós and Ruiz-Omeñaca, 2005

Type species: *Galvesaurus herreroi* Barco, Canudo, Cuenca-Bescós and Ruiz-Omeñaca, 2005
Holotype: A dorsal vertebra (CLH-16); figured in Pérez-Oñate *et al.*, 1994: Fig. 2; Cuenca-Bescós *et al.*,

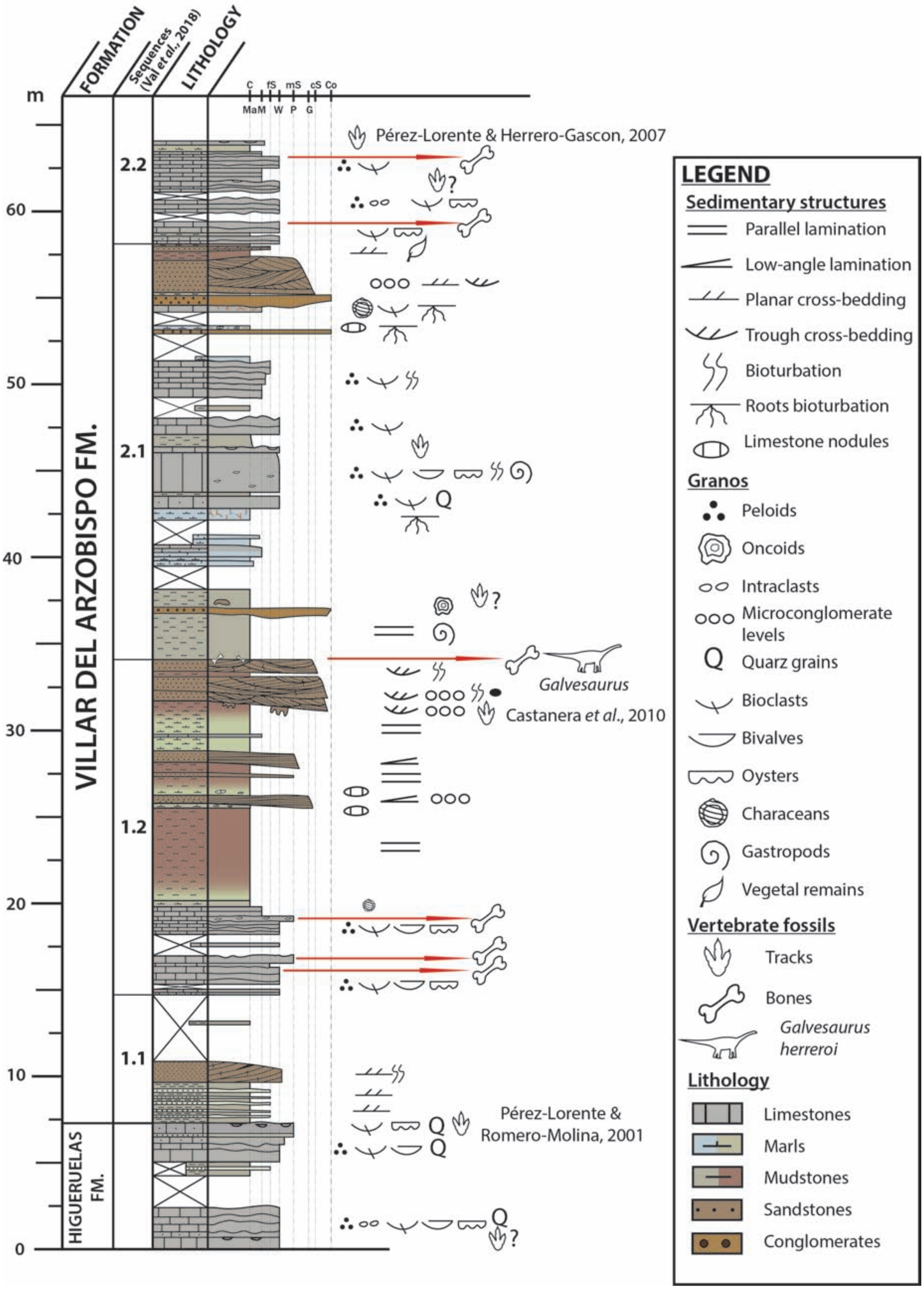


Figure 3. Stratigraphic section 'Río Alfambra' (RA), with the main fossil sites.
Figura 3*. Sección estratigrafía 'Río Alfambra' (RA), con los principales yacimientos de fósiles.*

1997: Fig. 3; Barco, 2003: Figs. 34-43, 44c; 1; Barco, 2005: Fig. 3c; lams. 1, 2; Barco *et al.*, 2005: Fig. 11; Sánchez-Hernández, 2005: Fig. 2; Barco, 2009: Fig. 4.3.1; Barco and Canudo, 2012: Fig. 2).

Paratype: 4 cervical vertebrae (CL-2; GAL00/CL/48; CL (CBC) 15-4; MPZ-2003/884); 2 cervical ribs (GAL00/CL/60; GAL00/CL/181); 3 dorsal spines (CL-JMH; GAL00/CL/86; GAL00/CL/62); a sacrum (GAL01/CL/90); 2 dorsal ribs (CLH-5; GAL01/CL/102) and a dorsal rib fragments (; CLH-22); 6 caudal vertebrae (CLH-8; CLH-15; GAL00/CL/35; CLH; CL (CBC)-31 two fused vertebrae); a haemal arch (without an acronym, fused to CL(CBC)-31); right scapula (CLH-14); both humeri (CLH-1 right, CLH-4 left); right ischium (CLH-6); and a sternal plate (CLH-7).

Assigned material: a fragment of the right coracoid fragment (CL-CBC-908), a fragment of the right pubis (GAL01/CL/150).

