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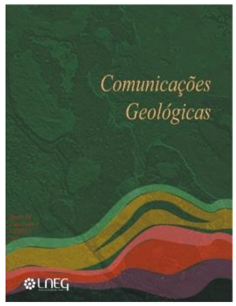
A review of the new sauropod material from the Els Nerets locality (UpperCretaceous, South-Central Pyrenees): estimating species diversity



Revisão de novo material de dinossáurios saurópodes da localidade de Els Nerets (Cretácico Superior, sul-centro dos Pirenéus): estimando diversidade de espécies

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Abstract: Titanosauria is the only sauropod taxa present in the Late Cretaceous of Europe. One of the most diverse localities in the Southern Pyrenees is the lower Maastrichtian site of Els Nerets (Tremp, Catalonia, Spain). The present work reviews the new sauropod material discovered in recent years together with the classical specimens from the site in order to establish the Minimum Number of Individuals (MNI) through the relationships between the appendicular elements. The results show the presence of three adult individuals (based on histological observations) of different sizes, suggesting the occurrence of two distinct, indeterminate species. Although they are similar, morphological comparisons with other Ibero-Armorican titanosaurs suggests that the individuals from Els Nerets cannot be confidently assigned to any of them given the fragmentary nature of the material and the lack of recognisable autapomorphies. However, this work improves on our understanding of the Els Nerets titanosaur diversity.

Keywords: Sauropodomorpha, Titanosauria, Europe, Ibero-Armorica, Lleida

Resumo: Titanosauria é único grupo presente no Cretácico Superior da Europa. Uma das localidades com maior diversidade na região sul dos Pirenéus é a jazida do Maastrichtiano inferior de Els Nerets (Tremp, Catalunha, Espanha). O presente trabalho pretender rever novo material de saurópodes encontrado em Els Nerets nos últimos anos juntamente com exemplares clássicos provenientes desta localidade de forma a estabelecer o Número Mínimo de Indivíduos (MNI) através da comparação dos elementos apendiculares. Os resultados demonstram a presença de três indivíduos adultos (baseado em observações histológicas) de diferentes tamanhos, sugerindo a existência de duas espécies distintas e indeterminadas. Apesar de similares, a comparação morfológica com outros titanossáurios Iberoarmoricanos sugere que os indivíduos de Els Nerets não podem ser referidos com segurança a nenhuma destas formas devido à sua natureza fragmentária e à ausência de autapomorfias. Contudo, este estudo permite melhorar o nosso conhecimento sobre a diversidade em titanossáurios de Els Nerets.

Palavras-chave: Sauropodomorpha, Titanosauria, Europa, Ibero-Armórica, Lérida

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1. Introduction

Titanosauria is the only clade of sauropod dinosaurs from the continental palaeoenvironments of south-western Europe during the Upper Cretaceous (*e.g.* Díez Díaz *et al*. 2016). In the Ibero-Armorican domain (present-day areas of the Iberian Peninsula and France), the titanosaurian fossil record comprises bones, teeth, tracks, eggs and even skin impressions, with up to five species described: *Ampelosaurus atacis* (Le Loeuff, 1995), *Atsinganosaurus velauciensis* (Garcia *et al.*, 2010), *Lirainosaurus astibiae* (Sanz *et al.*, 1999), *Lohuecotitan pandafilandi* (Díez Díaz *et al*., 2016), and *Garrigatitan meridionalis* (Díez-Díaz *et al.*, 2021). Nevertheless, several authors estimated a higher diversity in the region (*e.g.* Ortega *et al.*, 2015; Vila *et al.*, 2012; Díez Díaz *et al*., 2013) based on the analysis of fragmentary remains found in more than 20 localities. Attempts to establish the titanosaurian diversity or the erection of new taxa in these localities include morphological descriptions, comparison with known taxa, and the search for autapomorphies. For instance, partial skeletons or isolated elements from Lo Hueco (Cuenca), Chera (Valencia), Bellevue (Aude, France), Presa de Tremp, Peguera-1, Molí del Baró-2 (Catalunya), Serraduy (Aragón), Fox-Amphoux-Métisson and Massecaps (France) point out to several indeterminate but distinct taxa (Canudo, 2001; Company *et al.*, 2009; Vila *et al.*, 2012; Díez-Díaz *et al.*, 2012, 2013; Páramo *et al.*, 2020).

In the Tremp Basin, the Els Nerets locality has yielded indeterminate sauropod remains that could represent distinct species (Casanovas *et al.*, 1995; Pereda Suberbiola *et al.*, 2004). In the present work, after the description of new specimens, and the counts of Minimum Number of Individuals (MNI), we assess the alpha diversity based on the relative size and histological features for each individual. Finally, we discuss how the new forms from Els Nerets impacts on the late Campanian-late Maastrichtian titanosaurian diversity of south-western Europe.

2. Geological and geographical setting

The Els Nerets locality (Fig. 1) is found northeast of Vilamitjana village, Tremp (Lleida province in Catalonia, Spain) in the Tremp

Basin, a piggy-back type foreland basin in the south-central Pyrenees (Riera *et al.*, 2009). The Els Nerets site is located on top of the Aren Sandstone Formation and within the La Posa Formation of Cuevas (1992), a marine to continental transition unit of the Tremp Group. This unit, also referred to 'Lower Grey Unit' (sensu Rosell *et al.*, 2001) consists of alternating levels of marly-limestones and grey mudstones with interdigitated sandy levels, which have been interpreted as lagoon deposits (Cuevas, 1992). The locality is dated around 70-71 Ma, in the early Maastrichtian (Riera *et al.*, 2009), within the chron C31r (Fondevilla *et al.*, 2019), and the sauropod bones were recovered from two stratigraphic layers vertically separated by around 1.5 m. Based on the sedimentation rate calculated by Fondevilla *et al.* (2016), this separation would equal a lapse of time over 8.33 ka.

