

Historical Biology

An International Journal of Paleobiology

ISSN: (Print) (Online) Journal homepage: <https://www.tandfonline.com/loi/ghbi20>

A new titanosaur (Dinosauria: Sauropoda) from the Upper Cretaceous of Velaux-La-Bastide Neuve (southern France)

Verónica Díez Díaz , Géraldine Garcia , Xabier Pereda Suberbiola , Benjamin Jentgen-Ceschino , Koen Stein , Pascal Godefroit & Xavier Valentin

To cite this article: Verónica Díez Díaz , Géraldine Garcia , Xabier Pereda Suberbiola , Benjamin Jentgen-Ceschino , Koen Stein , Pascal Godefroit & Xavier Valentin (2020): A new titanosaur (Dinosauria: Sauropoda) from the Upper Cretaceous of Velaux-La-Bastide Neuve (southern France), *Historical Biology*, DOI: [10.1080/08912963.2020.1841184](https://doi.org/10.1080/08912963.2020.1841184)

To link to this article: <https://doi.org/10.1080/08912963.2020.1841184>



Published online: 21 Dec 2020.



Submit your article to this journal [↗](#)



View related articles [↗](#)



View Crossmark data [↗](#)



A new titanosaur (Dinosauria: Sauropoda) from the Upper Cretaceous of Velaux-La-Bastide Neuve (southern France)

Verónica Díez Díaz^{a,b}, Géraldine Garcia^c, Xabier Pereda Suberbiola^d, Benjamin Jentgen-Ceschino^{e,f}, Koen Stein^{e,g}, Pascal Godefroit^g and Xavier Valentin^{c,h}

^aMuseum für Naturkunde, Leibniz-Institut für Evolutions-und Biodiversitätsforschung, Berlin, Germany; ^bHumboldt Universität zu Berlin, Germany; ^cLaboratoire de Paléontologie, Evolution, Paléoécosystèmes et Paléoprimatologie (PALEVOPRIM, UMR 7262 CNRS INEE), Université de Poitiers, Poitiers cedex, France; ^dFacultad de Ciencia y Tecnología, Departamento de Geología, Universidad del País Vasco/Euskal Herriko Unibertsitatea, Bilbao, Spain; ^eEarth System Science – AMGC, Vrije Universiteit Brussel, Brussels, Belgium; ^fEvolution & Diversity Dynamics Lab, Liège University, Liège, Belgium; ^gDirectorate 'Earth and History of Life', Royal Belgian Institute of Natural Sciences, Brussels, Belgium; ^hPalaios Association, Valdivienne, France

ABSTRACT

Remains of *Garrigatitan meridionalis* nov. gen. et sp. were found in two bonebeds of sequence 2 from the upper Campanian site of Velaux-La Bastide Neuve (Aix-en-Provence Basin, Bouches du Rhône department). The vertebrate assemblage is dominated by dinosaurs, including the titanosaur *Atsinganosaurus velauciensis*. *Garrigatitan meridionalis* presents three diagnostic characters: hourglass-shaped humeri (proximal and distal thirds of almost the same transversal width) in anterior and posterior views, ilium with a broad rounded hollow slightly posterior to the base of the pubic peduncle, proximolateral margin of the femur only slightly medially deflected. *Garrigatitan* was a small to medium-sized sauropod (sub/adult individuals between 4–6 metres and 2–2.5 tonnes), showing anatomical differences with *Atsinganosaurus*, and with the other Late Cretaceous Ibero-Armorican titanosaurs. Large titanosaurian specimens found at Velaux-La Bastide Neuve could belong to adult *Garrigatitan* individuals reaching a body length of at least 12 metres. Histological analysis of long bones shows features similar to other Late Cretaceous European titanosaurs, indicating that all individuals had reached skeletal maturity (presence of an EFS, heavy remodelling HOS 12 to 14). The new taxon is recovered within the clade Lirainosaurinae. *Garrigatitan meridionalis* increases the diversity of Late Cretaceous titanosaurs within the Ibero-Armorican Island.

ARTICLE HISTORY

Received 19 August 2020
Accepted 20 October 2020

KEYWORDS

France; *Garrigatitan meridionalis*; Late Cretaceous; Lirainosaurinae; Sauropoda; Titanosauria

Introduction

Since the 19th Century, Late Cretaceous deposits from southeastern France have yielded titanosaurian sauropod fossils (see e.g. Matheron 1869; Lapparent 1947; Le Loeuff 1992; Buffetaut et al. 1999). Most of the fossil sites are located in Aude, Bouches-du-Rhône, Dordogne, Haute-Garonne, Hérault, and Var departments (see Díez Díaz 2013, CD6 supplementary file for more detailed information and references), but titanosaurian species have only been properly described from two sites: Bellevue (Aude department) and Velaux-La Bastide Neuve (Bouches-du-Rhône). *Ampelosaurus ataxis* was described from the lower Maastrichtian of Bellevue, in Campagne-sur-Aude (Le Loeuff 1995, 2005a), and *Atsinganosaurus velauciensis* from the upper Campanian of Velaux-La Bastide Neuve, in Velaux (Garcia et al. 2010). New excavation campaigns were conducted in 2009 and 2012 in Velaux-La Bastide Neuve, and the new remains led to a more detailed description and emended diagnosis of *Atsinganosaurus velauciensis*, together with histologic analyses of long bones and ribs (Díez Díaz et al. 2018). However, several titanosaurian bones from this assemblage show divergences at anatomical and histological levels, indicating the presence of a second taxon in this site.

It is worth emphasising that Velaux-La Bastide Neuve would not be the first site from the Ibero-Armorican Island in which more than one titanosaurian species occurs. Other examples include:

- In France: in the late Campanian – early Maastrichtian Fox-Amphoux-Métisson site (Var department) two tooth

morphotypes have been identified (Díez Díaz et al. 2012); in the lower Maastrichtian Bellevue site, it is highly possible that a second taxon is present besides *Ampelosaurus ataxis* (Vila et al. 2012, B. Vila personal communication 2020; VDD personal observation 2010), as all the remains from this site and the ones referred to this species deserve a revision.

- In Spain: in the middle to late Campanian Chera site (Valencia), two taxa are known, including *Lirainosaurus astibiae* (Díez Díaz et al. 2015); in the late Campanian – early Maastrichtian Lo Hueco site (Cuenca), there is at least one more titanosaur besides *Lohuecotitan pandafileandi* (Knoll et al. 2013, 2015; Díez Díaz et al. 2014; Páramo et al. 2015a, 2015b, 2020).

Furthermore, occasionally the same taxon has also been found in at least two sites:

- *Lirainosaurus*: in the Spanish fossiliferous sites of Laño (upper Campanian, Condado de Treviño) and Chera (mid to upper Campanian, Valencia) (Sanz et al. 1999; Díez Díaz et al. 2015).
- *Ampelosaurus*: its presence has been suggested in several sites from the lower Maastrichtian of France and Spain (Le Loeuff 1995; Buffetaut et al. 1999; Knoll et al. 2013).
- Knoll et al. (2019) have identified some similarities between a fragmentary skull from the late Campanian – early Maastrichtian Fox-Amphoux-Métisson site and the fragmentary neurocranial wall of the same age from Velaux-La Bastide Neuve referred to *Atsinganosaurus* (Díez Díaz et al. 2018).

- Teeth with similar morphologies have been found in the late Campanian – early Maastrichtian Fox-Amphoux-Métisson (France) and Lo Hueco (Spain) sites (Díez Díaz et al. 2012, p. 2014).

All this information suggests complex titanosaurian systematic and palaeobiogeographic relationships that existed in the Ibero-Armorican Island during the Late Cretaceous.

In this contribution, we describe new titanosaurian remains from Velaux-La Bastide Neuve and compare them with other European titanosaurs, focusing primarily on the sympatric *Atsinganosaurus velauciensis*.

Geological setting

Velaux-La Bastide Neuve is mostly known for its reptile assemblage, which includes several unique taxa (for example Godefroit et al. 2017; Vullo et al. 2018), recovered from three different sedimentological sequences. This fossiliferous site is located in the western part of the Aix-en-Provence Basin (Bouches du Rhône department, southern France) (Figure 1(a)) and has a late Campanian age, based of magnetostratigraphic analyses and biostratigraphic information derived from charophyte and dinosaur eggshell biozones (Cincotta et al. 2015). During the two field campaigns (2009 and 2012) a surface of 375 m² to a depth of 1.2 metres was excavated, which resulted in 100 m³ of overburden and matrix.

New material, particularly of titanosaurs, collected by Palaios/University of Poitiers/RBINS during both excavation campaigns, comes from the main bone-rich concentrations of sequence 2, B2 and B3 (Figure 1(b)) at the base of the lithological section. Sequence 2 presents a thickness of ca. 1 metre (Cincotta et al. 2015, figure 2). It is important to state that none of the titanosaurian remains recovered from sequence 2 were found in articulation or association (Díez Díaz et al. 2018, Figure 1(b)), with the exception of the holotype (four articulated posterior dorsal vertebrae) of *Atsinganosaurus* (Garcia et al. 2010). The majority of the titanosaurian remains were recovered in level B2, including the ones referred to *Atsinganosaurus velauciensis*. Only three titanosaurian remains were collected from level B3 (Figure 1(b and c)): the ilium MMS/VBN.12.32 referred to *Atsinganosaurus*, and a sacrum (MMS/VBN.09.170) and a humerus (MMS/VBN.12.82) which could not be referred to *Atsinganosaurus* because of their anatomical differences (see below). There is little separation between

the type stratum and that producing the referred material, besides that of *Atsinganosaurus* is from the same unit. This situation makes the comparison between the specimens referred to *Atsinganosaurus* and those of the new taxon really important, so the titanosaurian diversity of this site can be correctly assessed.

The diverse titanosaurian elements were found disarticulated in a lenticular conglomeratic sandstone, and result from the transport of decayed carcasses originating from different settings in a river channel, in the context of fluvial environment (Robin et al. 2019). Dinosaur specimens represent 38% of the vertebrate remains collected from sequence 2 (Cincotta et al. 2015), with most of these belonging to titanosaurs (25%). The vertebrate assemblage, with predominantly terrestrial and freshwater taxa (Robin et al. 2019), is abundant and diversified, including rhabdodontid iguanodontians (*Matheronodon provincialis* [Godefroit et al. 2017]), ankylosaurian remains, theropod teeth, an ontogenetic series of cranial and post-cranial elements of the eusuchian crocodyliform *Allodaposuchus precedens* (Martin et al. 2016), pleurodiran and cryptodiran turtle carapaces, the new genus of azhdarchid pterosaur *Mistralazhdarcho magii* (Vullo et al. 2018), hybodont shark teeth (Meristonoides), and a mawsoniid parasphenoid bone referred to *Axelrodichthys megadromos* (Cavin et al. 2020).

Methodology

Taxonomic description

We use ‘Romerian’ terms (Wilson 2006) for the anatomical structures (e.g. ‘centrum’, not ‘corpus’) and their orientation (e.g. ‘anterior’, not ‘cranial’). The landmark-based terminology for vertebral laminae (Wilson 1999) and fossae (Wilson et al. 2011) is used in the discussion of vertebral anatomy and in Figures 2 and 4. We use the anatomical terminology for the sacrum of sauropod dinosaurs proposed by Wilson (2011). All measurements are provided in Table 2.

For conciseness and clarity, *Garrigatitan meridionalis* is compared mainly with European titanosaurian taxa: *Ampelosaurus atacis* from the lower Maastrichtian of Campagne-sur-Aude (Aude, France) (Le Loeuff 1995, 2005a), *Atsinganosaurus velauciensis* from the upper Campanian of Velaux-La Bastide Neuve (Bouches-du-Rhône, France) (Garcia et al. 2010; Díez Díaz et al. 2018), *Normanniasaurus genceyi* from the Albian of Le Havre (Normandy, France) (Le Loeuff et al. 2013), *Lirinosaurus astibiae* from the upper

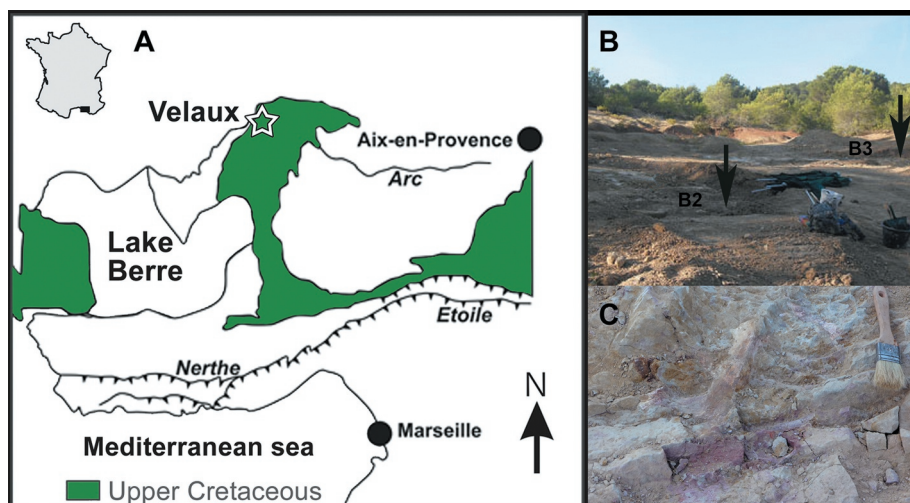


Figure 1. (a) Simplified geological map of the western Aix-en-Provence Basin (Bouches-du-Rhône, France). The star indicates the location of the Velaux-La Bastide Neuve site. (b) View of one part of the lithological section with the stratigraphical position of the rich fossiliferous levels B2 and B3 from sequence 2. (c) Detail of the *in situ* sacrum (MMS/VBN.09.170) of the titanosaur *Garrigatitan meridionalis* during its excavation.

Table 1. Bones of *Garrigatitan meridionalis*, from the Upper Cretaceous of Velaux-La Bastide Neuve (France), sampled for bone histology and summary of histologic observations. Bone tissue types and histologic ontogenetic stages (HOS) after Klein and Sander (2008), Stein et al. (2010). Remodelling stages (RS) after Mitchell et al. (2017).

