SPANISH JOURNAL OF PALAEONTOLOGY

Updating titanosaurian diversity (Sauropoda) from the Late Cretaceous of Spain: the fossil sites of Laño and Chera

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Díez Díaz, V., Pereda Suberbiola, X. & Company, J. 2015. Updating titanosaurian diversity (Sauropoda) from the Late Cretaceous of Spain: the fossil sites of Laño and Chera. [Revisión de la diversidad de titanosaurios (Sauropoda) del Cretácico Superior de España: los yacimientos de Laño y Chera]. *Spanish Journal of Palaeontology*, 30 (2), 293-306.

Manuscript received 23 March 2015
Manuscript accepted 09 September 2015

ABSTRACT

Three titanosaurian sauropods are well-known from the Campanian-Maastrichtian of the Ibero-Armorican Island (southwestern Europe): *Lirainosaurus astibiae* from Spain, and *Ampelosaurus atacis* and *Atsinganosaurus velauciensis* from France. However, a higher titanosaurian diversity has been suggested for this island, a hypothesis that has gained traction in recent years as a result of new discoveries in fossil sites from Spain and southern France. An estimation of the titanosaurian diversity in the late Campanian-early Maastrichtian of the Iberian Peninsula is made here on the basis of the available information from the three fossil sites that have yielded the best preserved fossil remains: Laño (Condado de Treviño), Chera (Valencia), and Lo Hueco (Cuenca). The results confirm the hypothesis of a higher titanosaurian diversity in the Iberian Peninsula: from one to, at least, three taxa. Moreover, we also suggest the presence of two different titanosaurian morphotypes in the site of Chera, with one of them representing *Lirainosaurus.*

Keywords: Dinosauria, Sauropoda, Titanosauria, Campanian-Maastrichtian, Iberia.

RESUMEN

A día de hoy se conocen tres saurópodos titanosaurios en el Campaniense-Maastrichtiense del Dominio Ibero-Armoricano (suroeste de Europa): *Lirainosaurus astibiae* en España, y *Ampelosaurus atacis* y *Atsinganosaurus velauciensis* en Francia. Sin embargo, varios autores han sugerido una mayor diversidad de los titanosaurios iberoarmoricanos, una hipótesis que está ganando fuerza en los últimos años gracias al descubrimiento de nuevos yacimientos en España y el sur de Francia. En este trabajo se realiza una estimación de la diversidad de titanosaurios en el Campaniense superior-Maastrichtiense inferior de la Península Ibérica a partir de la información obtenida en los tres yacimientos donde se han encontrado los restos fósiles mejor preservados: Laño (Condado de Treviño), Chera (Valencia) y Lo Hueco (Cuenca). Los resultados confirman la hipótesis de una mayor diversidad de titanosaurios en la Península Ibérica, pasando de uno a, al menos, tres taxones. Igualmente, se sugiere la presencia de dos morfotipos diferentes de titanosaurios en el yacimiento de Chera, siendo uno de ellos *Lirainosaurus.*

Palabras clave: Dinosauria, Sauropoda, Titanosauria, Campaniense-Maastrichtiense, Iberia.

https://doi.org/10.7203/sjp.30.2.17258

1. INTRODUCTION

The first titanosaurian remains recovered in the Iberian Peninsula mainly consist of fragmentary or badly preserved fossil bones. Lapparent & Aguirre (1956, 1957) described some appendicular remains found in the Tremp Basin (Maastrichtian) of Lleida, and identified them as belonging to *Hypselosaurus* sp. and *Titanosaurus* cf. *indicus* (both considered now as *nomina dubia*). Since then, more than ten Late Cretaceous fossil sites with titanosaurian remains have been discovered, some of them located in the provinces of Álava, Guadalajara, Segovia, and Soria (Lapparent *et al.*, 1957; Sanz & Buscalioni, 1987; Pereda-Suberbiola *et al*., 1999; Ortega & Pérez-García, 2009; Royo-Torres, 2009), although nearly all of these titanosaurian remains were found isolated and/or are badly preserved (Fig. 1). This situation changed in the last two decades thanks to the discovery of important fossil sites that have yielded titanosaurian remains in Spain: Laño (Condado de Treviño), Chera (Valencia), and Lo Hueco (Cuenca). Thanks to the information gathered in these three sites we can estimate the titanosaurian diversity from the Late Cretaceous (late Campanian to early Maastrichtian) of the Iberian Peninsula.

Lirainosaurus astibiae was described on the basis of fossil remains found at the end of the 20th century in the Laño quarry (Sanz *et al*., 1999). This site is located in a sand quarry between the villages of Laño and Albaina (Condado de Treviño, northern Spain). Laño has yielded one of the most important and diversified European continental vertebrate assemblages from the Late Cretaceous, including remains of bony fishes, amphibians, lizards, snakes, turtles, crocodilians, pterosaurs, dinosaurs and mammals (Astibia *et al*., 1990, 1999a; Pereda Suberbiola *et al*., 2000, 2015). In the Laño quarry, three fossiliferous beds dated as late Campanian (Corral *et al*., 2016) are known within an alluvial system composed mainly of fluvial sands and silts: L1A, L1B, and L2 (Fig. 2). All the titanosaurian remains recovered in the fossil site of Laño have been assigned to the taxon *Lirainosaurus astibiae* (Sanz *et al.*, 1999; Díez Díaz, 2013). Both cranial (basicrania and teeth) and postcranial (axial, appendicular, girdle elements, and osteoderms) remains of *Lirainosaurus astibiae* have been discovered in these three beds (Sanz *et al.*, 1999; Díez Díaz *et al.*, 2011, 2012a, 2013a, b).

