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Additional Information

1 Paléontologie des Vertébrés/Vertebrate Palaeontology
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6 **First dinosaur and turtle remains from the latest Cretaceous shallow marine deposits of**
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8 **Albaina (Laño quarry, Iberian Peninsula)**
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13 Premiers restes fossiles de dinosaure et de tortue dans les dépôts marins littoraux fincrétacés
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15 d'Albaina (carrière de Laño, Péninsule ibérique)
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4 ABSTRACT
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6 We report here on new vertebrate fossils from the latest Cretaceous of Albaina (Laño quarry,
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8 Condado de Treviño), northern Iberian Peninsula. They consist of an incomplete hadrosauroid
9 femur, and two partial plates of turtles, one belonging to a Pleurodira (Bothremydidae), the
10 other one to an indeterminate taxon, probably corresponding to a Pan-Cryptodira. They are
11 the first dinosaur and turtle remains found in the Late Maastrichtian sublittoral beds of
12 Albaina. Other components of this shallow marine vertebrate fauna are selachians (sharks,
13 rays), actinopterygians (pycnodonts, teleosts) and marine reptiles (mosasaurids, plesiosaurs).
14
15 The Albaina femur is one of the few hadrosauroid remains from the Late Maastrichtian of
16 Europe found in marine environments, and the first one described from this kind of deposits
17 in the Iberian Peninsula. The histological structure of the bone indicates that it belongs to an
18 immature individual of small size.
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Keywords: Hadrosauroidea, Bothremydidae, Pan-Cryptodira, Condado de Treviño, Late Maastrichtian, Spain.

RÉSUMÉ

De nouveaux fossiles de vertébrés découverts à Albaina (carrière de Laño, Condado de Treviño), 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 (Bothremydidae) et l'autre à un taxon indéterminé, correspondant probablement à 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 (pycnodontes et

1 téléostéens) et des reptiles marins (mosasauridés et plésiosaures). Le fémur d'Albaina est l'un
2 des rares fossiles d'hadrosauroïde découverts dans un environnement marin dans le
3 Maastrichtien supérieur d'Europe, et le premier décrit dans ce type de dépôts dans la
4 Péninsule ibérique. La structure histologique de l'os indique qu'il appartient à un individu
5 immature de petite taille.

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16 *Mots clés:* Hadrosauroidea, Bothremydidae, Pan-Cryptodira, Condado de Treviño,
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18 Maastrichtien supérieur, Espagne.
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23 **1. Introduction**

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25 The Laño quarry is a disused silica sand quarry embracing the villages of Albaina and
26 Laño in the Condado de Treviño, which is an exclave of Burgos province (Spain) in the
27 northern Iberian Peninsula (Fig. 1). The quarry is located about 30 km south to the city of
28 Vitoria-Gasteiz (Álava). Some deposits uncovered by sand quarrying at this point have
29 revealed one of the most noteworthy Campanian-Maastrichtian vertebrate sites of Europe by
30 its taxonomic diversity, and provided relevant information about the composition and
31 affinities of both terrestrial-freshwater and shallow marine vertebrate faunas from the latest
32 Cretaceous of the Ibero-Armorican Domain in southwestern Europe (Astibia et al., 1990,
33 1999; Pereda-Suberbiola et al., 2000, in review).

34
35 Vertebrate fossils accumulate at two different stratigraphic units: the lower one contains
36 the so-called Laño 1 and Laño 2 sites, ascribed to the Late Campanian-Early Maastrichtian
37 interval, while the upper one, mainly located in the vicinity of the Albaina village, are
38 ascribed to the Late Maastrichtian. Therefore, there exists an important time gap between the
39 two stratigraphic units, which is represented in the Laño quarry by a low-angle unconformity
40 (Baceta et al., 1999; Berreteaga, 2008 and references). The fluvial beds of sites Laño 1 and 2
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1 have yielded a diversified vertebrate association that consists of nearly 40 species, including
2 actinopterygians, lissamphibians, squamates, turtles, crocodyliforms, dinosaurs, pterosaurs
3 and mammals (see Pereda-Suberbiola et al., in review for an updated list). The sublittoral beds
4
5 of the Albaina site have yielded a diverse vertebrate assemblage so far composed of 37 taxa,
6
7 including sharks and rays (Cappetta and Corral, 1999), pycnodontiforms and teleosteans
8 (Poyato-Ariza et al., 1999), mosasaurids and plesiosaurians (Bardet et al., 1999, 2013).
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16 In this paper, we describe three new interesting fossils from the Late Maastrichtian
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18 sublittoral beds of the Albaina site (Laño quarry): the first identifiable dinosaur bone and two
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20 isolated turtle plates. Their identity and palaeontological significance are also discussed in
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22 detail.
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25 *Institutional abbreviations.- MCNA, Museo de Ciencias Naturales de Álava/Arabako
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27 Natur Zientzien Museoa, Vitoria-Gasteiz, Spain; LU, Luberri - Oiartzungo Ikasgune
28
29 Geologikoa Museoa, Oiartzun, Spain.*

35 2. Geological setting

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37 The detailed geology of the Laño quarry (including the Albaina beds) has been well
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39 discussed in other publications (Astibia et al. 1990, 1999; Baceta et al., 1999; Gómez-Alday,
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41 1999; Pereda-Suberbiola et al., 2000, in review; Berreteaga, 2008). Geologically, the area lies
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43 on the southern limb of the Miranda-Treviño syncline (central part of the Sub-Cantabrian
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45 Synclinorium). Quarrying has exposed at least a 70 m section of terrigenous and carbonate
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47 rocks of Late Cretaceous-Paleogene age that records continental to shallow marine
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49 environment within the southern Basque-Cantabrian Basin.
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53 The Late Cretaceous succession is subdivided into three unnamed formations, considered
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55 equivalent to the Sedano, Sobrepeña plus Valdenoceda, and Torme formations (Berreteaga,
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57 2008; see also Floquet, 1991, 1998), which reflect substantive changes in lithology and fossil
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1 content (Fig. 1). The basal part of the succession (equivalent to the Sedano Fm.) comprises
2 fluvial silty and sandy facies, where terrestrial and freshwater vertebrate fossils occur (Laño 1
3 and 2 sites), and is overlain by massively sand bar which was the commonly targeted bed in
4 the quarry. The sedimentary structures are consistent with channel areas within an extensive
5 braided river system (Gómez-Alday, 1999; Pereda-Suberbiola et al., 2000).

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

9 The upper part of the exposed section (equivalent to the Torme Formation cropping out in
10 the Villarcayo area, Burgos Province, North-Castilian Platform) is composed of grey poorly
11 cemented sandstones and yellowish friable calcarenites, deposited during the maximum
12 transgression of the sea into this area. The maximum thickness of this formation throughout
13 the Laño area is about 10 to 12 m. Contrary to the invertebrate macrofossils (i.e. gastropods,
14 bivalves, ammonites, crustaceans), which are rather scarce in these carbonate rocks, fishes,
15 marine reptiles and layers of accumulated orbitoidids are characteristic. The upper unit
16 represents a shallow marine sublittoral environment. According to the selachian association, a
17 Late –but not latest– Maastrichtian age is given for the Albaina beds (Cappetta and Corral,
18 1999).

47 3. Material and methods

48 The vertebrate material described here was collected by breaking out calcarenite rocks
49 fallen from the upper beds of the Laño quarry face. These beds have been primarily targeted
50 for their content in marine vertebrate remains (Bardet et al, 1999, 2013; Cappetta and Corral,
51 1999; Poyato-Ariza et al., 1999). The dinosaur bone was found by two of us (G.M., J.L.) in
52 recently fallen blocks, whereas the turtle plates were already in the MCNA collection as a
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1 result of regular prospecting in the fossil site by another of us (J.C.C.). Fossil preparation and
2 conservation was done in the MCNA laboratory, using standard preparation techniques.
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5 Thin sections were made from the mid-shaft of the femur LU-JL-LAÑ001, which is
6 assumed to contain the most complete growth record of the bone (Sander, 2000; Stein and
7 Sander, 2009). The samples were cut and polished processed according to current techniques
8 (Lamm, 2013).
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18 **4. Systematic Palaeontology**

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20 *4.1. Testudines*

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22 Cf. PAN-CRYPTODIRA Joyce, Parham and Gauthier, 2004
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25 Cf. Pan-Cryptodira indet.
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30 *Material.* MCNA 15055, a partial peripheral plate lacking the medial and latero-posterior
31 regions (Fig. 2A-C).
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35 *Description.* The plate lacks its medial region. For this reason, the width/length cannot be
36 estimated. It is a peripheral that does not contact the plastron, but is close to the plastral
37 bridge. This plate is crossed by a sulcus located between two marginal scutes. Considering
38 that the most distal region of this kind of sulci is always anteriorly directed, this plate is
39 identified as a left peripheral. The angle between the dorsal and the ventral surfaces is greater
40 in the anterior region than in the posterior one (Fig. 2B-C). Therefore, the anterior margin
41 corresponds to that located nearest to the plastral bridge, this plate being a posterior
42 peripheral. Although the width of this plate is not known (i.e. the length between the medial
43 and distal margins), the ventral surface covered by the marginal scutes is relatively narrow,
44 substantially less than half of the width of the plate (Fig. 2B). A well-developed change of
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1 level, which does not match the ventro-medial margin of the marginal scutes, is present. It is
2 parallel to that margin, being more medially located. The outer surface is partially altered.
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4 However, several discontinuous dichotomous sulci are preserved. Therefore, this plate was
5 ornamented. Because the medial region is not preserved, it is not possible to know if the
6 pleural scutes overlapped the peripheral plates. It is interpreted that, if such overlap occurs, it
7 would be short, because the marginal scutes cover all the preserved dorsal region of the
8 peripheral plate.