<i>G. meridionalis</i> sample and number of thin section	Bone	Preserved length (mm)	Core location	Bone tissue type	2 nd osteon generations in the inner/mid/outer cortex respectively	HOS/RS
MMS/VBN.12.82.LM	Right humerus	±700	Posterior side, around the mid-shaft	H	5/4/4	14/12
MMS/VBN.09.47.LM	Left humerus	487	Posterior side, beneath the mid-shaft	H	5/5/4	14/13
MMS/VBN.09.A.016.LM	Right humerus	585	Posterior side, around the mid-shaft	F	4/4/3	12/11
MMS/VBN.00.013.LM	Right femur	790	Posterior side, in the mid-shaft	G	6/5/3	13/11+

$$\log M(\text{g}) = 2.754 \times \log \text{PerH} + \text{F} - 1.097 \quad (2)$$

And for size estimates we used the equation proposed by Seebacher (2001):

$$M(\text{kg}) = 214.44 \times L(\text{m})^{1.46} \quad (3)$$

in which M: body mass, PerH+F: sum of the perimeters of the humerus and femur in mm, L: body length.

Institutional Abbreviations: MMS/VBN, Musée Moulin Seigneurial/Velaux-La Bastide Neuve, Bouches-du-Rhône, France.

Anatomical Abbreviations: ala, alar arm; ca, capitulum; cpol, centropostzygapophyseal lamina; dif, dorsal intercostal foramen; iped, ischial peduncle; NC, neural canal; PO, postzygapophysis, podl, postzygodiapophyseal lamina; posdf, postzygospinodiapophyseal fossa; posl, postspinal lamina; PP, parapophysis, pped, pubic peduncle; prdl, posterior centrodiapophyseal lamina; prsdf, prezygospinodiapophyseal fossa; sdf, spinodiapophyseal fossa; spdl, spinodiapophyseal lamina; spof, spinopostzygapophyseal fossa; spol, spinopostzygapophyseal lamina; sprl, spinoprezygapophyseal lamina; tu, tuberculum; vif, ventral intercostal foramen.

Systematic palaeontology

Dinosauria Owen 1842

Saurischia Seeley 1887

Sauropoda Marsh 1878

Titanosauriformes Salgado et al. 1997

Titanosauria Bonaparte and Coria 1993

Lithostrotia Upchurch et al. 2004

Lirainosaurinae Díez Díaz et al. 2018

Garrigatitan gen. nov.

Type and only included species.

Garrigatitan meridionalis sp. nov.

Etymology

Garriga, from the Occitan word ‘garriga’ (‘garrigue’ in French), which is derived from the old Provençal word ‘garric’, for a typically Mediterranean low vegetation composed mainly of drought-resistant shrubs which is abundant in the environment of the Velaux-La Bastide Neuve locality; and titan, giant in Greek mythology, a common suffix for titanosaurs.

Type locality and horizon

As for type and only species.

Diagnosis

See diagnosis for type and only species below.

Garrigatitan meridionalis gen. et sp. nov.

Holotype

MMS/VBN.09.170: sacrum with part of the left ilium.

Referred specimens

MMS/VBN.02.99: cervical vertebra; MMS/VBN.09.A.016, MMS/VBN.09.47: two humeri; MMS/VBN.12B.12a: left ilium; MMS/VBN.12B.12b: right ischium.

Tentatively referred specimens

MMS/VBN.12B.011: cervical rib; MMS/VBN.12.82: right humerus; MMS/VBN.09.A.017: right ulna; MMS/VBN.00.13: left femur.

Etymology

From the Latin word ‘meridionalis’ meaning ‘southern’, for southern France.

Type locality

La Bastide Neuve, Velaux; Aix-en-Provence Basin, Bouches-du-Rhône, France (Figure 1).

Type horizon

‘Begudian’ (local stage) sandstones, upper Campanian, Upper Cretaceous (Garcia et al. 2010; Cincotta et al. 2015). The holotype and paratype were recovered from level B3 of sequence 2, and the referred material from level B2 of the same sequence.

Diagnosis

Member of Titanosauria, having the following autapomorphies (marked with an asterisk), as well as a unique combination of characters not seen in other Late Cretaceous European titanosaurs: medium sized titanosaur (sub/adults with a body length of ca. 4–6 metres and body mass of ca. 2–2.5 tonnes, adults could reach a body length between 12 and 16 metres) with (1) posterior cervical vertebrae with a wide neural canal, (2) posterior cervical vertebrae with an anteroposteriorly compressed and paddle-shaped neural spine (not wider than the centrum), (3) posterior cervical vertebral postzygapophyses widely separated and with laterally oriented articular surfaces, (4) hourglass-shaped humeri (proximal and distal thirds of almost the same transversal width) in anterior and posterior views*, (5) ilium with a broad rounded hollow slightly posterior to the base of the pubic peduncle*, (6) proximolateral margin of the femur only slightly medially deflected*.

Description and comparisons

All measurements are indicated in Table 2.

Table 2. Measurements (in mm) of the remains of the titanosaur *Garrigatitan meridionalis*, and both metacarpals referred to *Atsinganosaurus velauciensis*, from the Late Cretaceous Velaux-La Bastide Neuve site (France). Abbreviations: AP: anteroposterior; LM: lateromedial; Max: maximum; Min: minimum; Min. Cir. Diaph.: minimum circumference of the diaphysis; PP: pubic peduncle; ECC (eccentricity index) (Wilson and Carrano 1999); mid-shaft mediolateral width divided by the anteroposterior width. *preserved length.

CERVICAL VERTEBRA									
	Centrum length (w/ condyle)	Centrum length (wo/ condyle)	Centrum length (posterior)	Centrum height (posterior)	Centrum width (posterior)	Neural arch height	Neural spine height		
MMS/VBN.02.99	-	*61		100	129	242	184		
HUMERI									
	Preserved length	Min. transversal width	Min. AP width	ECC	Min. Cir. Diaph.	Max. width proximal end	Max. width distal end		
MMS/VBN.09.47	482	96	42	2.29	250	*243	*124		
MMS/VBN.09A.016	590	80	30	2.67	230	*201	*172		
MMS/VBN.12.82	610	118	35	3.37	230	-	-		
ULNA									
	Preserved length	Min. transversal width	Min. AP width	ECC	Min. Cir. Diaph.	Max. width proximal end	Max. width distal end		
MMS/VBN.09-A.017	660	104	36	3	348	*350	*69		
METACARPALS									
	Length	AP width diaphysis	LM width diaphysis	AP width proximal articularion	LM width proximal articularion	AP width distal articularion	LM width distal articularion		
MMS/VBN.12.18	300	60	20	110	-	60	-		
MMS/VBN.02.107	310	50	30	110	-	60	-		
FEMUR									
	Preserved length	Min. transversal width	Min. AP width	ECC	Min. Cir. Diaph.	Max. width proximal end	Max. width distal end		
MMS/VBN.00.13	810	90	60	1.50	273	*198	*177		
ISCHIUM									
	Preserved length	PP articular surface	Distal edge width						
MMS/VBN.012.12b	*48,5	17	*13						

Cervical vertebra

Garcia et al. (2010) described the isolated specimen MMS/VBN.02.99 as a dorsal vertebra referred to *Atsinganosaurus*. But, because of its general morphology, the position of the ribs, and the development of the neural spine, we interpret this specimen as a posterior cervical (Figure 2). This vertebra, which preserves its posterior half, together with the neural spine and the proximal part of the ribs, is generally poorly preserved. However, besides its general preservation, we can observe that it probably was anteroposteriorly short and dorsoventrally tall, as the cervical vertebrae described for *Ampelosaurus*, *Mansourasaurus*, *Mendozasaurus* and *Isisaurus* (Sallam et al. 2018). The centrum is opisthocelous, with a slight dorsoventral compression. Because of its preservation the presence of pleurocoels in the lateral surfaces cannot be confirmed. The diapophyses are located above the junction between the centrum and the neural arch, and the parapophyses are placed ventrolaterally on the centrum. A sdf is present above the diapophysis, and delimited posteriorly by the postzygapophyses. This fossa is narrower than in the cervicals of *Atsinganosaurus* due to the anteroposterior compression of the neural arch. The postzygapophyses are better developed than in *Atsinganosaurus* and strongly laterally directed. They surpass the posterior edge of the centrum. Both are widely separated and no tpol is preserved. The articular surfaces of the postzygapophyses face ventrolaterally at ca. 45° from the horizontal axis. The neural canal is wide, and delimited by both vertically-oriented cpol. Two conspicuous and well-developed spol extend from the dorsal surface of the postzygapophyses to the distal edge of the posterior surface of the neural spine, meeting at its middle point. A deep and triangular spof is delimited by the two spol, as in *Atsinganosaurus*. There is no posl. The neural spine is anteroposteriorly compressed, not bifurcated, and with a rounded distal edge, having a paddle-shaped outline (albeit not wider than the centrum) in anterior and posterior views. A similar morphology has been described in the posteriormost cervical and anteriormost dorsal vertebrae of several somphospondylans (Gomani 2005; Bonaparte et al. 2006; Calvo et al. 2007; D’Emic 2012). However, the laminar contribution to the lateral expansion differs between taxa (Gallina 2011; Gallina and Apesteguía 2015; González Riga et al. 2018). Only in *Garrigatitan*, *Futalognkosaurus*, *Mendozasaurus*, *Quetecsaurus* (Gallina 2011; González Riga and Ortiz David 2014) and *Alamosaurus* (Tykoski and Fiorillo 2016) is it known to be formed entirely by the spdl, and among these taxa *Mendozasaurus* is distinct in that this lateral expansion results in the neural spine being wider than the centrum. This morphology of the neural spine, together with the separation between the postzygapophyses, their development and their lateral orientation, the wide neural canal, are not present in *Atsinganosaurus*. This taxon presents more closely placed postzygapophyses, as well as neural spines with straighter distal and lateral edges. The posterior cervical vertebra C3-265 of *Ampelosaurus* also presents separated postzygapophyses, a deep and wide spof between them, and vertical cpol. But such a comparison must be made with caution due to the incomplete preservation of the neural spine of C3-265.

Sacrum

This sacrum (MMS/VBN.09.170) (Figures 3–4), together with the humerus MMS/VBN.12.82, was recovered from level B3 (2 m above level B2 in which the rest of the referred specimens of *Garrigatitan* as well as the bones referred to *Atsinganosaurus* [Garcia et al. 2010; Díez Díaz et al. 2018] were found).

Sacral vertebrae

This sacrum is formed by five sacral vertebrae; however, the first one is likely missing, as titanosaurian sacra are usually formed by 6

sacrals (Huene 1929), with the exception of some derived lithostrotians that have 7, including *Neuquensaurus* (Salgado et al. 2005; D’Emic and Wilson 2011). The total preserved length is ca. 50 cm. Most of the structures of this sacrum are highly fused, including the centra and neural spines (whose distal tips are broken off), as in *Atsinganosaurus velauciensis*, although the junctions between the vertebrae are thickened in this latter taxon. As the distal tips of the neural spines are lost, the presence of a supraspinous rod cannot be confirmed. Nevertheless, when compared with the development of this rod and of the neural spines in the sacrum of *Atsinganosaurus*, it seems more probable that the sacrum of *Garrigatitan* had no supraspinous rod, or at the least it was less (or more poorly) developed than in *Atsinganosaurus* (it is interesting to keep in mind that the presence of this rod could be a diagnostic feature within Titanosauria [Poropat et al. 2016]). The sacrum is more dorsoventrally compressed than the one referred to *Atsinganosaurus*. Thanks to the broken surfaces, the inner structure of the sacral elements can be observed, and there is no camellate tissue; this, however, could also be the result of the dorsoventral compression of the specimen. The ventral surfaces of the centra – only the third, fourth and fifth vertebrae have their ventral surfaces preserved – show a ventral keel, as in *Atsinganosaurus*. The lateral sides of the centra are obscured, so that the presence of pleurocoels cannot be assessed. The presence and development of the transverse foramina between the centra and the ribs cannot be observed, either. The tubercula of the ribs are thickened, and their dorsal surface is flat and differentiated from the rest of the rib. The distal end of this thickened surface – the alar arm of the rib (*sensu* Wilson 2011) – connects with the dorsal edge of the ilium. This connection between the alar arm of the sacral ribs and the dorsal edge of the ilium creates a robust structure, especially between the second and the fourth sacrals. These thickened dorsal surfaces in the tuberculum of the sacral ribs have been also observed in *Atsinganosaurus*, although this structure is not as robust in the latter taxon. An intricate complex formed by laminae and fossae is found between the tuberculum and the neural spines. The anterior surface of the first preserved sacral is so damaged that no structures can be discerned. From every dorsal surface, three laminae extend to the neural spine: prdl, podl and spdl. The spdl are vertical, but the prdl and podl are almost horizontal. The prdl and its anterior podl are usually connected at the base of the neural spine, and the new lamina extends vertically to the dorsal tip of the neural spine. A deep prsdf is present between the prdl and the spdl, and a posdf is developed between the podl and the spdl. Although the posterior surface of the last sacral is poorly preserved, a small spol is present, whereas a posl appears to be absent. These laminae and fossae complexes differ from the ones present in the sacrum of *Atsinganosaurus*, where these are also more variable between the vertebrae, and even not bilaterally symmetrical in the same vertebra (e.g. some of the vertebrae have more than three laminae diverging from the thickened dorsal surface of the tuberculum, even accessory laminae that start in other laminae). Ventrally, the capitulum is an almost dorsoventrally flat structure, with the costoventral junction and the acetabular arm expanded anteroposteriorly. The distal ends of the acetabular arms of the ribs are not preserved, but the presence of intercostal junctions between them and with the base of the ilium can be hypothesised, forming the sacricostal yoke, as typical of Eusauropoda (see e.g. Wilson 2011). Deep dorsal and ventral intercostal foramina are present between the sacral ribs. A sacrum is known in the Spanish taxon *Lohuecotitan*, but only details on its sacricostal yoke and tubercula of the ribs can be assessed. In *Lohuecotitan*, the tubercula are transversely less developed and have an hourglass-shape, and the vertebrae have a camellated bone tissue, in contrast with *Garrigatitan*.