Description

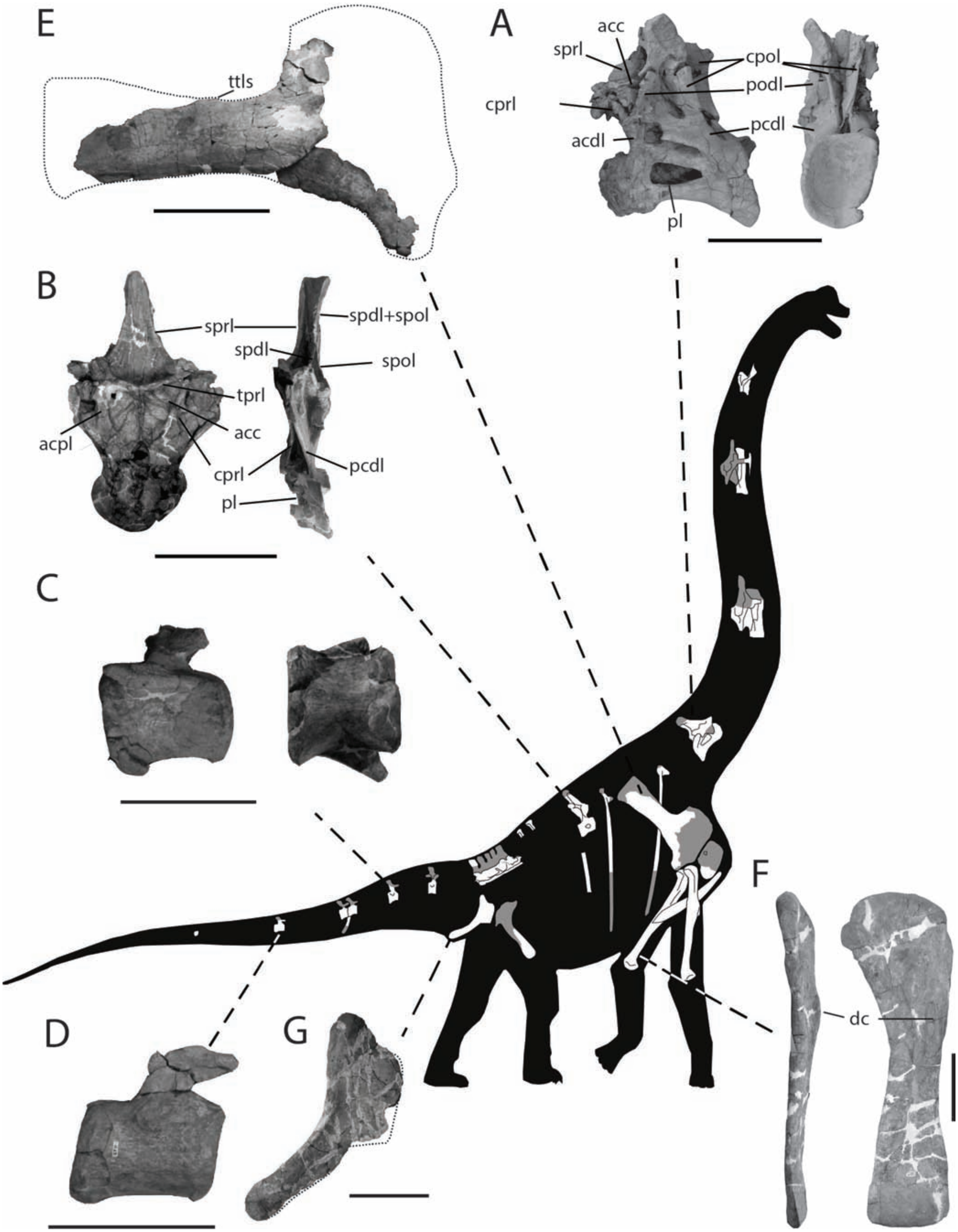
Galvesaurus is represented by an incomplete specimen, lacking any cranial remains and with only a few vertebrae preserved (4 cervical, 1 dorsal, 1 sacrum and 6 caudal). Barco *et al.* (2005) and Barco (2009) provide an extended description of the bones. Here we only describe as succinctly as possible those elements that have been reinterpreted and are relevant for the cladistics analysis.

The cervical vertebrae are generally poorly preserved, usually with the neural arch and the spine eroded, so that the description is based on CL-2, which is the best-preserved vertebra. CL-2 could be situated between the tenth and the thirteenth position (Barco, 2009) (Fig. 4A). The centrum of CL-2 is opisthocoelous, and subcircular in section. It is elongated anteroposteriorly, though not very markedly, with an elongation index aEI (after Chure *et al.*, 2010) of 1.77 (Table 1). Ventrally, the centrum shows a groove limited to the middle part. It also presents pleurocoels in its lateral faces, drop-shaped (Fig. 4A) and divided by a thin lamina, which marks an anterior and a posterior excavation; this division is also observed in GAL00/CL/48 centrum. Internally, it shows strongly-developed pneumaticity, divided internally into camerae and camellae. The neural arch of the vertebra possesses a well-developed system of laminae (Fig. 4A), as shown by all the eusauropods (Wilson, 2002). These laminae include: anterior centrodiapophyseal (acdl) and posterior centrodiapophyseal (pcdl), centroprezygapophyseal (cprl), which are divided dorsally into lateral and medial cprl, intraprezygapophyseal (tprl), centropostzygapophyseal (cpol), prezygodiapophyseal (podl, postzygodiapophyseal (podl) and spinoprezygapophyseal (sprl). Acdl and pcdl are the only laminae that connect the neural arch with the centrum, the rest of the laminae being connected directly with them instead of the centrum. An accessory lamina connects podl with sprl, delimiting a narrow and deep fossa between the two laminae (Fig. 4A). The neural spine is short and simple, even though the distal end is eroded, and is situated above the central part of the centrum. Middle cervical vertebrae as GAL00/CL/48 and MPZ-2003/884, are more elongated than CL-2, having the first one a aEI of 4.23 for its centrum (Table 1). The cervical ribs associated with GAL00/CL/48 do not go beyond the caudal margin of the centrum, having a higher projection towards that margin than towards the cranial margin.