Lirainosaurus astibiae was the first Iberian titanosaur to be properly described (Sanz *et al.*, 1999). Ten years later, some postcranial remains referred to *Lirainosaurus* cf. *astibiae* were described from the late Campanian-early Maastrichtian of Chera (Valencia) (Company *et al.*, 2009a). However, after careful study of all the titanosaurian material recovered from this fossil site, including vertebrae and limb bones, several morphological differences have been noted, which means that there were probably two titanosaurian morphotypes at Chera. We will briefly discuss this hypothesis in this work. In Sacedón (Guadalajara), one caudal vertebra was referred to cf. *Lirainosaurus* (Ortega & Pérez-García, 2009), but it does not have any diagnostic features that can allow us to unambiguously refer it to *Lirainosaurus* or any other titanosaurian genus (Díez Díaz, 2013). Thus far, no other titanosaurian taxon has been defined in the Iberian Peninsula, but the discovery of the exceptional fossil site of Lo Hueco near Fuentes (Cuenca, late Campanian-early Maastrichtian) will change this situation in the future. Although the study of the titanosaurian remains of Lo Hueco is still in its first phase, interesting specimens hinting at greater diversity have recently been published (e.g., Díez Díaz & Ortega, 2013; Knoll *et al.*, 2013a, b; Díez Díaz *et al*., 2014a, b, c; Vidal *et al.*, 2014).

The Tremp Basin (south-central Pyrenees) has several Maastrichtian sites that have also yielded titanosaurian

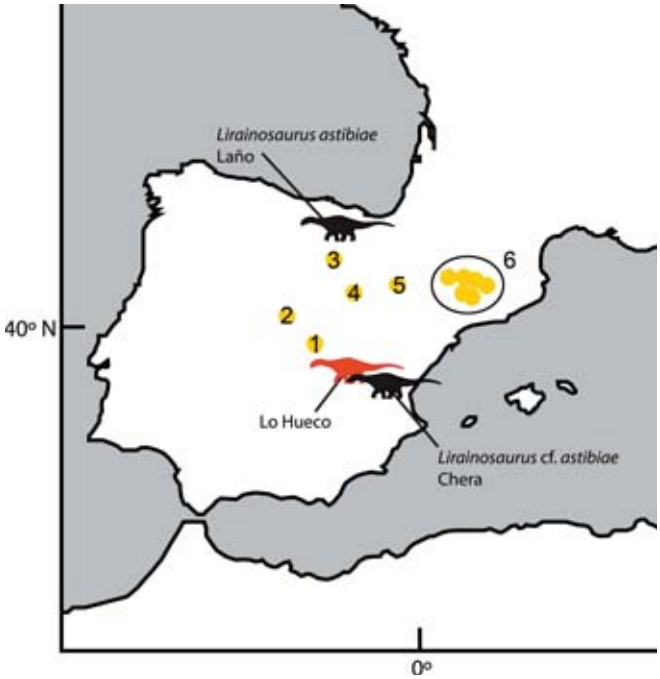


Figure 1. Map of the Iberian Peninsula showing the Late Cretaceous fossil sites that have yielded titanosaurian remains. The sauropods indicate the sites with known titanosaurian taxa. Fossil sites: **1.** Sacedón (Guadalajara, Ortega & Pérez-García, 2009); **2.** Armuña (Segovia, Sanz & Buscalioni, 1987); **3.** Apellaniz (Álava, Pereda Suberbiola *et al*., 1999); **4.** Cubilla (Soria, Lapparent *et al*., 1957; Le Loeuff, 1993; Pereda Suberbiola & Ruíz-Omeñaca, 2001); **5.** Serraduy (Huesca, Canudo, 2001). **6.** Fossil sites from the Tremp Basin, Lleida (Lapparent & Aguirre, 1956, 1957; Casanovas *et al.*, 1987; Masriera & Ullastre, 1988; Casanovas-Cladellas & Santafé-Llopis, 1993; Casanovas-Cladellas *et al*., 1995; López Martínez *et al*., 2001; Vila *et al*., 2006; Sellés *et al*., 2015). Modified from Díez Díaz (2013).

remains (e.g., Lapparent & Aguirre, 1956, 1957; Casanovas *et al.*, 1987; Masriera & Ullastre, 1988; Casanovas-Cladellas & Santafé-Llopis, 1993; Casanovas-Cladellas *et al.*, 1995; Vila *et al.*, 2012), but most of them are badly preserved – poor preservation, isolated bones, etc. –, so their ascription to a known titanosaurian taxon is not possible. In the upper Maastrichtian La Solana site, near Tous (Valencia), scanty titanosaurian material has been recovered (Company *et al.*, 2009b, 2013), but it has never been described in detail.

In this work we will estimate the titanosaurian diversity in the latest Cretaceous of the Iberian Peninsula on the basis of the available information from the three upper Campanian-lower Maastrichtian fossil sites that have yielded the best preserved fossil remains: Laño (Condado de Treviño), Chera (Valencia), and Lo Hueco (Cuenca).

Institutional Abbreviations: MCNA, Museo de Ciencias Naturales de Álava/Arabako Natur Zientzien Museoa, Vitoria-Gasteiz, Spain; MGUV, Museo de Geología de la Universidad de Valencia, Burjassot, Spain; UPV/EHU, Universidad del País Vasco/Euskal Herriko Unibertsitatea, Leioa, Bizkaia.

2. *LIRAINOSAURUS ASTIBIAE* FROM THE FOSSIL SITE OF LAÑO (CONDADO DE TREVIÑO)

Most of the titanosaurian remains found in Laño were described in detail several years after the initial description of Sanz *et al.* (1999) (see Díez Díaz *et al.*, 2011, 2012a, 2013a, b). New bones were also studied and described, and the diagnosis of *Lirainosaurus astibiae* was modified. However, a proper comparison of the elements found in the different field seasons and levels was not realized.

Pereda-Suberbiola *et al.* (2000) produced a detailed taphonomic analysis of the Laño quarry thanks to the information recovered in the L1A level in the 1995 field season. Table 1 provides detailed information about the number of titanosaurian remains recovered in the field seasons.