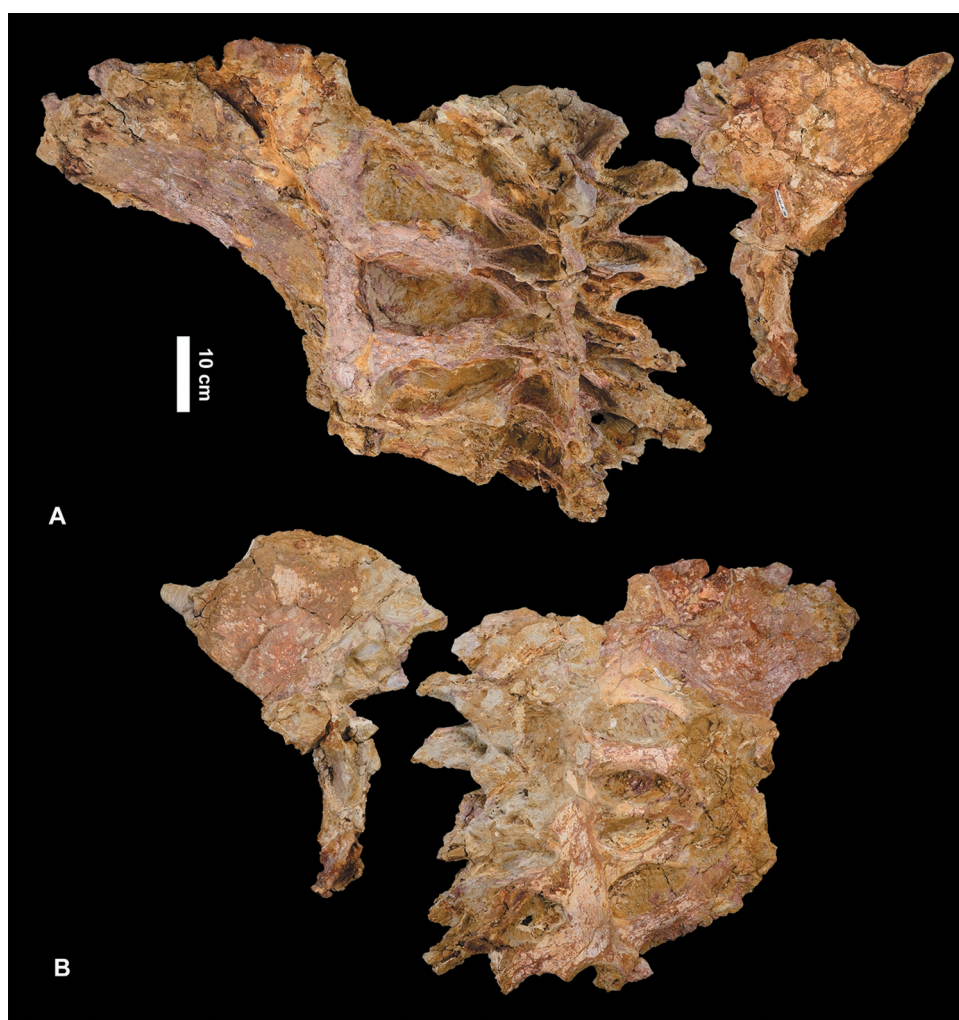


Figure 3. Sacrum (MMS/VBN.09.170), holotype of the titanosaur *Garrigatitan meridionalis* from the Late Cretaceous Velaux-La Bastide Neuve site (France) in (a) dorsal and (b) ventral views.

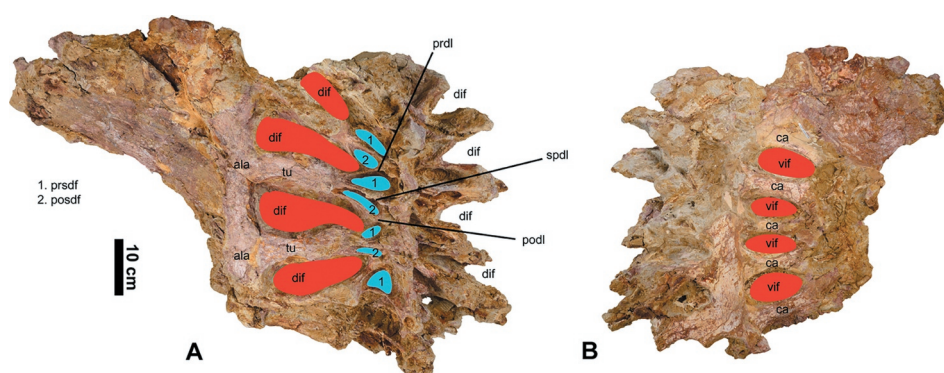


Figure 4. Sacrum (MMS/VBN.09.170), holotype, without the right ilium, of the titanosaur *Garrigatitan meridionalis* from the Late Cretaceous of Velaux-La Bastide Neuve (France) in (a) dorsal and (b) ventral views, highlighting the laminae and fossae patterns. Abbreviations as in the text. Fossae in the neural arch are shown in blue, intercostal foramina in red.

Ilium

The left ilium is completely fused to the sacral ribs. The right one is broken off and poorly preserved. The dorsal margin of the preacetabular process is rounded, horizontal, and laterally deflected, unlike in *Lirainosaurus* and *Lohuecotitan*. The highest part of the dorsal margin of the preacetabular process seems to be located

anterior to the base of the pubic peduncle. The base of the pubic peduncle is robust and longer anteroposteriorly than lateromedially. A second ilium has been found (MMS/VBN.12B.012a) associated with a right ischium (MMS/VBN.12B.12b) from level B2. This specimen is better preserved, so a detailed description and comparison is given below.

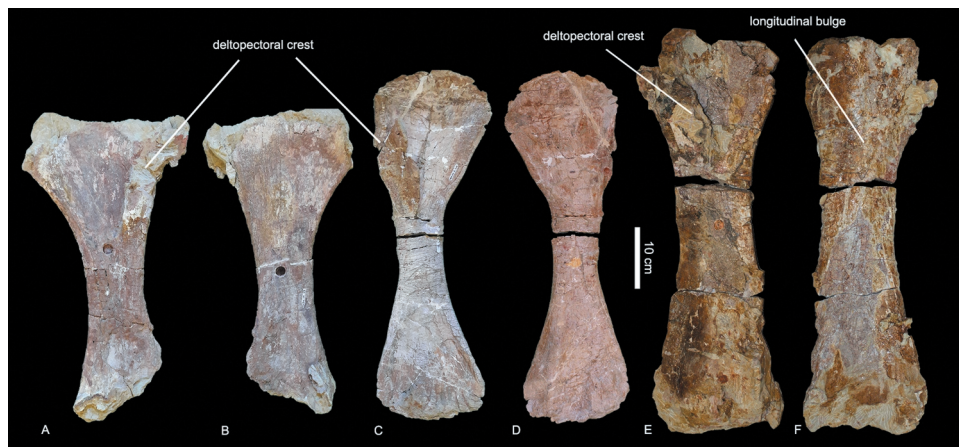


Figure 5. Humeri of the titanosaur *Garrigatitan meridionalis* from the Late Cretaceous Velau-La Bastide Neuve site (France). Left humerus (MMS/VBN.09.47) in (a) anterior and (b) posterior views; right humerus (MMS/VBN.09.A.016) in (c) anterior and (d) posterior views; and right humerus (MMS/VBN.12.82) in (e) anterior and (f) posterior views.

Forelimb

Humerus

Two humeri are referred to *Garrigatitan* (Figure 5): MMS/VBN.09.47 (Figure 5(a-b)) and MMS/VBN.09.A.016 (Figure 5(c-d)). MMS/VBN.09.47 is a left humerus with incomplete proximal and distal extremities, but their lateromedial expansion is clearly noticeable, just as it is in the right humerus MMS/VBN.09.A.016. This lateromedial expansion of the humeral proximal third differentiates *Garrigatitan* from *Atsinganosaurus*, *Ampelosaurus*, *Lirainosaurus*, *Magyarosaurus* and *Opisthocoelicaudia* (Borsuk-Białynicka 1977), in which only the medial edge is expanded. The proximal third of the humeri of *Garrigatitan* is also more transversally expanded than in the preserved humeri referred to *Mansourasaurus* (Sallam et al. 2018). The humeral diaphyses of *Garrigatitan* are anteroposteriorly compressed, with the anterior surfaces of the proximal and distal ends concave, and the posterior surface flat/slightly convex. No bulges or tuberosities are present in the anterior or posterior surfaces. The deltopectoral crest is not complete in any specimen (only its base is preserved), but it did not reach the middle of the shaft, as it does in *Atsinganosaurus*, *Lirainosaurus*, *Ampelosaurus*, *Magyarosaurus*, *Opisthocoelicaudia* and *Mansourasaurus*. The base of the deltopectoral crest has the same thickness throughout all its length, contrary to *Atsinganosaurus* and *Opisthocoelicaudia*. When compared with *Atsinganosaurus*, the humeri of *Garrigatitan* are more robust (however, not as much as those of the Asian taxon *Opisthocoelicaudia*), and their morphology is more similar to those of some other European titanosaurs (e.g. *Ampelosaurus* and *Lirainosaurus*). In addition, the eccentricity index (ECC *sensu* Wilson and Carrano 1999) shows that the humeri of *Garrigatitan* (mean ECC: 2.48) were neither the most anteroposteriorly compressed (*Atsinganosaurus* mean ECC: 3.45), nor the closest to a more circular cross-section of the diaphysis (*Lirainosaurus* mean ECC: 2) among European titanosaurs. Besides this, the lateromedial expansion of the proximal and distal extremities starts closer to the middle of the diaphysis, when compared with the humeri referred to *Atsinganosaurus* (i.e. the diaphyses of the humeri of *Atsinganosaurus* seem straighter in anterior and posterior views). The humeri of *Garrigatitan* have transversely relatively wider distal extremities (almost the same width as the proximal third) in comparison to other Ibero-Armorican titanosaurs, especially when compared to *Atsinganosaurus*. This hourglass-shape outline of the humerus is visible in anterior and posterior views.

Pelvic girdle

Ilium

One fragmentary left ilium is preserved (MMS/VBN.12B.012a) (Figure 6(a-b)). It consists of the dorsal part of the acetabulum, most of the pre- and postacetabular processes of the iliac blade, the ischial peduncle, and part of the pubic peduncle. The preacetabular process is horizontal and slightly laterally projected, like in *Lohuecotitan*, and contrary to the ilium of *Lirainosaurus*, which has a vertical preacetabular lobe. The postacetabular process is vertical and slightly laterally projected as well. The ischial peduncle is reduced, contrasting with the better developed ischial peduncle present in *Paludititan*, and it is located anterior to the postacetabular process of the iliac blade. A broad, rounded hollow is present slightly posterior to the base of the pubic peduncle, but it is not triangular, as the one present in *Lirainosaurus* (Díez Díaz et al. 2013b). The acetabulum is not as concave as in *Paludititan*. This ilium is pneumatized, as in *Atsinganosaurus* (Díez Díaz et al. 2018), *Lirainosaurus* (Díez Díaz et al. 2013b), *Diamantinasaurus* (Poropat et al. 2015), and other derived titanosaurs (see Cerda et al. 2012). However, this could be a convergence with *Euhelopus*, as it also has pneumatized ilia (see Wilson and Upchurch 2009; Mannion et al. 2013). The main differences from the fragmentary ilium ascribed to *Atsinganosaurus* are the C-shaped cross-section of the pubic peduncle (considered as one of its autapomorphies), and the hollow present near the base of the pubic peduncle in *Garrigatitan* (absent in *Atsinganosaurus*).

Ischium

One right ischium (MMS/VBN.12B.12b) (Figure 6(c-d)) was found close to the ilium MMS/VBN.12B.12a. It has a plate-like morphology, with a sigmoidal shape. The iliac peduncle is incomplete, its distal edge is missing. This plate-like morphology and the absence of an emargination in the anterior margin of the ischiadic blade are common features in titanosaurs (Wilson 2002; Upchurch et al. 2004; González Riga et al. 2009), contrary to some lithostrotions, as *Opisthocoelicaudia* (Borsuk-Białynicka 1977). The acetabular margin is flat, as also observed in *Ampelosaurus* (Le Loeuff 2005a, figure 4.17) and *Atsinganosaurus*, and it is not well differentiated from the iliac peduncle. The iliac peduncle seems to be robust, as in *Ampelosaurus* and *Paludititan*, and contrasting with *Atsinganosaurus*. The pubic peduncle is long, and clearly differentiated from the anteroventral edge, which is not well preserved distally. The ischia of *Ampelosaurus* and *Paludititan* have a more boomerang-like morphology and their pubic peduncle is also well

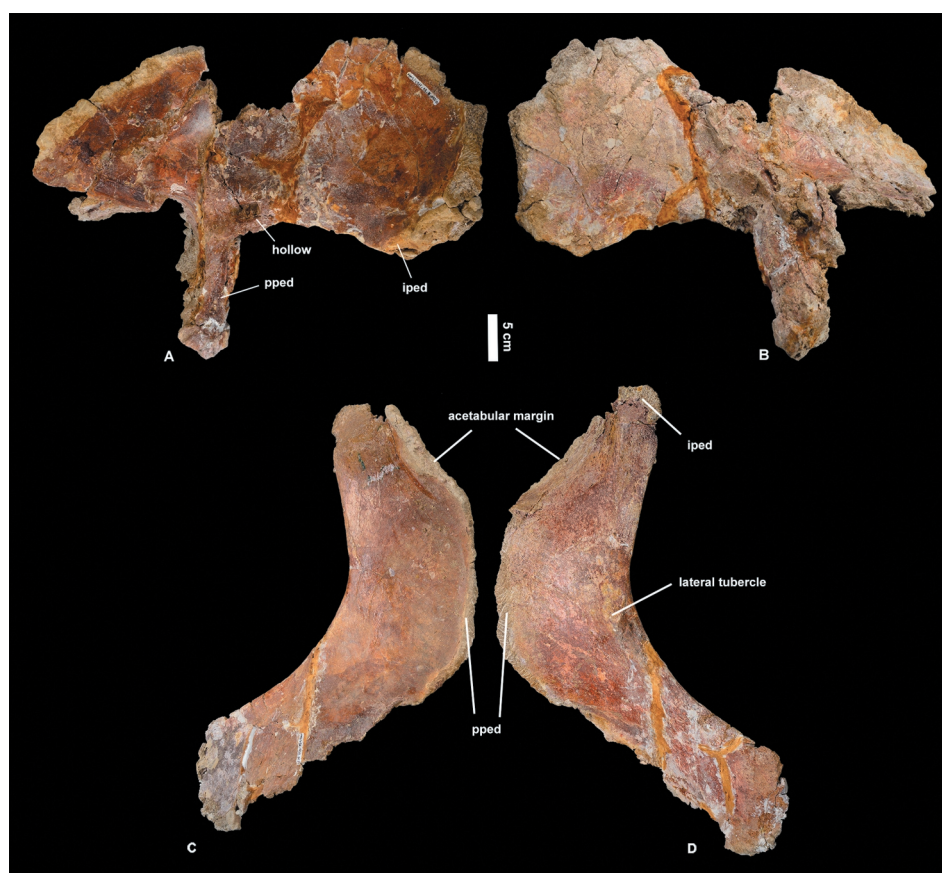


Figure 6. Pelvic elements of the titanosaur *Garrigatitan meridionalis* from the Late Cretaceous Velaux-La Bastide Neuve site (France). Left ilium (MMS/VBN.12B.012a) in (a) lateral and (b) medial views; and right ischium (MMS/VBN.12B.12b) in (c) medial and (d) lateral views. Abbreviations as in the text.

differentiated from the distal blade. The ischial blade is a straight plate whose thickness decreases towards its distal edge. At the base of the iliac peduncle, a lateral tubercle is present near the posterior edge of the proximal part of the blade. A similar prominence appears in the ischium of *Atsinganosaurus*, although it is more robust and developed in this one. This lateral ridge could correspond to the bulge interpreted by Borsuk-Białynicka (1977) as the attachment point for *m. flexor tibialis internus III* (see also Poropat et al. 2015). This lateral tubercle or tuberosity seems to be a diagnostic feature within Titanosauria (Carballido et al. 2017). Besides these differences, the ischium of *Garrigatitan* is larger than the one of *Atsinganosaurus*, and lacks the lateral prominence that appears in this latter taxon near the middle of its blade, close to its ventral margin.