The only dorsal vertebra preserved is CLH-16, which corresponds to middle dorsal (fifth to seventh) (Barco, 2009). It is notably more developed lateromedially than anteroposteriorly (Fig. 4B). Although the anterior surface of the centrum is eroded, it can be described as opisthocoelous. It is shortened anterioposteriorly, with an aEI amounting to 0.67 (after Chure *et al.,* 2010) (Table 1). The centrum presents a small pleurocoel in its left-lateral surface, with an angular dorsal margin. Internally, moreover, the centrum is practically hollow, with just one thin lamina in the middle part (Fig. 4B), so it can be defined as cam-

	Length of centrum	**Posterior surface width of centrum**	**Height of centrum**	**E. I. (Chure *et al.* 2010)**
Cervical CL-2	36.6 cm	19.5 cm	22 cm	1.77
Cervical GAL00/CL/48	62 cm	18.7 cm	12 cm	4.23
Dorsal CLH-16	10.8 cm	20.8 cm	15.8 cm	0.67

Table 1. Relevant measures of the cervical and dorsal vertebrae of *Galvesaurus*.
Tabla 1. *Principales medidas de las vértebras cervicales y dorsales de* Galvesaurus.


E
ttls
A
acc
sprl
cprl
cpol
podl
pcdl
acdl
pl
B
sprl
spdl+spol
spdl
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tprl
acc
acpl
cprl
pcdl
pl
C
F
dc
D
G

erate. The neural arch constitutes at least two-thirds of the height of the vertebra, and shows a well-marked lateromedial expansion (Fig. 4B). Like the cervical vertebrae, it has a well-developed system of laminae (Fig. 4B), comprising: anterior centrodiapophyseal (acdl) and posterior centrodiapophyseal (pcdl), anterior centroparapophyseal (acpl) intraprezygapophyseal (tprl), centroprezygapophyseal (cprl), prezygodiapophyseal (prdl), prezygoparapophyseal (prpl), centropostzygapophyseal (cpol), spinoprezygapophyseal (sprl), spinopostzygapophyseal (spol) and spinodiapophyseal (spdl). Tprl and cprl are connected with one another by an accessory lamina (Fig. 4B). The vertebra has a rhomboidal hyposphene in its posterior face, but no hypantrum. The neural spine shows two fossae delimited by the laminae spdl and sprl and lacks triangular aliform processes. However, the dorsal spines CL-JMH and GAL/00/CL/62, which correspond to posterior dorsal vertebrae, do have triangular "aliform" processes. Dorsal ribs are none of them totally complete, lacking a well-preserved proximal part, although it seems that they were not pneumatized. In cross-section, anterior ribs (GAL/00/CL/102) show a plank-like shape, meanwhile those in a posterior position have subtriangular cross-section (CLH-22).

The sacrum is made up of five fused vertebrae, cylindrical in shape, slightly opisthocoelous, and lacking pleurocoels. The transverse processes of the vertebrae are connected with one another by the laminae prdl and podl, which form a practically continuous lamina. The neural spines are eroded, except the spine of S5, which preserves its distal end, albeit disarticulated from the rest of the spine. This allows a length of 28 cm to be estimated for the spine of S5, which is around 2.33 times more than the length of the centrum (~12 cm). The sacral ribs are connected at their distal ends by a sacricostal yoke, which presents in its ventral margin a shallow concavity between S1 and S4. This can be interpreted as the contribution to the acetabulum of the sacrum.

The caudal centra preserved correspond to anterior and middle vertebrae (Fig. 4C and D). All of them are solid, without pneumatic cavities or pleurocoels. Their anterior and posterior articular faces are slightly concave, so they are amphicoelous. Their ventral surface is convex transversely, and they have well-marked chevron facets (Fig. 4C), except CLH, which is one of the posterior middle vertebrae. The transverse processes are triangular in shape, developing in a middle position on the dorsal margin of the centrum. Their ventral surface is oriented slightly ventrally, whereas the dorsal surface is flat. The neural arches are simple, without laminae, located in the anterior part of the centra in the anterior vertebrae, migrating slightly towards the posterior in the middle vertebrae. No neural spines are preserved. The only haemal arch preserved lacks a crus bridging its dorsal margin, and the haemal canal would constitute approximately a quarter of the total length of the haemal arch.

Only the right scapula of *Galvesaurus* was found. This was poorly preserved, having lost a great part of the proximal lamina and the distal part of the scapular blade (Fig. 4). The acromion process is broad, being at least twice as wide as the blade, and its dorsal margin is concave. Due to the poor preservation of the proximal lamina, we estimated the orientation of the coracoid articulation and the glenoid (Fig. 4E). The scapular blade shows a slight dorsoventral expansion and has a 'D-shaped' transverse section. Its dorsal margin presents a small tubercle (Fig. 4E), which corresponds to the insertion of the *trapezius* and *levator scapulae* muscles (Meers, 2003). The right coracoid is poorly preserved, with only its cranioventral margin preserved, which is convex and has a subrounded contour. This suggests a rounded shape for

Figure 4. *Galvesaurus herreroi* skeletal reconstruction based on the holotype. A) Middle cervical vertebra in lateral and posterior view. B) Middle dorsal vertebra in anterior and lateral view. C) Anterior caudal vertebra in lateral and ventral view. D) Middle caudal vertebra in lateral view. E) Right scapula in lateral view. F) Left humerus in lateral and anterior view. G) Right ischium in lateral view. Scale bar: 30 cm, except in C and D, which measure 15 cm. Grey represents parts of the bones not preserved. Abbreviations: acc: accessory lamina, acdl: anterior centrodiapophyseal lamina, acpl: centroparapophyseal cpol: centropostzygapophyseal lamina, cprl: centroprezygapophyseal lamina, dc: deltopectoral crest, pcdl: posterior centrodiapophyseal lamina, podl: postzygodiapophyseal lamina, pl: pleurocoel, spdl: spinodiapophyseal lamina, spol: spinopostzygapophyseal lamina, sprl: spinoprezygapophyseal lamina, tprl: intraprezygapophyseal lamina, ttls: trapezius and levator scapulae tubercle.

