



General Palaeontology, Systematics and Evolution (Vertebrate Palaeontology)

First dinosaur and turtle remains from the latest Cretaceous shallow marine deposits of Albaina (Laño quarry, Iberian Peninsula)



Premiers restes fossiles de dinosaure et de tortue dans les dépôts marins littoraux fini-crétacés d'Albaina (carrière de Laño, péninsule Ibérique)

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ABSTRACT

We report here on new vertebrate fossils from the latest Cretaceous of Albaina (Laño quarry, Condado de Treviño), northern Iberian Peninsula. They consist of an incomplete hadrosauroid femur and two partial plates of turtles, one belonging to a Pleurodira (Bothremyidae), the other one to an indeterminate taxon, probably corresponding to a Pan-Cryptodira. They are the first dinosaur and turtle remains found in the Late Maastrichtian sublittoral beds of Albaina. Other components of this shallow marine vertebrate fauna are selachians (sharks, rays), actinopterygians (pycnodonts, teleosts) and marine reptiles (mosasaurids, plesiosaurs). The Albaina femur is one of the few hadrosauroid remains from the Late Maastrichtian of Europe found in marine environments, and the first one described from this kind of deposits in the Iberian Peninsula. The histological structure of the bone indicates that it belongs to an immature individual of small size.

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RÉSUMÉ

De nouveaux fossiles de vertébrés découverts à Albaina (carrière de Laño, Condado de Treviño), dans le Nord de la péninsule Ibérique, sont décrits. Il s'agit d'un fémur incomplet d'hadrosauroïde et de deux plaques partielles de tortue, l'une appartenant à un Pleurodira (Bothremyidae) et l'autre à un taxon indéterminé, correspondant probablement à

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Pan-Cryptodira ; ce sont les premiers restes de dinosaure et de tortue trouvés dans les dépôts sub-littoraux d'âge Maastrichtien supérieur d'Albaina. Les autres éléments de cette faune marine de vertébrés sont des sélaciens (requins et raies), des actinoptérygiens (pseudodontes et téléostéens) et des reptiles marins (mosasauridés et plésiosaures). Le fémur d'Albaina est l'un des rares fossiles d'hadrosauroïde découverts dans un environnement marin dans le Maastrichtien supérieur d'Europe, et le premier décrit dans ce type de dépôts dans la péninsule Ibérique. La structure histologique de l'os indique qu'il appartient à un individu immature de petite taille.

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1. Introduction

The Laño quarry is a disused silica sand quarry embracing the villages of Albaina and Laño in the Condado de Treviño, which is an exclave of Burgos province (Spain) in the northern Iberian Peninsula (Fig. 1). The quarry is located about 30 km south of the city of Vitoria-Gasteiz (Álava). Some deposits uncovered by sand quarrying at this point have revealed one of the most noteworthy Campanian–Maastrichtian vertebrate sites of Europe by its taxonomic diversity, and provided relevant information about the composition and affinities of both terrestrial–freshwater and shallow marine vertebrate faunas from the Latest Cretaceous of the Ibero-Armorican Domain in southwestern Europe (Astibia et al., 1990, 1999; Pereda-Suberbiola et al., 2000).

Vertebrate fossils accumulate at two different stratigraphic units: the lower one contains the so-called Laño 1 and Laño 2 sites, ascribed to the Late Campanian–Early Maastrichtian interval, while the upper one, mainly located in the vicinity of the Albaina village, is ascribed to the Late Maastrichtian. Therefore, there exists an important time gap between the two stratigraphic units, which is represented in the Laño quarry by a low-angle unconformity (Baceta et al., 1999; Berreteaga, 2008 and references). The fluvial beds of sites Laño 1 and 2 have yielded a diverse vertebrate association that consists of nearly 40 species, including actinopterygians, lissamphibians, squamates, turtles, crocodyliforms, dinosaurs, pterosaurs and mammals (Pereda-Suberbiola et al., 2000). The sublittoral beds of the Albaina site have yielded a diverse vertebrate assemblage so far composed of 37 taxa, including sharks and rays (Cappetta and Corral, 1999), pycnodontiforms and teleosteans (Poyato-Ariza et al., 1999), mosasaurids and plesiosaurs (Bardet et al., 1999, 2013).

In this paper, we describe three new interesting fossils from the Late Maastrichtian sublittoral beds of the Albaina site (Laño quarry): the first identifiable dinosaur bone and two isolated turtle plates. Their identity and palaeontological significance are also discussed in detail.

Institutional abbreviations. MCNA, Museo de Ciencias Naturales de Álava/Arabako Natur Zientzien Museoa, Vitoria-Gasteiz, Spain; LU, Luberrí-Oiartzungo Ikasgune Geologikoa Museoa, Oiartzun, Spain.

2. Geological setting

The detailed geology of the Laño quarry (including the Albaina beds) has been extensively discussed in other

publications (Astibia et al., 1990, 1999; Baceta et al., 1999; Berreteaga, 2008; Gómez-Alday, 1999; Pereda-Suberbiola et al., 2000). Geologically, the area lies on the southern limb of the Miranda-Treviño syncline (central part of the Sub-Cantabrian Synclinorium). Quarrying has exposed at least a 70-m section of terrigenous and carbonate rocks of Late Cretaceous–Paleogene age that records continental to shallow marine environment within the southern Basque–Cantabrian Basin.

The Late Cretaceous succession is subdivided into three unnamed formations, considered equivalent to the Sedano, Sobrepeña plus Valdenoceda, and Torme formations (Berreteaga, 2008; see also Floquet, 1991, 1998), which reflect substantive changes in lithology and fossil content (Fig. 1). The basal part of the succession (equivalent to the Sedano Fm.) comprises fluvial silty and sandy facies, where terrestrial and freshwater vertebrate fossils occur (Laño 1 and 2 sites), and is overlain by a massive sand bar, which was the commonly targeted bed in the quarry. The sedimentary structures are consistent with channel areas within an extensive braided river system (Gómez-Alday, 1999; Pereda-Suberbiola et al., 2000).

Above this interval, a succession of sandy lutites, occasionally microconglomeratic, pedogenic carbonates and silty grey mudstones with plant remains and unidentifiable black bone fragments represent an alluvial–palustrine system (Gómez-Alday, 1999).

