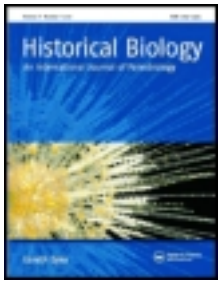


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# A new hadrosaurid dentary from the latest Maastrichtian of the Pyrenees (north Spain) and the high diversity of the duck-billed dinosaurs of the Ibero-Armorican Realm at the very end of the Cretaceous

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In the latest Maastrichtian, the European hadrosauroid fauna was more diverse than those of North America and Asia. The European record of hadrosaurid dentaries is an example of this diversity, and most of the sites with mandibular remains are located in the Ibero-Armorican Realm. Within the Iberian Peninsula, most of the remains are located in the Tremp Basin (South Central Pyrenees). Two of the three valid hadrosaurid taxa defined in this basin are from the Blasi sites (Arén, Huesca province): *Arenysaurus ardevoli* (Blasi-3) and *Blasisaurus canudoi* (Blasi-1). A new locality in Blasi (Blasi 3.4) has provided a new dentary from an indeterminate euhadrosaurid. This dentary presents some characters intermediate between *Arenysaurus* and *Blasisaurus*, some characters similar to *Pararhabdodon isonensis* (from the nearby province of Lleida), and some characters of its own. Nevertheless, due to its fragmentary character, without dentition or its edentulous anterior part, it cannot be determined above the level of Euhadrosauria. It thus represents a fourth Iberian euhadrosaurian taxon in the Ibero-Armorican Realm, different from *Arenysaurus, Blasisaurus* and *Pararhabdodon*, increasing the diversity of hadrosauroids in this realm at the very end of the Cretaceous.

**Keywords:** Hadrosauridae; Late Cretaceous; dentary; paleobiodiversity; Iberian Peninsula



## Introduction

The paleobiodiversity of the European duck-billed dinosaurs of the Maastrichtian distinguishes them from those from North America and Asia (Prieto-Márquez et al. 2007; Dalla Vecchia 2009; Pereda-Suberbiola, Canudo, Company, et al. 2009; Pereda-Suberbiola, Canudo, Cruzado-Caballero, et al. 2009; Prieto-Márquez and Wagner 2009; Cruzado-Caballero, Pereda-Suberbiola and Ruiz-Omeñaca 2010; Cruzado-Caballero, Ruiz-Omeñaca and Canudo 2010). This mixed European fauna was due to the connection of Asia and Europe by means of 'semi-permeable' barriers that were emerged or submerged depending on changes in the climate and sea level (Prieto-Márquez and Wagner 2009). A series of geo-dispersal events is likely to have occurred. The first event probably took place during the Santonian–Campanian of Asia and explains the presence of the non-hadrosaurid hadrosauroid *Tethyshadros insularis* Dalla Vecchia, 2009 and the basal hadrosaurid *Telmatosaurus transsylvanicus* (Nopcsa, 1903) (Cruzado-Caballero, Pereda-Suberbiola et al. 2010). Afterwards, no later than the middle to late Campanian, another dispersal event of hadrosaurines and lambeosaurines is likely to have taken place. The periods of isolation during high-sea-level times may have facilitated the survival of non-hadrosaurid hadrosauroids and basal hadrosaurids (i.e. *Tethyshadros* and *Telmatosaurus*) in the Maastrichtian of Europe (Pereda-Suberbiola, Canudo, Company, et al. 2009). These taxa took refuge in the European islands and underwent varying degrees of reduction in size probably due to insular dwarfism (Dalla Vecchia 2009; Prieto-Márquez and Wagner 2009; Benton et al. 2010; Weishampel et al. 2010). As a result of the different geo-dispersal events and the periods of isolation, the European fauna was the only one where non-hadrosaurid hadrosauroids, non-euhadrosaurian hadrosaurids, hadrosaurines and lambeosaurines co-existed in the Maastrichtian. In other continents (Asia, North America and South America) the more basal forms became extinct before the Campanian.

The European record is based on many fragmentary specimens with a good representation of dentaries (from France, Italy, Romania, Spain and The Netherlands; Figure 1). Most of the sites with remains of dentaries are located in the Pyrenees (south France and north Spain) and are Maastrichtian in age (Table 1). The French record is very fragmentary, and most of it probably belongs to juvenile specimens (Laurent et al. 2002; Laurent 2003), while the Spanish record presents at least 13 specimens of adult and juvenile individuals. Three of these dentaries come from the Blasi sites in Arén (Huesca province; Cruzado-Caballero, Ruiz-Omeñaca, Gaete et al. 2010; Figure 2). The Blasi sites are the richest in cranial and