Figura 4*. Reconstrucción del esqueleto de* Galvesaurus herreroi *basada en el holotipo. A) Vértebra cervical media en vistas lateral y posterior. B) Vértebra dorsal media en vistas anterior y lateral. C) Vértebra caudal anterior en vistas lateral y ventral. D) Vértebra caudal media en vista lateral. E). Escápula derecha en vista lateral. F) Húmero izquierdo en vista lateral y anterior. G) Isquion derecho en vista lateral. La barra de escala equivale a 30 cm, excepto en C y D, que equivale a 15 cm. El color gris representa partes de los huesos no preservadas. Abreviaturas: acc: lámina accesoria, acdl: lámina centrodiapofisial anterior, acpl: lámina centroparapofisial, cpol; lámina centropostzigapofisial, cprl: lámina centroprezigapofisial, dc: cresta deltopectoral, pcdl: lámina centrodiapofisial posterior, podl: lámina postzigapofisial, pl: pleurocelo, spdl: lámina espinodiapofisial, spol: lámina espinopostzigapofisial, sprl: lámina espinoprezigapofisial, tprl: lámina intraprezigapofisial, ttls: tubérculo del trapezius y levator scapulae.*

the coracoid (Fig. 4). There is also a sternal plate that is oval in shape, with the posterolateral margin curved. It has a maximum anteroposterior length of 64 cm, yielding a ratio to the length of the humerus of 0.45, which is less than the 0.75 typical of somphospondylan sauropods (Upchurch *et al.*, 2004).

The humerus has a generally straight shape, with an elliptical midshaft cross-section (Fig. 4F). The proximomedial corner has a notch that somewhat resembles the *triosseum* foramen of birds' humerus and that has been observed in other sauropods, such as *Tehuelchesaurus* (Carballido *et al.*, 2011). The deltopectoral crest is narrow, and is limited to the proximolateral margin of the humerus, developing only up to the middle part of the diaphysis (Fig. 4F). The articular surface of the condyles is restricted to the distal portion of the humerus. They are slender humeri, with an RI (*sensu* Wilson and Upchurch, 2003) of 0.25.

Regarding the pelvic girdle, the right ischium is almost complete (Fig. 4G) and 65 cm in length, with a proximal shaft trapezoidal in shape, with the pubic and iliac peduncles constraining the acetabular articulation, which keeps the same transverse width throughout its length. The iliac peduncle is triangular in shape, but does not show any constriction, whereas the pubic peduncle shows a partially rectangular shape, since it is somewhat eroded. The ischial blade is elongated and narrow; its distal end is not expanded (Fig. 4G). It articulates with the proximal shaft at an angle of about 100°, which indicates that the juncture of the ischial blades of both ischia would be almost coplanar. The right pubis is only represented by the distal end of the pubic shaft, which is not expanded and is 40 cm in length. On the basis of this length, we estimate a total length for the pubis of between 95-100 cm, which would equal 145% of the length of the ischium.

Phylogenetic analysis

The phylogenetic analysis resulted in 50000 most parsimonious trees (MPTs) with a length of 1380 steps, CI = 0.360 and RI = 0.718.

In all the trees *Galvesaurus* is recovered within Titanosauriformes, as a sister taxon of *Lusotitan*, together constituting a sister clade to the others Brachiosauridae, (Fig. 5). The characters that allow *Galvesaurus* to be included within Titanosauriformes are: i) a length/height ratio of the posterior articular surface of the middle cervical vertebrae higher than 4 (C142: 1); ii) scapula with the acromion process lying nearly at glenoid level (C283: 0); iii) gracile humerus (with an RI less than 0.27, *sensu* Wilson and Upchurch, 2003) (C304: 0); and iv) pubis larger (+120%) than ischium (C334: 1). The clade Brachiosauridae (*Galvesaurus+Lusotitan+*more derived Brachiosauridae) is supported by the following characters: i) Anterior and middle dorsal vertebrae with zygapophyseal articulation horizofig.ntal or slightly posteroventrally oriented (C171:0), ii) Neural spine of anterior dorsal vertebrae with a minimums width / length lower than 0.5 (C174:1), iii) Middle and posterior dorsal vertebrae neural spine with triangular aliform processes present and project far laterally (as far as caudal zygapophyses) (C196:2). In addition, according to this phylogenetic hypothesis, the characters that could be diagnostic of *Galvesaurus* within the latter clade would be: i) middle and posterior dorsal centrum strongly compressed in transverse section (with a ratio of the height to the width below 0.8) (C195: 2); ii) sacral vertebral centra without pleurocoels in their lateral surfaces (C219: 0); and iii) amphicoelous anterior caudal centra (C231: 0). A list of the synapomorphies that characterize the clades relevant to *Galvesaurus* is provided in Appendix 2.

Discussion

Age of Galvesaurus

Previous research attributed *Galvesaurus* to a Tithonian-Berriasian age (Barco *et al.*, 2005; Royo-Torres *et al.*, 2009). However, Aurell *et al.* (2016) date the Villar del Arzobispo Fm. as middle-upper Tithonian by the presence of benthic foraminifer *Anchispirocyclina lusitanica,* and the absence of the middle Berriasian charophyte *Globator maillardii incrassatus*, which it is present in the overlaying Aguilar del Alfambra Fm. Recently Campos-Soto *et al.* (2017) consider Villar del Arzobispo Fm. as late Kimmeridgian in age, based on the presence of benthic foraminifer *Alveosepta jaccardi-personata,* although this dating was performed in the Penyagolosa sub-basin. Posteriorly, Val *et al.* (2018), found this foraminifer in the lower part of Villar del Arzobispo Fm. in Galve sub-basin, with its presence being limited to sequence S1. Thus, S1 corresponds to latest Kimmeridgian, whereas the rest of the formation would date as early Tithonian. Besides, ^{87}Sr/^{86}Sr isotope data confirm the dating, giving the formation a time span from 152.5 to 151 Ma.

As we have determined, the *Galvesaurus* site is situated in the lower part of the formation in question, just at the top of sequence S1 (Fig. 3), which means that this sauropod can be ascribed to the latest Kimmeridgian-Early Tithonian, with an estimated