Large specimens tentatively referred to *Garrigatitan*

Several titanosaurian bones found in level B2 (with the exception of the humerus MMS/VBN.12.82, which was recovered from level B3) show a noticeable difference in size when compared with the rest of the recovered specimens referred to *Garrigatitan*, but also *Atsinganosaurus*. However, and as stated below, the duplicated specimens clearly show anatomical differences with those of *Atsinganosaurus*, so they will be here regarded as tentatively belonging to large individuals of *Garrigatitan* (the hypothesis of one single individual comprising all these large bones will not be presented here, as they were not found associated or in articulation).

The hypothesis of the presence of a third titanosaurian taxon has been also assessed. No Upper Cretaceous sites with more than two titanosaurian taxa are known to date, and, as previously indicated, there is little separation between the type stratum and that producing

the referred material to both *Atsinganosaurus* and *Garrigatitan* (less than 1 metre). Besides, the different levels studied at Velaux-La Bastide Neuve seem to reflect rapid flooding events (Cincotta et al. 2015), without a real taxonomical implication between them. Because of this information, we currently consider the referral of these large specimens to *Garrigatitan* to be a more parsimonious hypothesis than the presence of three different titanosaurian taxa in this site.

Cervical rib

A right anterior cervical rib, which lacks its distal portion and the tuberculum, has been recovered (MMS/VBN.12B.011) (Figure 7). The capitulum is robust, convex ventrally and concave dorsally. A wide ridge connects the anteroposteriorly broad articulation with the parapophysis and the connection with the tuberculum, which is missing. Posterior to this ridge a concave surface can be observed, but no hollow or foramina are present. A short and rounded anterior process can be observed, although its complete preservation can not be confirmed. The capitulum narrows posteriorly rapidly to form the slender rib, which follows a horizontal axis and shows a D-shaped cross-section. No pneumatic features seem to be present. The main difference of this specimen with the cervical rib ascribed to *Atsinganosaurus* (MMS/VBN.12 A.004) is the anteroposterior extension, robusticity and ventral convexity of the capitulum of MMS/VBN.12B.011 (see also Diez Díaz et al. 2018, Figure 3(a, d and g)).

Humerus

The right humerus MMS/VBN.12.82 (Figure 5(e and f)) was collected from the same level from where the sacrum was recovered. This

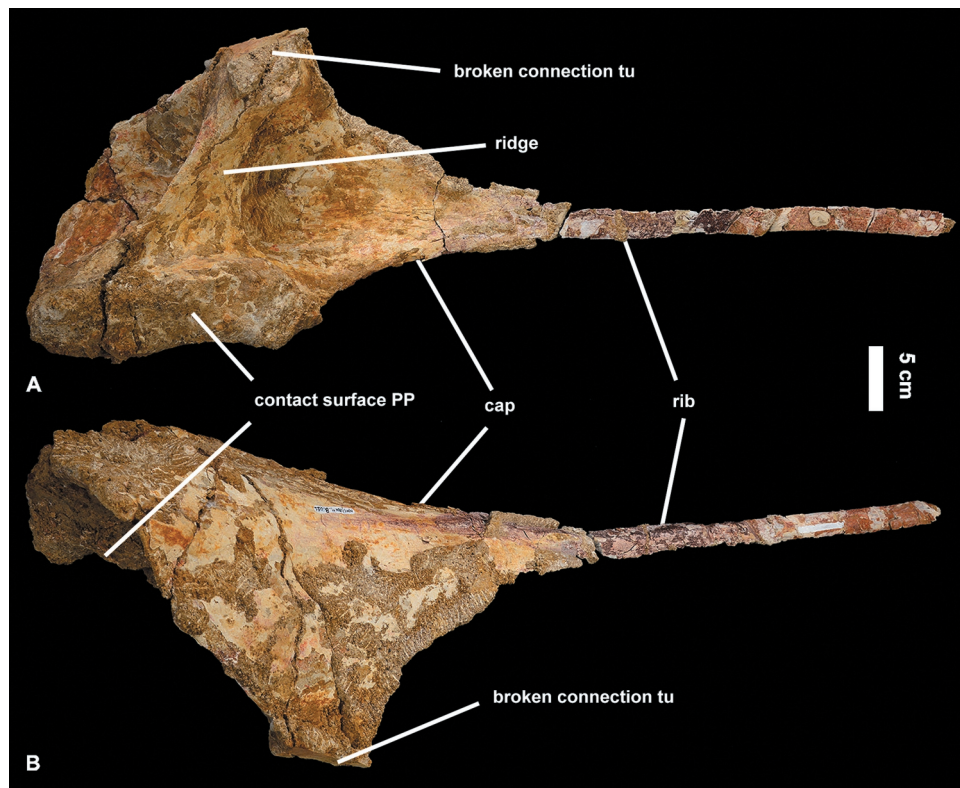


Figure 7. Right anterior cervical rib (MMS/VBN.12B.011) of the titanosaur *Garrigatitan meridionalis* from the Late Cretaceous Velaux-La Bastide Neuve site (France) in (a) dorsal and (b) lateral views. Abbreviations as in the text.

humerus, although not completely preserved, is larger than the ones referred to *Atsinganosaurus*. Neither the proximal nor the distal ends are not preserved. The humeral diaphysis is more anteroposteriorly compressed than that of the smaller humeri referred to *Garrigatitan*, with an ECC closer to that of the humeri of *Atsinganosaurus* (ECC: 3.37). The deltopectoral crest is not complete, but its base is more medially oriented – as in many titanosauriforms (Mannion et al. 2013) – than those of *Atsinganosaurus* or the smaller humeri of *Garrigatitan*. A wide longitudinal bulge appears in the middle of its proximal posterior half. The histological analyses also highlight some differences between this humerus and the smaller referred to *Garrigatitan* (see below). However, and besides the noted differences with *Garrigatitan*, this humerus is referred to this new taxon as its general anatomy is more similar to it than to *Atsinganosaurus* (e.g. transversely wider diaphysis and distal third than those of the humeri referred to *Atsinganosaurus*).

Ulna

A large right ulna (MMS.VBN.09.A.017; preserved length ca. 66 cm, preserved maximum proximal width ca. 35 cm) has been found (Figure 8); it is poorly preserved. It is transversely compressed, especially in its proximal third. This compression is mainly taphonomical, but a slight anatomical compression cannot be ruled out. This preservation makes it impossible to check the angle formed by the arms of the proximal end. A ridge extends along its lateral surface from the posterior edge of the proximal end, but the distal tip of this ridge is not preserved. This ridge is the broken base of the anterolateral arm, which delimits, together with the large anterior arm, a shallow radial articulation. The distal half has a quadrangular cross-section, although its distal articular surface is not preserved. It is difficult to make a detailed

comparison, but the general outline of the specimen is very similar to the ulna C3-1296 of *Ampelosaurus*: both are large (although the one referred to *Ampelosaurus* is comparatively smaller, ca. 50 cm) and robust elements, with the proximal edge lateromedially compressed, and greatly expanded in comparison with the quadrangular and poorly expanded distal edge. The olecranon is low, although it is more noticeable than in C3-1296. The general morphology and size of this specimen is completely different from those of the ulna referred to *Atsinganosaurus* (preserved length 42 cm). Le Loeuff (2005b) also figures a large ulna (58 cm) referred to *Magyarosaurus dacus*, from the Late Cretaceous of Romania. The Velaux-La Bastide Neuve specimen is the largest titanosaurian ulna found in Europe so far.

Femur

MMS/VBN.00.13 is a slender left femur, with the proximal and distal extremities eroded (Figure 9). Its diaphysis is straighter than in other titanosaurian femora, and its distal end is more transversely expanded than its proximal end. The anterior surface is not as well preserved as the posterior one. The cross-section of the straight diaphysis is elliptical (ECC: 1.46). The proximolateral margin is only slightly medially deflected, a condition that is not typical for Titanosauriformes (Salgado et al. 1997; Wilson and Sereno 1998; Wilson 2002; Mannion et al. 2013), and has a well-developed lateral bulge. The fourth trochanter is well-developed, and it is posteromedially located, above the middle of the shaft, similar to the femur referred to *Opisthocoelicaudia* (Borsuk-Białynicka 1977). However, no smaller tuberosities are present laterally to the fourth trochanter in MMS/VBN.00.13. The femoral morphology is clearly different from that of other European taxa, especially in the medial deflection of the proximolateral margin, and the development of the

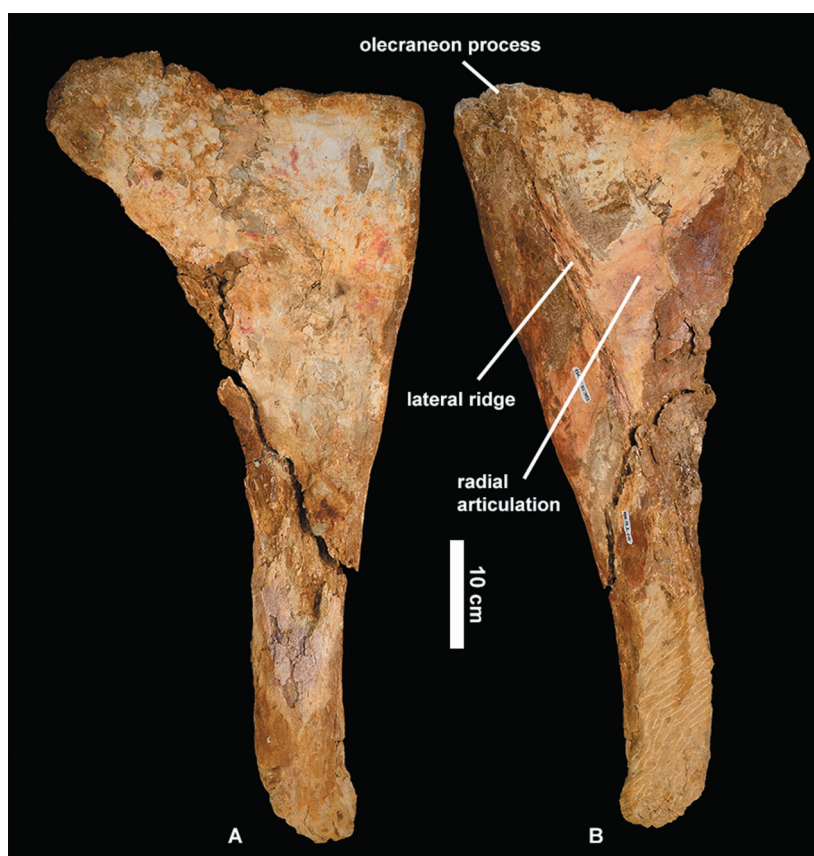


Figure 8. Right ulna (MMS.VBN.09.A.017) of the titanosaur *Garrigatitan meridionalis* from the Late Cretaceous Velaux-La Bastide Neuve site (France) in (a) medial and (b) lateral views.

fourth trochanter. But we prefer to be cautious about interpreting and comparing these features, as they could be due to taphonomical deformations.

New specimens referred to *Atsinganosaurus*

Metacarpals

The metacarpals are oriented as Poropat et al. (2015, page, p. 1010) did for describing the metacarpal remains of *Diamantinasaurus*, as if they lay 'side-by-side on a flat surface with the long axis of each distal articular end oriented transversely. This means that each element has its palmar surface facing ventrally, its external surface facing dorsally, and lateral and medial surfaces. [...] Thus, the external surface will be termed dorsal, and the palmar, ventral'.

Two metacarpal I? remains have been recovered (MMS/VBN.02.107 and MMS.VBN.12.18, Figure 10), but their preservation makes a detailed description and comparison with other taxa not possible. Both are highly similar to the left metacarpal I MMS/VBN.09.113 referred to *Atsinganosaurus*, specially MMS/VBN.02.107, which is the most complete of the two. Their straight diaphyses are highly dorsoventrally compressed. Their proximal ends are more expanded and compressed than the distal ones. The proximal ends present a projection of the lateral apex, which creates a concave edge of the lateral surface of the diaphyses, visible in dorsal and ventral views. The proximal articular surface is dorsoventrally compressed, and shows a triangular outline. The distal articulation with the metacarpal II can be observed both in ventral and lateral views (Figure 10(e and f)). The distal end of MMS/VBN.02.107 has a squared-like outline and a lateral

apex, as in *Rapetosaurus* (Curry Rogers 2009). The main difference of these metacarpals with those referred to *Atsinganosaurus* is their size, being the ones described in this work almost two times larger.

Histologic observations

Heavy bone remodelling including several crosscutting generations of secondary osteons (*sensu* Stein et al. 2010; Mitchell et al. 2017) is the main histologic pattern of the samples. Trabeculae are broken at the base of the cores, leading the medullary cavity – cortex transition to be abrupt into a cortex with distorted secondary osteons (MMS/VBN.09.47, MMS/VBN.00.013 and MMS/VBN.12.82). These secondary osteons are clearly visible in MMS/VBN.12.82 and MMS/VBN.00.013, and form one-fifth of the cortex thickness in MMS/VBN.00.013 (Figure 11(c)).