Here, we emphasize the taphonomic information recovered in the 1997 field season, as several titanosaurian remains were found close together in the L1A level at this time, meaning that they likely belong to a single individual. In addition, we compare the elements that appeared in the

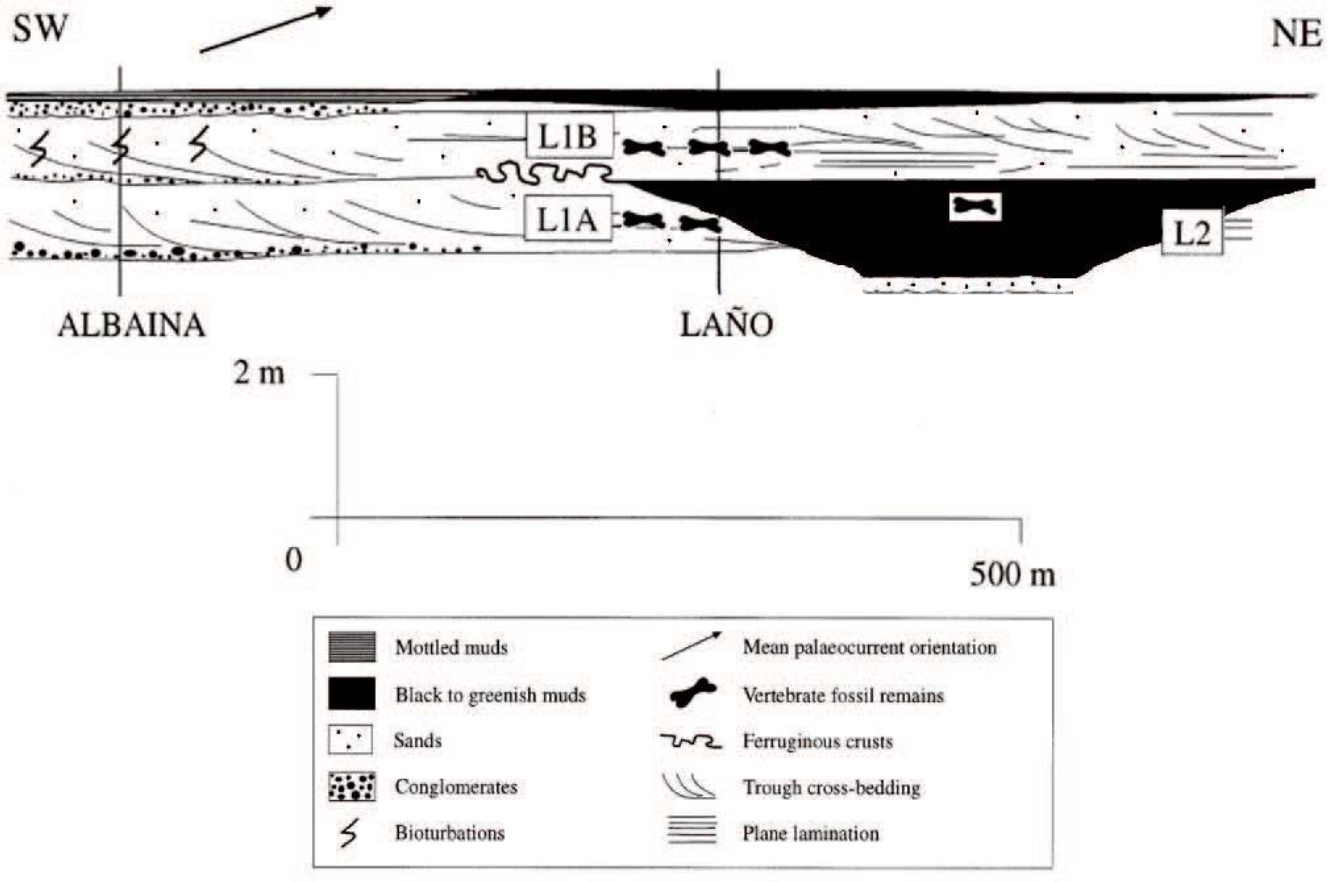


Figure 2. Channel cross-section from SW to NE of the Laño quarry (Condado de Treviño). Modified from Pereda-Suberbiola *et al.* (2000).

different levels (i.e., L1A, L1B, and L2) to confirm that only a single titanosaurian taxon is present in the fossil site of Laño.

Table 1. Information regarding the titanosaurian remains recovered from the fossil Laño fossil site during seven field seasons. Additional titanosaurian material consists of isolated teeth found in L1A.

Field Season	Recovered macrofossils	Titanosaurian remains	Type of identified titanosaurian remains	Fossiliferous levels
1988	≥ 90	10	Axial remains, 2 humeri	L1A, L1B
1989	≥ 27	3	2 caudals, 1 femur	L1B, L2
1990	≥ 40	2	1 femur	L1
1992	≥ 100	13	1 tooth, axial and appendicular remains	L1B
1993	≥ 50	6	1 tooth, 1 scapulocoracoid, 1 caudal vertebra	L1A, L2
1995	1053	16	7 teeth, 5 vertebrae, 2 femora	L1A
1997	≥ 2000	25	Cranial and postcranial remains	L1A, L1B

2.1. Methods

The methodology followed during the 1997 field season was the same as in the 1995 season (see Pereda Suberbiola *et al.*, 2000): detailed excavation with taphonomic notes, and mapping following a square grid system.

For this work only the fossil remains referred as titanosaurian sauropod in the table of taphonomic features used in the field (the same as in the 1995 field season) were taken into account (see model of taphonomic file features in Astibia *et al*., 1999b: fig. 8; also Pereda Suberbiola *et al*., 2000: fig. 5). These remains are housed at the Museo de Ciencias Naturales de Álava (MCNA, Vitoria-Gasteiz). Although several bones were prepared before the beginning of this work, others had to be prepared and/or restored. The laboratory phase of this work was carried out in the Stratigraphy and Palaeontology Department of the Universidad del País Vasco/Euskal Herriko Unibertsitatea (UPV/EHU, Bilbao), principally with mechanical techniques.

This discovery during the 1997 field season highlights the possibility of the presence of one individual of *Lirainosaurus astibiae* in L1A, which can help with the comparison of other remains found in Laño, but also in Chera (Valencia).

2.2. Taphonomic comments from the 1997 field season

More than 1800 vertebrate fossil remains were recovered in L1A, and 200 in L1B. Twenty-three remains were referred to as titanosaurian in L1A, and two in L1B. All of the titanosaurian remains found in L1A in the 1997 season belong to the posterior part of the animal – hindlimb and pelvic girdle bones, one haemal arch, and anterior and middle caudal vertebrae –, except for one tooth. Although the remains appeared dispersed, they seem to be organized in an axis of ca. 5 m (Fig. 3). Eleven bones were disarticulated but in close association. This complex consists of bones of the pelvic girdle and the most anterior caudal vertebrae (Fig. 4).