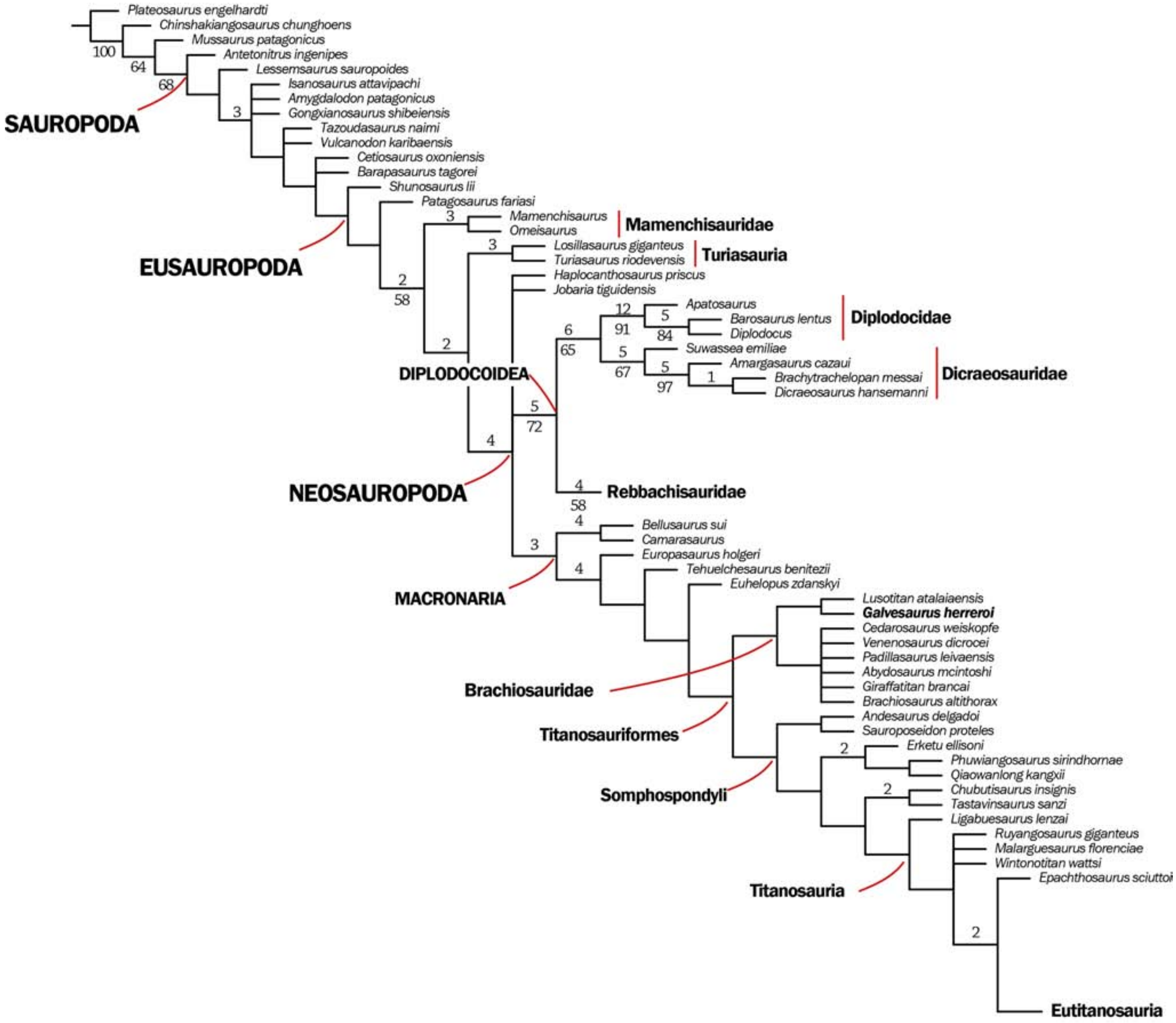

Figure 5. Strict consensus tree of the 50,000 most parsimonious trees (MPTs). Numbers over nodes represent Bremer supports over 2. Numbers below branches represent bootstrap values over 50 after a thousand replications.

***Figura 5.** Árbol de consenso estricto de los 50000 árboles más parsimoniosos (MPTs). Los números sobre los nodos representan soportes de Bremer con valores por encima de 2. Los números bajos las ramas representan valores de bootstrap por encima de 50 después de mil replicaciones.*

occurrence span of 1.5 Ma. This delimits and narrows the temporal range of *Galvesaurus* to the Upper Jurassic, ruling out its presence during the Early Cretaceous.

Phylogenetic position of Galvesaurus *and its palaeobiogeographic implications*

Neosauropoda is an extensive clade defined above all by cranial characters, as well as others from the carpals, astragalus and tibia (Wilson and Sereno, 1998; Upchurch *et al.*, 2004), elements that are not preserved in *Galvesaurus*. However, *Galvesaurus* shares several characters that allow it to be included within this clade. These characters are the presence of deep pleurocoels in the presacral vertebrae; cervical pleurocoels divided by a septum; five or more sacral vertebrae; the anterior position of the neural arches in the middle caudal vertebrae; the lack of a crus bridging in the haemal arches; and ischia that present a distal end with a flattened (almost coplanar) section.

Macronaria is defined mainly by cranial and metacarpal characters (Wilson and Sereno, 1998; Wilson, 2002; Upchurch *et al.*, 2004). Once again, the incompleteness of the *Galvesaurus* skeleton hampers its inclusion in this clade. Nevertheless, *Galvesaurus* shares some features that allow us to include it in Macronaria, such as the presence of triangular 'aliform' processes in the neural spines of the middle and posterior dorsal vertebrae. This character is also present in some derived eusauropods, such as *Omeisaurus* or *Turiasaurus*, but in Neosauropoda it is only present in Macronaria, since it disappears in Diplodocoidea. A synapomorphy of Macronaria is also opisthocoelous centra in posterior dorsal vertebrae with, even though in some titanosauriforms this character is less developed. For *Galvesaurus*, this character is inferred from the shape of the first sacral centrum, which is slightly opisthocoelous.

Galvesaurus has several characteristics that support its inclusion in Titanosauriformes, such as the presence of camellae in presacral vertebrae (Wedel, 2003),having compressed caudal centra (Mocho *et al.*, 2017), the anterior position of the neural arch in the middle caudal vertebrae (Salgado *et al.*, 1997; D'Emic, 2012), the posterior orientation of the haemal arches, and anterior dorsal ribs with a plank-like cross-section (Wilson, 2002), although the latter is absent in basal macronarians such as *Camarasaurus,* which has a sub-circular section. There are also several synapomorphies of Titanosauriformes that are unknown in *Galvesaurus* due to the incompleteness of its remains, as well as a few that are not shared by *Galvesaurus*, such as the presence of proximal pneumatic cavities in the dorsal ribs (Wilson and Sereno, 1998), although the ribs preserved in *Galvesaurus* are scarce and there is no proximal part that is well preserved. However, we think that the evidence that supports its inclusion is stronger. This includes the results of other phylogenetic analyses, such as the one performed by D'Emic (2012) on Titanosauriformes, in which the author considers *Galvesaurus* to be a possible member of this clade.