Secondary osteons are mature and rounded to elliptical in shape. Under cross-polarised light, alternating bright and dark lamellar layers within these osteons are characteristic of type two osteons *sensu* Ascenzi and Bonucci (1968) (arrow in Figure 11(a, b, d and e)). In the long bones of *Garrigatitan meridionalis*, four to six generations of secondary osteons can be recognised in the innermost cortex, four to five generations in the mid cortex and three to four generations in the outer cortex (see Table 1 below for details). Elliptical osteons have the long axis preferentially oriented parallel to the periosteal surface in transverse section, a feature also seen in other titanosaurian sauropods such as *Ampelosaurus ataxis* and *Atsinganosaurus velauciensis* (Klein et al. 2012; Díez Díaz et al. 2018 – Figure 11(a and e)). No open resorption cavities were observed in the innermost cortex.



Figure 9. Left femur (MMS/VBN.00.13) of the titanosaur *Garrigatitan meridionalis* from the Late Cretaceous Velaux-La Bastide Neuve site (France) in (a) posterior, (b) distal (posterior towards top), (c) lateral, (d) proximal (posterior towards top), (e) anterior, and (f) medial views.

Some interstitial primary bone tissue is preserved between the secondary osteons, mostly restricted to the outermost cortex, but also here and there extending down halfway into the cortex (MMS/VBN.09.A.016, MMS/VBN.09.47 and MMS/VBN.00.013). Large areas of primary bone in the outermost cortex can be seen in MMS/VBN.09.A.016 and MMS/VBN.00.013. These zones are highly vascularised with mature circumferentially oriented primary osteons. Some lines of arrested growth (LAGs) are present and are quite densely packed, but with primary vascular canals in between (Figure 11(a and d)), indicative of the onset of an External Fundamental System (EFS – *sensu* Klein and Sander 2008). However, the outer cortex of specimen MMS/VBN.00.013 is less vascularised than that of MMS/VBN.09.A.016, but shows a vascular canal opening to the periosteal surface (arrow in Figure 11(b)). It is not unlikely that the outermost μm -thick layer of the cortical samples is missing because of weathering or mechanical preparation, as the bones are very brittle, but not to an extent that could hamper assessment of maturity.

Following Klein and Sander (2008) and Stein et al. (2010), the studied specimens range from Histologic Ontogenetic Stage (HOS) 12 and 13 (MMS/VBN.09.A.016 and MMS/VBN.00.013, respectively)

to HOS 14, given the presence of type F-G bone tissues in MMS/VBN.09.A.16 and MMS/VBN.00.013 (Figure 11(a and d)), and the complete remodelled type H bone tissue of the cortex in MMS/VBN.12.82 and MMS/VBN.09.47 (Figure 11(e)). Given the multiple crosscutting secondary osteon generations throughout the cortex, the remodelling stages (RS) (*sensu* Mitchell et al. 2017) range from RS 11 to 13.

In longitudinal sections, the osteonal boundaries are more difficult to distinguish, and so are the different crosscutting generations. Nonetheless, remodelling is widespread, with very elongated secondary osteons, meaning they are mainly oriented in the long bone axis direction. Some Volkmann's canals can be seen running oblique to the long bone axis. These oval osteons are present only in MMS/VBN.12.82 and become numerous towards the top of this core (Figure 11(e), Table 1).

Phylogenetic analysis

Ten MPTs were obtained, with 184 steps. The calculated Consistency Index (CI) is 0.533, and the Retention Index (RI) is



Figure 10. Metacarpals of the titanosaur *Atsinganosaurus velauciensis* from the Late Cretaceous Velaux-La Bastide Neuve site (France). Left metacarpal I (MMS/VBN.02.107) in (a) dorsal, (b) distal (dorsal towards top), (c) medial, (d) proximal (ventral towards bottom), (e) ventral, and (f) lateral views; and metacarpal I? (MMS.VBN.12.18) in (g) dorsal/ventral? and (h) ventral/dorsal? views.

0.631 (Figure 12). The general topology of the consensus tree is similar to the one obtained by Díez Díaz et al. (2018). However, one of the main differences is that the placement of several basal titanosaurs (two of them are the European *Lohuecotitan* and *Paludititan*) remains unresolved. Furthermore, the nodes Titanosauria and Lithostrotia cannot be defined. No more comments on these taxa will be made here, as a more complete phylogenetic work about the Late Cretaceous titanosaurian faunas from Europe is currently in preparation. In this work we will only focus on the phylogenetic relationships of *Garrigatitan*. Our phylogenetic analysis recovers *Garrigatitan* as closely related to *Ampelosaurus* within Lirainosaurinae, defined by Díez Díaz et al. (2018) as the

clade including *Lirainosaurus astibiae*, *Ampelosaurus atacis*, their common ancestor, and all of its descendants. No autapomorphies have been recovered for *Garrigatitan*.

Discussion

Ontogeny

In general, all the sampled specimens of *Garrigatitan meridionalis* show similar histologic features. The samples do not represent a growth series but closely comparable developmental stages. The bones were quite well preserved as osteocytes are visible in every

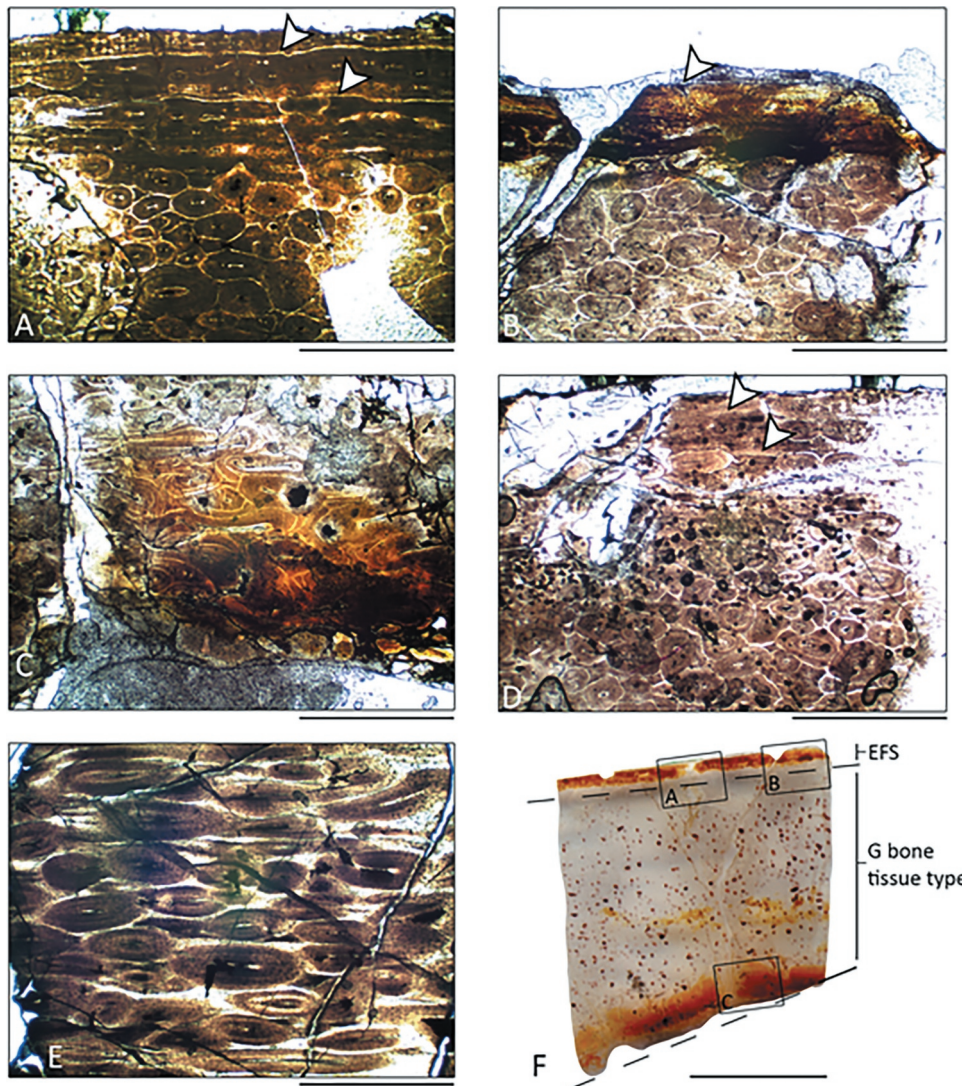


Figure 11. Bone histology of the titanosaur *Garrigatitan meridionalis* from the Late Cretaceous Velaux-La Bastide Neuve site (France). A–D and F) transverse sections. E) longitudinal section. (a) Outermost cortex of MMS/VBN.00.13 showing the edge of the remodelling front and LAG's (arrows) defining an EFS onset. (b) Open vascular canal (arrow) in the EFS onset of MMS/VBN.00.13. (c) Crushed, distorted secondary osteons at the innermost cortex of MMS/VBN.00.13. (d) Outermost cortex of MMS/VBN.09.A016 showing the edge of the remodelling front and LAG's (arrows) defining an EFS onset. (e) Heavily remodelled cortex of MMS/VBN.12.82. The main axis of secondary osteons is elongated parallel to the periosteal surface. (f) Overview of the sample of MMS/VBN.00.13. Black boxes locate microphotos A to C. All microphotos' scale bar = 1 mm. Core scale bar = 5 mm.

part of the cortex, the cortex itself is not completely fractured, and there is no evidence of extensive recrystallisation. Heavy remodelling is the main histologic pattern in the long bones of *Garrigatitan meridionalis*, comparable to that of the small European titanosaurs *Lirainosaurus astibiae* (adult specimen descriptions and Figure 5 in Company 2011), or *Magyarosaurus dacus* (Stein et al. 2010), and also found in *Atsinganosaurus velauciensis* (Díez Díaz et al. 2018). However, there are some features indicating residual growth in MMS/VBN.09.A.016 and MMS/VBN.00.013: (i) the EFS onset is highly vascularised albeit mature primary osteons are not very dense between the LAGs, and (ii) there are open vascular canals to the periosteal surface of the bone. This suggests that the remodelling process would have begun early in the ontogeny of this titanosaur compared to non-titanosaurian sauropods, at a rate that surpassed the apposition rate. This is consistent with the histology of juveniles of the titanosaur *Rapetosaurus krausei* (Rogers et al. 2016). If the haversian bone deposition rate is assumed to be constant throughout ontogeny (Mitchell and Sander 2014), the combination of a slow apposition rate with heavy remodelling prior to reaching the final

body size involves some kind of size reduction and/or insular dwarfism comparable to other titanosaurs in the Late Cretaceous European archipelago (e.g. *Lirainosaurus astibiae*, *Magyarosaurus dacus*, *Atsinganosaurus velauciensis* – Stein et al. 2010; Company 2011; Díez Díaz et al. 2018).

Among the sampled humeri, MMS/VBN.12.82 is intriguing because of its size, cortical thickness and ontogenetic status. Its cortex is clearly the thickest of all the samples. Even though this humerus is significantly longer than MMS/VBN.09.47 and MMS/VBN.09.A.016 (70.0 cm vs. 48.7–58.5 cm), its ontogenetic status is almost identical (type H and F bone tissues respectively). Longitudinal sections also underline diverging features in MMS/VBN.12.82 compared to the other sections. Only specimen MMS/VBN.12.82 shows clear elliptical secondary osteons (Figure 11(e)) distributed among normal (very elongated) ones throughout the cortex in longitudinal section. This implies that these osteons are obliquely oriented in relation to the long axis of the bone, an unusual pattern for neosauropods (Klein et al. 2012). It seems unlikely that Volkmann's canals could have

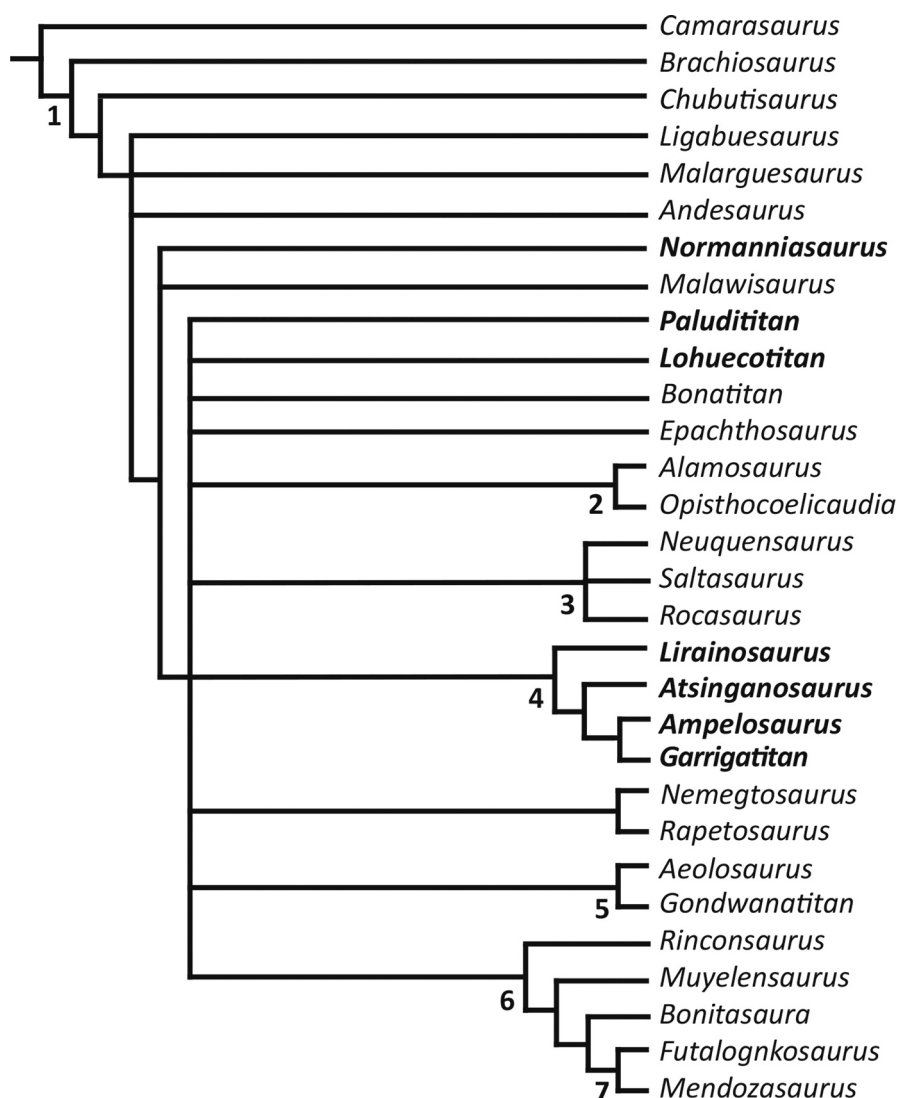


Figure 12. Phylogenetic hypothesis highlighting the position of *Garrigatitan*. Strict consensus tree of 10 MPTs and 184 steps, with a consistency index (CI) of 0.533 and a retention index (RI) of 0.631. The European taxa are highlighted in the cladogram. The nodes marked up are (1) Titanosauriformes, (2) Opisthocoelicaudiinae, (3) Saltosaurinae, (4) Lirainosaurinae, (5) Aeolosaurinae, (6) Rinconsauria, and (7) Lognkosauria. The nodes Titanosauria and Lithostrotia were not recovered.

been sectioned throughout the entire cortex mimicking secondary osteons only in MMS/VBN.12.82. The other sections show a normal longitudinal pattern of secondary osteons from the innermost cortex to the outermost one. As the radial section of MMS/VBN.12.82 shows normal histologic features similar to the other transverse sections, it is excluded that the MMS/VBN.12.82 longitudinal section was not cut along the long axis of the bone. Therefore, because of the similarity in histological maturity and difference in size, it is unlikely that MMS/VBN.12.82 followed the same growth trajectory as the other *Garrigatitan* individuals. It could represent a potential case of sexual dimorphism or a pathological individual of the same taxon. However, testing this hypothesis would require additional specimens, and thus lies beyond the scope of this paper.