2.3. *Lirainosaurus* in the Laño vertebrate assemblage (Table 2)

Approximately 3500 macrofossil remains have been recovered from Laño in the 7 field seasons between 1988 and 1997. Within this impressive number, almost 150 remains were assigned to *Lirainosaurus astibiae*, with the titanosaurian sauropod the most abundant dinosaur of the Laño site in terms of number of fossils. As previously stated, these titanosaurian remains were found in L1A, L1B and L2. However, the bones found in L2 were fewer and more poorly preserved, making comparisons more difficult. Most of the titanosaurian remains are isolated teeth that were found in L1A through screen washing of the silty sediments (Pereda Suberbiola *et al*., 2000).

MCNA 14464 is the most complete ilium found for *Lirainosaurus astibiae*, but because of its preservation it is impossible to check the presence of the triangular hollow that appears at the base of the pubic peduncle in lateral view, which is a diagnostic feature of *L. astibiae* found in other iliac fragments (Díez Díaz *et al*., 2013b). Although anteroposteriorly compressed because of its preservation, the anterior caudal vertebrae MCNA 14441 and 14444 have a similar general morphology as the holotype MCNA 7458 of *Lirainosaurus astibiae*: (1) stout centra with a prominent and very convex posterior condyle, and (2) a high neural spine inclined slightly posteriorly with a complex lamination (e.g., presence of a postzygodiapophyseal lamina) (see Díez Díaz *et al*., 2013a for a more detailed description).

Two braincases described by Díez Díaz *et al*. (2011) were found in different levels. MCNA 7439 comes from L1A, whereas MCNA 13913 was found in L1B. Both share the presence of basal tubera foramina –a diagnostic feature of *Lirainosaurus*–, absence of subcondylar depressions or foramina, and the general morphology of their cranial elements, grooves and foramina.

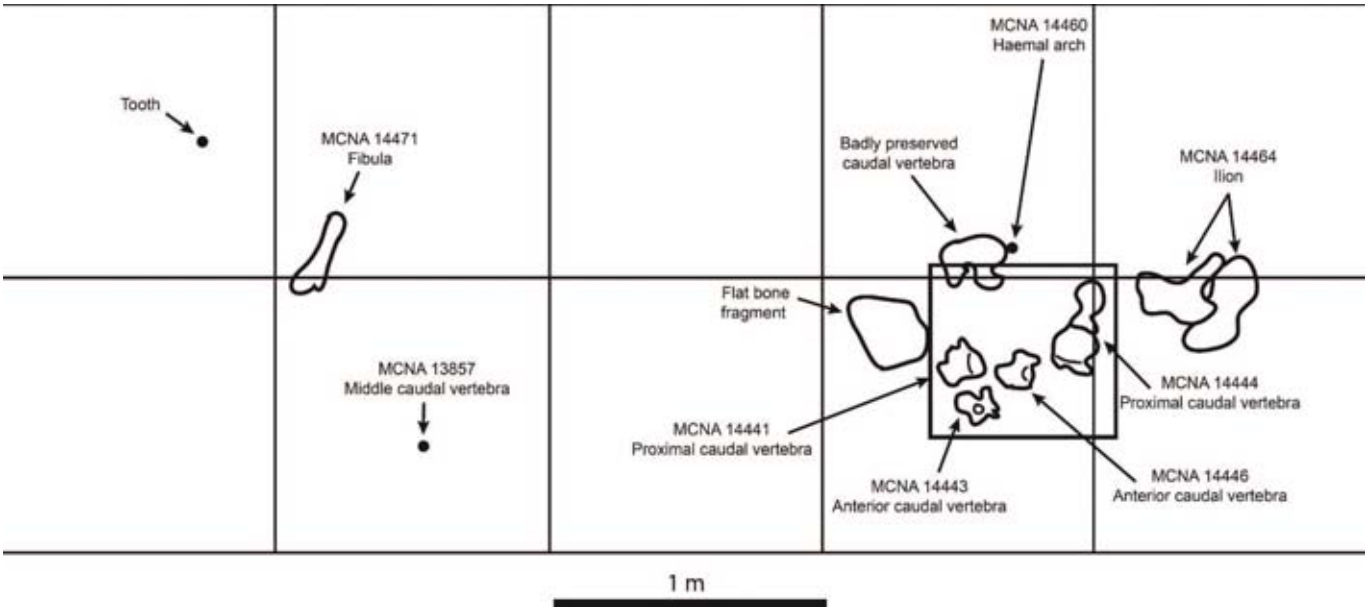
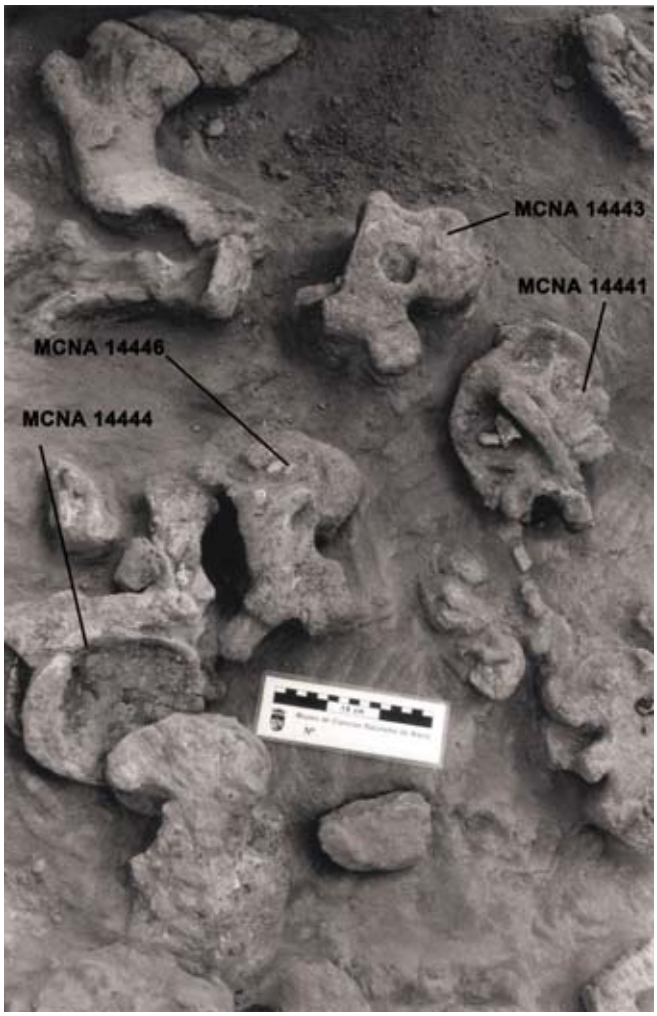