It is important to note that *Galvesaurus* and *Lusotitan atalaiensis* (Lusitanian basin, Portugal, Kimmeridgian-Tithonian in age)*,* form a clade sister to all other Brachiosauridae, with which they share some affinities. Brachiosauridae is defined by Wilson and Sereno (1998) as the most inclusive clade that includes *Brachiosaurus altithorax* but excludes *Saltasaurus loricatus*. The synapomorphies that characterize this clade according to Wilson and Sereno (1998) are: i) subrectangular muzzle (twice as long as wide, ii) elongate cervical centra (reaching a maximum of seven times as long as wide), iii) centra with deep accessory depressions, iv) elongate humerus (subequal to the femur in length); and v) humerus with prominent deltopectoral crest. *Galvesaurus* complies with the characters related to cervicals, has a gracile humerus (but we cannot compare its length with the femur), but it does not have such a prominent deltopectoral crest as *s.s.* Brachiosauridae. Furthermore, a rounded dorsolateral corner in the humerus and an abbreviated pubic peduncle in the ischium, as shown by *Galvesaurus*, are considered by D'Emic (2012) to be synapomorphies of Brachiosauridae.

Galvesaurus and *Lusotitan* appear in the analysis as sister taxa, defined by two synapomorphies: i) the middle to posterior dorsal vertebrae have pleurocoels with their dorsal margin angular (C188: 1), and ii) the posterior dorsal centra have slightly opisthocoelous articular faces (C207: 1). Mocho *et al.* (2017) also described as similarities the presence of dorsoventrally compressed caudal vertebrae, the anterior displacement of the neural arches in the middle caudal vertebrae, the absence of a lateral groove in the ischium, and a dorsoventrally restricted deltopectoral crest. For this reason, Mocho *et al.*, (2017) consider arduous to differentiate *Galvesaurus* from *Lusototitan*, and they do not exclude the possibility of both taxa being synonymous. However, we have recognized several characters displayed by *Galvesaurus* that are not shared with *Lusotitan* and are relevant as phylogenetic characters (Fig. 6): such as the absence of pneumatic foramina in sacral centra (present in *Lusotitan*); flat ventral surface of the sacral centra (whereas *Lusotitan* presents a keel-like structure on its ventral surface; and slender pubic shaft, without a marked distal expansion (*Lusotitan* pubis has a circular expansion).

For all the reasons expounded above, we consider *Galvesaurus* to be a brachiosaurid sauropod, with great affinities with *Lusotitan*, but constituting different taxa, and with both of them being basal forms of the clade Brachiosauridae. However, we consider this hypothesis to be fallible since both sauropods are rather incomplete, relative low support of all clades in this region of the cladogram (Fig. 5) and hence there is a lack of data, especially in relation to cranial characters. Thus, this hypothesis needs to be tested with new, more complete specimens.

The Titanosauriformes was a widespread group of sauropods that probably appeared at the end of the Middle Jurassic (D'Emic, 2012) and extended across Europe, Gondwana and North America in the Late Jurassic (Fig. 7), although it seems that they did not reach Asia until the Early Cretaceous (Wilson and Upchurch, 2009; D'Emic, 2012). The inclusion of