The locality was first excavated in the middle 1980s and 1990s (Casanovas *et al.*, 1985, 1987, 1995) and revisited later in 2003 and in the 2010s. The site has yielded fossil remains of theropods, hadrosaurids, titanosaurs, crocodylomorphs, eggshells, fish remains, Carophytales, fern spores, and pollen (see references in Conti *et al.*, 2020).

3. Material and methods

The studied samples include the specimens IPS-901, 36325, 36326 and 897 and IPSN-23 from the upper stratigraphic level, originally described by Casanovas *et al.* (1987, 1995) and currently housed in the Museu de l'Institut Català de Paleontologia Miquel Crusafont. The new material found in recent excavations from the lower fossiliferous level (MCD-6731, 6733b, 6705, 7030, 8641-42 and 9886) is currently housed in the Museu de la Conca Dellà. Anatomical descriptions followed the Romerian terminology (Romer, 1956). In addition, the individuals from Els Nerets have been compared with other Ibero-Armorican titanosaurs. At the same time, the Minimum Number of Individuals (MNI) has been obtained and primarily calculated, together with the performance of a histological analysis and a HOS (Histological Ontogenetic Stage) evaluation after Klein and Sander (2008) (see Appendix for the Extended Methods and taxonomic comparisons).

Institutional Abbreviations. IPS (Museu de l'Institut Català de Paleontologia Miquel Crusafont, Cerdanyola del Vallès, Catalonia, Spain), MCD (Museu de la Conca Dellà, Isona i Conca Dellà, Catalonia, Spain).

4. Results

4.1. Systematic palaeontology

DINOSAURIA Owen, 1842
SAURISCHIA Seeley, 1887
SAUROPODA Marsh, 1878
MACRONARIA Sereno, 1997
TITANOSAURIFORMES Salgado *et al.*, 1997
TITANOSAURIFORMES indet.

Material. right humerus IPS-36325 and dorsal vertebra IPS-897 (individual 1); and the left femur IPS-36326 (individual 2, described in Casanovas *et al.*, 1987, 1995)

TITANOSAURIA Bonaparte and Coria, 1993
TITANOSAURIA indet.

Material. Middle caudal centra (IPS-901, MD-6733b), distal caudal centra (MCD-8641, MCD-8642), scapular fragment (MCD-6731), right ulna (MCD-6705), partial left femur (MCD-9886) (Fig. 2) (individual 3).

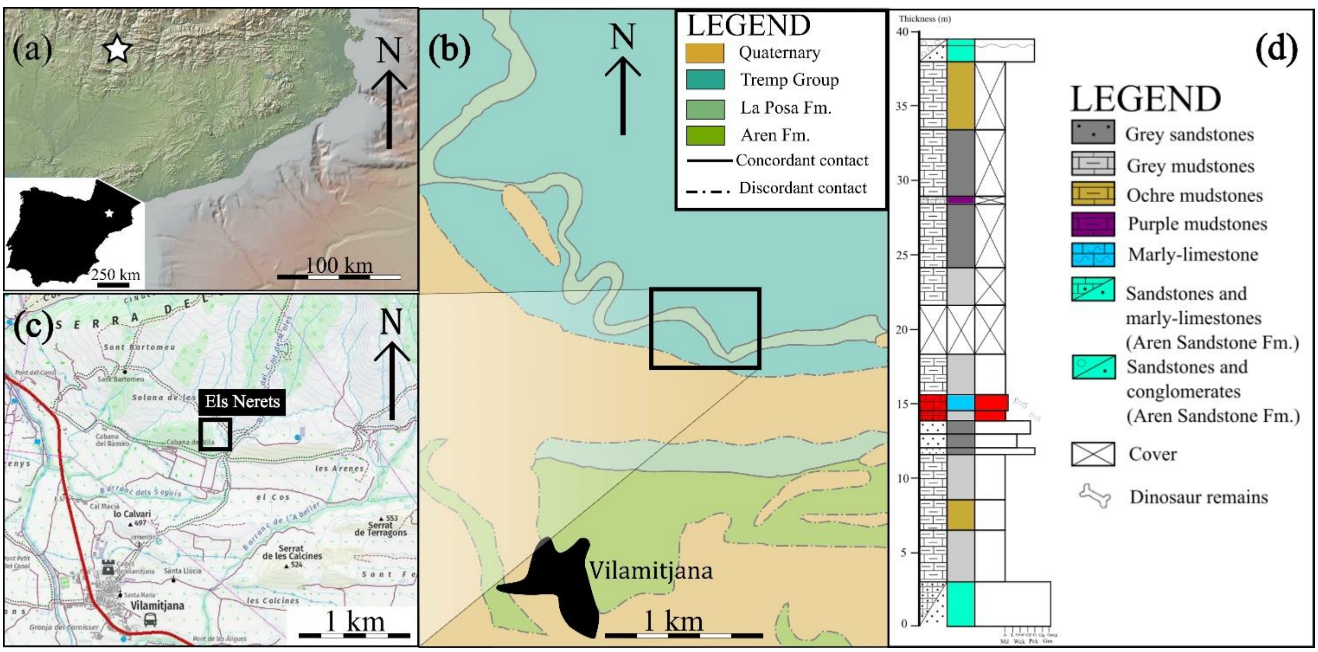

Figure 1. Geographic and geological setting of the paleontological site of Els Nerets: Regional location of Els Nerets in Catalonia and the Iberian Peninsula (a) Geological setting of Els Nerets (b) Topographic map of the Els Nerets area (c) Geological section at Els Nerets site (fossiliferous levels are shown in red/dark gray) (d). Images modified from GeoMapApp, ICGC, and Google Earth. Section modified from Fondevilla *et al.* (2019).