Figure 3. Quarry map of the Laño bone assemblage (L1A level) in 1997, showing the remains of *Lirainosaurus astibiae* recovered. The bold square remarks the caudal vertebrae detailed in the Fig. 4. Each grid measures 1 meter high x 1 meter wide.



More than 40 titanosaurian caudal vertebrae have been recovered from Laño (Díez Díaz *et al*., 2013a). Anteriormost caudal vertebrae have only been found in L1A, whereas anterior and middle caudal vertebrae were found in L1A and L1B, sharing the same general morphology: (1) procoely, (2) slight lateral compression, (3) dorsally restricted condyle, (4) flat ventral surface, (5) posteroventral articulation for the haemal arches, and (6) low neural spine located anteriorly in the centrum. Distal caudal vertebrae were also recovered in L2, and all of them show the same features: (1) amphiplatyan or only slightly convex, spool-like, elongated centra, and (2) a neural arch located anteriorly on the centrum.

One fragmentary ilium was found in L1A (MCNA 13861) and two in L1B (MCNA 7466, 8609). All of them include fragments of the acetabulum, the junction of the iliac blade and the proximal part of the pubic peduncle. They have a highly pneumatized internal structure and show a triangular hollow at the base of the pubic peduncle in lateral view (Díez Díaz *et al*., 2013b).

One femur has been found in L1A (MCNA 7468) and two in L1B (MCNA 1817, 3160). MCNA 7468 is the best preserved and most complete of the three. All of the femora have an anteroposteriorly compressed shaft with an elliptical cross-section. They also present a medial

Figure 4. Proximal-anterior caudal vertebrae of *Lirainosaurus astibiae* found in Laño (L1A level) during the 1997 field season. Modified from Díez Díaz (2013).

Table 2. The Eccentricity Index (ECC) and Robustness Index (RI) of the titanosaurian appendicular elements found at the Laño (in grey) and Chera fossil sites ascribed to *Lirainosaurus* and to a second morphotype. The ECC has been calculated as the mid-shaft mediolateral width divided by the anteroposterior width (Wilson & Carrano, 1999), and the RI has been calculated as the average of the greatest widths of the proximal and distal ends and the mid-shaft divided by the length of the element (Wilson & Upchurch, 2003).

		HUMERI			ULNAE		FEMORA			TIBIAE	
		Specimen	RI	ECC	Specimen	RI	Specimen	RI	ECC	Specimen	RI
LAÑO	*Lirainosaurus*	MCNA 7463	-	2.023	MCNA 3157	0.279	MCNA 1817	-	1.916	MCNA 2203	-
		MCNA 7464	0.269	1.461			MCNA 3160	-	2.581	MCNA 13860	0.237
		MCNA 7465	0.257	2.461			MCNA 7468	0.219	1.685		
		MCNA 7472	-	2.075							
CHERA							MGUV 17194	-	2.6		
							MGUV 17235	0.2	2.24		
							MGUV 17819	-	1.89		
	Titan.	MGUV 16431	-	1.24	MGUV 17045	0.18	MGUV 16450	-	3.65	MGUV 17843	0.2
		MGUV 17552	-	1.59	MGUV 17274	-	MGUV 17294	0.25	2.33		
		MGUV 17683	-	1.47							

deflection and a lateral bulge. The femoral head is directed dorsomedially. The fourth trochanter is a poorly developed ridge and it is located on the posteromedial surface of the diaphysis. They only vary in terms of their femoral eccentricity (see Table 5 in Díez Díaz *et al*., 2013b).

One tibia has been found at each of the Laño levels: in L1A (MCNA 13860), L1B (MCNA 7471), and L2 (MCNA 2203). The tibia is the bone of *Lirainosaurus* that shows the highest morphological variation. The specimen MCNA 7471 is robust, with a concave anterior edge and a more rounded proximal end that has a deeper and narrower surface for articulation with the fibula. MCNA 13860 is a slender tibia, with a more compressed diaphysis and the proximal end has a shallow surface for the reception of the fibula. In MCNA 2203, the anterior edge is straighter than in the other specimens. However, despite these differences, the Laño tibiae share the following features: (1) the cnemial crest is an expanded flat rounded ridge projecting anterolaterally, (2) there is a prominent anteromedial ridge close to the distal end that delimits two concave surfaces, one anteriorly located and the other medially directed (these ridges are more conspicuous in MCNA 2203), and (3) the surfaces for the ascending process of the astragalus and for the posteroventral process of the tibiae are not well pronounced (see Díez Díaz *et al*., 2013b).

The two fibulae found in L1A (MCNA 9410, 14471) and the one in L1B (MCNA 7472) also present several differences (Díez Díaz *et al*., 2013b). The fibulae from L1A are more robust and show a greater curvature of shaft and more expanded proximal ends than the fibula from L1B. However, the latter specimen is not well preserved (it is eroded in some places and has an iron crust covering most of the surface of the bone), and so a more detailed comparison of other structures (e.g., ridges, trochanters, surface scars, etc.) is not possible.

Counting the duplicated titanosaurian remains recovered from Laño (i.e., basicrania, scapulae, coracoids, humeri, ilia, femora, tibiae, and fibulae), taking into account the level at which they appeared, and comparing their morphology, we can confirm that, at least, five titanosaurian individuals were present (two in L1A, two in L1B, and one in L2).