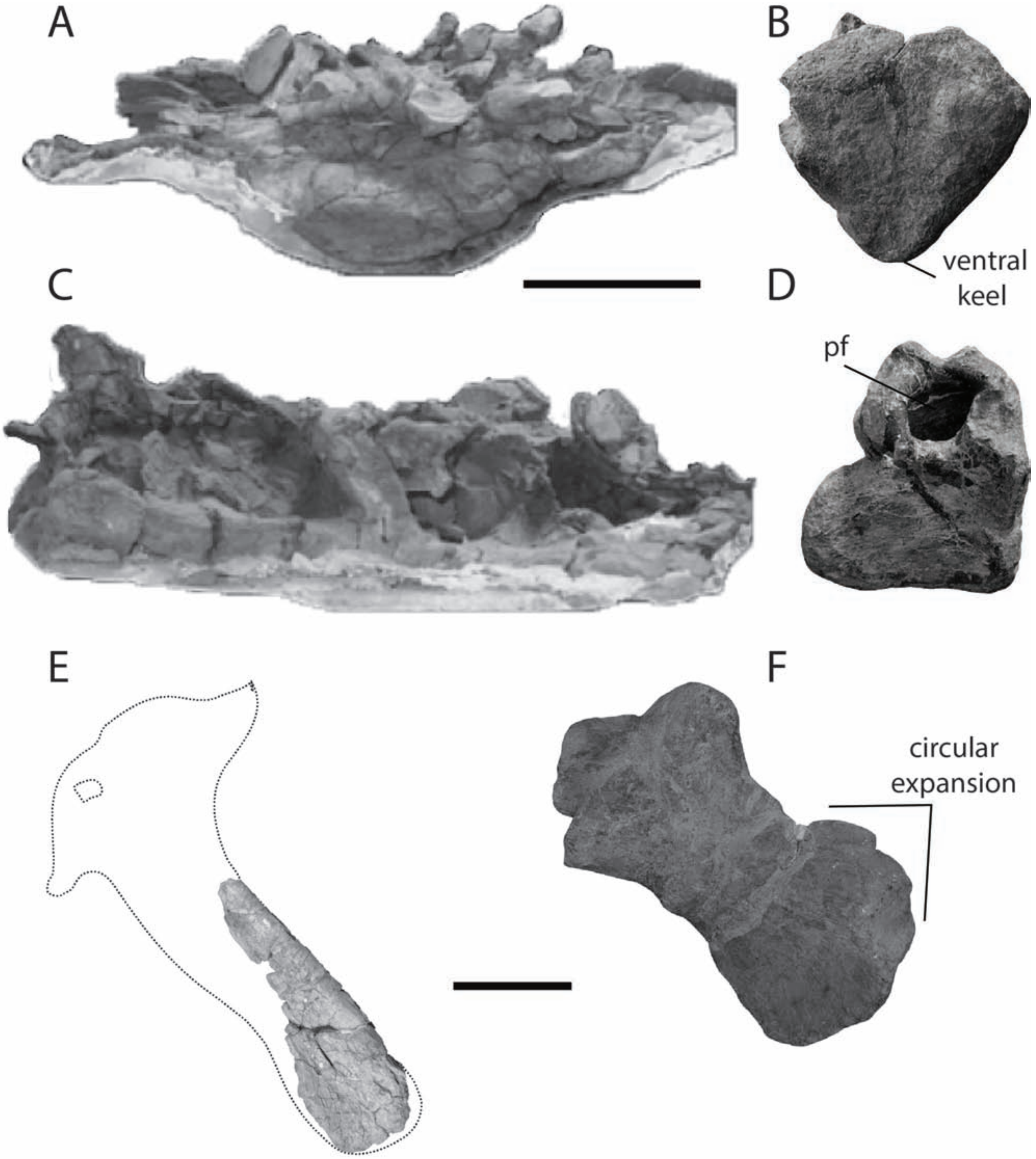

Figure 6. Comparison of the distinctive elements between *Galvesaurus* and *Lusotitan*. Sacrum of *Galvesaurus* (A, C) and sacral vertebra of *Lusotitan* (B, D) in anterior and right lateral view. Note the flat ventral surface in A and the absence of pneumatic foramen in C, whereas B shows a keel ventrally and D has pneumatic foramina. Right pubis of *Galvesaurus* (E) and left pubis of *Lusotitan* (F) in lateral view (F is a mirrored view, to resemble the right pubis). Note the slender pubic shaft of E, whilst F shows a circular expansion. Bones of *Lusotitan* modified from Mocho *et al.* (2018). Scale bar equals 15 cm for sacra and 20 cm for pubes. Pf: pneumatic foramen.

***Figura 6**. Comparación de los elementos distintivos entre* Galvesaurus *y* Lusotitan*. Sacro de* Galvesaurus *(A, C) y vértebra sacra de* Lusotitan *(B, D) en vistas anterior y lateral derecha. Nótese la superficie ventral plana en A y la ausencia de foramen neumático en C, mientras que B muestra una quilla ventral y D tiene un foramen neumático. Pubis derecho de* Galvesaurus *(E) y pubis izquierdo de* Lusotitan *(F) en vista lateral (F es una vista reflejada, para representar al pubis derecho). Obsérvese la delgada rama púbica de E, mientras que F muestra una expansión circular. Huesos de* Lusotitan *modificados de Mocho* et al. *(2018). La barra de escala equivale a 15 cm para los sacros y 20 cm para los pubis. Pf: foramen neumático.*

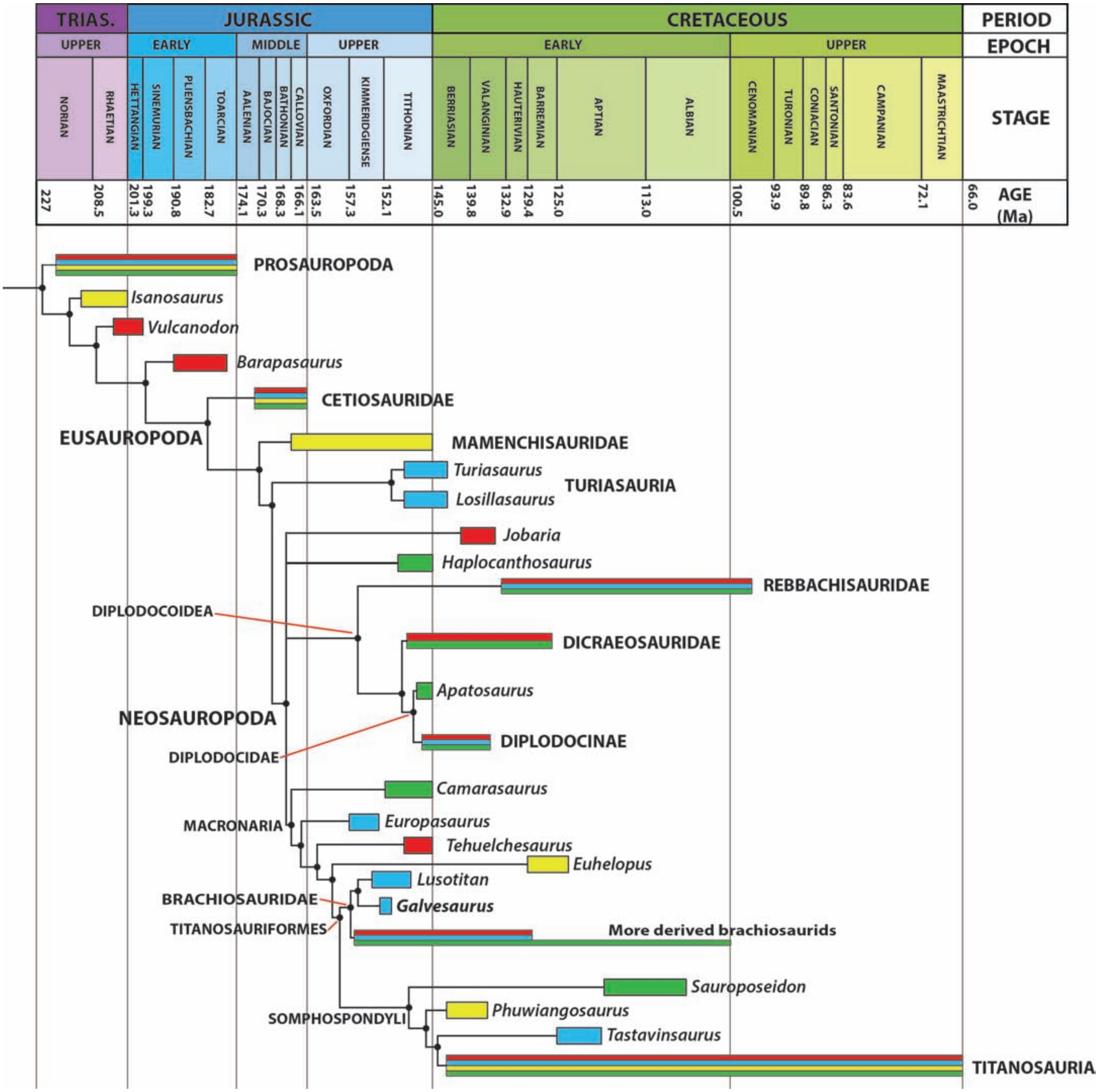

Figure 7. Time-calibrated phylogeny showing the temporal range and palaeobiogeography of the main clades of the sauropods (green = North America; blue = Europe; red = Gondwana; yellow = Asia). Ages taken from IUGS (2018).