The upper part of the exposed section (equivalent to the Torme Formation cropping out in the Villarcayo area, Burgos Province, North-Castilian Platform) is composed of grey poorly cemented sandstones and yellowish friable calcarenites, deposited during the maximum transgression of the sea into this area. The maximum thickness of this formation throughout the Laño area is about 10 to 12 m. Contrary to the mollusc and arthropod macrofossils (i.e. gastropods, bivalves, ammonites, crustaceans), which are rather scarce in these carbonate rocks, selachians, actinopterygians, marine reptiles and layers of accumulated orbitoidids are characteristic. The upper unit represents a shallow marine sublittoral environment. According to the selachian association, a Late–but not Latest–Maastrichtian age is given for the Albaina beds (Cappetta and Corral, 1999).

3. Material and methods

The vertebrate material described here was collected by breaking out calcarenite rocks fallen from the upper beds

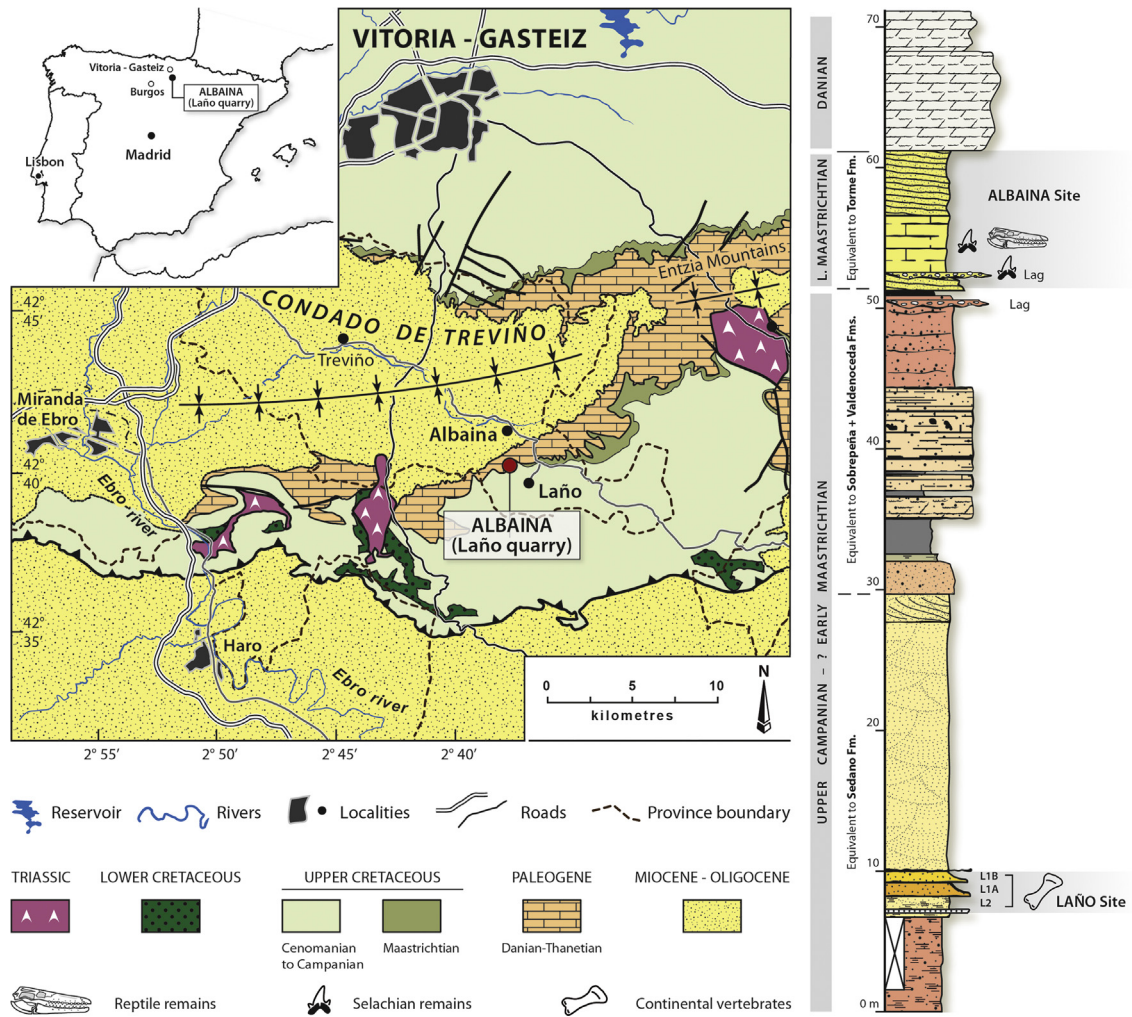


Fig. 1. (Color online.) Simplified geological map of the south-central part of the Basque–Cantabrian Region and stratigraphic column of the Laño quarry showing the position of the fossil vertebrate beds (map compiled from the Spanish National Geologic Map, MAGNA 1:50,000; the column follows standard lithologic patterns). Albaina location is also indicated in the inset map of Iberia.

Fig. 1. (Couleur en ligne.) Carte géologique simplifiée de la partie sud-centrale de la région Basco-Cantabrique et colonne stratigraphique de la carrière de Laño montrant la position des niveaux fossilifères à vertébrés (carte d'après la carte géologique nationale d'Espagne, MAGNA 1:50 000; la colonne suit les modèles lithologiques standards). La localisation d'Albaina est aussi indiquée sur l'encart représentant la carte de l'Espagne.

of the Laño quarry face. These beds have been primarily targeted for their content in marine vertebrate remains (Bardet et al., 1999, 2013; Cappetta and Corral, 1999; Poyato-Ariza et al., 1999). The dinosaur bone was found by two of us (G.M., J.L.) in recently fallen blocks, whereas the turtle plates were already in the MCNA collection as a result of regular prospecting in the fossil site by another of us (J.C.C.). Fossil preparation and conservation was done in the MCNA laboratory, using standard preparation techniques.

Thin sections were made from the midshaft of the femur LU-JL-LAÑO01, which is assumed to contain the most complete growth record of the bone (Sander, 2000; Stein and Sander, 2009). The samples were cut and polished according to current techniques (Lamm, 2013).

4. Systematic palaeontology

4.1. Testudines

cf. PAN-CRYPTODIRA Joyce, Parham and Gauthier, 2004
cf. Pan-Cryptodira indet.

Material. MCNA 15055, a partial peripheral plate lacking the medial and latero-posterior regions (Fig. 2A–C).