Figura 1. Enquadramento geográfico e geológico do sítio paleontológico de Els Nerets; localização de Els Nerets na região de Catalunha e da Península Ibérica (a) enquadramento geológico de Els Nerets (b) mapa topográfico da área de Els Nerets (c) secção geológica do sítio de Els Nerets (níveis fossilíferos estão em vermelho/cinzento escuro) (d). Imagens modificadas de GeoMapApp, ICGC, e Google Earth. Secção modificada de Fondevilla *et al.* (2019).

Figure 2. New sauropod material from Els Nerets. Right femur MCD-9886 in posterior (a) view; right ulna MCD-6705 in medial (b), anterior (c), lateral (d) and posterior (e) views; middle caudal vertebra MD-6733b in anterior (f), posterior (g) and left lateral (h) views; middle caudal vertebra IPS-901 in dorsal (i), anterior (j), left lateral (k) and posterior (l) views; distal caudal vertebra MCD-8641 in dorsal (m) and ventral (n) views; distal caudal vertebra MCD-8642 in lateral left (o) and dorsal (p) views; Fragment of right scapular blade MCD-6731 in lateral (q) view. Scale: 10 cm.

Figura 2. Novo material de saurópodes proveniente de Els Nerets. Fémur direito MCD-9886 em vista posterior (a); ulna direita MCD-6705 em vistal medial (b), anterior (c), lateral (d) e posterior (e); vértebra caudal média MD-6733b em vista anterior (f), posterior (g) e lateral esquerda (h); vértebra caudal média IPS-901 em vista dorsal (i), anterior (j), lateral esquerda (k) e posterior (l); vértebra caudal distal MCD-8641 em vistal dorsal (m) e ventral (n); Vértebra caudal distal MCD-8642 em vista lateral esquerda (o) e dorsal (p); Fragmento da lâmina escapular direita MCD-6731 em vista lateral (q). Escala: 10 cm.

4.2. Description

Middle caudal centra (IPS-901, MCD-6733b): Centra are procoelous. The centra are longer than tall with a ventral concavity and lack the neural arch, although both present pedicel fragments in the anterior half of the centra and do not present any vertebral processes.

Distal caudal centra (MCD-8641-42): MCD-8642 is a biconvex centrum (63 mm anteroposteriorly and 24 mm dorsoventrally) lacking neural arch. The dorsal and ventral surfaces are flattened. The posterior articular surface bears a dorsoventrally developed medial groove. MCD-8641 is morphologically very similar to MCD-8642, although it is smaller (57 mm anteroposteriorly and 20 mm dorsoventrally) and lacks a medial groove.

Scapula fragment (MCD-6731): It is a fragment of scapular blade intensely fractured. It has a smooth surface and a D-shaped proximal section.

Ulna (MCD-6705): The ulna is slender with a Robustness Index (RI) between 0.19-0.2 (after Wilson and Upchurch, 2003). It preserves almost the entire length, lacking only parts of the proximal and distal ends. The proximal end has a triradiate section. The anteromedial process is the most developed whereas the anterolateral one is the most robust and presents a ventral tilt. The olecranon process is at the same level with the proximal articulation and is as robust as the anteromedial process. Between the wedge-like olecranon and the anteromedial process there is a pronounced fossa (on anterior view) that is larger than the articular surface for the radius. The shaft of the ulna is straight and triangular in cross-section. Although the distal end is not preserved, part of the concave distal articular surface of the radius is observed.

Femur (MCD-9886): It is a partial right femur of moderate-large size (proximodistal preserved length: 860 mm, estimated complete length of 1093 mm). The shaft is anteroposteriorly compressed, probably due to diagenetic factors, and the cross-section at midshaft is elliptical (180 mm x110 mm, eccentricity of 164%). Both the anterior and posterior surfaces are flat and smooth. The fourth trochanter is elliptical (100 mm proximodistally and 55 mm mediolaterally) and it is located at the posteromedial margin of the femur, near the centre of the proximodistal axis of the shaft.

5. Discussion

We conducted a taxonomic (species-level) diversity assessment in the Els Nerets locality based on the minimum number of individuals (MNI) found in the site and their respective ontogenetic ages. To perform the analyses, we integrate the newly described material and the historical specimens described by Casanovas *et al.* (1987, 1995) (see Appendix). With a MNI of three titanosaurian individuals (two from the upper level, and another one from the lower level), the palaeohistological analysis of the bones reveals that all individuals were adults (see Appendix), as shown by their high HOS (Klein and Sander, 2008). For Individual 1, the humerus is small and shows a high HOS (12) with a type F bone tissue; this indicates that the species reached a small body size (about 5 m) at adulthood (measures based on Mazzetta *et al.*, 2004).

For Individuals 2 and 3, the appendicular elements (femora and ulna) are of medium size and show a range of HOS values between 12 to 14 and type bone tissues F and G (sensu Klein and Sander, 2008), indicating that the individuals probably belonged to a different species than Individual 1, as they reached a larger body size (7 m and 9 m, respectively) in adulthood. Similarities in morphology, size, and HOS, may suggest that both individuals could belong to the same species.

Individual 1 can only be classified in a sauropod group as derived as Titanosauriformes based on the camellate internal structure of its associate dorsal centra (D'Emic, 2012). For Individual 2, despite its morphological resemblance to the femur of Individual 3 and those of the Ibero-Armorican taxa, the presence of a medial deflection of its proximal third only allows for its classification as a macronarian (D'Emic, 2012). Its assignment to Titanosauria is uncertain as its eccentricity index is 164%, much below the 185% which is considered the minimum for Titanosauria. However, since it has been suggested that both Individuals 2 and 3 may belong to the same species, Individual 2 could be also considered a titanosaur. For Individual 3, the long and wide anterior process in the ulna and the apparent placement of the neural arches on the anterior half of the middle caudal centra, are two synapomorphies of Titanosauriformes (D'Emic, 2012; Gorscak and O'Connor, 2019). The ventral concavity in the anterior caudal vertebrae is common in Titanosauria (D'Emic, 2012) and thus we assign Individual 3 to Titanosauria indet., although the future discovery of new material from the same individual might confirm a more precise classification.