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20 *Discussion.* The limited information provided by this element prevents its accurate
21 systematic allocation. Characters such as the absence of the autapomorphic ornamental
22 pattern of Dortokidae, a clade of basal Pan-Pleurodira recognized in the continental deposits
23 of Laño, as well as its larger size, allow excluding its assignment to that group. The absence
24 of tubercles confirms that this specimen cannot be assigned to Solemydidae, another clade of
25 turtles recognized in Laño. The presence of an ornamental pattern composed by discontinuous
26 and dichotomous sulci is shared with Bothremydidae (Pleurodira), the third clade recognized
27 in Laño. However, characters such as the relatively narrow ventral development of the
28 marginal scutes allow excluding its assignment to this group. This ornamental pattern has also
29 been identified in several undetermined pan-cryptodiran taxa recognized both in the Early and
30 Late Cretaceous of Western Europe (see Pérez-García et al., 2009; Pérez-García and
31 Murelaga, 2014), generally referred as “chelydroids” in aspect, and probably belonging to
32 different clades. Although all or at least some of these poorly known taxa have fontanelles
33 between the costal and the peripheral plates, the absence of information on the medial region
34 of MCNA 15055 does not allow comparing this character.

1 PLEURODIRA Cope, 1864
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3 PELOMEDUSOIDES Cope, 1868
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5 BOTHREMYDIDAE Baur, 1891
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7 BOTHREMYDINAE Baur, 1891
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9 BOTHREMYDODDA Baur, 1891 sensu Gaffney, Tong and Meylan, 2006
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11 BOTHREMYDINI Baur, 1891 sensu Gaffney, Tong and Meylan, 2006
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13 FOXEMYDINA Gaffney, Tong and Meylan, 2006
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15 cf. *Polysternon atlanticum*
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23 *Material.* MCNA 10863, the almost complete medial half of a sixth left costal plate (Fig.
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25 2D-F).
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30 *Description.* The only broken margin corresponds to the distal one. Therefore, the
31 preserved region of this costal plate allows knowing the morphology of the margins which
32 contacted with the neural series and with other costals. The antero-medial contact with a
33 neural is observed (Fig. 2E, F). The posterior region of this neural was relatively wide in
34 relation to its length. An approximately parallel margin to the axial axis suture, which is
35 interpreted as the medial contact with another costal plate, is developed in the medial edge of
36 the preserved costal. The postero-medial edge of this plate corresponds to the suture with
37 another costal, the medial area of contact of the last costals of the carapace being developed in
38 zigzag.
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51 The medial region of MCNA 10863 is covered by a portion of a vertebral scute. The sulci
52 separating this scute and two pleural ones are observed (Fig. 2E, F). Therefore, this plate is an
53 even-numbered costal. Given this, plus its curvature, and the described contact with other
54 plates, this element can be attributed to a sixth left costal. Taken this into account, this plate
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1 antero-medially contacts the sixth neural, medially the sixth right costal, and postero-medially
2 the seventh right costal. Consequently, the neural series is interpreted as discontinuous (i.e.
3 not continuous between the nuchal and the suprapygal plates), being composed of six plates.
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5 The best preserved areas show that the plate was ornamented by discontinuous and
6 dichotomous sulci (Fig. 2E).
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16 *Discussion.* Despite its limited information, it is possible to observe that MCNA 10863
17 shares several characters with Bothremydidae: a discontinuous neural series, the posterior
18 region of the last neural being noticeably wider than long; the morphology and arrangement
19 of the contact between the vertebral and the pleural scutes; and finally, the ornamental pattern.
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25 The only bothremydid from the European Late Cretaceous record hitherto characterized by
26 the presence of six neurals is *Iberoccitanemys* Pérez-García, Ortega, and Murelaga, 2012.
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29 However, variability in this character is known in some bothremydid taxa, as *Chedighaii*
30 *hutchisoni* Gaffney, Tong and Meylan, 2006, from the Late Cretaceous of United States, in
31 which the number of neurals varies from six to seven. In Late Cretaceous taxa from
32 southwestern Europe represented by several specimens, such as *Iberoccitanemys*, *Rosasia*
33 Carrington da Costa, 1940 and *Foxemys* Tong, Gaffney, and Buffetaut, 1998, the so far
34 known number of these plates is constant (being seven in the latter two taxa). However,
35 unpublished material of *Polysternon provinciale* (Matheron, 1869) reveals variability in the
36 neural series (six or seven plates). Therefore, some specimens of *Polysternon provinciale* with
37 the same number of neurals as in *Iberoccitanemys* are known. The Laño bothremydid
38 *Polysternon atlanticum* (the only bothremydid species currently identified here *sensu* Pérez-
39 García et al., 2010) has been recognized by relatively scarce and disarticulated material.
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41 Lapparent de Broin and Murelaga (1999) indicated that its neural series includes at least seven
42 neurals, the costals 8 medially meeting. However, the morphology of the medial region of the
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1 sixth costal MCNA 7051 from Laño (see plate 5.12 in Lapparent de Broin and Murelaga,
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3 1999) is similar to that of the specimen MCNA 10863 from Albaina. Therefore, we recognize
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5 that a neural series composed of six plates can be present in some *Polysternon atlanticum*
6
7 specimens. MCNA 10863 cannot be referred to *Polysternon provinciale* because thin
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9 striations composed of parallel streaks are absent on the carapace. Therefore, the plate from
10
11 Albaina probably belongs to *Polysternon atlanticum*, the only bothremydid recognized in
12
13 Laño. However, given the limited availability of characters, and the described compatibility of
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15 this element with other European representatives of Foxemydina, i.e. *Iberoccitanemys* (taking
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17 into account its morphology, but also the arrangement of the neural and the costals with which
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19 it is in contact), we opted for its identification as cf. *Polysternon atlanticum*.
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4.2. Dinosauria

ORNITHISCHIA Seeley, 1887

ORNITHOPODA Marsh, 1881

HADROSAUROIDEA Cope, 1869 sensu Sereno, 1986

Hadrosauroidea indet.

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

Description. LU-JL-LAÑ001 consists of the medial and distal parts of a right femur, which is broken just below the fourth trochanter (not preserved in the specimen). The bone shows evidences of erosion, especially on the distal condyles (Fig. 3A-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-D). The cross-section at the preserved proximal

1 end of the shaft is ovoid, wider than long; the medial side is longer anteroposteriorly than the
2 lateral one. The anterior surface of the shaft is convex whereas the posterior surface is slightly
3 concave. Although eroded, the distal condyles seem to have been well-developed. They are
4 expanded anteriorly and posteriorly to form an H-shaped outline in distal view (Fig. 3E). The
5 anterior intercondylar groove for the passage of the extensor tendons is deep and U-shaped; it
6 is partially enclosed by expansions of both medial and distal condyles. In anterior view, the
7 medial condyle is wider than the lateral one and is located distally below it (Fig. 3A). In distal
8 view, the intercondylar flexor groove is deep, U-shaped, and narrower than the anterior
9 groove. The medial posterior condyle is wider and more projected than the lateral one, with a
10 slightly medial orientation (Fig. 3B). The lateral condyle is projected perpendicular to the
11 long axis of the femur. The posterolateral surface of the lateral condyle shows a shallow
12 vertical groove for the *M. ilio-fibularis*.
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33 Measurements of femur LU-JL-LAÑ001:
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35 - Length (as preserved) = 155 mm
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37 - Minimum transverse width of shaft = 48 mm
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39 - Maximum anteroposterior length of shaft = 32 mm
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41 - Perimeter of shaft = 130 mm
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43 - Maximum transverse width of distal end = 60 mm
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50 *Discussion.* The combination of femoral characters observed in LU-JL-LAÑ001, i.e.
51 straight distal shaft, anteroposterior expansion of the distal condyles, and deep, nearly closed
52 intercondylar extensor groove on the distal end, allow us to assign the specimen to the clade
53 Hadrosauroidea (see Horner et al., 2004; Prieto-Márquez, 2008; Xing et al., 2012:
54 supplement). We follow here the stem-based definition of Hadrosauroidea by Sereno (1998):
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1 all hadrosauriforms closer to *Parasaurolophus* Parks, 1922 than to *Iguanodon* Mantell, 1825.
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3 It should be noted that the development of a deep intercondylar extensor groove, with the
4 edges of the groove meeting or nearly meeting anteriorly to enclose an extensor tunnel, has
5 been regarded by Wu and Godefroit (2012) as a synapomorphy of Hadrosauridae, a clade
6 defined by these authors as the most recent common ancestor of *Bactrosaurus* Gilmore, 1933
7 and *Parasaurolophus*, plus all the descendants of this common ancestor (see Sereno, 2005 and
8 Prieto-Márquez, 2010 for different definitions). According to Wu and Godefroit (2012), a
9 deep intercondylar extensor groove is absent in non-hadrosaurid ornithopods, including in
10 basal iguanodontians such as rhabdodontids, which subsisted in Europe until the latest
11 Cretaceous (Weishampel et al., 2003; Ösi et al., 2012).

12 In Europe, hadrosauroid femora have been found in several Maastrichtian localities, from
13 the Iberian Peninsula to Crimea passing through northern and central Europe (see Cruzado-
14 Caballero, 2012 for a list). Some of these femora have been referred in the literature to
15 Hadrosauridae indet. or Euhadrosauria indet. (see Dalla Vecchia, 2006; Cruzado-Caballero,
16 2012), but others belong to taxa like *Telmatosaurus* Nopcsa, 1903 (Weishampel et al., 1993),
17 *Tethyshadros* Dalla Vecchia, 2009 (late Campanian to early Maastrichtian according to Dalla
18 Vecchia, 2009b), “*Orthomerus*” (now regarded as a *nomen dubium*; see Brinkmann, 1988;
19 Horner et al., 2004) and the lambeosaurines *Arenysaurus* Pereda-Suberbiola et al., 2009 and
20 *Blasisaurus* Cruzado-Caballero, Pereda-Suberbiola & Ruiz-Omeñaca, 2010.