Description. The plate lacks its medial region. For this reason, the width/length cannot be estimated. It is a peripheral that does not contact the plastron, but is close to the plastral bridge. This plate is crossed by a sulcus located

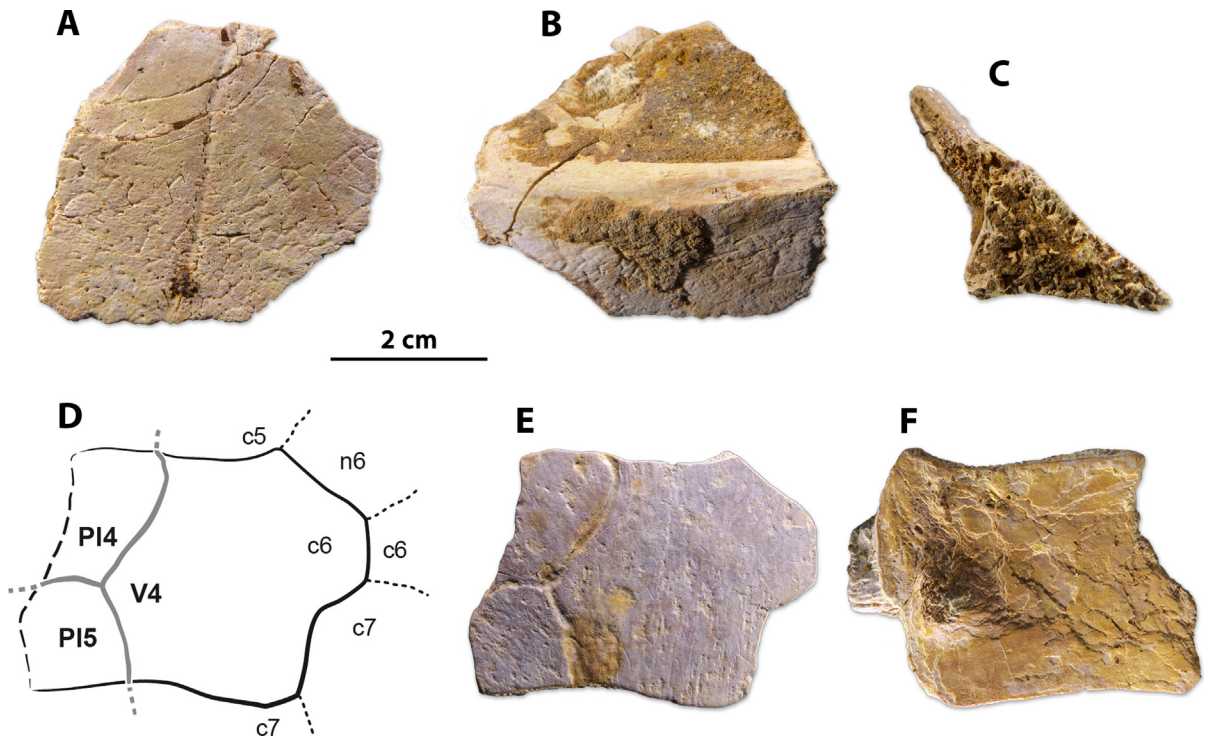


Fig. 2. (Color online.) Albaina turtles. A–C. MCNA 15055, cf. Pan-Cryptodira indet., partial peripheral plate in dorsal, ventral and anterior views. D–F. MCNA 10863, cf. *Polysternon atlanticum* (Bothremydidae), sixth left costal plate, interpretative schema, dorsal and ventral views. The continuous lines represent the preserved margins of the plate, the dashed lines are broken edges, and the dotted lines correspond to the hypothetical reconstruction of the adjacent plates. Black lines represent the sutures between plates; grey and wider lines indicate the border of the scutes. Abbreviations: c, costal plate, n, neural plate; PL, pleural scute; V, vertebral scute.

Fig. 2. (Couleur en ligne.) Tortues d'Albaina. A–C. MCNA 15055, cf. Pan-Cryptodira indet., plaque périphérique partielle en vues dorsale, ventrale et antérieure. D–F. MCNA 10863, cf. *Polysternon atlanticum* (Bothremydidae), 6^e plaque costale gauche, schéma interprétatif et vues dorsale et ventrale. Les lignes continues représentent les bords préservés de la plaque, les lignes discontinues les bords cassés, et les lignes en pointillé correspondent à une reconstitution hypothétique des plaques adjacentes. Les traits noirs représentent les sutures entre les plaques, et les traits gris plus épais les frontières entre les écailles. Abréviations : c, plaque costale, n, plaque neurale ; Pl, écaille pleurale ; V, écaille vertébrale.

between two marginal scutes. Considering that the most distal region of this kind of sulci is always anteriorly directed, this plate is identified as a left peripheral. The angle between the dorsal and the ventral surfaces is greater in the anterior region than in the posterior one (Fig. 2B and C). Therefore, the anterior margin corresponds to that located nearest to the plastral bridge, this plate being a posterior peripheral. Although the width of this plate is not known (i.e. the length between the medial and distal margins), the ventral surface covered by the marginal scutes is relatively narrow, substantially less than half of the width of the plate (Fig. 2B). A well-developed change of level, which does not match the ventro-medial margin of the marginal scutes, is present. It is parallel to that margin, being more medially located. The outer surface is partially altered. However, several discontinuous dichotomous sulci are preserved. Therefore, this plate was ornamented. Because the medial region is not preserved, it is not possible to know if the pleural scutes overlapped the peripheral plates. It is interpreted that, if such overlap occurs, it would be short, because the marginal scutes cover all the preserved dorsal region of the peripheral plate.

Discussion. The limited information provided by this element prevents its accurate systematic allocation. Characters, such as the absence of the autapomorphic ornamental pattern of Dortokidae, a clade of basal Pan-Pleurodira recognized in the continental deposits of Laño, as well as its larger size, allow excluding its assignment to that group. The absence of tubercles confirms that this specimen cannot be assigned to Solemydidae, another clade of turtles recognized in Laño. The presence of an ornamental pattern composed by discontinuous and dichotomous sulci is shared with Bothremydidae (Pleurodira), the third clade recognized in Laño. However, characters, such as the relatively narrow ventral development of the marginal scutes allow excluding its assignment to this group. This ornamental pattern has also been identified in several undetermined pan-cryptodiran taxa recognized both in the Early and Late Cretaceous of Western Europe (see Pérez-García and Murelaga, 2014; Pereda-Suberbiola et al., 2009a), generally referred as “chelydroids” in aspect, and probably belonging to different clades. Although all or at least some of these poorly known taxa have fontanelles between the costal and the peripheral plates, the absence of information on the

medial region of MCNA 15055 does not allow comparing this character.