In sum, we have recognized the presence of a small-sized and two medium-sized sauropod individuals in the Els Nerets locality: the smallest reaching a body length up to 5 m, and the medium-sized forms with 7 m and 9 m, being the largest the specimen recognized as a member of Titanosauria. The comparisons with other Upper Cretaceous Ibero-Armorican titanosaurs (see Appendix) show that, although the Els Nerets specimens share similarities with some of them, they cannot be assigned to any of the known taxa due to the absence of diagnostic characters. We cannot rule out that the differences observed with other titanosaurian species may be due to intraspecific, ontogenetic changes, or dimorphism (*e.g.* Páramo *et al.*, 2020) for Individuals 2 and 3, so further research is needed.

6. Conclusions

The study of the sauropod material from the Els Nerets locality (Lleida, South-Central Pyrenees) indicates the occurrence of three individuals with mature histologic ontogenetic stages (HOS 12-14). The three adult individuals show differences in size and may represent two different species, but the observed synapomorphies only allow for the classification of Individual 3 (and Individual 2 if considered a member of the same species) as Titanosauria indet., whereas Individual 1 can only be assigned to Titanosauriformes. The fragmentary nature of the specimens hinders the comparison with the known Ibero-Armorican titanosaurs and prevents the assignment of the Els Nerets taxa to any of them. Therefore, more complete specimens are needed in order to better classify the new forms as new taxa or as an already known species. However, the integration of anatomical studies, histological analyses and body size estimates is considered to be an efficient tool to differentiate between individuals and provide diversity estimations.

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Appendix 1. Supplementary information

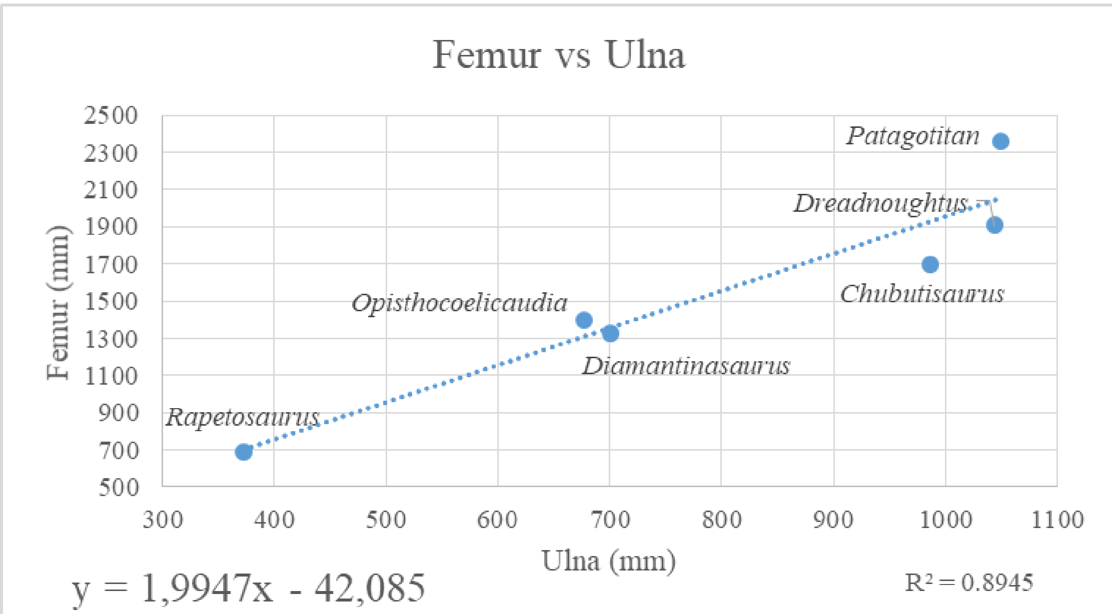
Appendix 1.1. Materials and methods

The Minimum Number of Individuals (MNI) was primarily calculated on counts of non-replicated elements present in a single stratigraphic level. Secondarily, it was determined in terms of size and age characteristics of such elements. This is, for each non-replicated appendicular element from a single stratigraphic level, we calculated the expectable lengths of the respective elements found in the same level. To do so, we compiled femoral and ulnar lengths of four articulated or complete titanosaurian skeletons that preserve both elements in their entirety (Appendix Table 1), then plotted the respective lengths and performed a linear regression to produce an allometric equation relating these dimensions (Appendix Figures 1 and 2), allowing one to be estimated from the other (Appendix Table 2). For femoral vs. humeral length, we used the allometric equation $y = 0.9637x + 0.208$ of González-Riga *et al*. (2016).

Appendix Table 1: Proximodistal lengths of humeri, femora, and ulnae in articulated titanosaurian specimens. Abbreviations: Lh, humeral length; Lf, femoral length; Lu, ulnar length. Measurements are in mm.