21 The general morphology of the hadrosauroid femora is quite conservative, but some
22 individual variation has been observed (Brett-Surman and Wagner, 2007). Few ontogenetic
23 changes have been documented in the limb bones (i.e., femora) and at least immature
24 specimens of basal hadrosauroids can provide reliable information for taxonomic and
25 phylogenetic inferences (Prieto-Márquez, 2011). LU-JL-LAÑ001 looks roughly like two
26 hadrosauroid femora from Els Nerets, Lleida (Casanovas et al., 1985) and Peguera, Barcelona
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(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. Waiting for the discovery of new material, the Albaina femur is here referred to Hadrosauroidea 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 per cent 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, 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 · (circumference of femur in mm)^b, where a = 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 allow to infer the ontogenetic stage of the individuals when perished (Chinsamy and Hillenius, 2004; Chinsamy-Turan, 2005; Reid, 2012 and references therein). The reduced 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 (Company et al., in review). Bone microstructure of juvenile dinosaurs is clearly different from that of submature or mature individuals, and has been described in a variety of groups (Horner et al., 2000, 2009; Klein and Sander, 2008; Cerdá et al., 2013)

The cortical bone at mid-shaft is largely dominated by a well-vascularised, uninterrupted primary fibrolamellar bone tissue. The vascular network is mainly organized into a laminar to plexiform pattern, composed of longitudinal and circumferential primary vascular canals, with

1 occasional radial anastomoses (Fig. 4A). The vascular canals are completely filled by osteonal
2 bone, indicating the complete formation of the primary osteons. Vascular arrangement
3 remains more or less constant throughout the cortex, except in the periosteal surface where it
4 becomes reticular (irregular distribution of vascular canals) (Fig. 4B). Nevertheless, there is
5 no appreciable reduction in vascular density towards the bone surface. In this part of the
6 compacta, many vascular canals open to the subperiosteal surface (Fig. 4B-C) suggesting
7 intensive bone deposition (i. e., bone growth). Isolated secondary osteons or small clusters are
8 mainly restricted to the middle and deep cortex. Growth lines are completely absent.

9
10 The high degree of osteonal development around the vascular canals, the presence of a
11 regularly organized fibro-lamellar tissue along the entire cortex, and the formation of
12 secondary osteons in the deep and middle cortex suggest that the examined specimen was not
13 from an early juvenile individual. The described histological organization is clearly different
14 from that of the early juveniles in which there is a slight degree of osteonal development
15 around the vascular canals (nearly all of them not organized and longitudinally oriented), the
16 fast-growing woven bone is the dominant histological type, and there is little evidence of
17 secondary remodeling in the compacta (Horner et al., 2000, 2009; Klein and Sander, 2008;
18 Cerdá et al., 2013). Nonetheless, the well-vascularized sub-periosteal region of the cortex,
19 provided with reticular canals opening to the outer surface, reveal that the specimen belongs
20 to a still growing individual of small size (a late juvenile-young adult: Horner et al., 2000).
21 There is no evidence of growth rings, slow-growing bone tissues (e.g. lamellar or parallel-
22 fibred bones), advance of the Haversian reworking or gradual reduction in vascular density
23 towards bone surface, which are distinctive features of more skeletally mature individuals.
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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 defined there. It belongs to a clade of primitive 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, both being 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 lineage 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*, 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). So that bothremydids are the most abundant and diverse clade of turtles currently recognized in the European uppermost 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 recognized as marine littoral forms, or with the ability to use the coastlines to migrate (Lapparent de Broin and Werner, 1998). The bothremydids defined in the Late Cretaceous of Europe are considered as 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; Gude et al., 2013). Therefore, and taking into account the environment in which the three clades of turtles recognized in the

1 continental deposits of Laño lived, the occurrence of Bothremydidae in Albaina appears more
2 probable than that of the representatives of the other two clades.
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5 The presence of an indeterminate Pan-Cryptodira has also been reported in the Spanish
6 uppermost Cretaceous site of Lo Hueco (Cuenca) (Pérez-García et al., 2009). The presence of
7 unpublished “chelydroid”-like taxa has been also recognized in other Late Cretaceous sites of
8 Western Europe. These taxa, recognized as aquatic forms, could correspond to freshwater or
9 marine turtles (Pérez-García et al., 2009; Gude et al., 2013). No sea turtle has been identified
10 in the uppermost Cretaceous of the Basque-Cantabrian Region, to the exception of scapular
11 remains of an *Allopleuron*-like chelonoid from the Santonian of San Pantaleón de Losa
12 (Burgos) studied by Bardet et al. (1993). Only another indeterminate Pan-Cryptodira has been
13 mentioned in Mesozoic levels of the Basque-Cantabrian Region, more precisely from the
14 Hauterivian-Barremian of Vega de Pas (Cantabria) (Pérez-García and Murelaga, 2014).
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16 Therefore, the peripheral plate found in Albaina allows the identification of a fourth taxon
17 in the Laño quarry. Unlike taxa so far described there, this form probably belongs to Pan-
18 Cryptodira.
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6.2. Dinosauria

LU-JL-LAÑ001 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 reelaboration

1 processes in these beds (Pereda-Suberbiola et al., 2000, in review). Consequently, the Laño
2 quarry provides information of the occurrence of hadrosauroids in Iberia as early as the Late
3 Campanian: Laño is currently the only Iberian site where hadrosauroid material has been
4 found together with rhabdodontid and titanosaurian remains, the locality of Els Nerets in the
5 south-central Pyrenees of Lleida attesting of a similar dinosaur association is currently
6 regarded as Late Maastrichtian in age (Sellés and Vila, in review). The association of
7 hadrosauroids with *Rhabdodon* is unusual in the latest Cretaceous of southern France: it has
8 only been mentioned in the Late Maastrichtian Vitrolles-La-Plaine locality of Provence
9 (although an artefact due to reworking cannot be excluded; see Valentin et al., 2012).

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11 It is interesting to note that the Albaina femur was found in marine deposits that have
12 yielded benthic foraminifera, invertebrates, selachians, osteichthyes and marine reptiles,
13 including turtles (Cappetta and Corral, 1999; Pereda-Suberbiola et al., in review). In addition
14 to the Laño quarry, hadrosauroid fossils have been reported from various Late Maastrichtian
15 marine sites of Europe: the Maastrichtian type area (Limburg and Liège; see Weishampel et
16 al., 1999; Jagt et al., 2003; Mulder et al., 2005; Buffetaut, 2009 and references), Midi-
17 Pyrénées (Paris and Taquet, 1973; Laurent et al., 1999, 2002; Laurent, 2003; Bilotte et al.,
18 2010), southern Bavaria (Wellnhofer, 1994), northwestern Bulgaria (Godefroit and
19 Motchurova-Dekova, 2010), and the Crimean Peninsula (Riabinin, 1945). The relative
20 abundance of hadrosauroid remains in Late Maastrichtian marine deposits of the European
21 archipelago probably reflects the dominance of these herbivorous dinosaurs on nearby
22 landmasses, as suggested by the large amount of fossils found in contemporaneous continental
23 sites of Europe and especially in the Ibero-Armorian Domain (see Dalla Vecchia, 2009a;
24 Prieto-Márquez et al., 2013). The occurrence of hadrosauroid fossils in shallow marine
25 environments can be interpreted as the result of the passive transport of floating carcasses

1 over fairly long distances from the mainland (Buffetaut, 1994; Godefroit and Motchurova-
2 Dekova, 2010).

3 Horner (1979) listed the dinosaur specimens from Upper Cretaceous marine deposits of
4 North America and noted the relative abundance of hadrosaurines (unadorned or solid crested
5 hadrosaurids), primarily in the Western Interior, suggesting that may have inhabited coastal
6 environments. Horner (1979) also noticed that approximately one-half of the specimens
7 belong to young or juvenile individuals the size or smaller than the type of *Claosaurus agilis*
8 (Marsh, 1872) (femur length 670 to 676 mm; Lull and Wright, 1942), and over three-quarters
9 of the specimens are from individuals smaller than the type of *Hadrosaurus foulkii* Leidy,
10 1858 (femur length 1055 mm; Prieto-Márquez et al., 2006b). According to Godefroit and
11 Motchurova-Dekova (2010), the overrepresentation of immature specimens in marine
12 deposits can be explained taphonomically as the result of an attritional death profile of the
13 fossil accumulation (instead of a local catastrophic event), with a selective mortality of
14 younger and smaller individuals (see Lauters et al., 2008).

15 Lambeosaurines and non-hadrosaurid hadrosauroids have been reported in Europe (Dalla
16 Vecchia, 2009a; Pereda-Suberbiola et al., 2009b; Prieto-Márquez et al., 2013). The possible
17 presence of hadrosaurines (Cruzado-Caballero et al., 2010b) has been questioned by Prieto-
18 Márquez et al. (2013). With regard to the hadrosauroid records from the Late Maastrichtian
19 marine deposits of Europe, the specimens are mostly fragmentary and not diagnostic beyond
20 Hadrosauroidea gen. et sp. indet. All these specimens, with the exception of “*Orthomerus*
21 *weberi*” from Crimea (estimated femur length 750-800 mm; Riabinin, 1945), belong to small
22 individuals (i.e., femur length of “*Orthomerus dolloi*”: 495 mm, Seeley, 1883; femur length of
23 the Bavarian taxon: 340 mm, Wellnhofer, 1994). We can wonder if the small size of the
24 specimens reflects the presence of immature individuals or of small-bodied adults. The
25 Albaina femur is presently the only hadrosauroid specimen found in the marine facies of
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1 Europe that has been studied from a histological point of view. The analysis indicates that the
2 specimen belongs to a not fully-grown individual of a moderate-size species.
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8 **7. Conclusions**
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10 The Laño quarry (northern Iberian Peninsula) is one of the most noteworthy Late
11 Cretaceous vertebrate sites of Europe, with abundant fossils found in two different
12 stratigraphic units: the lower one contains the Laño sites, of fluvial origin, which have yielded
13 a diverse vertebrate assemblage composed of dinosaurs and other continental vertebrates,
14 ascribed to the Late Campanian-Early Maastrichtian; the Late Maastrichtian overlying marine
15 beds of Albaina are rich in selachian, actinopterygian and mosasaurid teeth found in
16 association with benthic foraminifera and invertebrates. New vertebrate fossils collected from
17 fallen calcarenitic blocks of the quarry are the first turtle and dinosaur specimens discovered
18 to date in the sublittoral beds of Albaina. They consist of two partial turtle plates, one of them
19 belonging to a Bothremydidae (Pleurodira) and the other probably to an indeterminate Pan-
20 Cryptodira, and a partial femur of a hadrosauroid ornithopod. Although the presence of
21 Bothremydidae was previously known in the older continental levels of Laño, the other turtle
22 taxon cannot be attributed to any of those recorded there so far, thus this discovery enlarges
23 our knowledge of the vertebrate diversity from the Laño quarry. With regard to the ornithopod
24 femur, it is the first hadrosauroid specimen described from Late Maastrichtian marine deposits
25 of the Iberian Peninsula, and one of the scarce dinosaur remains found in European marine
26 environments of this age. The examination of the histological features of the femur suggests
27 that it belongs to an immature, still growing (a late juvenile-young adult) individual of small
28 size. Based on comparisons with other hadrosauroid taxa, its estimate body length at death
29 was approximately 3 m. This and other finds suggest an overrepresentation of immature
30 hadrosauroid specimens in the Late Cretaceous marine deposits.