PAN-PLEURODIRA Joyce, Parham and Gauthier, 2004
 PLEURODIRA Cope, 1864
 PELOMEDUSOIDES Cope, 1868
 BOTHREMYDIDAE Baur, 1891
 BOTHREMYDINAE Baur, 1891
 BOTHREMYDODDA Baur, 1891 sensu Gaffney, Tong and Meylan, 2006
 BOTHREMYDINI Baur, 1891 sensu Gaffney, Tong and Meylan, 2006
Foxemydina Gaffney, Tong and Meylan, 2006
 cf. ***Polysternon atlanticum***

Material. MCNA 10863, the almost complete medial half of a sixth left costal plate (Fig. 2D–F).

Description. The only broken margin corresponds to the distal one. Therefore, the preserved region of this costal plate documents the morphology of the margins, which contacted with the neural series and with other costals. The antero-medial contact with a neural is observed (Fig. 2E, F). The posterior region of this neural plate was relatively wide in relation to its length. An approximately parallel margin to the axial axis suture, which is interpreted as the medial contact with another costal plate, is developed in the medial edge of the preserved costal. The postero-medial edge of this plate corresponds to the suture with another costal, the medial area of contact of the last costals of the carapace being developed in zigzag.

The medial region of MCNA 10863 is covered by a portion of a vertebral scute. The sulci separating this scute and two pleural ones are observed (Fig. 2E, F). Therefore, this plate is an even-numbered costal. Given this, plus its curvature, and the described contact with other plates, this element can be attributed to a sixth left costal. Taken this into account, this plate antero-medially contacts the sixth neural, medially the sixth right costal, and postero-medially the seventh right costal plates. Consequently, the neural series is interpreted as discontinuous (i.e. not continuous between the nuchal and the suprapygal plates), being composed of six plates. The best preserved areas show that the plate was ornamented by discontinuous and dichotomous sulci (Fig. 2E).

Discussion. Despite its limited information, it is possible to observe that MCNA 10863 shares several characters with Bothremydidae: a discontinuous neural series, the posterior region of the last neural being noticeably wider than long; the morphology and arrangement of the contact between the vertebral and the pleural scutes; and finally, the ornamental pattern.

The only bothremydid from the European Late Cretaceous record hitherto characterized by the presence of six neurals is *Iberoccitanemys* Pérez-García, Ortega, and Murelaga, 2012. However, variability in this character is known in some bothremydid taxa, as *Chedighaii hutchisoni* Gaffney, Tong and Meylan, 2006, from the Late Cretaceous of United States, in which the number of neurals varies from six to seven. In Late Cretaceous taxa from southwestern Europe represented by several specimens, such as *Iberoccitanemys*,

Rosasia Carrington da Costa, 1940 and *Foxemys* Tong et al., 1998, the so far known number of these plates is constant (being seven in the latter two taxa). However, unpublished material of *Polysternon provinciale* (Matheron, 1869) reveals variability in the neural series (six or seven plates). Therefore, some specimens of *Polysternon provinciale* with the same number of neurals as in *Iberoccitanemys* are known. The Laño bothremydid *Polysternon atlanticum* (the only bothremydid species currently identified here sensu Pérez-García et al., 2010) has been recognized by relatively scarce and disarticulated material. Lapparent de Broin and Murelaga (1999) indicated that its neural series includes at least seven neurals, the costals 8 medially meeting. However, the morphology of the medial region of the sixth costal MCNA 7051 from Laño (see plate 5.12 in Lapparent de Broin and Murelaga, 1999) is similar to that of the specimen MCNA 10863 from Albaina. Therefore, we recognize that a neural series composed of six plates may be present in some *Polysternon atlanticum* specimens. MCNA 10863 cannot be referred to *Polysternon provinciale* because thin striations composed of parallel streaks are absent on the carapace. Therefore, the plate from Albaina probably belongs to *Polysternon atlanticum*, the only bothremydid recognized in Laño. However, given the limited availability of characters and the described compatibility of this element with other European representatives of *Foxemydina*, i.e. *Iberoccitanemys* (taking into account its morphology, but also the arrangement of the neural and the costals with which it is in contact), we opted for its identification as cf. *Polysternon atlanticum*.

4.2. Dinosauria

ORNITHISCHIA Seeley, 1887
 ORNITHOPODA Marsh, 1881
 HADROSAUROIDEA Cope, 1869 sensu Sereno, 1986
 Hadrosauroida indet.

Material. LU-JL-LAÑ001, a fragmentary right femur (Fig. 3).

Description. LU-JL-LAÑ001 consists of the medial and distal part of a right femur, which is broken just below the fourth trochanter (not preserved in the specimen). The bone shows evidence of erosion, especially on the distal condyles (Fig. 3A and B). As preserved, the femur is 155 mm long for a maximum distal width of 60 mm (see measurements below); it probably corresponds to a femur that did not exceed 380 mm in length when complete. The shaft is straight in lateral and medial views (Fig. 3C and D). The cross-section at the preserved proximal end of the shaft is ovoid, wider than long; the medial side is longer anteroposteriorly than the lateral one. The anterior surface of the shaft is convex whereas the posterior surface is slightly concave. Although eroded, the distal condyles seem to have been well-developed. They are expanded anteriorly and posteriorly to form an H-shaped outline in distal view (Fig. 3E). The anterior intercondylar groove for the passage of the extensor tendons is deep and U-shaped; it is partially enclosed by expansions of both medial and distal condyles. In anterior view, the medial condyle is