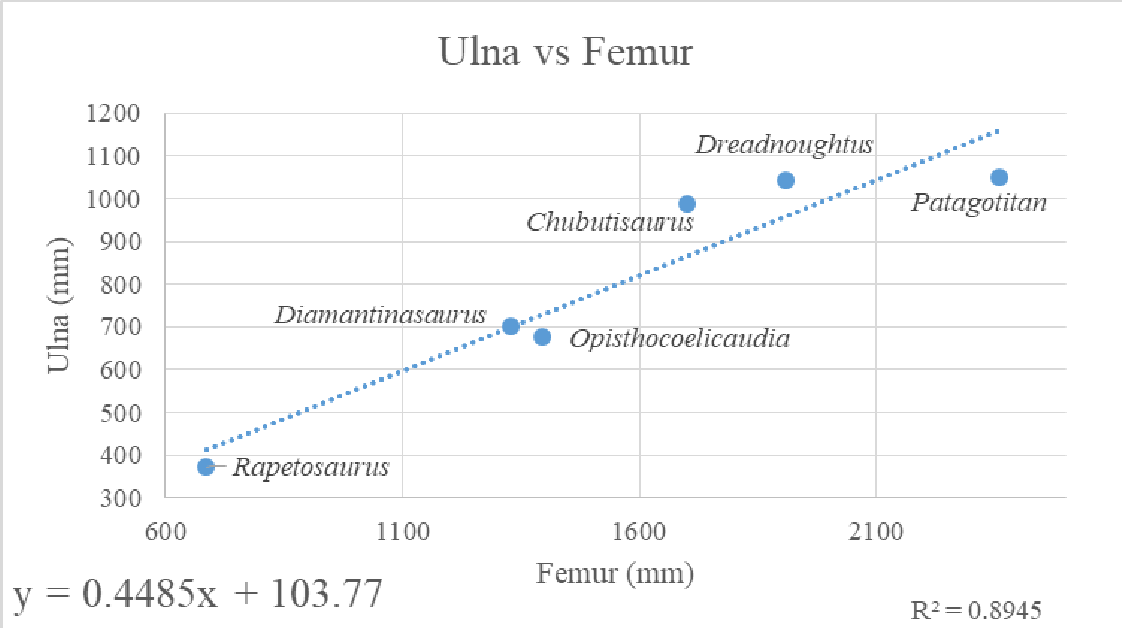
Anexo Tabela 1. Comprimentos proximodistais dos úmeros,fémures e ulnas em exemplares articulados de titanossáurios. Abreviaturas: Lh, comprimento umeral; Lf, comprimento femoral; Lu, comprimento ulnar. Medidas estão em mm.

Taxon	Specimen	Source	Lh	Lf	Lu
Rapetosaurus krausei	FMNH PR 2209	Curry-Rogers, 2009	524	687	372
Diamantinasaurus matildae	AODF 603	Poropat *et al.*, 2015	1068	1330	700
Opisthocoelicaudia skarzynskii	ZPAL MgD-I/48	Borsuk-Bialinicka, 1977	1000	1395	677
Dreadnoughtus schrani	MPM-PV 1156	Ullmann and Lacovara, 2016	1600	1910	1044
Chubutisaurus insignis	MACN 18222	Carballido *et al.*, 2011	1460	1700	987



Appendix Figure 1: Linear regression for titanosaurian femoral and ulnar proximodistal lengths. Data extracted from Supplementary Table 1.

Apêndice Figura 1: Regressão linear para os comprimentos proximodistais dos fémures e ulnas de titanossáurios. Dados retirados da Tabela Suplementar 1.



Appendix Figure 2: Linear regression for titanosaurian ulnar and femoral proximodistal lengths. Data extracted from Supplementary Table 1.

Apêndice Figura 2: Regressão linear para os comprimentos proximodistais das ulnas e fémures de titanossáurios. Dados retirados da Tabela Suplementar 1.

The histological analysis and the HOS (Histological Ontogenetic Stage) evaluation follow the methods of Klein and Sander (2008). The humerus (IPS-36325), ulna (MCD-6705), and femora (IPS-36326, MCD-9886) were core drilled (circular diamond crown, 1420 rpm, at 350 W) and a thin section (around 30 µm) was later prepared at the Servei de Làmines primes de la Universitat Autònoma de Barcelona.

The individuals from Els Nerets have been compared with other Ibero-Armorican titanosaurs: *Ampelosaurus atacis* (Le Loeuff, 1995, 2005), *Atsinganosaurus velaucensis* (García *et al*., 2010; Díez Díaz *et al*., 2018), *Garrigatitan meridionalis* (Díez Díaz *et al*., 2021), *Lirainosaurus astibiae* (Company *et al*., 2009; Díez Díaz *et al*., 2013a, 2013b), *Lohuecotitan pandafilandi* (Díez Díaz *et al*., 2016); and the titanosaur from Orcau-1 locality (Tremp Basin, Catalonia, Spain; Vila *et al*., 2018).

Appendix 1.2. Institutional Abbreviations

AODF (Australian Age of Dinosaurs Fossil, Winton, Queensland, Australia), FMNH (Field Museum of Natural History, Chicago, USA), IPS (Museu de l'Institut Català de Paleontologia Miquel Crusafont, Cerdanyola del Vallès, Catalonia, Spain), MACN (Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina), MCD (Museu de la Conca Dellà, Isona i Conca Dellà, Catalonia, Spain), MPM (Museo Padre Molina, Río Gallegos, Argentina), ZPAL MgD (Instytut of Paleobiologii, Polish Academy of Sciences, Warsaw, Poland).

Appendix 1.3. Results

Appendix 1.3.1. Minimum Number of Individuals

After integrating the historical material and the newly described specimens from the Els Nerets locality, we found two non-replicated elements (humerus and femur) in the upper stratigraphic level and two more elements (femur and ulna) in the lower level (Supplementary Table 2).

Appendix Table 2: Proximodistal length (mm) of the appendicular elements of each fossiliferous level. Values in parenthesis represent the percentage difference between the calculated value in relation with the element estimated value in each stratigraphic level. The Real measurement (Rm) results from the direct measure of the parts preserved of the piece. The Estimated value (Ev) is obtained based on the estimation of the bone size compared with complete specimens present in other taxa. The Calculated value (Cv) results from the use of linear correlation equations (see Supplementary Figures 1 and 2).