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27
References
28

- 29
30 Alexander, R.M., 1989. Dynamics of dinosaurs and other extinct giants. Columbia University
31
32 Press, New York, 167 p.
33
34 Astibia, H., Buffetaut, E., Buscalioni, A.D., Cappetta, H., Corral, C., Estes, R., García
35
36 Garmilla, F., Jaeger, J.-J., Jiménez Fuentes, E., Le Loeuff, J., Mazin, J.M., Orue-
37
38 Etxebarria, X., Pereda-Suberbiola, J., Powell, J.E., Rage, J.-C., Rodríguez Lázaro, J.,
39
40 Sanz, J.L., Tong, H., 1990. The fossil vertebrates from Laño (Basque Country, Spain);
41
42 new evidence of the composition and affinities of the Late Cretaceous continental faunas
43
44 of Europe. *Terra Nova* 2, 460–466.
45
46
47 Astibia, H., Corral, J.C., Murelaga, X., Orue-Etxebarria, X., Pereda-Suberbiola, X. (Coords.),
48
49 1999. Geology and palaeontology of the Upper Cretaceous vertebrate-bearing beds of the
50
51 Laño quarry (Basque-Cantabrian Region, Iberian Peninsula). *Estud. Mus. Cienc. Nat.*
52
53 Alava. 14 (Núm. Espec. 1), 1–380.
54
55
56
57
58
59
60
61
62
63
64
65

- 1 Baceta, J.I., Pujalte, V., Orue-Etxebarria, X., 1999. The vertebrate fossil-bearing sites of the
2 Laño quarry (Basque-Cantabrian Region): stratigraphical and palaeogeographical
3 context. *Estud. Mus. Cienc. Nat. Alava.* 14 (Núm. Espec. 1), 13–28.
4
- 5 Bardet, N., Corral, J.C., Pereda-Suberbiola, X., 1993. Primeros restos de reptiles marinos en
6 el Cretácico superior de la Cuenca Vasco-Cantábrica. *Estud. Mus. Cienc. Nat. Alava.* 8,
7 27–35.
8
- 9 Bardet, N., Corral, J.C., Pereda-Suberbiola, X., 1999. Marine reptiles from the uppermost
10 Cretaceous of the Laño quarry (Iberian Peninsula). *Estud. Mus. Cienc. Nat. Alava.* 14
11 (Núm. Espec. 1), 373–380.
12
- 13 Bardet, N., Martín, G., Corral, J.C., Pereda-Suberbiola, X., Astibia, H., 2013. New
14 mosasaurid teeth (Reptilia: Squamata) from the Maastrichtian of Albaina (Laño quarry,
15 Condado de Treviño). *Spanish J. Palaeontol.* 28, 69–78.
16
- 17 Baur, G., 1891. Notes on some little known American fossil tortoises. *Proc. Acad. Nat. Sci.*
18 Phila. 43, 411–430.
19
- 20 Berreteaga, A., 2008. Estudio estratigráfico, sedimentológico y paleontológico de los
21 yacimientos con fósiles de vertebrados del Cretácico final de la Región Vasco-
22 Cantábrica. Doctoral Thesis, Universidad del País Vasco/Euskal Herriko Unibertsitatea
23 (UPV/EHU), Leioa, 410 p.
24
- 25 Bilotte, M., Laurent, Y., Téodori, D., 2010. Restes d'Hadrosaure dans le Crétacé terminal
26 marin de Larcan (Petites Pyrénées, Haute-Garonne, France). *Carnets de Géologie Letter*
27 2010/02 (CG2010_L02), 1–10.
28
- 29 Brett-Surman, M.K., 1989. A revision of the Hadrosauridae (Reptilia: Ornithischia) and their
30 evolution during the Campanian and Maastrichtian. Ph.D. dissertation, George
31 Washington University, Washington, D.C., 272 p.
32
- 33
- 34
- 35
- 36
- 37
- 38
- 39
- 40
- 41
- 42
- 43
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- 55
- 56
- 57
- 58
- 59
- 60
- 61
- 62
- 63
- 64
- 65

- 1 Brett-Surman, M.K., Wagner, J.R., 2007. Discussion of character analysis of the appendicular
2 anatomy in Campanian and Maastrichtian North American hadrosaurids – variation and
3 ontogeny. In: Carpenter, K. (Ed.), Horns and Beaks: Ceratopsian and Ornithopod
4 Dinosaurs. Indiana University Press, Bloomington, pp. 135–169.
- 5
- 6 Brinkman, D., 2011. The size-frequency distribution of hadrosaurs from the Dinosaur Park
7 Formation of Alberta, Canada. In: Hadrosaur Symposium Abstract volume. Drumheller,
8 pp. 16–20.
- 9
- 10 Brinkmann, W., 1988. Zur Fundgeschichte und Systematik der Ornithopoden (Ornithischia,
11 Reptilia) aus der Ober-Kreide von Europa. Documenta Naturae 45, 1–157.
- 12
- 13 Buffetaut, E., 1994. The significance of dinosaur remains in marine sediments: an
14 investigation based on the French record. Berliner Geowiss. Abh. 13, 125–133.
- 15
- 16 Buffetaut, E. 2005. Late Cretaceous vertebrates from the Saint-Chinian area (southern
17 France): a review of previous research and an update on recent finds. Acta Palaeontol.
18 Roman. 5, 39–48.
- 19
- 20 Buffetaut, E. 2009. An additional hadrosaurid specimen (Dinosauria: Ornithischia) from the
21 marine Maastrichtian deposits of the Maastricht area. Carnets de Géologie Letter 2009/03
22 (CG2009_L03), 1–4.
- 23
- 24 Cappetta, H., Corral, J.C., 1999. Upper Maastrichtian selachians from the Condado de
25 Treviño (Basque-Cantabrian Region, Iberian Peninsula). Estud. Mus. Cienc. Nat. Alava.
26 14 (Núm. Espec. 1), 339–372.
- 27
- 28 Carrington da Costa, J., 1940. Un novo quelónio fóssil. Com. Serv. Geol. Portugal 21, 105–
29 125.
- 30
- 31 Casanovas-Cladellas, M.L., Santafé-Llopis, J.V., Isidro-Llorens, A., 1993. *Pararhabdodon*
32 *isonense* n. gen. n. sp. (Dinosauria). Estudio morfológico, radiotomográfico y
33 consideraciones biomecánicas. Paleontol. Evol 26–27, 121–131.
- 34
- 35
- 36
- 37
- 38
- 39
- 40
- 41
- 42
- 43
- 44
- 45
- 46
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- 51
- 52
- 53
- 54
- 55
- 56
- 57
- 58
- 59
- 60
- 61
- 62
- 63
- 64
- 65

- 1 Casanovas, M.L., Santafé Llopis, J.V., Sanz, J.L., Buscalioni, A.D., 1985. *Orthomerus*
2
3 (Hadrosaurinae, Ornithopoda) del Cretacio superior del yacimiento de “Els Nerets”
4
5 (Tremp, España). *Paleontol. Evol.* 19, 155–162.
6
7
- 8 Casanovas, M.L., Pereda-Suberbiola, X.P., Santafé, J.V., Weishampel, D.B., 1999. First
9 lambeosaurine hadrosaurid from Europe: paleobiogeographical implications. *Geol. Mag.*
10
11 136, 205–211.
12
13
- 14 Cerdá, I.A., Pol, D., Chinsamy, A., 2013. Osteohistological insight into the early stages of
15 growth in *Mussaurus patagonicus* (Dinosauria, Sauropodomorpha). *Hist. Biol.* 26, 110–
16
17 121.
18
19
- 20 Chinsamy-Turan, A., 2005. The microstructure of dinosaur bone: Deciphering biology with
21 fine-scale techniques. Johns Hopkins University Press, Baltimore, 216 p.
22
23 Chinsamy, A., Hillenius, W., 2004. Physiology of nonavian dinosaurs. In: Weishampel, D.B.,
24
25 Dodson, P., Osmólska H. (Eds.), *The Dinosauria*, 2nd ed. University of California Press,
26
27 Berkeley, pp. 643–659.
28
29
- 30 Company, J., Cruzado-Caballero, P., Canudo, J.I., in review. Presence of diminutive
31 hadrosaurids (Dinosauria: Ornithopoda) from the Maastrichtian of the south-central
32 Pyrenees (Spain). *J. Iberian Geol.*
33
34 Cope, E.D., 1864. On the limits and relations of the Raniformes. *Proc. Acad. Sci. Phila.* 16,
35 181–183.
36
37 Cope, E.D., 1868. On the origin of genera. *Proc. Acad. Sci. Phila.* 20, 242–300.
38
39 Cope, E.D., 1869. Synopsis of the extinct Batrachia, Reptilia and Aves of North America.
40
41 Trans. Am. Phil. Soc. 14 (1870), 1–252.
42
43
- 44 Cruzado-Caballero, P., 2012. Restos directos de dinosaurios hadrosáuridos (Ornithopoda,
45 Hadrosauridae) del Maastrichtiense superior (Cretácico Superior) de Arén (Huesca).
46
47 Doctoral Thesis, Universidad de Zaragoza, Zaragoza, 410 p.
48
49
- 50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