3. PRESENCE OF *LIRAINOSAURUS* IN THE FOSSIL SITES OF CHERA (VALENCIA)

3.1. Introduction

Company *et al*. (2009a) described the first titanosaurian remains from the Late Cretaceous of Valencia Province, which consisted of axial and appendicular bones. The fossils come from several exposures in the Chera area, 60 km west of the city of Valencia. The dinosaur-bearing beds are ascribed to the Sierra Perenchiza Formation, dated as late Campanian-early Maastrichtian (Company, 2004; Company et *al*., 2005). The vertebrate remains in the Chera area are mainly restricted to the clayley-rich beds which correspond with the lower part of palustrine carbonate sequences deposited in shallow, freshwater environments, which exhibit extensive evidence of pedogenic modification.

More than 95 % of the titanosaurian remains from Chera were collected from a fossiliferous horizon named “Chera 0”,

where dinosaur, crocodilian and turtle skeletal elements tend to be disarticulated and unassociated. Most of the recovered bones show scanty evidences of weathering and abrasion, suggesting a limited transport and short subaerial exposition before burial. Other fossiliferous outcrops in the Chera area (Chera 1, Chera 1c, La Castellana 2) have produced scanty and fragmentary material of titanosaurian dinosaurs. The collection of six different-sized -some of them partially preserved- titanosaurian femora in Chera 0 suggests the presence of, at least, six different individuals in this locality. Additional fragmentary titanosaurian remains found in other fossiliferous beds of the same area increase to nine the minimum number of individuals recovered from the Chera sites.

These titanosaurian remains were referred to *Lirainosaurus* cf. *astibiae* on the basis of several features shared with the material of Laño: e.g., the presence of a dorsal prominence and a ventral ridge on the medial surface of the scapula, and the general morphology of the caudal vertebrae and the coracoid (see Company et *al*., 2009a for a more detailed description). Nevertheless, after the complete study of the remains of *Lirainosaurus* from Laño and the revision of the diagnosis of *Lirainosaurus astibiae*, a revision of the material from Chera is needed.

After a preliminary study, several differences have been highlighted, not only between parts of the material of Chera and Laño, but also between some elements from Chera. Consequently, a new hypothesis is proposed: that there may be two different titanosaurian morphotypes in the fossil sites of Chera, with one of them representing *Lirainosaurus*. Here we will advance an initial comparison between the fossil remains from both localities, but a more detailed study examining the titanosaurian remains of Chera will be an important future research goal.

3.2. Titanosaurian remains referred to *Lirainosaurus*

Some of the remains recovered from Chera show similarities and share autapomorphies with those of the genus *Lirainosaurus* from Laño. However, other elements present some disparities, and could belong to a different titanosaurian morphotype.

The following titanosaurian remains are here referred to the genus *Lirainosaurus*. We keep the taxonomic ascription to *Lirainosaurus* cf. *astibiae* published by Company *et al*. (2009a) as the fossils exhibit some differences from the bones of *Lirainosaurus* from the Laño site. The description of some elements (i.e., the haemal arches MGUV 17168, 17192, 17332, the scapula MGUV 17645, the coracoid MGUV 17238, the sternal plate MGUV 16446) ascribed to *Lirainosaurus* cf. *astibiae* is detailed in the work of Company *et al*. (2009a). In this work, we will focus on the elements newly referred to this genus, or that show some differences from the original description.

3.2.1. Axial skeleton

MGUV 17320 is a fragmentary dorsal centrum with the base of its neural arch. The centrum has large and deep, eyed-shaped pleurocoels, and a large and heart-shaped concave posterior articular surface. The pcdl (posterior centrodiapophyseal lamina) is not ventrally bifurcated, as is also the case in the dorsal vertebrae from Laño (Díez Díaz *et al*., 2013a).

MGUV 17169 is a proximal-anterior caudal vertebra missing most of its neural arch (Company *et al*., 2009a). The centrum is short and procoelous, with a large and prominent condyle and an anterior articular surface with a circular outline. There are no lateral pleurocoels and it presents both lateral transverse processes with a triangular profile in anterior and posterior views. This general morphology resembles that of some proximal caudal vertebrae from Laño (MCNA 14444: Díez Díaz *et al*., 2013a). The anterior caudal MGUV 17897 presents a similar morphology as those of *Lirainosaurus* (e.g., MCNA 14443, 14446), although the neural arch seems to have a more complex lamination, with several accessory laminae not present in the Laño material. Three middle caudal vertebrae are ascribed to *Lirainosaurus* (MGUV 17017, 17105). The general morphology of these vertebrae is very similar to those of *Lirainosaurus* (e.g., MCNA 7457, 13388), i.e., they are procoelous, with slight lateral compression, flat ventral surface, and with a posteroventral articulation for the haemal arches. Two posterior caudal vertebrae have been recovered (MGUV 17028 and 17693), and also present a similar morphology to that of the posterior caudal vertebrae of *Lirainosaurus* (e.g., MCNA 7454 and 14435), being slightly procoelous, with long and dorsoventrally compressed centra. MGUV 17028 preserves long and anteriorly directed prezygapophyses, and a low and anteroposteriorly elongated neural spine.

3.2.2. Appendicular skeleton (Table 2)

The femora MGUV 17194, 17235, and 17819 (this last one is not as well preserved as the others) present similar features as the femora of *Lirainosaurus astibiae*. The shaft is slender and straight, anteroposteriorly compressed, with an elliptical cross-section. The lateral edge is straight, and the medial one is concave, although less so than in the femora from Laño (Díez Díaz *et al*., 2013b). The fourth trochanter is a ridge on the posteromedial surface of the diaphysis, and it is more developed than in the femora from Laño. The average femoral eccentricity is higher than 2.2.

3.3. Titanosaurian remains that cannot be ascribed to *Lirainosaurus*

The study of additional caudal vertebrae and appendicular remains from Chera suggests a noticeable variability in several remains previously referred to *Lirainosaurus* cf. *astibiae,* or not yet published. Only some brief comments will be provided in this work in order to compare them with the remains referred to *Lirainosaurus*. This study suggests the presence of a second titanosaurian taxon in the fossil site of Chera. However, it is important to keep in mind that these differences in the morphotypes could be related to ontogenetic changes or sexual dimorphism.