Estimation of body size and mass for *Garrigatitan*

The estimated body length of *Atsinganosaurus velauciensis* was not correctly calculated in Díez Díaz et al. (2018) – Seebacher's (2001) equation was incorrectly used –, so it is re-calculated here. The body length range varies between 5.32 to 8.95 metres (ca. 5 to 9 metres), being smaller than previously suggested, and achieving lengths

more closely comparable to *Lirainosaurus astibiae* (ca. 4 to 6 metres, Díez Díaz et al. 2013b).

Using the smallest specimens of *Garrigatitan meridionalis* result in a body size of 4.37 metres (*sensu* Seebacher 2001), and a body mass of 1.85 tonnes (*sensu* Packard et al. 2009) to 2.2 tonnes (*sensu* Campione and Evans 2012), whereas with the largest specimens the same dimensions are 5.31 metres (*sensu* Seebacher 2001), and 2 tonnes (*sensu* Packard et al. 2009) to 2.45 tonnes (*sensu* Campione and Evans 2012), respectively. As the histological analyses indicate that no juvenile individuals were sampled, we tentatively suggest for the adults of *Garrigatitan* a body length of ca. 4 to 6 metres, and a body mass of ca. 2 to 2.5 tonnes. With these values *Garrigatitan* could be recognised as a small to medium sized titanosaur, being smaller than *Atsinganosaurus*, and with a similar length to *Lirainosaurus* (Díez Díaz et al. 2013b, 2018). However, the calculations show that the largest *Lirainosaurus* individuals could have been slightly heavier (ca. 1 ton) than those of *Garrigatitan*. Indeed, *Garrigatitan* and *Atsinganosaurus* seem to have been generally more slender than the Iberian titanosaur.

It is important to keep in mind that these equations only use the circumferences of the humeri and femora, and that the appendicular remains of *Garrigatitan* are relatively longer than the ones of

Atsinganosaurus (especially the ulna and the femur). In addition, the remains referred to *Garrigatitan* are not well preserved, and they were not found in articulation or associated, so they could very well belong to different individuals. Because of this, these body values should be used with caution, although they might serve as an approximation.

Phylogenetic relationships of *Garrigatitan* and palaeobiogeographical considerations

Garrigatitan is placed within the lithostrotian clade *Lirainosaurinae*, and is closely related with *Ampelosaurus*. This relationship can also be confirmed thanks to a detailed comparison of the remains ascribed to *Garrigatitan* with the ones referred to *Ampelosaurus*: both titanosaurs share the posterior laminae and fossae pattern, as well as the morphology, of the posterior cervical vertebrae; and the size (although most of the specimens referred to *Garrigatitan* are smaller) and robust anatomy of the humeri, ulnae and ischia. However, several differences between these taxa are obvious: e.g. the ulnar olecranon process is more developed in *Ampelosaurus*, and the femora are completely different.

Although further work is needed to better understand the complex relationships of Late Cretaceous titanosaurs from the Ibero-Armorican Island, the phylogenetic analysis supports that the taxa *Atsinganosaurus*, *Ampelosaurus* and *Garrigatitan* from southern France and *Lirainosaurus* from Spain are closely related, grouped in the clade *Lirainosaurinae*. Other titanosaurian taxa from the Campanian-Maastrichtian of Europe, such as *Paludititan* from Transylvania and *Lohuecotitan* from central Spain are included within a large polytomy, comprising most lithostrotians as well as *Lirainosaurinae*. *Lohuecotitan* and *Paludititan* appear grouped together as basal lithostrotians in eight of the ten MPT. In the other two MPT *Lohuecotitan* is placed as basal lithostrotian, and *Paludititan* appears as sister taxon of *Rinconsauria*. These two taxa would represent a second lineage of European titanosaurs different from *lirainosaurines*, but still more work on the phylogeny and biogeography of these titanosaurian groups is needed to assess this hypothesis.

From a palaeobiogeographical perspective, Díez Díaz et al. (2018) have proposed as a working hypothesis that the *Lirainosaurinae* clade was endemic to the Ibero-Armorican Island, and that it may be an example of a relict lineage of titanosaurs that evolved from a stock of older (Early Cretaceous?) Laurasian titanosaurs. One outstanding feature of the vertebrate faunas from the Late Cretaceous of Europe is the high number of relictual taxa, which could be explained by the archipelago palaeogeography (Csiki-Sava et al. 2015). They include dinosaurs (rhabdodontid ornithomorphs, struthiosaurine ankylosaurs), crocodyliforms (atoposaurids), squamates (borioteiid lizards), turtles (kallokibotionin meiolaniforms), and mammals (zhelestid eutherians, kogaionid multituberculates) (see references in Csiki-Sava et al. 2015). Tennant et al. (2016) restricted atoposaurid crocodyliforms to the Late Jurassic of Western Europe, but Venczel and Codrea (2019) expanded again their temporal span until the Maastrichtian thanks to the discovery of a new *Theriosuchus*-like crocodyliform from Romania, which seems to be more closely related to Atoposauridae than to Paralligatoridae. These evolutionary lineages, which originated prior to the Late Cretaceous, probably survived in refugia all across the Santonian-Maastrichtian European archipelago. A similar scenario could be suggested for the *lirainosaurine* lineage among titanosaurian sauropods.

Diversity of Campanian-Maastrichtian titanosaurs from the Ibero-Armorican Island

Our knowledge regarding the diversity and distribution of Campanian-Maastrichtian titanosaurs from the Ibero-Armorican

Island has greatly improved in recent years thanks to discoveries made in France and Spain (Le Loeuff 1995, 2005a; Garcia et al. 2010; Díez Díaz et al. 2011, 2012, 2013a, 2013b, 2014, 2015, 2016, 2018; Knoll et al. 2013, 2015; Páramo et al. 2020). Currently, five genera and species have been identified: *Ampelosaurus atacis*, *Atsinganosaurus velaucienensis* and *Garrigatitan meridionalis* from southern France, and *Lirainosaurus astibiae* and *Lohuecotitan pandaflandi* from the Iberian Peninsula. Based on phylogenetic analyses such as the one presented in this work, all these titanosaurs except *Lohuecotitan* are members of the clade *Lirainosaurinae*.

Atsinganosaurus and *Garrigatitan* occur together in the upper Campanian site of Velaux-La Bastide Neuve. The most numerous titanosaurian appendicular specimen found in this site is the humerus: three humeri have been referred to *Garrigatitan*, and three more to *Atsinganosaurus*. None of them have been found associated. In the case of *Garrigatitan* they do not show similar sizes, so the presence of at least two small-sized sub/adult and one medium-sized adult *Garrigatitan* individuals can be suggested. The most complete humeri described for *Atsinganosaurus* are both left and right specimens and have similar sizes, and although they were not found close between them, their referral to the same individual can not be ruled out. However, the presence of another fragmentary humerus and two left tibia confirms the presence of at least two adult *Atsinganosaurus* individuals in the Velaux-La Bastide Neuve site.

The presence of two distinct titanosaurs in the same locality is a common feature observed in the Ibero-Armorican sites, although there are exceptions (e.g. only a single titanosaur is known in Laño: *Lirainosaurus*). In Bellevue (Aude), a great morphological variability has been observed in the material assigned to *Ampelosaurus*, mainly within the appendicular remains (Vila et al. 2012), suggesting the presence of a second titanosaur. *Garrigatitan* shares many similarities with *Ampelosaurus*, and it cannot be excluded that part of the material found in the Bellevue site actually belongs to *Garrigatitan*. In order to test this hypothesis, a detailed review of all the titanosaurian specimens found in Bellevue would be welcome.

It is also interesting to highlight that some titanosaurs from the Late Cretaceous of Europe, including *lirainosaurines* from the Ibero-Armorican Island, are rather small animals in comparison with Late Cretaceous titanosaurs from other continents. Adult individuals of *Lirainosaurus* and *Atsinganosaurus*, and sub/adult *Garrigatitan* individuals reached lengths between 4 to 9 metres, and a body weight ranging from 2 to 6 tonnes (Table 3). Benson et al. (2018) calculated for the Transylvanian taxon *Magyarosaurus* a weight of 750 kg, while for the French titanosaur *Ampelosaurus* they obtained a weight of 2.5 tonnes (Benson et al. 2018, Dataset S1). A slowdown of the growth rate is coupled with a drastic body size reduction, and possibly correlated reduction in metabolic rate, in the small-sized *Magyarosaurus* and *Lirainosaurus* (Stein et al. 2010; Company 2011). The more normal-sized *Ampelosaurus* shows a similar reduction in growth rate but not in body size, possibly indicating also a reduced metabolic rate (Klein et al. 2012). These changes are interpreted as the result of dwarfing, an example of island life-related adaptations on the European archipelago during the Late Cretaceous (Klein et al. 2012; Csiki-Sava et al. 2015).

Small to medium-sized *lirainosaurines* (*Lirainosaurus*, *Atsinganosaurus* and the sub/adult individuals of *Garrigatitan*) coexisted in the Ibero-Occitanian area during the late Campanian. The normal-sized *lirainosaurines* *Ampelosaurus* and larger indeterminate titanosaurs are more frequently found in Maastrichtian sites of the Ibero-Armorican Island, namely in Languedoc and the southern Pyrenees of Aragon and Catalonia (Vila et al. 2012, 2018). However, and as previously stated, *Garrigatitan* adult individuals could have presented larger body sizes than the ones calculated in this work. Indeed, *Garrigatitan* is closely phylogenetic

Table 3. Length and weight estimates for the Late Cretaceous Ibero-Armorican titanosaurs *Lirainosaurus*, *Atsinganosaurus* and *Garrigatitan*. The values have been taken and updated from Díez Díaz et al. (2013b, 2018). The estimates have been calculated using the equations proposed by Packard et al. (2009) (¹ in the table), Campione and Evans (2012) (² in the table), and Seebacher (2001) (³ in the table).

	Lirainosaurus	Atsinganosaurus	Garrigatitan
Humerus and femur for min. PerH+F	MCNA 7463 and 14,465	MMS/VBN.09.A.018 and 09.126	MMS/VBN.09A.016 and 00.13
Humerus and femur for max. PerH+F	MCNA 7464 and 14,468	MMS/VBN.00.12 and 00.12	MMS/VBN.09.47 and 00.13
Min. mass¹	1540,23 Kg	2464,19 Kg	1845,6 Kg
Max. mass¹	2917,91 Kg	3612,92 Kg	2005,03 Kg
Min. mass²	1743,51 Kg	3201,92 Kg	2203,53 Kg
Max. mass²	3989,69 Kg	5258,28 Kg	2453,32 Kg
Min. length³ (using min. mass¹)	3,86 m	5,32 m	4,37 m
Min. length³ (using min. mass²)	4,2 m	6,37 m	4,62 m
Max. length³ (using max. mass¹)	5,98 m	6,92 m	4,93 m
Max. length³ (using max. mass²)	7,41 m	8,95 m	5,31 m

related with *Ampelosaurus*, which also has a large ulna referred to it. It could be hypothesised that the adult individuals of both taxa could achieve similar body sizes. A body length between 12 and 16 metres long has been estimated for the Australian titanosaur *Diamantinasaurus*, whose ulna measures 70 cm (Poropat et al. 2015) and probably had a body weight of ca. 23 tonnes (Benson et al. 2018). Extrapolating these data, the largest individuals of *Ampelosaurus* (largest ulna: 50 cm) and *Garrigatitan* (ulna: ca. 66 cm) could have also achieved similar body lengths, being ca. 3 times longer than the small sub/adult individuals lengths calculated in this work. The histological analyses do conclude that all the sampled bones present similar developmental stages. However, and previously indicated, it is not possible to confirm if this difference in body size between individuals is related to sexual dimorphism or any pathology.

Conclusions

In this work we describe new titanosaurian remains from the upper Campanian fossil-site of Velaux-La Bastide Neuve (southeastern France). A new genus and species is erected based on them: *Garrigatitan meridionalis* is a small to medium-sized titanosaur (length of ca. 4 to 6 metres, and body mass of approximately 2 to 2.5 tonnes for sub/adult individuals, ca. 12 to 16 metres for adult individuals) diagnosed by a unique combination of characters, including three (4 and 6) as autapomorphies: (1) posterior cervical vertebrae with a wide neural canal, (2) posterior cervical vertebrae with an anteroposteriorly compressed and paddle-shaped neural spine (not wider than the centrum), (3) posterior cervical vertebrae postzygapophyses with a wide separation between them and laterally oriented articulation surfaces, (4) hourglass-shaped humeri (proximal and distal thirds of almost the same transversal width) in anterior and posterior views, (5) ilium with a broad rounded hollow slightly posterior to the base of the pubic peduncle, (6) proximolateral margin of the femur only slightly medially deflected. It is noticeable that, despite the size differences between several appendicular bones referred to *Garrigatitan*, all of these show similar histological features, thus representing close developmental stages. This could mean that several taxa are present in the material here referred to *Garrigatitan*. A similar case was reported for *Magyarosaurus* from the Hateg Basin of Romania (Stein et al. 2010), however the second taxon in the Hateg assemblage was significantly larger in size (double humerus length), and showed less advanced HOS. Alternatively, the slight size differences in the *Garrigatitan* materials could be related to sexual dimorphism. Unfortunately, assessing this hypothesis is not possible with the current available limited material.