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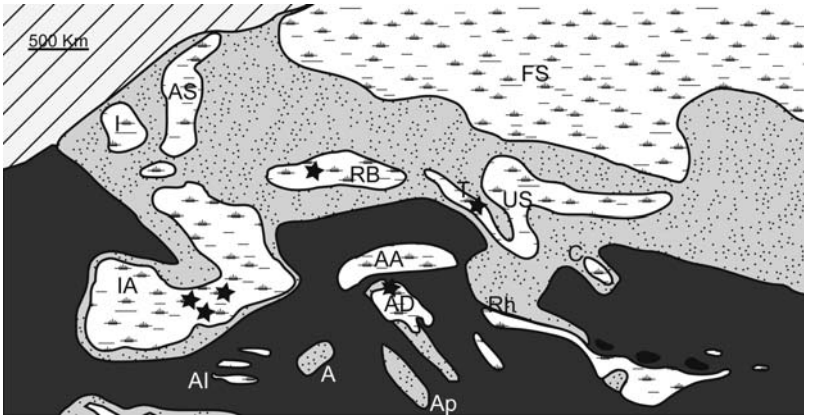


Figure 1. Simplified paleogeographical map of Europe during the Late Cretaceous (Maastrichtian), redrawn from Pereda-Suberbiola (2009, fig. 2), with the distribution of the known European hadrosauroid dentaries. A, Apennine platform; AA, Australpine island; AD, Adriatic-Dinaric island; AI, Alboran islands; Ap, Apulian platform; AS, Anglo-Scottish island; C, Crimean island; FS, Fennoscandian shield; I, Irish island; IA, Ibero-Armorican island; RB, Rhenish-Bohemian island; Rh, Rhodope; T, Transylvanian basin; US, Ukrainian shield. Plot marks: forest, exposed land; dotted, epicontinental seas; dark grey, oceanic basins; striped, unknown; black, volcanics.



postcranial hadrosaurid remains described in the latest Maastrichtian of Spain (López-Martínez et al. 2001; Cruzado-Caballero et al. 2005; Pereda-Suberbiola, Canudo, Cruzado-Caballero, et al. 2009; Cruzado-Caballero, Pereda-Suberbiola and Ruiz-Omeñaca 2010; Cruzado-Caballero, Ruiz-Omeñaca and Canudo 2010). The aim of this paper is to describe a new dentary from the new locality Blasi 3.4 and to try to assess the diversity of the European hadrosauroids of the Latest Cretaceous on the basis of the preserved dentaries.

## Geological and chronological framework

The Tremp Group (see references in Rosell et al. 2001) is part of the south-Pyrenean foreland basin infill that took place during the Upper Cretaceous and Paleogene. This formation is the result of sediment deposition in continental settings (fluvial environments) and transitional marine-continental settings (mainly lagoonal environments). Such stratigraphic units change laterally to each other as well as with the marine Arén Formation (coastal environments). The age of the Tremp Group (Oms et al. 2007; Riera et al. 2009) ranges from Maastrichtian to Paleocene, and in the area of the studied material it has been dated by means of magnetostratigraphy (Oms and Canudo 2004; Pereda-Suberbiola, Canudo, Cruzado-Caballero, et al. 2009; Vila et al. 2012). Thus all the findings reported here can be integrated within a robust chronostratigraphic framework to show that the levels with hadrosauroid mandibles are found in a stratigraphic position close to one another (see Figure 3) around the boundary between chrons C29r and C30n (i.e. ca. 66.2 Ma).

### *Institutional abbreviations*

IPS, Institut Català de Paleontologia (formerly Institut de Paleontologia Dr Miquel Crusafont), Sabadell, Spain; MDE, Museé des dinosaures, Espéraza, France; MGUV, Museo de Geología, Universitat de València, Valencia, Spain; MNHN, Museúm national d'Histoire naturelle, Paris, France; MPV, Museo Municipal de Ciencias Naturales de Valencia, Valencia, Spain; MPZ, Museo Paleontológico de la Universidad de Zaragoza, Zaragoza, Spain.

## The Ibero-Armorican record of dentaries from the Maastrichtian

The Ibero-Armorican record consists of 19 dentaries, 6 from France and 13 from Spain (Figure 4).

### *The French record*

Of the six French dentaries described, three are well preserved, whereas the other three are very fragmentary. The three best-preserved dentaries comprise two from the site of Cassagnau-2 (Marignac-Laspeyres, Department of Haute-Garonne; MDE-Cas2-02, 248) and one from the site of Le Bexen (Fontjoncouse, Department of Aude; MDE-Fo1-10). According to Laurent (2003), all of them belong to juvenile individuals.