- 1 Cruzado-Caballero, P., Pereda-Suberbiola, X., Ruiz-Omeñaca, J.I., 2010a. *Blasisaurus*
2
3 *canudoi* gen. et sp. nov., a new lambeosaurine dinosaur (Hadrosauridae) from the Latest
4
5 Cretaceous of Arén (Huesca, Spain). Can. J. Earth Sci. 47, 1507–1517.
6
7 Cruzado-Caballero, P., Ruiz-Omeñaca, J.I., Canudo, J.I., 2010b. Evidencias de la coexistencia
8
9 de dinosaurios hadrosaurinos y lambeosaurinos en el Maastrichtiano superior de la
10
11 Península Ibérica (Arén, Huesca, España). Ameghiniana 47, 153–154.
12
13
14 Cruzado-Caballero, P., Canudo, J.I., Moreno-Azanza, M., Ruiz-Omeñaca, J.I., 2013. New
15
16 material and phylogenetic position of *Arenysaurus ardevoli*, a lambeosaurine dinosaur
17
18 from the late Maastrichtian of Arén (northern Spain). J. Vert. Paleontol. 33, 1367–1384.
19
20
21 Dalla Vecchia, F.M., 2006. *Telmatosaurus* and the other hadrosaurids of the Cretaceous
22
23 European archipelago. An overview. Natura Nascosta 32, 1–55.
24
25
26 Dalla Vecchia, F.M., 2009a. European hadrosaurs. In: Colectivo Arqueológico-
27
28 Paleontológico Salense (Ed.), Actas de las IV Jornadas Internacionales sobre
29
30 Paleontología de Dinosaurios y su Entorno. Salas de los Infantes, Burgos, pp. 45–74.
31
32
33 Dalla Vecchia, F.M., 2009b. *Tethyshadros insularis*, a new hadrosauroid dinosaur
34
35 (Ornithischia) from the Upper Cretaceous of Italy. J. Vert. Paleontol. 29, 1100–1116.
36
37
38 Floquet, M., 1991. La plate-forme nord-castillane au Crétacé supérieur (Espagne). Arrière-
39
40 pays ibérique de la marge passive basco-cantabrique. Sédimentation et vie. Mém. Géol.
41
42
43 Univ. Dijon 14, 1–925.
44
45
46 Floquet, M., 1998. Outcrop cycle stratigraphy of shallow ramp deposits, the Late Cretaceous
47
48 series on the Castilian Ramp (Northern Spain). SEPM Spec. Publ. 60, 343–361.
49
50
51 Gaffney, E.S., Tong, H., Meylan, P.A., 2006. Evolution of the side-necked turtles: the
52
53 families Bothremydidae, Euraxemydidae, and Araripeemydidae. Bull. Am. Mus. Nat. Hist.
54
55
56 300, 1–700.
57
58
59
60
61
62
63
64
65

- 1 Gilmore, C.W., 1933. On the dinosaurian fauna of the Iren Dabasu Formation. Bull. Amer.
2
3 Mus. Nat. Hist. 67, 23–78.
- 4
5 Godefroit, P., Motchurova-Dekova, N., 2010. Latest Cretaceous hadrosauroid (Dinosauria:
6
7 Ornithopoda) remains from Bulgaria. C. R. Palevol 9, 163–169.
- 8
9 Gómez-Alday, J.J., 1999. Stratigraphic and depositional environments of the Upper
10 Cretaceous of the Laño quarry. Evidence of diapiric activity. Estud. Mus. Cienc. Nat. de
11
12 Alava 14 (Núm. espec. 1), 29–35.
- 13
14 Gudeo, I.L., Pérez-García, A., Murelaga, X., Zuluaga, M.C., Alonso-Olazabal, A., Suárez-
15
16 Bilbao, O., Ortega, L.A., 2013. Estudio isotópico de estroncio en tortugas del Cretácico
17 superior de España. Libro de resúmenes del IX Congreso Ibérico - Congreso Nacional de
18
19 Geoquímica, Soria, pp. 54–55.
- 20
21 Horner, J.R., 1979. Upper Cretaceous dinosaurs from the Bearpaw Shale (marine) of south-
22
23 central Montana with a checklist of Upper Cretaceous dinosaur remains from marine
24
25 sediments in North-America. J. Paleontol. 53, 566–577.
- 26
27 Horner, J.R., Makela, R., 1979. Nest of juveniles provides evidence of family structure among
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65
dinosauria. Nature 282, 296–298.
- Horner, J.R., Ricqlès, A. de, Padian, K., 2000. Long bone histology of the hadrosaurid
dinosaur *Maiasaura peeblesorum*: growth dynamics and physiology based on an
ontogenetic series of skeletal elements. J. Vert. Paleontol. 20, 115–129.
- Horner, J.R., Ricqlès, A. de, Padian, K., Scheetz, R.D., 2009. Comparative long bone
histology and growth of the “hypsilophodontid” dinosaurs *Orodromeus makelai*,
Dryosaurus altus, and *Tenontosaurus tilletti* (Ornithischia: Euornithopoda). J. Vert.
Paleontol. 29, 734–747.

- 1 Horner, J.R., Weishampel, D.B., Forster, C.A., 2004. Hadrosauridae. In: Weishampel, D.B.,
2
3 Dodson, P., Osmolska, H. (Eds.), *The Dinosauria*, 2nd ed. University of California Press,
4
5 Berkeley, pp. 438–463.
6
7 Jagt, J.W.M., Mulder, E.W.A., Schulp, A.S., Dortangs, R.W., Fraaije, R.H.B., 2003.
8
9 Dinosaurs from the Maastrichtian-type area (southeastern Netherlands, northeastern
10 Belgium). *C. R. Palevol.* 2, 67–76.
11
12 Joyce, W.G., Parham, J.F., Gauthier, J.A., 2004. Developing a protocol for the conversion of
13 rank-based taxon names to phylogenetically defined clade names, as exemplified by
14 turtles. *J. Paleontol.* 78, 989–1013.
15
16 Klein, N., Sander, P.M., 2008. Ontogenetic stages in the long bone histology of sauropod
17
18 dinosaurs. *Paleobiology* 34, 247–263.
19
20 Lamm, E.T., 2013. Preparation and sectioning of specimens. In: Padian, K., Lamm, E.T.
21
22 (Eds.), *Bone Histology of Fossil Tetrapods: Advancing Methods, Analysis and*
23
24 Interpretation. University of California Press, Berkeley, pp. 55–160.
25
26 Lapparent de Broin, F. de, Murelaga, X., 1996. Une nouvelle faune de chéloniens dans le
27 Crétacé supérieur européen. *C. R. Acad. Sci. Paris (IIa)* 323, 729–735.
28
29 Lapparent de Broin, F. de, Murelaga, X., 1999. Turtles from the Upper Cretaceous of Laño
30 (Iberian Peninsula). *Est. Mus. Cien. Nat. Alava* 14 (Núm. espec. 1), 135–211.
31
32 Lapparent de Broin, F. de, Werner, C., 1998. New late Cretaceous turtles from the Western
33 Desert, Egypt. *Ann. Paléontol.* 84, 131–214.
34
35 Lapparent de Broin, F. de, Murelaga Bereikua, X., Codrea, V., 2004. Presence of Dortokidae
36 (Chelonii, Pleurodira) in the earliest Tertiary of the Jibou Formation, Romania:
37 paleobiogeographical implications. *Acta Palaeontol. Roman.* 4, 203–215.
38
39 Laurent, Y., 2003. Les faunes de vertébrés continentaux du Maastrichtien supérieur d'Europe:
40 systématique et biodiversité. *Strata (Sér. 2)* 41, 1–81.
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

- 1 Laurent, Y., Bilotte, M., Le Loeuff, J., 2002. Late Maastrichtian continental vertebrates from
2 southwestern France: correlation with marine fauna. *Palaeogeogr. Palaeoclimatol.*
3
4 Palaeoecol.
- 5 187, 121–135.
- 6
7 Laurent, Y., Cavin, L., Bilotte, M., 1999. Découverte d'un gisement à vertébrés dans le
8 Maastrichtien supérieur des Petites-Pyrénées. *C.R. Acad. Sci. Paris (II)* 328, 781–787.
- 9
10 Lauters, P., Bolotsky, Y.L., van Itterbeeck, Godefroit, P., 2008. Taphonomy and age profile of
11 a latest Cretaceous dinosaur bone bed in far Eastern Russia. *Palaios* 23, 153–162.
- 12
13 Leidy, J., 1858. *Hadrosaurus foulkii*, a new saurian from the Cretaceous of New Jersey,
14 related to the *Iguanodon*. *Proc. Acad. Nat. Sci. Philadelphia* 10, 213–218.
- 15
16 Lull, R.S., Wright, N.E., 1942. Hadrosaurian dinosaurs of North America. *Geol. Soc. Am.*
17 Spec. Paper 40, 1–242.
- 18 Mantell, G.A., 1825. Notice on the *Iguanodon*, a newly discovered fossil reptile, from the
19 sandstone of Tilgate Forest, in Sussex. *Phil. Trans. Roy. Soc. London* 115, 179–186.
- 20
21 Marsh, O.C., 1881. Principal characters of American Jurassic dinosaurs. Part V. *Am. J. Sci.*
22 (3) 21, 167–170.
- 23
24 Marsh, O.C., 1872. Notice on a new species of *Hadrosaurus*. *Am. J. Sci.* (3) 3, 301.
- 25
26 Matheron, P., 1869. Notice sur les reptiles fossiles des dépôts fluvio-lacustres crétacés du
27 basin à lignite de Fuveau. *Mém. Acad. Imp. Sci. B.-L. Arts*, Marseille, pp. 345–379.
- 28
29 Mulder, E.W.A., 1984. Resten van *Telmatosaurus* (Ornithischia, Hadrosauridae) uit het
30 Boven-Krijt van Zuid-Limburg. *Grondb. Hamer* 38, 108–115.
- 31
32 Mulder, E.W.A., Jagt, J.W.M., Schulp, A.S., 2005. Another record of a hadrosaurid dinosaur
33 from the Maastrichtian type area (The Netherlands, Belgium): Seeley (1883) revisited.
34 Bull. Inst. R. Sci. Nat. Belg. Sci. Terre 75, 201–206.
- 35
36 Nopcsa, F., 1931. Sur des nouveaux restes de Tortues du Danien du Midi de la France. *Bull.*
37 Soc. Géol. France 1, 223–236.
- 38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