Figura 7. *Filogenia calibrada temporalmente, mostrando el intervalo temporal y la paleobiogeografía de los principales clados de saurópodos (verde = Norte América; azul = Europa; rojo = Gondwana; amarillo = Asia). Edades tomadas de IUGS (2018).*

Galvesaurus in Brachiosauridae (Fig. 7) sheds new light on the abundance of this group and of titanosauriform sauropods in Iberia during the Late Jurassic. Titanosauriformes is represented during the Tithonian by the brachiosaurids *Galvesaurus* and *Lusotitan*, and there are also several teeth (Rauhut, 2000, Royo-Torres *et al*., 2014) and a femur (Canudo *et al*., 2010) that could be assigned to Titanosauriformes. This femur could correspond to one of the two already-defined taxa, or belong to a new one, because it is the only Jurassic femur of a titanosauriform from Iberia. Contemporaneously, there were other groups of sauropods during the Tithonian, such as the turiasaurs *Turiasaurus, Losillasaurus* (Royo-Torres *et al*., 2009) and *Zby* (Mateus *et al*., 2012), the non-titanosauriform macronarian *Lourinhasaurus* (Mocho *et al*., 2014) and the diplodocid *Dinheirosaurus* (Antunes and Mateus, 2003). Within this great diversity, there are sauropods during Late Jurassic that show a certain endemism to Iberia, as turiasaurs, though they extend to North America during Early Cretaceous (Royo-Torres *et al*., 2017b), whereas other forms have a wider distribution, as diplodocids or brachiosaurids. The latter appear during the Middle Jurassic and flourish during the Late Jurassic, with members in North America (*Brachiosaurus,* Riggs, 1903), Africa (*Giraffatitan*, Janensch, 1914) and Europe (*Europasaurus*, Carballido and Sander, 2014; *Lusotitan,* Mocho *et al*., 2016; and *Galvesaurus*), and dubious presence in South America (Mannion *et al*., 2017). This almost global presence continues during Early Cretaceous, with several brachiosaurids in North America (Mannion *et al*., 2017) and Africa (McPhee *et al.,* 2016). In Europe, they are only represented by the Iberian brachiosaurid *Soriatitan* (Royo-Torres *et al*., 2017a).

Conclusions

Galvesaurus herreroi was a brachiosaurid titanosauriform sauropod from the latest Kimmeridgian to early Tithonian (1.5 Ma time span) of the Maestrazgo Basin of Spain. This position is supported by the review of the paratype and the description of new, unpublished material, namely a right coracoid and a fragment of the right pubis and the recalibration of the age range of Villar del Arzobispo Fm. in the Galve sub-basin.

Galvesaurus herreroi is recovered as a sister taxon of *Lusotitan atalaiensis*, from the Kimmeridgian-Tithonian of the Lusitanian basin. This clade is supported by the angular dorsal margin of the pleurocoels of the dorsal vertebrae and an opistocoelic sacrum. This phylogenetic position confirms the presence of titanosauriform sauropods in the Upper Jurassic of Spain, previously known only from fragmentary remains, and supports a closer relation between the faunas of the Maestrazgo and Lusitanian basins.

Hence, we can conclude that at least two different species of brachiosaurids inhabited the transitional environments of Iberia during the Kimmeridgian-Tithonian, in a highly diverse sauropod ecosystem with North America and/or Gondwana influences, and endemic particularities. Nevertheless, the incompleteness of *Galvesaurus* leaves a degree of uncertainty in the matter. Further discoveries will help to confirm or change our hypothesis.

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Appendix 1

Galvesaurus herreroi scoring for Carballido *et al.* (2017) data matrix

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?????????? ?????????? ?01112210? 010012??0? 111000?0?0
?0?-?10?11 1110-01?11 0001112?0? 011000110? 0110221001
11110?10?1 1012110?0? 0??2???010 0000?00100 ?0000?—-0
001000??0? 000?????1? ??11????01 1000?1?0?0 000000001?
10100100?? ?????????? ?????????? ???1???000 01011000??
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???????00? 0?

Changes on *Lusotitan atalaienses* codification in Carballido *et al.* (2017) data matrix

136 (2 ?), 161 (? 1), 178 (? 1), 189 (? 1), 195 (? 1), 207 (? 1), 219 (? 1), 299 (0 ?), 309 (? 1), 310 (? 1), 311 (? 1), 313 (? 0&1), 338 (? 1), 339 (? 0), 340 (? 0), 342 (? 1), 348 (0 1), 367 (? 0), 368 (? 1), 370 (? 0), 371 (? 1), 373 (? 1), 374 (? 1), 412 (? 1)

Appendix 2

Unambiguous synapomorphies for the main sauropod clades

Node 104, Neosauropoda: 171 (0 1), 246 (0 1), 363 (0 1), 376 (0 1).
Node 106, Macronaria: 93 (0 1), 96 (0 1), 157 (1 0), 174 (1 0), 207 (0 2), 320 (0 1), 321 (0 1), 337 (0 1), 342 (0 1), occasionally 165 (0 1), 283 (0 1).
Node 107, *Galvesaurus+Lusotitan*: 188 (0 1), 207 (2 1).
Node 108, Brachiosauridae (*Galvesaurus+Lusotitan+*other Brachiosauridae): 171 (1 0), 174 (0 1), 196 (1 2).
Node 109, Titanosauriformes: 18 (0 1), 100 (1 2), 106 (1 0), 109 (0 1), 142 (0 1), 195 (0 1) 283 (1 0), 304 (1 0), 334 (0 1), 355 (1 2), occasionally 353 (1 2).
Node 116, Somphospondyli: 178 (0 1), Char. 185 (0 1).
Node 117, more derived Brachiosauridae: 169 (1 0), 173 (0 2), 181 (0 1), 203 (1 0), 205 (0 1), 228 (0 1).
Node 121, Titanosauria: 163 (1 0), 166 (0 1).

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