3.3.1. Axial skeleton

Although a number of caudal vertebrae recovered from the Chera sites are procoelous and have restricted condyles, they also show striking differences with the caudals of *Lirainosaurus.* Three middle-posterior caudals (MGUV 17016, 17682, and 17785) cannot be referred to *Lirainosaurus*: the centra are not dorsoventrally compressed, in fact they have a subquandrangular (i.e., laterally compressed) profile in posterior view, and present a well developed anterior articulation for the haemal arches. Further comparisons are difficult due to the bad preservation of the caudal centra of some European titanosaurs (e.g., *Atsinganosaurus* Garcia *et al*., 2010). The posterior caudal MGUV 17096 shows a more rounded cross-section of the centrum, and both anterior and posterior articular surfaces present vertical grooves.

3.3.2. Appendicular skeleton (Table 2)

Three partial humeri (MGUV 16431, 17552, and 17683) seem somewhat different to those referred to *Lirainosaurus* from Laño. Although none of them are complete, they are better preserved than those here referred to *Lirainosaurus* cf. *astibiae*. The most striking differences from the humeri of *Lirainosaurus* are the slenderness of the diaphysis in comparison with the lateromedially expanded proximal end, and the roughly subcircular cross-section at the midshaft. The eccentricity index varies between 1.2 and 1.6 (*Lirainosaurus* ECC = 2-2.5, see Díez Díaz *et al*., 2013b). As these humeri are noticeably smaller than those referred to *Lirainosaurus*, it should not be excluded that they are from juvenile individuals. It is important to highlight that eccentricity could vary ontogenetically in titanosaurs.

Two recovered ulnae (MGUV 17045, and 17274) show several differences from those of *Lirainosaurus* (Fig. 5c). Both specimens are well preserved, with MUGV 17045 complete. The ulnae are slender in comparison with that of *Lirainosaurus* from Laño (MCNA 3157), and the distal end is not expanded. The posterior edge is straighter than in the ulna of *Lirainosaurus.* The robustness index barely reaches the value of 0.2 (*Lirainosaurus* RI = ca. 0.28, see Díez Díaz *et al*., 2013b).

Two femora (MGUV 16450, and 17294 [which is complete]) present several differences from the femora of *Lirainosaurus* (Fig. 5a). These femora are more robust than those of *Lirainosaurus*, and the fourth trochanter is not as laterally biased. The femoral eccentricity index surpasses the value of 2.3 (being higher than 3.6 in MGUV 16450) (*Lirainosaurus* ECC = 2-2.6, see Díez Díaz *et al*., 2013b).

One left tibia (MGUV 17843) cannot be referred to *Lirainosaurus* (Fig. 5b). The main differences from the tibiae of *Lirainosaurus* are: (1) the rounded profile of the proximal articulation, (2) the reduced anterolateral expansion of the cnemial crest and the presence of a lateral protuberance that delimits a deep and narrow concavity on the proximal third, (3) the distal third is slightly concave anteriorly and it is delimited by both stout medial and lateral ridges, (4) the distal third is convex posteriorly, (5) the distal articulation is anteroposteriorly compressed, and (6) the diaphysis is transversely compressed in the upper half and anteroposteriorly compressed in the lower one. It presents a similar robustness index as *Lirainosaurus*: ca. 2.0.

Figure 5. Titanosaurian remains from Chera referred to the second morphotype. **a)** Left femur MGUV 17294. **b)** Left tibia MGUV 17843. **c)** Left ulna MGUV 17045.

3.3.3. Titanosaurian remains referred to Titanosauria indet. because of their preservation

Company *et al*. (2009a) referred to *Lirainosaurus* cf. *astibiae* all the titanosaurian remains found at the Chera sites. As we have seen, some of them present enough

differences to suggest that they may belong to a different titanosaurian morphotype rather than *Lirainosaurus*. Besides, a number of elements (fragmentary or not) do not preserve enough morphological characters to permit their assignment to either of the two titanosaurian morphotypes found at Chera, or to any other known taxon. Three dorsal centra (MGUV 17229, 17295, 17315), fourteen badly preserved caudal remains (MGUV 16438, 16448, 17027, 17094, 17314, 17090, 17092, 17093, 17097, 17101, 17337, 17513, 17539, 17243), five fragmentary humeri (MGUV 17165, 17166, 17286, 16449, 17721), and the femur MGUV 16454 were ascribed to *Lirainosaurus* by Company *et al*. (2009a), but because of their incomplete preservation we cannot confirm this hypothesis and regard them as from indeterminate titanosaurs.

4. BRIEF COMMENTS ON THE TITANOSAURIAN DIVERSITY OF THE FOSSIL SITE OF LO HUECO (CUENCA)

The fossil site of Lo Hueco (Cuenca) was discovered in 2007 during the construction of the Madrid-Levante highspeed railway. The faunal assemblage, palynological data, and stratigraphical context suggest a late Campanian to early Maastrichtian age for the site (Barroso-Barcenilla *et al*., 2009). More than 70% of the approximately 10,000 recovered, disarticulated vertebrate remains are titanosaurian bones, comprising more than 20 sets representing partial skeletons of several individuals (Ortega *et al*., 2008, 2015).

Preliminary studies have shed light on the presence of, at least, two different titanosaurian morphotypes at the site. This hypothesis is corroborated primarily from the cranial material, i.e., skulls (Knoll *et al*., 2013a, b) and teeth (Díez Díaz *et al*., 2014a). The cranial evidence shows that at Lo Hueco probably coexisted a titanosaur with close affinities with other remains from fossil sites of southern France (i.e., Massecaps in Cruzy, Fox-Amphoux-Métisson), and a second morphotype that corresponds to a new, still unnamed taxon (F. Ortega, pers. comm.). The presence of at least one other taxon in Lo Hueco has been confirmed thanks to the discovery of the so-called EC1 skeleton (Díez Díaz *et al*., 2014a). The EC1 skeleton was found partially articulated, and includes cervical, dorsal, sacral and caudal vertebrae, and several appendicular elements. The diagnostic characters observed in the vertebrae and in the appendicular bones confirm than this material is different from other previously known taxa.