- 1 Ösi, A., Prondvai, E., Butler, R., Weishampel, D.B., 2012. Phylogeny, histology and inferred
2 body size evolution in a new rhabdodontid dinosaur from the Late Cretaceous of
3 Hungary. PLoS ONE 7(9), e44318, 1–25.
- 4
- 5 Paris, J.-P., Taquet, P., 1973. Découverte d'un fragment de dentaire d'hadrosaurien (Reptile
6 dinosaurien) dans le Crétacé supérieur des Petites Pyrénées (Haute-Garonne). Bull. Mus.
7 Nat. Hist. Nat. Paris 130, 17–27.
- 8
- 9 Parks, W.A., 1922. *Parasauroplophus walkeri*, a new genus and species of crested trachodont
10 dinosaur. Univ. Toronto Stud. Geol. Ser. 13, 1–32.
- 11
- 12 Pereda-Suberbiola, X., Astibia, H., Murelaga, X., Elorza, J.J., Gómez-Alday, J.J., 2000.
13 Taphonomy of the Late Cretaceous dinosaur-bearing beds of the Laño Quarry (Iberian
14 Peninsula). Palaeogeogr. Palaeoclimatol. Palaeoecol. 157, 247–275.
- 15
- 16 Pereda-Suberbiola, X., Canudo, J.I., Company, J., Cruzado-Caballero, P., Barco, J.L., Lopez-
17 Martinez, N., Oms, O., Ruiz-Omeñaca, J.I., 2009a. The last hadrosaurid dinosaurs of
18 Europe: a new lambeosaurine from the uppermost Cretaceous of Arén (Huesca, Spain).
19 C. R. Palevol. 8, 559–572.
- 20
- 21 Pereda-Suberbiola, X., Canudo, J.I., Company, J., Cruzado-Caballero, Ruiz-Omeñaca, J.I.,
22 2009b. Hadrosauroid dinosaurs from the latest Cretaceous of the Iberian Peninsula. J.
23 Vert. Paleontol. 29, 946–951.
- 24
- 25 Pereda-Suberbiola, X., Ruiz-Omeñaca, J.I., Company, J., 2003a. Los dinosaurios hadrosaurios
26 del registro ibérico. Descripción de nuevo material del Cretácico superior de Laño
27 (Condado de Treviño). In: F. Pérez Lorente (Coord.), Reptiles mesozoicos de España.
28 Instituto de Estudios Riojanos, Logroño. Ciencias de la Tierra 26, 375–388.
- 29
- 30 Pereda-Suberbiola, X., Ruiz-Omeñaca, J.I., Ullastre, J., Masriera, A., 2003b. Primera cita de
31 un dinosaurio hadrosaurio en el Cretácico Superior del Prepirineo oriental (Peguera,
32 provincia de Barcelona). Geogaceta 34, 195–198.
- 33
- 34
- 35
- 36
- 37
- 38
- 39
- 40
- 41
- 42
- 43
- 44
- 45
- 46
- 47
- 48
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- 51
- 52
- 53
- 54
- 55
- 56
- 57
- 58
- 59
- 60
- 61
- 62
- 63
- 64
- 65

- 1 Pereda-Suberbiola, X., Corral, J.C., Astibia, H., Badiola, A., Bardet, N., Berreteaga, A.,
2
3 Buffetaut, E., Buscalioni, A.D., Cappetta, H., Cavin, L., Díez Díaz, V., Gheerbrant, E.,
4
5 Murelaga, X., Ortega, F., Pérez-García, A., Poyato-Ariza, F., Rage, J.C., Sanz, J.L.,
6
7 Torices, A. in review. Continental and marine vertebrate assemblages from the Late
8 Cretaceous of the Laño Quarry (Basque-Cantabrian Region, Iberian Peninsula): an
9 update. *J. Iber. Geol.*
- 10 Pérez-García, A., 2012. Las tortugas mesozoicas de la Península Ibérica. Doctoral Thesis,
11
12 Universidad Complutense de Madrid, Madrid, 415 p.
- 13 Pérez-García, A., de Lapparent de Broin, F., 2014. An update on the diachronous migration to
14 Europe of several Gondwanan lineages of pleurodiran turtles. In: Pankhurst, R.J.,
15 Castiñeiras, P., Sánchez Martínez, S. (Eds.). Abstract Book of Gondwana 15. Madrid, p.
16 137.
- 17 Pérez-García, A., Murelaga, X., 2014. Tortugas del Cretácico Inferior de la Cuenca Vasco-
18 Cantábrica: Registro Hauteriviense-Barremiense de Vega de Pas (Cantabria). *Geogaceta*
19 55, 79–82.
- 20 Pérez-García, A., Gasulla, J.M., Ortega, F., 2014. *Eodortoka morellana* gen. et sp. nov., the
21 first pan-pleurodiran turtle (Dortokidae) defined in the Early Cretaceous of Europe. *Cret.*
22 Res. 48, 130–138.
- 23 Pérez-García, A., Ortega, F., Murelaga, X., 2009. Una probable tortuga Pancryptodira del
24 Cretácico Superior de Lo Hueco (Cuenca, España). *Paleolusitana* 1, 365–371.
- 25 Pérez-García, A., Ortega, F., Murelaga, X., 2010. Ampliación de la distribución geográfica y
26 temporal de *Elochelys convenarum* (Chelonii, Bothremydidae) en el Cretácico Superior
27 de la Península Ibérica. *Ameghiniana* 47, 307–315.
- 28 Pérez-García, A., Ortega, F., Murelaga, X., 2012. A new genus of Bothremydidae (Chelonii,
29 Pleurodira) in the Cretaceous of Southwestern Europe. *Geobios* 45, 219–229.

- 1 Portis, A., 1882. Les Chéloniens de la Molasse vaudoise conservés dans le Musée Géologique
2 de Lausanne. Appendice concernant un nouveau genre de Chélonien de la Craie
3 supérieure de Fuveau. Mém. Soc. Paléontol. Suisse 9, 65–76.
4
5 Poyato-Ariza, F., Fielitz, C., Wenz, S., 1999. Marine actinopterygian fauna from the Upper
6 Cretaceous of Albaina (Laño quarry, northern Spain). Estud. Mus. Cienc. Nat. Alava 14
7 (Núm. espec. 1), 325–338.
8
9 Prieto-Márquez, A., 2008. Phylogeny and historical biogeography of hadrosaurid dinosaurs.
10 Ph.D. thesis, Florida State University, Tallahassee, Electronic Theses, Treatises and
11 Dissertations, Paper 460, 861 p.
12
13 Prieto-Márquez, A., 2010. Global historical biogeography of hadrosaurid dinosaurs. Zool. J.
14 Linn. Soc. Lond. 159, 503–525.
15
16 Prieto-Márquez, A., 2011. Cranial and appendicular ontogeny of *Bactrosaurus johnsoni*, a
17 hadrosaur dinosaur from the Late Cretaceous of northern China. Palaeontology 54, 773–
18 792.
19
20 Prieto-Márquez, A., Dalla Vecchia, F.M., Gaete, R., Galobart, À., 2013. Lambeosaurine
21 dinosaurs from the European Archipelago, with description of the new aralosaurin
22 Canardia garonnensis. PLoS ONE 8(7), e69835, 1–44.
23
24 Prieto-Márquez, A., Gaete, R., Rivas, G., Galobart, À., Boada, M., 2006a. Hadrosaur
25 dinosaurs from the Late Cretaceous of Spain: *Pararhabdodon isonensis* revisited and
26 *Koutalisaurus kohlerorum*, gen. et sp. nov. J. Vert. Paleontol. 26, 929–943.
27
28 Prieto-Márquez, A., Weishampel, D.B., Horner, J.R., 2006b. The dinosaur *Hadrosaurus*
29 *foulkii*, from the Campanian of the East Coast of North America, with a reevaluation of
30 the genus. Acta Palaeontol. Pol. 51, 77–98.
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

- 1 Reid, R.E.H., 2012. How dinosaurs grew. In: Brett-Surman, M.K., Holtz T.R. Jr., Farlow, J.O.
2 (Eds.), *The Complete Dinosaur*, 2nd ed. Indiana University Press, Bloomington, pp. 621–
3 635.
- 4
- 5 Riabinin, A.N., 1945. Dinosaurian remains from the Upper Cretaceous of the Crimea. Mat.
6 Vsessoyuzn. Nautsh. Geol. Razv. Inst. Paleont. Strat. Sbornik. 4, 4–10 (in Russian, with
7 English summary).
- 8
- 9 Sander, P.M., 2000. Longbone histology of the Tendaguru sauropods: implications for growth
10 and biology. *Paleobiology* 26, 466–488.
- 11
- 12 Scheyer, T.M., Pérez-García, A., Murelaga, X., 2012. Bone microstructure of selected fossil
13 turtle shell plates from the Cretaceous of Spain (Solemydidae and Dortokidae). In: Joyce,
14 W.G., Corsini, J.A., Werneburg, I., Rabi, M. (Eds.), *Abstracts of the Symposium on*
15 *Turtle Evolution*. Tübingen, p. 39.
- 16
- 17 Seeley, H.G., 1883. On the dinosaurs from the Maastricht beds. *Q. J. Geol. Soc. Lond.* 39,
18 246–253.
- 19
- 20 Seeley, H.G., 1887. On the classification of the fossil animals commonly named Dinosauria.
21 Proc. Roy. Soc. Lond. 43, 165–171.
- 22
- 23 Sellés, A.G., Vila, B., in review. Re-evaluation of the age of some dinosaur localities from the
24 southern Pyrenees by means of megaloolithid oospecies. *J. Iber. Geol.*
- 25
- 26 Sereno, P.C., 1986. Phylogeny of the bird-hipped dinosaurs (Order Ornithischia). *Natl. Geogr.*
27 Res. 2, 234–256.
- 28
- 29 Sereno, P.C., 1998. A rationale for phylogenetic definitions, with application to the higher-
30 level taxonomy of Dinosauria. *N. Jb. Geol. Palaontol. Abhandl.* 210, 41–83.
- 31
- 32 Sereno, P.C., 2005. Stem Archosauria – TaxonSearch. <http://www.taxonsearch.org/> (version
33 1.0).
- 34
- 35
- 36
- 37
- 38
- 39
- 40
- 41
- 42
- 43
- 44
- 45
- 46
- 47
- 48
- 49
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- 51
- 52
- 53
- 54
- 55
- 56
- 57
- 58
- 59
- 60
- 61
- 62
- 63
- 64
- 65