Apêndice Tabela 2: Comprimento proximodistal (mm) dos elementos apendiculares de cada nível fossilífero. Os valores entre parênteses representam a diferença percentual entre o valor calculado em relação ao valor estimado para o elemento em cada nível estratigráfico. A medição Real (Rm) resulta da medida direta dos segmentos preservados do elemento. O valor estimado (Ev) é obtido com base na estimativa do tamanho do osso em comparação com elementos completos presentes noutros taxa. O Valor calculado (Cv) resulta da utilização de equações de correlação linear (ver Figuras Suplementares 1 e 2).

	SPECIMEN	**Proximodistal Length**				
		Rm	**Ev**	**Cv**		
				Femur	Humerus	Ulna
Upper Level	Humerus (IPS-3625)	425	433	576 (-32,6%)	-	-
	Femur (IPS-36326)	567	855	-	693 (+60,0%)	-
Lower Level	Femur (MCD-9886)	860	1093	-	-	594 (-4,3%)
	Ulna (MCD-6705)	404	621	1196 (+9,5%)	-	-

By grouping the appendicular elements with proportional sizes from a particular stratigraphic level, we set a minimum number of three sauropod individuals.

Individual 1 includes the humerus IPS-36325 that is clearly too small (proximodistal length: 433 mm) to correspond with individuals of the other appendicular bones. Following allometric equations (Supplementary Table 2), for such a small humerus the corresponding femur would have a length of 417 mm, which is a significantly smaller value than that of the femur IPS-36326 (855 mm) recovered at the same stratigraphic level. An isolated centrum of a dorsal vertebra (IPS-897) described by Casanovas *et al.* (1995) is tentatively assigned to this individual due its size and stratigraphic provenance. Individual 2 is composed of the medium-sized femur IPS-36326 (855 mm).

Individual 3 is composed of the large-sized femur MCD-9886 (1093 mm), the ulna MCD-6705 (621 mm), six caudal vertebrae (IPS-901, MCD-6733b, IPSN-23, MCD-7030, MCD-8641 and MCD-8642) and tentatively the fragment of a scapular blade (MCD-6731). Four of the caudal vertebrae (MCD-6733b, MCD-7030, MCD-8641 and MCD-8642) have been assigned to this individual since they were found relatively close to one another at the same fossiliferous level, while IPS-901 and IPSN-23 (of which cannot be confidently said that were extracted from the same level as the other vertebrae) have been tentatively assigned to the same individual due to similarities in colour, preservation state and size. For the femur MCD-9886, the corresponding length of the ulna has been calculated at 578 mm, a value that falls very close to the proximodistal length (621 mm) of this element (MCD-6705).

Appendix 1.3.2. Paleohistological analysis

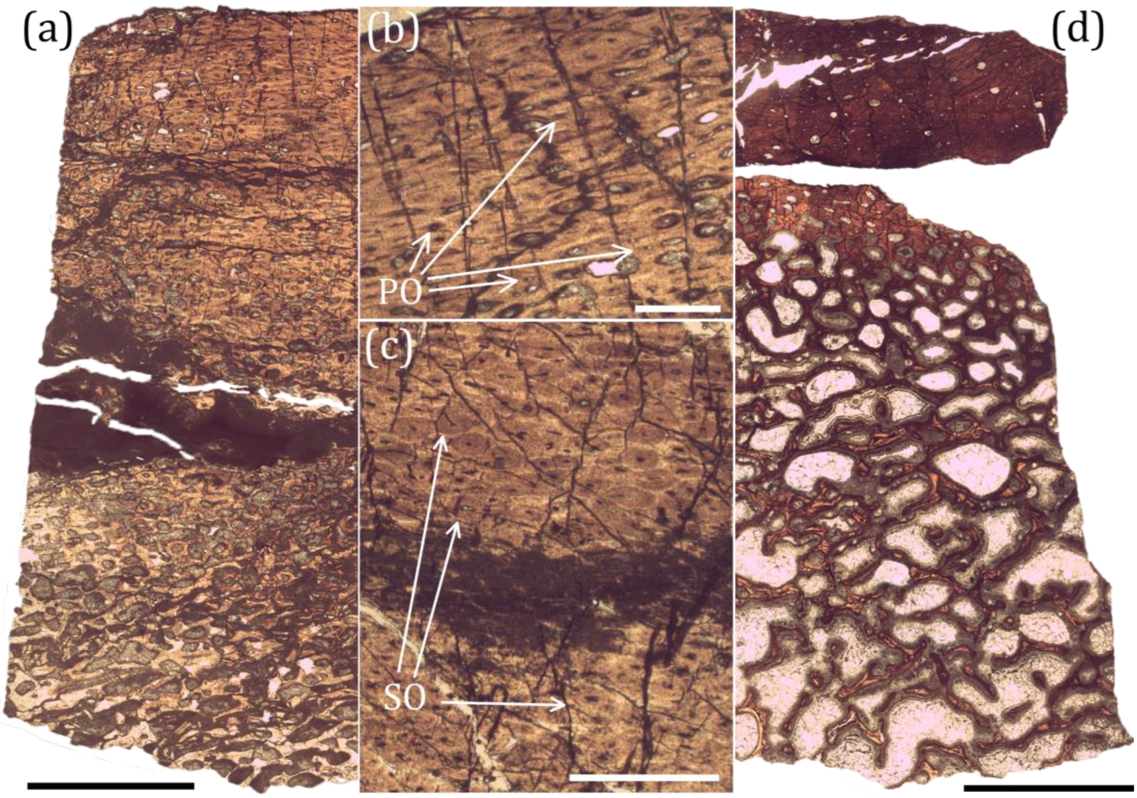
Femur MCD-9886 – Over the 75% of the thin-section is occupied by the medullary zone, but its external third consists in a gradual change to the cortex (see in Supplementary Figure 3a). The cortex preserves some primary structures as a slight longitudinal ordination pattern of the primary osteons (see in Supplementary Figure 3b) and a matrix with a laminar fibrolamellar bone tissue, although it also presents some secondary osteons. These three generations of secondary osteons are heterometric and accumulate in the transitional zone and in the periosteum. On the forementioned transitional zone (Supplementary Figure 3a), the secondary osteons show a bigger size. In addition, the degree of vascularization of the bone is low. No LAG's and/or EFS have been recognized. In the transitional zone from the medullary zone to the cortex and in the cortex itself, the bone tissue is established at F type. Due to the presence of a remodeling medullary zone, a zone with closed-packed secondary osteons and the presence of traces of primary bone tissue close to the periosteum, the ontogenetic stage is set at a HOS-12 value (after Klein and Sander, 2008).