To conclude, two different titanosaurs are present in the Velaux-La Bastide Neuve site of Provence: *Garrigatitan meridionalis* and *Atsinganosaurus velauciensis*. The general anatomy of the appendicular

remains is different between the two taxa; the neural spines of the cervical vertebrae have different morphologies, in addition to the differing size of the neural canal; the laminae and fossae patterns of their sacra are different; the autapomorphic pubic peduncle of *Atsinganosaurus* is not present in the ilium of *Garrigatitan*, and *Atsinganosaurus* does not have a hollow in the base of its pubic peduncle; finally, the morphology of the ischia and femora are also different between both. Most of these differences can be also recognised when comparing *Garrigatitan* to the Iberian titanosaur *Lirainosaurus* as well (with the exception of the hollow of the ilium).

The presence of two titanosaurian taxa in the same locality is not exclusive to Velaux-La Bastide Neuve, but appears to be the case in other Campanian-Maastrichtian Ibero-Armorican sites as well, such as Lo Hueco and Chera in Spain, and Fox-Amphoux-Métisson and probably Bellevue in southern France.

A phylogenetic analysis suggests that *Garrigatitan* is a member of Lirainosaurinae, grouping with *Atsinganosaurus*, and *Lirainosaurus* with *Ampelosaurus* as sister-taxon to this clade. Lirainosaurines from the late Campanian are small to medium-sized titanosaurs only known so far in the Ibero-Armorican Island. Other components of the titanosaurian fauna known from the Campanian-Maastrichtian of central and southern Europe are small to medium lithostrotians, suggesting a high taxonomic diversity.

Acknowledgments

We would like to acknowledge A. Montaufier for the photographs (with financial support of the Lisea-Vinci group), and C. Zafrá for the edition of the figures. We thank J. C. Corral and J. Alonso (Museo de Ciencias Naturales de Álava/Arabako Natur Zientzien Museoa, Vitoria-Gasteiz, Spain), B. Madarieta (Museo Vasco de Historia de la Medicina y de las Ciencias of Leioa, Spain), F. Ortega (Grupo de Biología Evolutiva, Universidad Nacional de Educación a Distancia, Spain), J. Le Loëuff (Musée des Dinosauriens d'Espéraza, France), and P. Barrett and S. Maidment (Natural History Museum London, U.K.). F. Holwerda (Utrecht University, Utrecht, The Netherlands) and E. Tschopp (American Museum of Natural History, New York, USA) helped in the development of the phylogenetic analysis, and P. Mannion (UCL, U.K.) is thanked for the photographs of *Normanniasaurus* and his useful comments and help. The Willi Hennig Society sponsors the use of the TNT cladistics software. BJC thanks J. Laval for producing the thin sections for histologic purposes, V. Fischer for his useful critics on the long bone histology part, and Khimaerai (J. Jentgen) for having helped a lot to produce the histologic figures. We would like to thank the editor G. Dyke, and the useful comments and suggestions provided by S. Poropat and two anonymous reviewers, which greatly improved this manuscript.

This work has been developed thanks to the collaboration between Palaios (a research association presided by XV), the University of Poitiers, the Velaux Municipality (Y. Guérin, J.-P. Maggi, and C. Peru) with its heritage, culture and technical services (M. Calvier) and association "Les amis du patrimoine" (L. Melih), the environment department from CD 13 (M. Bourrelly, T. Tortosa, G. Michel, N. Mouly, and S. Amico), the 'Service Départemental d'Incendie et de Secours' (SDIS 13), and numerous volunteers during the field campaigns in 2009 and 2012 (particularly N. Bardet, T. Beauprez, A. Bernet, S. Berton, A. Cincotta, M. Bournoneville, D. Brossens, S. Goolaerts, L. Guiraud, T. Hublin, P. Lauters, B. Mertens,

L. Villier and D. de Winter). This work was supported by the Ministry of Education and Communication (research grant VR1013 to Palaios association), the Bouches du Rhône department CD 13 proposals MAPADGAC23112010-1 and MAPADGAC16012014-1-AAPC. Research work of XPS was supported by the Spanish Ministerio de Ciencia e Innovación (project CGL2017-85038-P), the European Regional Development Fund, the Gobierno Vasco/Eusko Jaurlaritz (research group IT-1418-19) and the Universidad del País Vasco (UPV/EHU, research group PPG17/05), and that of BJC by a FRIA grant of the Fonds de la Recherche Scientifique. KS thanks the Fonds Wetenschappelijk Onderzoek for funding.

Disclosure statement

The authors declare no conflict of interest.

Funding

This work was supported by the European Regional Development Fund; Fonds de la Recherche Scientifique - FNRS; Fonds Wetenschappelijk Onderzoek; Spanish Ministerio de Ciencia e Innovación [CGL2017-85038-P]; Gobierno Vasco/Eusko Jaurlaritz [IT-1418-19]; Bouches du Rhône department CD 13 [MAPADGAC16012014-1-AAPC,MAPADGAC23112010-1]; French Ministry of Education and Communication [VR1013]; Universidad del País Vasco [PPG17/05].

ORCID

Verónica Díez Díaz  <http://orcid.org/0000-0002-9840-9829>

References

- Ascenzi A, Bonucci E. 1968. The compressive properties of single osteons. *Anat Rec.* 161(3):377–391. doi:10.1002/ar.1091610309.
- Benson RB, Hunt G, Carrano MT, Campione N. 2018. Cope's rule and the adaptive landscape of dinosaur body size evolution. *Palaeontology.* 61(1):13–48. doi:10.1111/pala.12329.
- Bonaparte JF, Coria RA. 1993. Un nuevo y gigantesco saurópodo titanosaurio de la Formación Río Limay (Albiano-Cenomanio) de la Provincia del Neuquén, Argentina. *Ameghiniana.* 30:271–282.
- 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. *Cret Res.* 27(3):364–376. doi:10.1016/j.cretres.2005.07.004.
- Borsuk-Bialynicka M. 1977. A new camarasaurid sauropod *Ophthocoelicaudia skarzynskii* gen. n., sp. n. from the Upper Cretaceous of Mongolia. *Palaeontol Pol.* 37:5–64.
- Buffetaut E, Le Loeuff J, Duffaud S, Cavin L, Garcia G, Tong H, Ward D; ACAP. 1999. Un nouveau gisement de vertébrés du Crétacé supérieur à Cruzy (Hérault, Sud de la France). *C R Acad Sci.* 328:203–208.
- Calvo JO, Porfiri JD, González-Riga BJ, Kellner AWA. 2007. A new Cretaceous terrestrial ecosystem from Gondwana with the description of a new sauropod dinosaur. *An Acad Bras Ciênc.* 79(3):529–541. doi:10.1590/S0001-37652007000300013.
- Campione NE, Evans DC. 2012. A universal scaling relationship between body mass and proximal limb bone dimensions in quadrupedal terrestrial tetrapods. *BMC Biol.* 10(1):60.
- Carballido JL, Pol D, Otero A, Cerda IA, Salgado L, Garrido AC, Ramezani J, Cúneo NR, Krause JM. 2017. A new giant titanosaur sheds light on body mass evolution among sauropod dinosaurs. *Proc Royal Soc London B.* 284:20171219.
- Cavin L, Buffetaut E, Dutour Y, Garcia G, Le Loeuff J, Mechin A, Méchin P, Tong H, Tortosa T, Turini E, et al. 2020. The last known freshwater coelacanth: new Late Cretaceous mawsoniid remains (Osteichthyes: Actinistia) from southern France. *PLOS ONE.* 15(6):e0234183. doi:10.1371/journal.pone.0234183.
- Cerda IA, Salgado L, Powell JE. 2012. Extreme postcranial pneumaticity in sauropod dinosaurs from South America. *Palaeontol Z.* 86(4):441–449. doi:10.1007/s12542-012-0140-6.
- Cincotta A, Yans Y, Godefroit P, Garcia G, Dejaj J, Benammi M, Amico S, Valentin X. 2015. Integrated paleoenvironmental reconstruction and taphonomy of a unique Upper Cretaceous vertebrate-bearing locality (Velaux, southeastern France). *PLOS ONE.* 10(8):e0134231. doi:10.1371/journal.pone.0134231.
- Company J. 2011. Bone histology of the titanosaur *Lirainosaurus astibiae* (Dinosauria: sauropoda) from the Latest Cretaceous of Spain. *Naturwissenschaften.* 98(1):67–78. doi:10.1007/s00114-010-0742-3.
- Company J, Pereda Suberbiola X, Ruiz-Omeñaca JI. 2009. Nuevos restos fósiles del dinosaurio *Lirainosaurus* (Sauropoda, Titanosauria) en el Cretácico Superior (Campaniano-Maastrichtiano) de la Península Ibérica. *Ameghiniana.* 46(2):391–405.
- Csiki Z, Codrea V, Jipa-Murzea C, Godefroit P. 2010. A partial titanosaur (Sauropoda, Dinosauria) skeleton from the Maastrichtian of Nălaț-Vad, Hațeg, Basin, Romania. *N Jb Geol Paläont Abh.* 258(3):297–324. doi:10.1127/0077-7749/2010/0098.
- Csiki-Sava Z, Buffetaut E, Ösi A, Pereda-Suberbiola X, Brusatte SL. 2015. Island life in the Cretaceous - faunal composition, biogeography, evolution, and extinction of land-living vertebrates on the Late Cretaceous European archipelago. *ZooKeys.* 469:1–161. doi:10.3897/zookeys.469.8439.
- Curry Rogers K. 2009. The postcranial osteology of *Rapetosaurus krausei* (Sauropoda: titanosauria) from the Late Cretaceous of Madagascar. *J Vertebr Paleontol.* 29(4):1046–1086. doi:10.1671/039.029.0432.
- D'Emic MD. 2012. The early evolution of titanosauriform sauropod dinosaurs. *Zool J Linn Soc.* 166:624–671. doi:10.1111/j.1096-3642.2012.00853.x.
- D'Emic MD, Wilson JA. 2011. New remains attributable to the Holotype of the Sauropod Dinosaur *Neuquensaurus australis*, with implications for saltasaurine systematics. *Acta Palaeontol Pol.* 56(1):61–73. doi:10.4202/app.2009.0149.
- Díez Díaz V. 2013. Revisión del dinosaurio saurópodo *Lirainosaurus astibiae*. (Titanosauria) del Cretácico Superior de la Península Ibérica. Comparación con otros titanosaurios del suroeste de Europa. Hipótesis filogenética y paleobiogeográfica [Unpublished Ph.D Thesis] (306 pp). Bilbao (Bilbao): Universidad del País Vasco/EHU.
- Díez Díaz V, Garcia G, Knoll F, Pereda Suberbiola X, Valentin X. 2012. New cranial remains of titanosaurian sauropod dinosaurs from the Late Cretaceous of Fox-Amphoux-Métisson (Var, SE France). *Proc Geol Assoc.* 123(4):626–637. doi:10.1016/j.pgeola.2012.04.002.
- Díez Díaz V, Garcia G, Pereda Suberbiola X, Jentgen-Ceschino B, Stein K, Godefroit P, Valentin X. 2018. The titanosaurian dinosaur *Atsinganosaurus velauciensis* (Sauropoda) from the Upper Cretaceous of southern France: new material, phylogenetic affinities, and palaeobiogeographical implications. *Cret Res.* 91:429–456. doi:10.1016/j.cretres.2018.06.015.
- 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). *Cret Res.* 68:49–60. doi:10.1016/j.cretres.2016.08.001.
- Díez Díaz V, Ortega F, Sanz JL. 2014. Titanosaurian teeth from the Upper Cretaceous of “Lo Hueco” (Cuenca, Spain). *Cret Res.* 51:285–291. doi:10.1016/j.cretres.2014.07.003.
- Díez Díaz V, Pereda Suberbiola X, Company J. 2015. Puesta al día de la diversidad de titanosaurios (Sauropoda) del Cretácico Superior de España. *Spanish J Paleontol.* 30(2):293–306.
- Díez Díaz V, Pereda Suberbiola X, Sanz JL. 2011. Braincase Anatomy of the Titanosaurian Sauropod *Lirainosaurus astibiae* from the Late Cretaceous of the Iberian Peninsula. *Acta Palaeontol Pol.* 56(3):521–533. doi:10.4202/app.2010.0043.
- Díez Díaz V, Pereda Suberbiola X, Sanz JL. 2013a. The axial skeleton of the titanosaur *Lirainosaurus astibiae* (Dinosauria: sauropoda) from the latest Cretaceous of Spain. *Cret Res.* 43:145–160. doi:10.1016/j.cretres.2013.03.002.
- Díez Díaz V, Pereda Suberbiola X, Sanz JL. 2013b. Appendicular skeleton and dermal armour of the Late Cretaceous titanosaur *Lirainosaurus astibiae* (Dinosauria: sauropoda) from Spain. *Palaeontol Electron.* 16(2):19A, 18p.
- Gallina PA. 2011. Notes on the axial skeleton of the titanosaur *Bonitasaura salgadoi* (Dinosauria-Sauropoda). *An Acad Bras Ciênc.* 83(1):235–246. doi:10.1590/S0001-37652011005000001.
- Gallina PA, Apesteguía S. 2015. Postcranial anatomy of *Bonitasaura salgadoi* (Sauropoda, Titanosauria) from the Late Cretaceous of Patagonia. *J Vertebr Paleontol.* 35(3):3, e924957. doi:10.1080/02724634.2014.924957.
- García G, Amico S, Fournier F, Thouand E, Valentin X. 2010. A new titanosaur genus (Dinosauria, Sauropoda) from the Late Cretaceous of southern France and its paleobiogeographic implications. *Bull Soc Géol France.* 181:269–277.
- Godefroit P, Garcia G, Gomez B, Stein K, Cincotta A, Lefevre U, Valentin X. 2017. Extreme tooth enlargement in a new Late Cretaceous rhabdodontid dinosaur from Southern France. *Sci Rep.* 7(1):13098. doi:10.1038/s41598-017-13160-2.
- Goloboff P, Farris J, Nixon K. 2008. TNT, a free program for phylogenetic analysis. *Cladistics.* 24(5):774–786. doi:10.1111/j.1096-0031.2008.00217.x.
- Gomani EM. 2005. Sauropod dinosaurs from the early Cretaceous of Malawi, Africa. *Palaeontol Electron.* 8(1):1–37.
- González Riga BJ, Mannion PD, Poropat SF, Ortiz David L, Coria JP. 2018. Osteology of the Late Cretaceous Argentinean sauropod dinosaur