- Stein, K., Sander, P.M., 2009. Histological core drilling: a less destructive method for studying bone histology. In: Brown, M.A., Kane, J.F., Parker, W.G. (Eds.), Methods in fossil preparation: Proceedings of the First Annual Fossil Preparation and Collections Symposium. Petrified Forest, pp. 69–80.
- Tong, H., Gaffney, E.S., Buffetaut, E., 1998. *Foxemys*, A new side-necked turtle (Bothremydidae: Pelomedusoides) from the Late Cretaceous of France. Am. Mus. Novit. 3251, 1–19.
- Valentin, X., Godefroit, P., Tabuce, R., Vianey-Liaud, M., Wu, W., Garcia, G., 2012. First Late Maastrichtian (Latest Cretaceous) vertebrate assemblage from Provence (Vitrolles-La-Pleine, southern France). In: Godefroit, P. (Ed.), Bernissart dinosaurs and Early Cretaceous Terrestrial Ecosystems. Indiana University Press, Bloomington, pp. 583–597.
- Weishampel, D.B., Jianu, C.-M., Csiki, Z., Norman, D.B., 2003. Osteology and phylogeny of Zalmoxes (n.g.), an unusual Euornithopod dinosaur from the latest Cretaceous of Romania. J. Syst. Palaeontol. 1, 65–123.
- Weishampel, D.B., Mulder, E.W.A., Dortangs, R.W., Jagt, J.W.M., Jianu, C.-M., Kuypers, M.M.M., Peeters, H.H.G., Schulp, A.S., 1999. Dinosaur remains from the type Maastrichtian: an update. Geologie en Mijnbouw 78, 357–365.
- Weishampel, D.B., Norman, D.B., Grigorescu, D., 1993. *Telmatosaurus transsylvanicus* from the Late Cretaceous of Romania: the most basal hadrosaurid dinosaur. Palaeontology 36, 361–385.
- Wellnhofer, P., 1994. Ein Dinosaurier (Hadrosauridae) aus der Oberkreide (Maastricht, Helvetikum-Zone) des bayerischen Alpenvorlandes. Mitteil. Bayer. Staatsamml. Palaeontol. Hist. Geol. 34, 221–238.
- Wu, W., Godefroit, P., 2012. Anatomy and relationships of Bolong yixianensis, an Early Cretaceous iguanodontoid dinosaur from Western Liaoning, China. In: Godefroit, P.

1 (Ed.), Bernissart dinosaurs and Early Cretaceous Terrestrial Ecosystems. Indiana
2 University Press, Bloomington, pp. 293–333.

3
4 Xing, H., Prieto-Márquez, A., Hai, S.-L., Yu, T.-X., 2012. Re-evaluation and phylogenetic
5 analysis of the hadrosaurine dinosaur *Wulagasaurus dongi* from the Maastrichtian of
6
7 northeast China. *Vert. PalAsiatica* 50, 160–169.
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
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1 **Caption of figures**
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6 **Fig. 1.** Simplified geological map of the south-central part of the Basque-Cantabrian Region
 7
 8 and stratigraphic column of the Laño quarry showing the position of the fossil vertebrate beds
 9
 10 (map compiled from the Spanish National Geologic Map, MAGNA 1:50.000; the column
 11 follows standard lithologic patterns). Albaina location is also indicated in the inset map of
 12 Iberia.
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 16 **Fig. 1.** Carte géologique simplifiée de la partie sud-centrale de la Région Basco-Cantabrique
 17
 18 et colonne stratigraphique de la carrière de Laño montrant la position des niveaux fossilifères
 19
 20 à vertébrés (carte d'après la Carte géologique nationale d'Espagne, MAGNA 1:50.000; la
 21
 22 colonne suit les modèles lithologiques standards). La localisation d'Albaina est aussi indiquée
 23
 24 sur l'encart d'Iberia.
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 32 **Fig. 2.** Albaina turtles. A-C, MCNA 15055, cf. Pan-Cryptodira indet., partial periferal plate in
 33 dorsal, ventral and anterior views. D-F, MCNA 10863, cf. *Polysternon atlanticum*
 34
 35 (Bothremydidae), sixth left costal plate, interpretative schema, dorsal and ventral views. The
 36
 37 continuous lines represent the preserved margins of the plate, the dashed lines are broken
 38 edges, and the dotted lines correspond to the hypothetical reconstruction of the adjacent
 39 plates. Black lines represent the sutures between plates; grey and wider lines indicate the
 40 border of the scutes. Abbreviations: c, costal plate, n, neural plate; PL, pleural scute; V,
 41
 42 vertebral scute.
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 52 **Fig. 2.** Tortues d'Albaina. A-C, MCNA 15055, cf. Pan-Cryptodira indet., plaque périphérique
 53 partielle en vues dorsale, ventrale et antérieure. D-F, MCNA 10863, cf. *Polysternon*
 54 *atlanticum* (Bothremydidae), 6^{ème} plaque costale gauche, schéma interprétatif et vues dorsale
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 56 et ventrale. Les lignes continues représentent les bords préservés de la plaque, les lignes
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1 discontinues les bords cassés, et les lignes en pointillé correspondent à une reconstitution
 2 hypothétique des plaques adjacentes. Les traits noirs représentent les sutures entre les plaques,
 3 et les traits gris plus épais les frontières entre les écailles. Abréviations : c, plaque costale, n,
 4 plaque neurale ; Pl, écaille pleurale ; V, écaille vertébrale.
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 13 **Fig. 3.** Albaina dinosaur. LU-JL-LAÑ001, Hadrosauroid indet., fragmentary right femur in
 14 anterior (A), posterior (B), medial (C), lateral (D) and distal (E) views. Abbreviations: ieg,
 15 intercondylar extensor (anterior) groove; ifg, intercondylar flexor (posterior) groove; lc,
 16 lateral condyle; mc, medial condyle.
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 23 **Fig. 3.** Dinosaur d'Albaina. LU-JL-LAÑ001, Hadrosauroid indet., fémur droit
 24 fragmentaire en vues antérieure (A), postérieure (B), médiale (C), latérale (D) et distale (E).
 25 Abréviations: ieg, sillon intercondylique extenseur (antérieur); ifg, sillon intercondylique
 26 flexeur (postérieur); lc, condyle latéral; mc, condyle médial.
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 35 **Fig. 4.** Transverse thin sections of the hadrosauroid femur LU-JL-LAÑ001 from Albaina. (A),
 36 General view of the middle to outer cortex showing a well vascularized fibro-lamellar bone
 37 tissue, with clusters of secondary osteons (Haversian reconstruction) restricted to the deeper
 38 regions of the compacta. (B), Detail of the outer cortex showing how the regular plexiform
 39 vascularity changes to a reticular pattern in the cortical periphery. Secondary osteons are
 40 absent in this external part of the cortex. (C) Enlargement of figure (B) showing sub-
 41 periosteal vascular canals opening to the outer surface, suggesting active growth.
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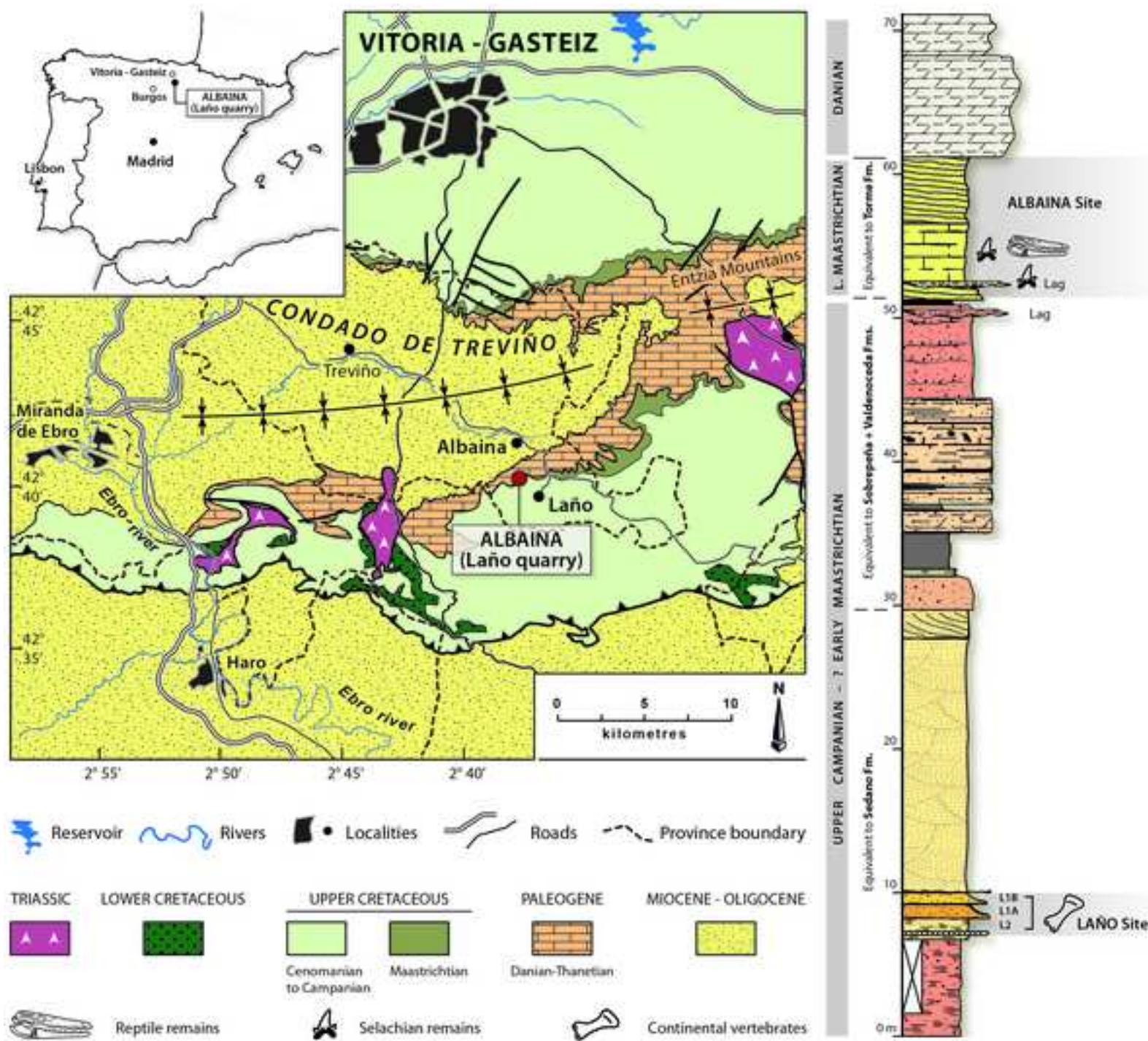
51
 52 Abbreviations: lv, longitudinal vascularity; po, primary osteons; pv, plexiform vascularity; rv,
 53 reticular vascularity; so, secondary osteons; vc, vascular canals. Scale bars: 1 mm (A-B), 0.25
 54 mm (C).
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1 **Fig. 4.** Lames minces transversales du fémur d'hadrosauroïde LU-JL-LAÑ001 d'Albaina.
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(A), vue générale du cortex moyen à externe montrant un tissu osseux fibro-lamellaire bien vascularisé, avec des clusters d'ostéones 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 ostéones secondaires sont absents dans la partie externe du cortex. (C), agrandissement de la figure (B) montrant les canaux vasculaires sub-périostés s'ouvrant vers la surface externe, ce qui suggère une croissance active. Abréviations: lv, vascularisation longitudinale; po, ostéones primaires; pv, vascularisation pléxiforme; rv, vascularisaton réticulaire; so, ostéones secondaires; vc, canaux vasculaires. Barres d'échelle : 1 mm (A-B), 0,25 mm (C).