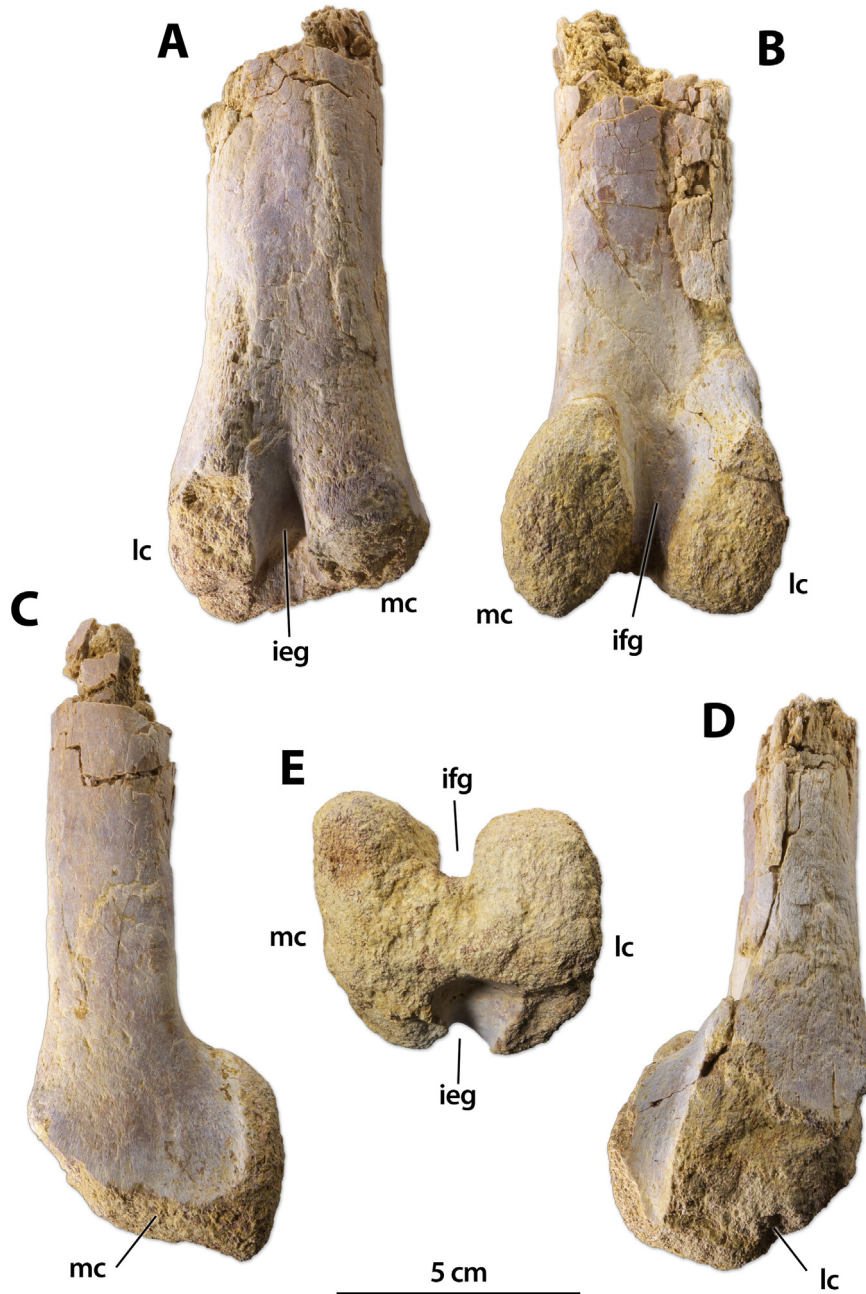


Fig. 3. (Color online.) Albaina dinosaur. LU-JL-LAÑ001, Hadrosauroidea indet., fragmentary right femur in anterior (A), posterior (B), medial (C), lateral (D) and distal (E) views. Abbreviations: ieg, intercondylar extensor (anterior) groove; ifg, intercondylar flexor (posterior) groove; lc, lateral condyle; mc, medial condyle.

Fig. 3. (Couleur en ligne.) Dinosaur d'Albaina. LU-JL-LAÑ001, Hadrosauroidea indet., fémur droit fragmentaire en vues antérieure (A), postérieure (B), médiale (C), latérale (D) et distale (E). Abréviations : ieg, sillon intercondyalaire extenseur (antérieur) ; ifg, sillon intercondyalaire flexeur (postérieur) ; lc, condyle latéral ; mc, condyle médial.

wider than the lateral one and is located distally below it (Fig. 3A). In distal view, the intercondylar flexor groove is deep, U-shaped, and narrower than the anterior groove. The medial posterior condyle is wider and more projected than the lateral one, with a slightly medial orientation (Fig. 3B). The lateral condyle is projected perpendicular to the long axis of the femur. The posterolateral surface of

the lateral condyle shows a shallow vertical groove for the *M. ilio-fibularis*.

Measurements of femur LU-JL-LAÑ001:

- length (as preserved) = 155 mm;
- minimum transverse width of shaft = 48 mm;
- maximum anteroposterior length of shaft = 32 mm;

- perimeter of shaft = 130 mm;
- maximum transverse width of distal end = 60 mm.

Discussion. The combination of femoral characters observed in LU-JL-LAÑ001, i.e. straight distal shaft, antero-posterior expansion of the distal condyles, and deep, nearly closed intercondylar extensor groove on the distal end, allow us to assign the specimen to the clade Hadrosauroidae (see Horner et al., 2004; Prieto-Márquez, 2008; Xing et al., 2012: supplement). We follow here the stem-based definition of Hadrosauroidae by Sereno (1998): all hadrosauriforms closer to *Parasaurolophus* Parks, 1922 than to *Iguanodon* Mantell, 1825. It should be noted that the development of a deep intercondylar extensor groove, with the edges of the groove meeting or nearly meeting anteriorly to enclose an extensor tunnel, has been regarded by Wu and Godefroit (2012) as a synapomorphy of Hadrosauridae, a clade defined by these authors as the most recent common ancestor of *Bactrosaurus* Gilmore, 1933 and *Parasaurolophus*, plus all the descendants of this common ancestor (see Sereno, 2005 and Prieto-Márquez, 2010 for different definitions). According to Wu and Godefroit (2012), a deep intercondylar extensor groove is absent in non-hadrosaurid ornithomorphs, including in basal iguanodontians, such as rhabdodontids, which subsisted in Europe until the Latest Cretaceous (Ősi et al., 2012; Weishampel et al., 2003).

In Europe, hadrosauroid femora have been found in several Maastrichtian localities, from the Iberian Peninsula to Crimea passing through northern and central Europe (see Cruzado-Caballero, 2012 for a list). Some of these femora have been referred in the literature to Hadrosauridae indet. or Euhadrosauria indet. (see Cruzado-Caballero, 2012; Dalla Vecchia, 2006), but others belong to taxa like *Telmatosaurus* Nopcsa, 1903 (Weishampel et al., 1993), *Tethyshadros* Dalla Vecchia, 2009 (Late Campanian to Early Maastrichtian according to Dalla Vecchia, 2009b), “*Orthomerus*” (now regarded as a *nomen dubium*; see Brinkmann, 1988; Horner et al., 2004) and the lambeosaurines *Arenysaurus* Pereda-Suberbiola et al., 2009a and *Blasisaurus* Cruzado-Caballero et al., 2010a.