Femur IPS-36326 – Similarly to IPS-36325, the femur presents an extended haversian system that takes up to three or four fifths of the thin-section. The haversian tissue is composed of multiple generations of heterometric secondary osteons, which sometimes present sharpey fibers. The external cortex is not well-preserved and its structures are obscured, although it is possible to recognize several secondary osteons close to the external margin of the bone. These characteristics indicate that this femur could be tentatively assigned to a mature ontogenetic stage, close to a HOS-13 value (after Klein and Sander, 2008).

Humerus IPS-6325 – Almost two thirds of the cortex is formed by the haversian tissue, starting from the medullary cavity (not preserved) to the external cortex, obliterating the original primary tissue. On the external third of the cortex there is a reduction in secondary osteon density that allows for the observation of primary osteons and fibrolamellar tissue, where it is possible to appreciate laminar and longitudinal vascularization. Primary osteons are organized longitudinally forming levels, whereas secondary osteons (see an example in Supplementary Figure 3c) are heterometric and more randomly distributed, and they are also abundant close to the periosteum. Due to their intense remodeling by haversian tissue, no LAGs nor EFS have been observed. After Klein and Sander (2008), the combination of said traits (internal cortex and periosteum dominated by F type tissue) allows us to establish a HOS-12.

Ulna MCD-6705 – The medullary region is highly developed on this sample, taking up to 70% of the section (see in Supplementary Figure 3d) and showing great vacuities that progressively reduce their size up to the external margin. In the preserved cortex there are only secondary osteons, distributed between three different generations. The intense remodeling of the thin-section impedes the observation either EFS or LAG's. The observed histological traits are compatible with the G type of bone tissue, defined by Klein and Sander (2008). With this, the histological ontogenetic stage that corresponds to the ulna should be a HOS-13 or maybe even a HOS-14, due to the great expansion of the medullary zone in the bone.

The histological analysis shows high HOS, ranging from 12-14 values (after Klein and Sander, 2008), for all the appendicular elements (humerus, femora, and ulna; Supplementary Table 2). These are obtained from the type of bone tissue (*e.g.* laminar fibrolamellar bone), its vascularity, and the presence of secondary osteons. In all the elements, the bone tissue is considered to be either type F or G (Klein and Sander, 2008). The resulting HOS values show, among other traits, a high amount (and multiple generations) of secondary osteons inside the cortical zone and a decrease in bone vascularization (reduction of the vascular canals). The high ontogenetic stages observed in all the samples are considered characteristic of adult individuals (Klein and Sander, 2008). It is of particular interest the high remodeling of the ulna of Individual 3 (MCD-6705), probably due to the expansion of the medullary zone, which in turn has allowed for a great development of the Haversian system. A common trait among the appendicular elements of all individuals is that no LAG's (Lines of Arrested Growth) and EFS (External Fundamental System) have been observed, a common trait for titanosaurs (Company, 2011).



Appendix Figure 3: Histological sections from Els Nerets material. a, Femur MCD-9886 depicting the medullary and the cortex zone (from bottom to top); b, Detail of the same femur, close to external cortex; c, Detail of the Humerus IPS-6325; d, Most of the ulna MCD-6705 is formed by the medullary zone, which is formed by great vacuities that progressively reduces their size up to periosteum. Abbreviations: PO, Primary Osteons; SO, Secondary Osteons. Scale bars in (a) and (d) equal 5 mm; (b) and (c) equal 1mm.

Apêndice Figura 3: Seções histológicas do material de Els Nerets. a, Femur MCD-9886 que mostra as zonas medular e do córtex (de baixo para cima); b, Detalhe do mesmo fémur, junto ao córtex externo; c, Detalhe do Humerus IPS-6325; d, Grande parte da ulna MCD-6705 é formada pela zona medular que é formada por grandes cavidades que reduzem progressivamente de tamanho até ao periósteo. Abreviaturas: PO, Ósteons Primários; SO, Ósteons Secundários. Escala em (a) e (d) igual a 5 mm; (b) e (c) igual a 1 mm.

Appendix 1.4. Discussion

Appendix 1.4.1. Paleohistological discussion

As a general premise, it is assumed that as an individual grows its degree of osteohistological maturity (including bone remodeling) increases and will therefore present higher ontogenetic histological stages (HOS) at adulthood (Klein and Sander, 2008). Following these authors, if we consider that two or more appendicular elements belong to the same individual, with a given body size and thus with the same ontogenetic stage, we will expect all their elements to have a similar HOS. Accordingly, the resulting HOS will indicate that body size corresponds to a particular ontogenetic stage (juvenile, subadult, adult) (Sander, 2000; Klein and Sander, 2008; Klein *et al*., 2012). In the case of titanosaurs, they have one isometric growth in the appendicular elements (Vila *et al*., 2013; Curry-Rogers *et al*., 2016) and therefore all appendicular elements of the same individual are expected to exhibit a similar HOS (Klein and Sander, 2008).