- Mendozasaurus neguyelap*: implications for basal titanosaur relationships. *Zool J Linn Soc.* 184(1):136–181. doi:10.1093/zoolinnean/zlx103.
- González Riga BJ, Ortiz David L. 2014. A new titanosaur (Dinosauria, Sauropoda) from the Upper Cretaceous (Cerro Lisandro Formation) of Mendoza Province, Argentina. *Ameghiniana.* 51(1):3–25. doi:10.5710/AMEGH.26.12.1013.1889.
- González Riga BJ, Previtera E, Pirrone CA. 2009. *Malarguesaurus florenciae* gen. et sp. nov., a new titanosauriform (Dinosauria, Sauropoda) from the Upper Cretaceous of Mendoza, Argentina. *Cret Res.* 30(1):135–148. doi:10.1016/j.cretres.2008.06.006.
- Huene F. 1929. Los Saurisquios y Ornithisquios del Cretáceo Argentino. *Anales Mus La Plata.* 2:1–196.
- Huene F. 1932. Die fossil Reptil-Ordnung Saurischia, ihre Entwicklung und Geschichte. *Monogr Geol Palaeontol.* 4:1–361.
- Klein N, Christian A, Sander PM. 2012. Histology shows that elongated neck ribs in sauropod dinosaurs are ossified tendons. *Biol Lett.* 8(6):1032–1035. doi:10.1098/rsbl.2012.0778.
- Klein N, Sander PM. 2008. Ontogenetic stages in the long bone histology of sauropod dinosaurs. *Paleobiology.* 34(2):247–263. [https://doi.org/10.1666/0094-8373\(2008\)034\[0247:OSITLB\]2.0.CO;2](https://doi.org/10.1666/0094-8373(2008)034[0247:OSITLB]2.0.CO;2).
- Knoll F, Lautenschlager S, Valentin X, Diez Díaz V, Pereda Suberbiola X, García G. 2019. First palaeoneurological study of a sauropod dinosaur from France and its phylogenetic significance. *Peer J.* 7:e7991. doi:10.7717/peerj.7991.
- Knoll F, Ridgely RC, Ortega F, Sanz JL, Witmer LM. 2013. Neurocranial osteology and neuroanatomy of a Late Cretaceous titanosaurian sauropod from Spain (*Ampelosaurus* sp.). *PLoS ONE.* 8(1):e54991. doi:10.1371/journal.pone.0054991.
- Knoll F, Witmer LM, Ridgely RC, Ortega F, Sanz JL. 2015. A new titanosaurian braincase from the Cretaceous “Lo Hueco” locality in Spain sheds light on neuroanatomical evolution within Titanosauria. *PLoS ONE.* 10(10):e0138233. doi:10.1371/journal.pone.0138233.
- Lapparent AF. 1947. Les dinosaouriens du Crétacé supérieur du Midi de France. *Mém Soc Géol France NS.* 56:1–54.
- Le Loeuff J. 1992. Les vertébrés continentaux du Crétacé supérieur d'Europe: Paléocologie, Biostratigraphie et Paléobiogéographie [Unpublished Ph.D. Thesis] Paris (France): Université Pierre et Marie Curie, Paris VI, Mém. Sci. Terre 92–293.
- Le Loeuff J. 1995. *Ampelosaurus atacis* (nov. gen., nov. sp.) un nouveau Titanosauridae (Dinosauria, Sauropoda) du Crétacé supérieur de la Haute Vallée de l'Aude (France). *C R Acad Sci Paris.* 321(IIa):693–699.
- Le Loeuff J. 2005a. Osteology of *Ampelosaurus atacis* (Titanosauria) from Southern France. In: Tidwell V, Carpenter K, editors. *Thunder-Lizards. The Sauropodomorph Dinosaurs.* Bloomington and Indianapolis: Indiana University Press; p. 115–137.
- Le Loeuff J. 2005b. Romanian Late Cretaceous dinosaurs: big dwarfs or small giants? *Hist Biol.* 17(1–4):15–17. doi:10.1080/08912960500376210.
- Le Loeuff J, Suteethorn S, Buffetaut E. 2013. A new sauropod dinosaur from the Albian of Le Havre (Normandy, France). *Oryctos.* 10:23–30.
- 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. *Zool J Linn Soc.* 168:98–206. doi:10.1111/zoj.12029.
- Marsh OC. 1878. Principal characters of American Jurassic dinosaurs. Part I. *Am J Sci.* s3-16(95):411–416. doi:10.2475/ajs.s3-16.95.411.
- Martin J, Delfino M, García G, Godefroit P, Berton S, Valentin X. 2016. New specimens of *Allodaposuchus precedens* from France: intraspecific variability and the diversity of European Late Cretaceous eusuchians. *Zool J Linn Soc.* 176(3):607–631. doi:10.1111/zoj.12331.
- Matheron P. 1869. Note sur les reptiles fossiles des dépôts fluvio-lacustres crétacés du bassin à lignite de Fuveau. *Bull Soc Géol France.* 26:781–795.
- Mitchell J, Sander PM. 2014. The three-front model: a developmental explanation of long bone diaphyseal histology of Sauropoda. *Biol J Linn Soc.* 112(4):765–781. doi:10.1111/bij.12324.
- Mitchell J, Sander PM, Stein KHW. 2017. Can secondary osteons be used as ontogenetic indicators in sauropods? Extending the histological ontogenetic stages into senescence. *Paleobiology.* 43(2):321–342. doi:10.1017/pab.2016.47.
- Nopcsa F. 1915. Die Dinosaurier der Siebenbürgischen Landsteile Ungarns. *Mitteil Jb kön Ungar Geol Reichsanst.* 23:3–24.
- Owen R. 1842. Report on British Fossil Reptiles. Part II. Report of the British Association for the Advancement of Science 11: 60–204.
- Packard GC, Boardman TJ, Birchard GF. 2009. Allometric equations for predicting body mass of dinosaurs. *J Zool.* 279(1):102–110. doi:10.1111/j.1469-7998.2009.00594.x.
- Páramo A, Mocho P, Ortega F. 2020. Three-dimensional analysis of the titanosaurian limb skeleton: implications for systematic analysis. *J Iber Geol.* doi:10.1007/s41513-020-00139-8.
- Páramo A, Ortega F, Sanz JL. 2015a. Two types of appendicular bones of titanosaurs (Dinosauria, Sauropoda) from Lo Hueco (Fuentes, Cuenca). 63rd Symposium for Vertebrate Palaeontology and Comparative Anatomy 24th Symposium of Palaeontological Preparation and Conservation with the Geological Curators' Group (Abstract Book)O. p. 100.
- Páramo A, Ortega F, Sanz JL. 2015b. Preliminary assessment of the morphological variability of appendicular bones of titanosaurs (Dinosauria, Sauropoda) from Lo Hueco (Fuentes, Cuenca). In: Reolid M, editor. *Libro de resúmenes de las XXXI Jornadas de Paleontología de la Sociedad Española de Paleontología.* p. 225–226.
- Poropat SF, Mannion PD, Upchurch P, Hocknull SA, Kear BP, Kundrat M, Tischler TT, Sloan T, Sinapius GHK, Elliott JA, et al. 2016. New Australian sauropods shed light on Cretaceous dinosaur palaeobiogeography. *Sci Rep.* 6(1):34467. doi:10.1038/srep34467.
- Poropat SF, Upchurch P, Mannion PD, Hocknull SA, Kear BP, Sloan T, Sinapius GHK, Elliott DA. 2015. Revision of the sauropod dinosaur *Diamantinasaurus matildae* Hocknull et al. 2009 from the mid-Cretaceous of Australia: implications for Gondwanan titanosauriform dispersal. *Gondwana Res.* 27(3):995–1033. doi:10.1016/j.gr.2014.03.014.
- Robin N, van Bakel BWM, Hyžný M, Cincotta A, García G, Charbonnier S, Godefroit P, Valentin X. 2019. The oldest freshwater crabs: claws on dinosaur bones. *Sci Rep.* 9:20220. doi:10.1038/s41598-019-56180-w.
- Rogers KC, Whitney M, D'Emic M, Bagley B. 2016. Precocity in a tiny titanosaur from the Cretaceous of Madagascar. *Science.* 352(6284):450–453. doi:10.1126/science.aaf1509.
- Salgado L, Apesteguía S, Heredia SE. 2005. A new specimen of *Neuquensaurus australis*, a Late Cretaceous saltasaurine titanosaur from north Patagonia. *J Vertebr Paleontol.* 25(3):623–634. [https://doi.org/10.1671/0272-4634\(2005\)025\[0623:ANSONA\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2005)025[0623:ANSONA]2.0.CO;2).
- Salgado L, Coria RA, Calvo JO. 1997. Evolution of titanosaurid sauropods I: phylogenetic analysis based on the postcranial evidence. *Ameghiniana.* 34(1):3–32.
- Salgado L, Gallina PA, Paulina Carabajal A. 2015. Redescription of *Bonattitan reigi* (Sauropoda: titanosauria) from the Campanian–Maastrichtian of the Río Negro Province (Argentina). *Hist Biol.* 27(5):525–548. doi:10.1080/08912963.2014.894038.
- Sallam HM, Gorscak E, O'Connor PM, El-Dawoudi IA, El-Sayed S, Saber S, Kora MA, Sertich JJW, Seiffert ER, Lamanna MC. 2018. New Egyptian sauropod reveals Late Cretaceous dinosaur dispersal between Europe and Africa. *Nat Ecol Evol.* 2(3):445–451. doi:10.1038/s41559-017-0455-5.
- Sander PM, Klein N, Stein K, Wings O. 2011. Sauropod bone histology and implications for sauropod biology. In: Klein N, Remes K, Gee CT, Sander PM, editors. *Biology of the Sauropod Dinosaurs: understanding the life of giants.* Bloomington: Indiana University Press; p. 276–302.
- 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. *Est Mus Cienc Nat Alava.* 14 (Número esp. 1):235–255.
- Seebacher F. 2001. A new method to calculate allometric length-mass relationships of dinosaurs. *J Vertebr Paleontol.* 21(1):51–60. [https://doi.org/10.1671/0272-4634\(2001\)021\[0051:ANMTCA\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2001)021[0051:ANMTCA]2.0.CO;2).
- Seeley HG. 1887. On the classification of the fossil animals commonly called Dinosauria. *Proc Royal Soc London.* 43(printed 1888):165–171.
- Stein K, Csiki Z, Rogers KC, Weishampel DB, Redelstorff R, Carballido JL, Sander PM. 2010. Small body size and extreme cortical bone remodeling indicate phyletic dwarfism in *Magyarosaurus dacus* (Sauropoda: titanosauria). *PNAS.* 107(20):9258–9263. doi:10.1073/pnas.1000781107.
- Stein K, Sander PM. 2009. Histological core drilling: a less destructive method for studying bone histology. In: Brown MA, Kane JF, Parker WG, editors. *Methods in Fossil Preparation: Proceedings of the First Annual Fossil Preparation and Collections Symposium, Petrified Forest National Park (Arizona, USA).* p. 69–80.
- Tennant JP, Mannion PD, Upchurch P. 2016. Evolutionary relationships and systematics of Atoposauridae (Crocodylomorpha: neosuchia): implications for the rise of Eusuchia. *Zool J Linn Soc.* 177(4):854–936. doi:10.1111/zoj.12400.
- Tykoski RS, Fiorillo AR. 2016. An articulated cervical series of *Alamosaurus sanjuanensis* Gilmore, 1922 (Dinosauria, Sauropoda) from Texas: new perspective on the relationships of North America's last giant sauropod. *J Syst Paleontol.* doi:10.1080/14772019.2016.1183150.
- Upchurch P, Barrett P, Dodson P. 2004. *Sauropoda.* In: Weishampel DB, Dodson P, Osmólska H, editors. *The Dinosauria.* 2nd ed. Berkeley: University of California Press; pp. 259–324.
- Venczel M, Codrea VA. 2019. A new Theriosuchus-like crocodyliform from the Maastrichtian of Romania. *Cret Res.* 100:24–38. doi:10.1016/j.cretres.2019.03.018.

- Vila B, Galobart À, Canudo JJ, Le Loeuff J, Dinarés-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. *Palaeogeogr Palaeoclimatol Palaeoecol.* 350-352:19–38. doi:10.1016/j.palaeo.2012.06.008.
- Vila B, Sellés AG, Galobart À, Canudo JJ, Marmi J, Gaete R. 2018. New titanosaurian findings from historical localities of the Treppe Basin (Maastrichtian, Pyrenees). In: Marzola M, Mateus O, Moreno-Azanza M, editors. Abstract book of the XVI Annual Meeting of the European Association of Vertebrate Palaeontology. Caparica (Portugal June 26th–July 1st); p. 194.
- Vullo R, Garcia G, Godefroit P, Cincotta A, Valentin X. 2018. *Mistralazhdarcho maggii* gen. et sp. nov., a new azhdarchid pterosaur from the Upper Cretaceous of southeastern France. *J Vertebr Paleontol.* 38(4):1–16. doi:10.1080/02724634.2018.1502670.
- Wilson JA. 1999. A nomenclature for vertebral laminae in sauropods and other saurischian dinosaurs. *J Vertebr Paleontol.* 19(4):639–653. doi:10.1080/02724634.1999.10011178.
- Wilson JA. 2002. Sauropod dinosaur phylogeny: critique and cladistic analysis. *Zool J Linn Soc.* 136:217–276.
- Wilson JA. 2006. Anatomical nomenclature of fossil vertebrates: standardized terms or lingua franca? *J Vertebr Paleontol.* 26(3):511–518. [https://doi.org/10.1671/0272-4634\(2006\)26\[511:ANOFVS\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2006)26[511:ANOFVS]2.0.CO;2).
- Wilson JA. 2011. Anatomical terminology for the sacrum of sauropod dinosaurs. *Contrib Mus Paleontol Univ Michigan.* 32:59–69.
- Wilson JA, Carrano MT. 1999. Titanosaurs and the origin of “Wide-Gauge”. *Trackways: A Biomechanical and Systematic Perspective on Sauropod Locomotion. Paleobiology;* p. 252–267.
- Wilson JA, D’Emic MD, Ikejiri T, Moacdieh EM, Withlock JA. 2011. A nomenclature for vertebral fossae in sauropods and other saurischian dinosaurs. *PLOS ONE.* 6(2):e17114. doi:10.1371/journal.pone.0017114.
- Wilson JA, Sereno PC. 1998. Early evolution and higher-level phylogeny of sauropod dinosaurs. *J Vertebr Paleontol.* 18(Suppl. to 2):1–68. (Society of Vertebrate Paleontology, Memoir 5). 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. *J Syst Palaeontol.* 7(2):199–239. doi:10.1017/S1477201908002691.