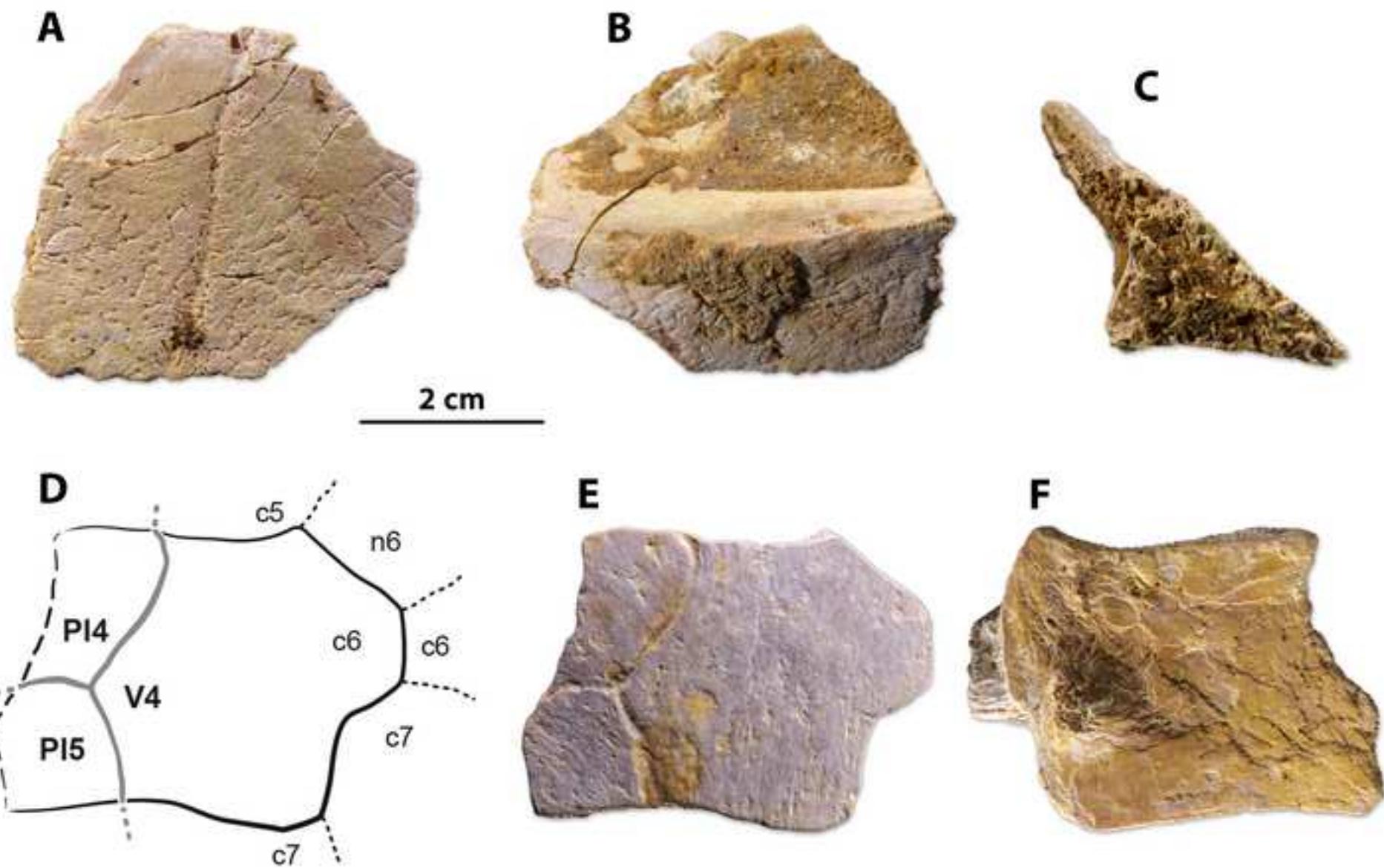
Figure

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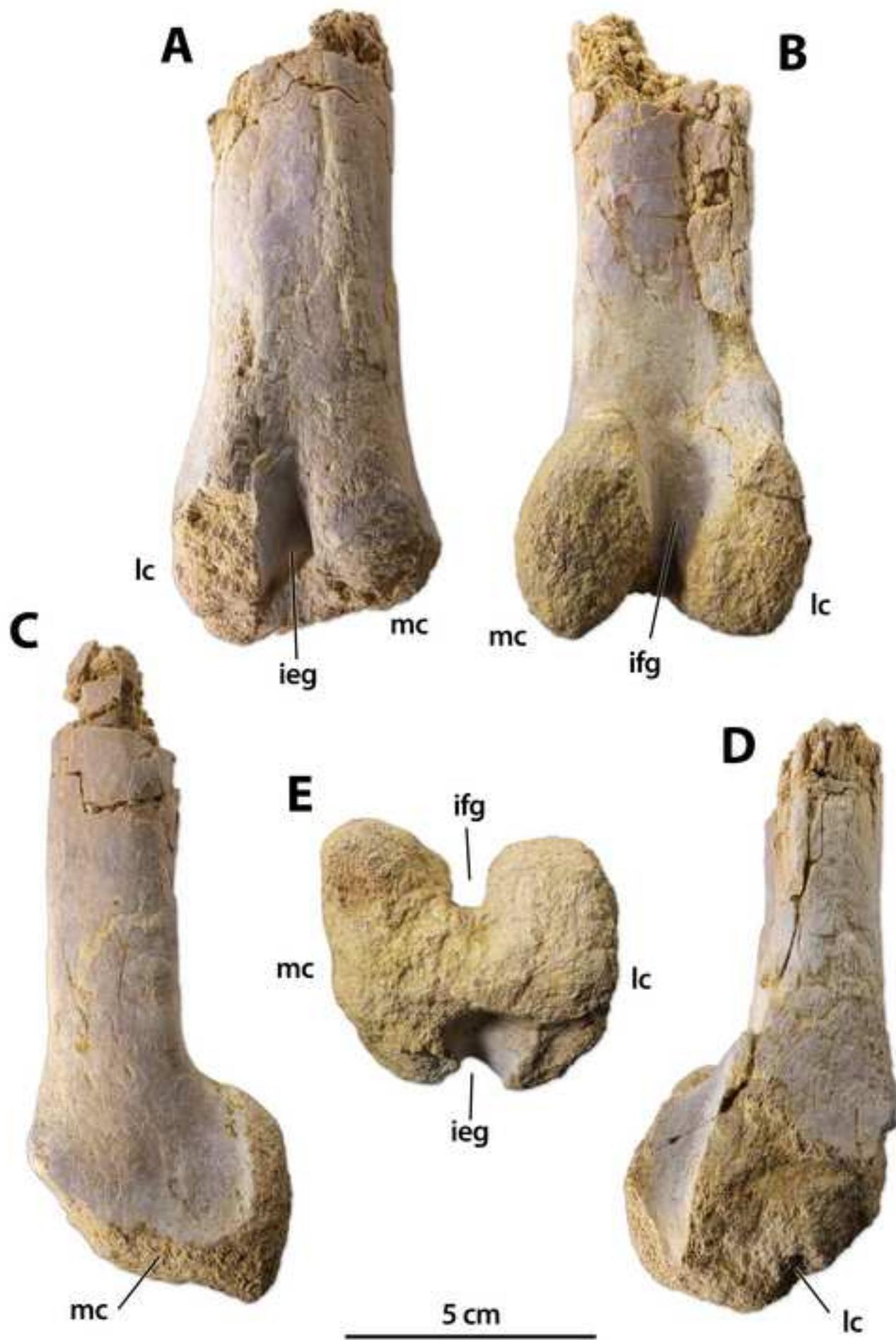
Figure

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