Appendix 1.4.2. Discussion on the taxonomy of the Els Nerets sauropod material

Titanosaurian species from the Ibero-Armorican region with small adult body sizes are *Lirainosaurus* (4-6 m; Díez Díaz *et al*., 2013b), *Atsinganosaurus* (6-9 m; Díez Díaz *et al*., 2021) and *Garrigatitan* (4-6 m; Díez Díaz *et al*., 2021). The slender humerus of Individual 1 (Casanovas *et al*., 1995) resembles the humeri of *Lirainosaurus* and *Atsinganosaurus* in terms of slenderness and while its deltopectoral crest is less proximodistally expanded than in the former, the humeral shaft is more robust (RI= 4.13, after Wilson and Upchurch, 2003) and straight than in the latter. The deltopectoral crest is fragmented and cannot be confidently compared but seems to be similar to *Atsinganosaurus*. Regarding *Garrigatitan*, the Els Nerets humerus does not share its general hourglass morphology, the lateromedial expansion of its proximal end, nor the constant width of its deltopectoral crest. As a note, the humerus from Els Nerets is much smaller and slender than that of the Orcau-1 titanosaur (Vila *et al*., 2018), which is considered to have a robust humerus together with a deltopectoral crest that appears to be more developed and expanded than in the humerus from Els Nerets. A dorsal centrum from Els Nerets (Casanovas *et al*, 1995), tentatively attributed to the same individual, is very similar to that of *Atsinganosaurus*, especially due to its oval section, but the Els Nerets specimen lacks both the lateral foramina and the ventral keel.

Anatomically, the two femora have very similar midshaft eccentricity indexes (170% for IPS-36326 (Casanovas *et al*., 1995) and 163% for MCD-9886) and comparable fourth trochanters in terms of size and position, although these characters are probably plesiomorphic for most titanosaurian femora (Vila *et al*., 2012, Páramo *et al*., 2020). The two femora have a similar HOS and a difference in size of about 22%, indicating that the individuals reached a remarkably disparate body size at adulthood. This suggests that they represent two different species, each with a different growth rate, or that differences in body size are due to intraspecific variability. In this regard, Company (2011) indicated that intraspecific variability relative to size for individuals of *Lirainosaurus* with the same HOS is about 4%. This variability can be significatively bigger in other Ibero-Armorican taxa according to Vila *et al*. (2022), and as a result of this, a big difference in size like the one between Individuals 2 and 3 from Els Nerets (22%) would still fall into the plausible values of intraspecific variability for *Ampelosaurus*. Therefore, Individuals 2 and 3 may be members of the same species. The body size for the individuals of this likely new species is more akin to that of *Ampelosaurus* (Mean value of 7.4 m; Vila *et al*., 2022) and *Lohuecotitan* (value of 8.1 m; Vila *et al*., 2022), to which they have been compared.

The femur of Individual 2 is slenderer than that of the titanosaur from Orcau-1 and *Ampelosaurus*, its eccentricity (163%) being more similar to *Lohuecotitan* (160%, based on Díez Díaz *et al*., 2016) and definitely lower than that of the titanosaur from Orcau-1 locality (>185%). However, the fourth trochanter of IPS-36326 is proximodistally shorter and it seems to be more prominent posteriorly (but since it is broken it cannot be known to what extent). It also lacks the trochanteric shelf present in *Lohuecotitan* (Díez Díaz *et al*., 2016). In sum, the fragmentary nature of the specimen prevents a confident assignment to any Ibero-Armorican species, and the lack of synapomorphies of more derived groups of sauropods restrings its taxonomic assignment to an indeterminate Macronaria.

For Individual 3, the middle caudal vertebrae (position determined by the lack of transverse processes, a plausible articulation with the haemal arch and by being longer than tall, after Díez Díaz *et al*., 2013a) present a slightly concave ventral surface and appear to be longer when compared to those of *Ampelosaurus* and *Lohuecotitan*, with a subtriangular section instead of the subcircular sections seen in the latter two taxa. The distal caudal vertebra of Els Nerets is rod-like and biconvex as in *Lirainosaurus* (Díez Díaz *et al*., 2013a), although contrary to the cylindrical centra of the Laño taxon, the dorsoventral surfaces of the Els Nerets centra are flat. The broken scapular blade is too fragmented to be confidently compared with similar pieces from the Ibero-Armorican taxa. The ulna from Els Nerets is similar to that of *Lohuecotitan* and *Ampelosaurus* in robustness and in the differential development of the proximal processes. The proximodistal fossa in the radial articular surface present in *Lohuecotitan* seems to be absent in the Els Nerets specimen. The latter is similar to *Lohuecotitan* in having a straighter shaft than *Ampelosaurus*. Lastly, the femur (Fig. 2a) is morphologically similar to that of *Lohuecotitan*, especially since the fourth trochanter of Els Nerets is visibly prominent medially in anterior view, unlike the straight profile of *Ampelosaurus*. Similarly to *Atsinganosaurus*, the fourth trochanter is more medially positioned than in *Lohuecotitan*, and the shaft eccentricity is higher, but not as much as in *Ampelosaurus*. Also, the trochanteric shelf present in *Lohuecotitan* is absent in Individual 3. It is also worth mentioning that the lateral bulge is poorly developed and located nearer the proximal end when compared to other Ibero-Armorican taxa. Even more similar to Els Nerets is the V-10 right femur from Presa de Tremp (Vila *et al*., 2012). Both share a straight shaft and a low, proximodistal ridge-like fourth trochanter that shows a proximodistal groove on the medial margin of the trochanter. The same cannot be said for the femur C3-1278 from Bellevue, which is more robust than MCD-9886 and its fourth trochanter is more medially developed than in Els Nerets (*e.g*. Vila *et al*., 2012). Additionally, the straight shaft from Els Nerets has a constant thickness proximally, unlike C3-1278.

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