5. THE TITANOSAURIAN DIVERSITY IN THE IBERO-ARMORICAN ISLAND

The first dinosaur described in the Late Cretaceous of Europe was the titanosaur *Hypselosaurus priscus,* found in the late Campanian-early Maastrichtian of Rognac (Bouches-du-Rhône Department) by Matheron (1869). Depéret (1899) found in Assignan (Hérault Department) some procoelic caudal centra that he identified as belonging to *Titanosaurus indicus*. However, these two taxa are considered today as *nomina dubia* (Le Loeuff, 1993; Wilson & Upchurch, 2003). Nowadays, two titanosaurian species are well known from the upper Campanian-lower Maastrichtian of southern France: *Ampelosaurus atacis* Le Loeuff, 1995 from the fossil site of Bellevue (Campagne-sur-Aude, Aude Department), and *Atsinganosaurus velauciensis* Garcia *et al*. 2010 from Velaux (Bouches-du-Rhône Department).

As in Spain, southern France is also riddled with more than 20 upper Campanian-lower Maastrichtian sites that have yielded titanosaurian remains, but the bones were often found isolated and/or are not well preserved in most of them – e.g., Le Mas d'Azil (Ariège Department [Le Loeuff, 1998]), Saint-Chinian (Hérault Department [Le Loeuff, 1993; Buffetaut, 2005]), Trets (Bouches-du-Rhône Department [Allain, 1998]) –. However, in some of these sites, i.e. Massecaps (Hérault Department; Buffetaut *et al*., 1999; Díez Díaz *et al*., 2013c), and Fox-Amphoux-Métisson (Var Department; Le Loeuff, 1993; Díez Díaz *et al*., 2012b), the future study of newly recovered remains (e.g., a new, still unnamed titanosaurian taxon from the fossil site of Massecaps [J. Le Loeuff, pers. com.]) will greatly improve the knowledge of the Late Cretaceous faunas from the Ibero-Armorican Island. Anyway, we can advance that at least three different titanosaurian taxa lived during the upper Campanian-lower Maastrichtian of southern France.

Several authors (Le Loeuff, 1992, 1993; Vila *et al*., 2012) suggested that there was probably a higher titanosaurian diversity in the Ibero-Armorican Island during the Late Cretaceous than previously hypothesized. The recent discovery of different morphotypes of teeth and femora that could not be ascribed to any of the titanosaurian taxa known to date in several Campanian-Maastrichtian fossil sites from Spain and southern France confirms this hypothesis (e.g., Díez Díaz *et al*., 2012b, 2013c, 2014a; Vila *et al*., 2012). Vila *et al*. (2012) ascribed four different femoral morphotypes to *Ampelosaurus atacis*, *Lirainosaurus astibiae*, *Atsinganosaurus velauciensis*, and the last one to a robust and indeterminate titanosaur. However, it is important to note that the titanosaurian femora from the fossil sites of Fox-Amphoux-Métisson and Bellevue that Vila *et al*. (2012) have assigned to cf. *Lirainosaurus* probably do not belong to this taxon (see Díez Díaz *et al*., 2013b).

6. CONCLUSION

In this work we have been able to accomplish several objectives:

We confirm the presence of a single titanosaurian taxon in the fossil site of Laño: *Lirainosaurus astibiae*. Although some bones (i.e., tibiae and fibulae) show differences between them, these are not enough to consider the presence of a second titanosaur in Laño besides *Lirainosaurus astibiae.* At present, these differences are explained as due to intraspecific variability.

The possible presence of two titanosaurian morphotypes at the fossil site of Chera is suggested from morphological differences of some skeletal elements from those of *Lirainosaurus astibiae*. However, some elements cannot be referred to either of these morphotypes due to their preservation. It is important to bear in mind that these differences in the morphotypes could be because of ontogenetic changes, or sexual dimorphism. Morphometric and histological analyses are needed to assess these hypotheses.

Currently, none of the titanosaurian remains found from Lo Hueco can be referred to *Lirainosaurus*. At least one of the two titanosaurian morphotypes from Lo Hueco is a new taxon.

Recent discoveries confirm that titanosaurian diversity in the late Campanian to early Maastrichtian of the Ibero-Armorican Island (and more specifically in the Iberian Peninsula) was higher than previously thought: from one known titanosaurian species in Spain (*Lirainosaurus*) and two in France (*Ampelosaurus* and *Atsinganosaurus*) to, at least, six or seven taxa as a result of discoveries in Laño, Chera, and Lo Hueco in Spain, and Bellevue, Velaux, Massecaps, and Fox-Amphoux-Métisson in France. This high diversity in an island of only 1,500,000 km^2 (Le Loeuff, 2005) makes southwestern Europe an important region for the study of Late Cretaceous sauropod evolution, as well for understanding their palaeobiogeography and palaeoecology.

ACKNOWLEDGEMENTS

We would like to acknowledge J.L. Sanz (Universidad Autónoma de Madrid, Spain), and F. Ortega (Universidad Nacional de Educación a Distancia, Spain) for access to the titanosaurian material from Lo Hueco, and their useful comments, J. Alonso and J.C. Corral (MCNA, Vitoria-Gasteiz, Spain) for access to the material of *Lirainosaurus* from Laño, and specially J.C. Corral for their help and comments during the PhD of the senior author and later during this project, and also X. Murelaga (Universidad del País Vasco/Euskal Herriko Unibertsitatea, Spain) for access to the taphonomic notes of the 1995 field season. The useful comments provided by H. Astibia (Universidad del País Vasco/Euskal Herriko Unibertsitatea), L. Filippi (Museo Argentino Urquiza, Rincón de los Sauces, Argentina), and M.J. Benton (University of Bristol, UK) greatly improved this manuscript. We would like to thank P. Mannion (Imperial College of London, UK) for revising the English grammar, but also for his useful comments. This research was supported by the projects of the Spanish Ministerio de Economía y Competitividad CGL2010-18851/BTE and CGL2013-47521-P (Secretaría de Estado de Investigación, Desarrollo e Innovación), the European Regional Development Fund, and the research group IT834-13 of the Basque Gouvernment (XPS, VDD). VDD was awarded with a Research Grant of the Sociedad Española de Paleontología, which partially supported this work.

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