The general morphology of the hadrosauroid femora is quite conservative, but some individual variation has been observed (Brett-Surman and Wagner, 2007). Few ontogenetic changes have been documented in the limb bones (i.e., femora) and at least immature specimens of basal hadrosauroids can provide reliable information for taxonomic and phylogenetic inferences (Prieto-Márquez, 2011). LU-JL-LAÑ001 looks roughly like two hadrosauroid femora from Els Nerets, Lleida (Casanovas et al., 1985) and Peguera, Barcelona (Pereda-Suberbiola et al., 2003b), but they show signs of erosion and/or deformation. The Albaina specimen apparently differs from the femora of *Telmatosaurus* (Weishampel et al., 1993) and *Arenysaurus* (Cruzado-Caballero et al., 2013) in the absence of a closed extensor tunnel (but an artefact due to erosion cannot be totally discarded for the Albaina femur). Moreover, the Albaina specimen lacks the elliptical foramen located just above the anterior distal condyles in several femora from Blasi 1 in Arén (Huesca) that could belong to *Blasisaurus* (Cruzado-Caballero, 2012). LU-JL-LAÑ001 differs from the

femora of “*Orthomerus dolloi*” Seeley, 1883 from Limburg (Mulder, 1984; Mulder et al., 2005) in having a U-shaped flexor groove (instead of V-shaped), and from the femur of an indeterminate hadrosauroid from Bavaria in that the flexor groove is not so wide (Wellnhofer, 1994). Comparisons with *Tethyshadros* are difficult because in the latter the femur is only available in lateral view (Dalla Vecchia, 2009b). The femur of both *Pararhabdodon* Casanovas, Santafé & Isidro, 1993 (Casanovas et al., 1999; Prieto-Márquez et al., 2006a) and *Canardia* Prieto-Márquez et al., 2013 from Midi-Pyrénées is presently not known. At last, the femora of “*Orthomerus weberi*” Riabinin, 1945 from the Crimea Peninsula and of an indeterminate hadrosauroid from Bulgaria (Godefroit and Motchurova-Dekova, 2010) are very fragmentary to make helpful comparisons. Pending the discovery of new material, the Albaina femur is here referred to Hadrosauroidae indet.

As noted above, the estimated total length of the Albaina femur would be around 35 cm. It is possible to estimate the body length of the Albaina hadrosauroid on the basis of more complete hadrosauroid specimens. The femur of the complete and articulated specimen of *Tethyshadros insularis* Dalla Vecchia, 2009 from the latest Cretaceous of Italy is 420 mm long, representing 11.6% of the total skeleton length (3620 mm from the tip of the snout to the distal end of the tail; see Dalla Vecchia, 2009b: table). In specimens of the hadrosaurine *Maiasaura peeblesorum* Horner and Makela, 1979 from North America, the femur length ranges from 13.3% to 15.5% of the body length (including different growth stages, from nestlings to adults; Horner et al., 2000: table 1). This ratio is similar in other hadrosauroid taxa, including basal and derived forms (see Brett-Surman, 1989). Thus, the Albaina individual was approximately 2.5–3 m in body length at death. Using the equation of Alexander (1989), the estimated body mass of this individual was approximately 95 kg [body mass in kg = a^b , where a (circumference of femur in mm) = 0.00016 and $b = 2.73$]. Histological studies by Horner et al. (2000) suggested that the late juvenile stage represented by individuals of about 3 m may reach an adult size of about twice, but we prefer to be cautious about this type of estimates until we have a better knowledge of both the mechanisms and growth rates in hadrosauroids (see Brinkman, 2011).

5. Bone histology of the hadrosauroid femur

Several bone slivers from the midshaft of the femur LU-JL-LAÑ001 were extracted in order to study its bone microstructure. The examination of bone histological features allows to infer the ontogenetic stage of the individuals when it perished (Chinsamy and Hillenius, 2004; Chinsamy-Turan, 2005; Reid, 2012 and references therein). The small dimensions of the bone (ca. 35 cm in length when reconstructed) suggest a probable young age for the specimen, if not the presence of a dwarf adult hadrosauroid. The occurrence of small-bodied dinosaurs was not rare in the Latest Cretaceous European archipelago (Csiki-Sava et al., 2015). Bone microstructure of juvenile dinosaurs is clearly different from that of submature or mature individuals, and has been described in a variety of groups (Cerdá et al., 2013; Horner et al., 2000, 2009; Klein and Sander, 2008).

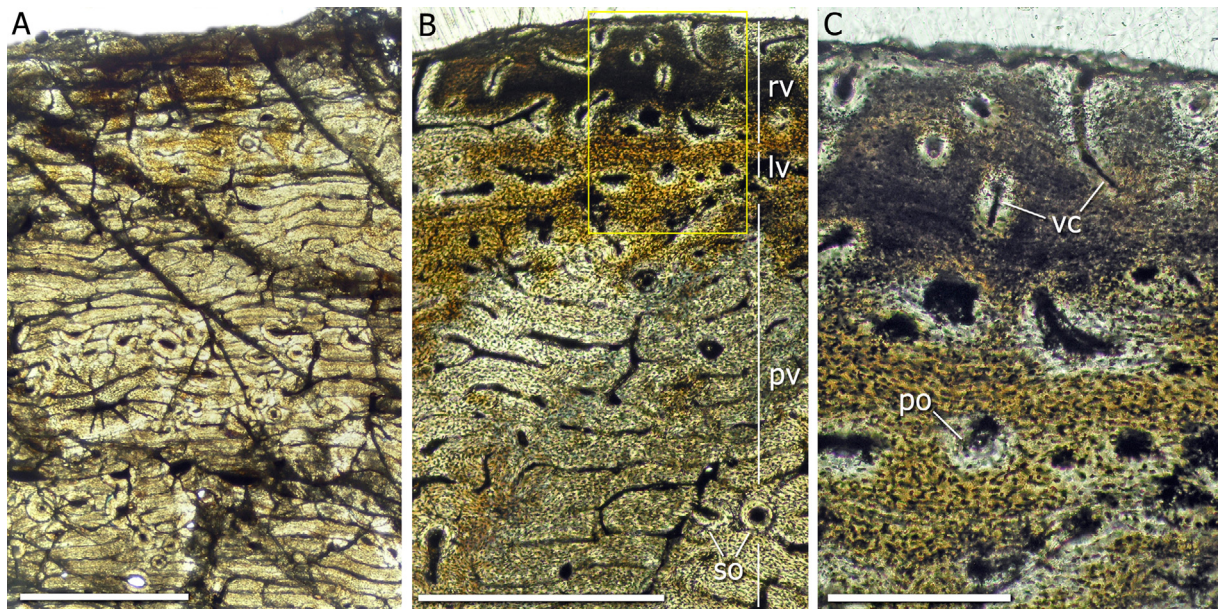


Fig. 4. (Color online.) Transverse thin sections of the hadrosauroid femur LU-JL-LAÑ001 from Albaina. A. General view of the middle to outer cortex showing a well-vascularized fibro-lamellar bone tissue, with clusters of secondary osteons (Haversian reconstruction) restricted to the deeper regions of the compacta. B. Detail of the outer cortex showing how the regular plexiform vascularity changes to a reticular pattern in the cortical periphery. Secondary osteons are absent in this external part of the cortex. C. Enlargement of part (B) showing sub-periosteal vascular canals opening to the outer surface, suggesting active growth. Abbreviations: lv, longitudinal vascularity; po, primary osteons; pv, plexiform vascularity; rv, reticular vascularity; so, secondary osteons; vc, vascular canals. Scale bars: 1 mm (A–B), 0.25 mm (C).

Fig. 4. (Couleur en ligne.) Lames minces transversales du fémur d'hadrosauroïde LU-JL-LAÑ001 d'Albaina. A. Vue générale du cortex moyen à externe montrant un tissu osseux fibro-lamellaire bien vascularisé, avec d'abondants ostéons secondaires (reconstruction haversienne) limités aux régions profondes de l'os compact. B. Détail du cortex externe montrant comment la vascularisation plexiforme régulière passe à un modèle réticulaire dans la périphérie du cortex. Les ostéons secondaires sont absents dans la partie externe du cortex. C. Agrandissement de la figure (B) montrant les canaux vasculaires sub-périostiques s'ouvrant vers la surface externe, ce qui suggère une croissance active. Abréviations : lv, vascularisation longitudinale ; po, ostéons primaires ; pv, vascularisation pléxiforme ; rv, vascularisation réticulaire ; so, ostéons secondaires ; vc, canaux vasculaires. Barres d'échelle : 1 mm (A–B), 0,25 mm (C).

The cortical bone at midshaft is largely dominated by a well-vascularised, uninterrupted primary fibro-lamellar bone tissue. The vascular network is mainly organized into a laminar to plexiform pattern, composed of longitudinal and circumferential primary vascular canals, with occasional radial anastomoses (Fig. 4A). The vascular canals are completely filled by osteonal bone, indicating the complete formation of the primary osteons. Vascular arrangement remains more or less constant throughout the cortex, except in the periosteal surface where it becomes reticular (irregular distribution of vascular canals) (Fig. 4B). Nevertheless, there is no appreciable reduction in vascular density towards the bone surface. In this part of the compacta, many vascular canals open to the sub-periosteal surface (Fig. 4B and C), suggesting intensive bone deposition (i. e., bone growth). Isolated secondary osteons or small clusters are mainly restricted to the middle and deep cortex. Growth lines are completely absent.

The high degree of osteonal development around the vascular canals, the presence of a regularly organized fibro-lamellar tissue along the entire cortex, and the formation of secondary osteons in the deep and middle cortex suggest that the examined specimen was not from an early juvenile individual. The described histological organization is clearly different from that of the early juveniles in which there is only a slight degree of osteonal development around the vascular canals (nearly all of them not organized

and longitudinally oriented), the fast-growing woven bone is the dominant histological type, and there is little evidence of secondary remodeling in the compacta (Cerdá et al., 2013; Horner et al., 2000, 2009; Klein and Sander, 2008). Nonetheless, the well-vascularized sub-periosteal region of the cortex, provided with reticular canals opening to the outer surface, reveals that the specimen belongs to a still growing individual of small size (a late juvenile-young adult: Horner et al., 2000). There is no evidence of growth rings, slow-growing bone tissues (e.g. lamellar or parallel-fibred bones), advance of the Haversian reworking or gradual reduction in vascular density towards bone surface, which are distinctive features of more skeletally mature individuals.

6. Implications

6.1. Testudines

The presence of three clades of turtles, all of them represented by taxa recognized as new forms, was notified in the continental levels of Laño (see Lapparent de Broin and Murelaga, 1996). A turtle currently identified as a terrestrial form (Scheyer et al., 2012), *Solemys vermiculata* Lapparent de Broin and Murelaga, 1996, was erected there. It belongs to a clade of basal turtles (Solemydidae). Solemydidae is known from the Late Jurassic to the Latest

Cretaceous of North America and Europe. The other two taxa are members of Pan-Pleurodira, and both are aquatic forms. One of them, *Dortoka vasconica* Lapparent de Broin and Murelaga, 1996, is of small size (being the estimated maximum length of the adults less than 20 cm), which belongs to a primitive clade of Pan-Pleurodira exclusively recorded in Europe from the Early Cretaceous to the Paleocene (Lapparent de Broin et al., 2004; Pérez-García et al., 2014). The third clade recognized is Bothremydidae (Pleurodira), represented by *Polysternon atlanticum*, and also defined in Laño (see Lapparent de Broin and Murelaga, 1999; Pérez-García et al., 2012). Although Bothremydidae is a clade of Gondwanan origin, several lineages of this group diachronically migrated to Europe (Pérez-García and Lapparent de Broin, 2014). Thus, bothremydids are the most abundant and diverse clade of turtles currently recognized in the European latest Cretaceous record. Representatives of these three groups of turtles have been found in numerous outcrops of the uppermost Cretaceous of southwestern Europe.

Some taxa of Bothremydidae have been interpreted as marine littoral forms, or with the ability to use the coastlines to migrate (Lapparent de Broin and Werner, 1998). The bothremydids found in the Late Cretaceous of Europe are considered to have been freshwater taxa. However, their identification in some deposits interpreted as located near the coastline suggests that they could live in environments with higher salinity than those in which the representatives of Dortokidae lived (Pérez-García, 2012; Guede et al., 2013). Therefore, and taking into account the environment in which the three clades of turtles recognized in the continental deposits of Laño lived, the occurrence of Bothremydidae in Albaina appears more probable than that of the representatives of the other two clades.

The presence of an indeterminate Pan-Cryptodira has also been reported in the Spanish uppermost Cretaceous site of Lo Hueco (Cuenca) (Pérez-García et al., 2009). The presence of unpublished “chelydroid”-like taxa has been also recognized in other Late Cretaceous sites of Western Europe. These taxa, recognized as aquatic forms, could correspond to freshwater or marine turtles (Guede et al., 2013; Pérez-García et al., 2009). No sea turtle has been identified in the uppermost Cretaceous of the Basque–Cantabrian Region, to the exception of scapular remains of an *Allopleuron*-like chelonoid from the Santonian of San Pantaleón de Losa (Burgos) studied by Bardet et al. (1993). Only another indeterminate Pan-Cryptodira has been mentioned in Mesozoic levels of the Basque–Cantabrian Region, more precisely from the Hauterivian–Barremian of Vega de Pas (Cantabria) (Pérez-García and Murelaga, 2014).

Therefore, the peripheral plate found in Albaina allows the identification of a fourth taxon in the Laño quarry. Unlike taxa so far described there, this form probably belongs to Pan-Cryptodira.

6.2. Dinosauria

LU-JL-LAÑO01 is the second hadrosauroid remain found in the Laño quarry, the first one being an isolated tooth

(MCNA 10510) from the fluvial deposits of the Laño 1 site, ascribed to the Late Campanian–Early Maastrichtian (Pereda-Suberbiola et al., 2003a). Buffetaut (2005) questioned the provenance of this tooth and suggested an accidental pollution from the Late Maastrichtian marine beds that overlie the older sandy and silty layers which have yielded the terrestrial and freshwater vertebrate remains. However, this hypothesis is rejected here because the hadrosauroid tooth MCNA 10510 was obtained by screen washing of the fossiliferous fluvial sands and silts of Laño 1, and there is no clear evidence of re-elaboration processes in these beds (Pereda-Suberbiola et al., 2000). Consequently, the Laño quarry provides information of the occurrence of hadrosauroids in Iberia as early as the Late Campanian: Laño is currently the only Iberian site where hadrosauroid material has been found together with rhabdodontid and titanosaurian remains, the locality of Els Nerets in the South-central Pyrenees of Lleida attesting of a similar dinosaur association is currently regarded as Late Maastrichtian in age (B. Vila, pers. comm.). The association of hadrosauroids with *Rhabdodon* is unusual in the latest Cretaceous of southern France: it has been mentioned only in the Late Maastrichtian Vitrolles–La Plaine locality of Provence (although an artefact due to reworking cannot be excluded; see Valentin et al., 2012).

It is interesting to note that the Albaina femur was found in marine deposits that have yielded benthic foraminifera, molluscs, arthropods, selachians, actinopterygians and marine reptiles, including turtles (Cappetta and Corral, 1999). In addition to the Laño quarry, hadrosauroid fossils have been reported from various Late Maastrichtian marine sites of Europe: the Maastrichtian type area (Buffetaut, 2009; Jagt et al., 2003; Limburg and Liège (see Weishampel et al., 1999; Mulder et al., 2005), Midi-Pyrénées (Bilotte et al., 2010; Laurent, 2003; Laurent et al., 1999, 2002; Paris and Taquet, 1973), southern Bavaria (Wellnhofer, 1994), northwestern Bulgaria (Godefroit and Motchurova-Dekova, 2010), and the Crimean Peninsula (Riabinin, 1945). The relative abundance of hadrosauroid remains in Late Maastrichtian marine deposits of the European archipelago probably reflects the dominance of these herbivorous dinosaurs on nearby landmasses, as suggested by the large amount of fossils found in contemporaneous continental sites of Europe and especially in the Ibero-Armorican Domain (see Dalla Vecchia, 2009a; Prieto-Márquez et al., 2013). The occurrence of hadrosauroid fossils in shallow marine environments can be interpreted as the result of the passive transport of floating carcasses over fairly long distances from the mainland (Buffetaut, 1994; Godefroit and Motchurova-Dekova, 2010).

Horner (1979) listed the dinosaur specimens from Upper Cretaceous marine deposits of North America and noted the relative abundance of hadrosaurines (unadorned or solid crested hadrosaurids), primarily in the Western Interior, suggesting that may have inhabited coastal environments. Horner (1979) also noticed that approximately one-half of the specimens belong to young or juvenile individuals the size or smaller than the type of *Claosaurus agilis* (Marsh, 1872) (femur length 670 to 676 mm; Lull and Wright, 1942), and over three-quarters of the specimens are from individuals smaller than the

type of *Hadrosaurus foulkii* Leidy, 1858 (femur length 1055 mm; Prieto-Márquez et al., 2006b). According to Godefroit and Motchurova-Dekova (2010), the overrepresentation of immature specimens in marine deposits can be explained taphonomically as the result of an attritional death profile of the fossil accumulation (instead of a local catastrophic event), with a selective mortality of younger and smaller individuals (see Lauters et al., 2008).

Lambeosaurines and non-hadrosaurid hadrosauroids have been reported in Europe (Dalla Vecchia, 2009a; Pereda-Suberbiola et al., 2009b; Prieto-Márquez et al., 2013). The possible presence of hadrosaurines (Cruzado-Caballero et al., 2010b) has been questioned by Prieto-Márquez et al. (2013). With regard to the hadrosauroid records from the Late Maastrichtian marine deposits of Europe, the specimens are mostly fragmentary and not diagnostic beyond *Hadrosauroidea* gen. et sp. indet. All these specimens, with the exception of “*Orthomerus weberi*” from Crimea (estimated femur length 750–800 mm; Riabinin, 1945), belong to small individuals (i.e., femur length of “*Orthomerus dolloi*”: 495 mm, Seeley, 1883; femur length of the Bavarian taxon: 340 mm, Wellnhofer, 1994). We can wonder if the small size of the specimens reflects the presence of immature individuals or of small-bodied adults. The Albaina femur is presently the only hadrosauroid specimen found in the marine facies of Europe that has been studied from a histological point of view. The analysis indicates that the specimen belongs to a not fully-grown individual of a moderate-size species.

7. Conclusions

The Laño quarry (northern Iberian Peninsula) is one of the most noteworthy Late Cretaceous vertebrate sites of Europe, with abundant fossils found in two different stratigraphic units: the lower one contains the Laño sites, of fluvial origin, which have yielded a diverse vertebrate assemblage composed of dinosaurs and other continental vertebrates, ascribed to the Late Campanian–Early Maastrichtian; the Late Maastrichtian overlying marine beds of Albaina are rich in selachian, actinopterygian and mosasaurid teeth found in association with benthic foraminifera and invertebrates. New vertebrate fossils collected from fallen calcarenitic blocks of the quarry are the first turtle and dinosaur specimens discovered to date in the sublittoral beds of Albaina. They consist of two partial turtle plates, one of them belonging to a *Bothremydidae* (*Pleurodira*) and the other probably to an indeterminate Pan-Cryptodira, and a partial femur of a hadrosauroid ornithopod. Although the presence of *Bothremydidae* was previously known in the older continental levels of Laño, the other turtle taxon cannot be attributed to any of those recorded there so far, thus, this discovery enlarges our knowledge of the vertebrate diversity from the Laño quarry. With regard to the ornithopod femur, it is the first hadrosauroid specimen described from Late Maastrichtian marine deposits of the Iberian Peninsula, and one of the scarce dinosaur remains found in European marine environments of this age. The examination of the histological features of the femur suggests that it belongs to an immature, still growing (a late juvenile-young adult)

individual of small size. Based on comparisons with other hadrosauroid taxa, its estimate body length at death was approximately 3 m.

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