An incomplete right dentary (MDE-Cas2-02, Hadrosauridae indet.) and a complete left dentary (MDE-Cas2-248, Euhadrosauria indet.) were found in the site of Cassagnau-2. This site is dated as upper Maastrichtian [Auzas Marls Formation; Laurent et al. 2002; Laurent 2003]. Both dentaries are gracile and anteroposteriorly short; MDE-Cas2-248 has a length of 160 mm (Figure 4(B)). The coronoid process is slightly projected anteriorly, and the posterodorsal edge is higher than the anterodorsal edge. In lateral view, several nutritional foramina are observed, and in MDE-Cas2-248 there is a large nutritional foramen near the symphyseal region. The dental battery of

Table 1. Latest Cretaceous hadrosauroid dentary record from Europe.

| Site/country | Formation | Age | Taxon | Remains | Reference |
|---|---|---|---|---|---|
| Ankerpoort-'t Nekami Quarry, province of Limburg, The Netherlands | Maastricht Formation, possibly Nekum Member | Upper Maastrichtian | Euhadrosauria indet. | NHMM 198027 Fragmentary right dentary | Buffetaut et al. (1985), Dalla Vecchia (2006) |
| Sânpetru, Hateg Basin, Transsylvania, Romania | Sânpetru Fromation | Maastrichtian | *Telmatosaurus transsylvanicus* | BMNH 3386 Holotype: a skull | Nopcsa (1903), Weishampel et al. (1993), Dalla Vecchia (2006) |
| Le Jadet, Department of Haute-Garonne, France | Calcarenites du Jadet Formation (Ausseing Group) | Upper Maastrichtian | Hadrosauridae indet. | MNHNP-sma 1 Fragmentary left dentary | Paris and Taquet (1973), Laurent (2003) |
| Cassagnau 2, Department of Haute-Garonne, France | Marnes d'Auzas Formation | Upper Maastrichtian (upper Campanian/ upper Maastrichtian in López-Martínez et al. 2001) | Hadrosauridae indet. Euhadrosauria indet. | MDE-Cas2-02 Rigth dentary; MDE-Cas2-248 Left dentary | Laurent (2003) |
| Le Bexen, Department of Aude, France | Marnes Rouges de Roquelongue Formation | Upper Maastrichtian (middle Maastrichtian in López-Martínez et al. 2001) | Hadrosauridae indet. | MDE-Fo1-01 Fragmentary right dentary; MDE-Fo1-03 Fragmentary left dentary; MDE-Fo-10 Fragmentary right dentary | Laurent et al. (1997), Laurent (2003) |
| Villaggio del Pescatore, Trieste, Italy | Liburnian Formation | Upper Campanian–Paleocene | *Tethyshadros insularis* | SC 57021 Holotype: a complete and articulated skeleton | Dalla Vecchia (2009) |
| Fontllonga, Province of Lleida, Spain | Conques? Formation (Tremp Group) | Upper Maastrichtian | Hadrosauroidea indet. | IPS 36338 Fragmentary left dentary | Casanovas-Cladellas et al. (1999b), Pereda-Suberbiola, Canudo, Cruzado-Caballero et al. (2009) |
| Les Llaus, Province of Lleida, Spain | Conques Formation (Tremp Group) | Upper Maastrichtian | *Koutalisaurus kohlerorum*[a] | IPS-SRA-27 Holotype: a rigth dentary | Casanovas-Cladellas et al. (1999a), Prieto-Márquez and Wagner (2009) |
| Basturs Poble, Province of Lleida, Spain | Conques Formation (Tremp Group) | Upper Maastrichtian | Hadrosauridae indet | At least three rigth dentaries | Prieto-Márquez et al. (2007) |
| La Solana, Province of Valencia, Spain | Villalba de la Sierra Formation | Upper Maastrichtian | Hadrosauridae indet. | MGUV 2200 Left dentary; MPV 181 Right dentary; MPV 182 Fragmentary right dentary; MPZ99/665 Left dentary. | Company Rodríguez (2004), Pereda-Suberbiola, Canudo, Cruzado-Caballero et al. (2009) |
| Blasi 1, Province of Huesca, Spain | Arén Formation | Upper Maastrichtian | *Blasisaurus canudoi* | | López-Martínez et al. (2001), Cruzado-Caballero, Pereda-Suberbiola and Ruiz-Omeñaca (2010) |
| Blasi 3, Province of Huesca, Spain | La Posa Formation (Tremp Group) | Upper Maastrichtian | *Arenysaurus ardevoli* | MPZ2008/258; left dentary | Pereda-Suberbiola, Canudo, Cruzado-Caballero et al. (2009) |
| Blasi 3.4, Province of Huesca, Spain | La Posa Formation (Tremp Group) | Upper Maastrichtian | Euhadrosauria indet. | MPZ2010/952; left dentary | This paper |
| Barranco Serraduy 1, Province of Huesca, Spain | La Posa Formation (Tremp Group) | Upper Maastrichtian | Hadrosauridae indet. | BS1-13; Fragmentary left dentary | Puértolas-Pascual et al. (2012) |
| Amor 2, Province of Huesca, Spain | Conques Formation (Tremp Group) | Upper Maastrichtian | Hadrosauridae indet. | MPZ2013/72; right dentary | Cruzado-Caballero et al. (2012) |

[a] This dentary was designated the holotype of *Koutalisaurus* by Prieto-Márquez et al. (2006); now a junior subjective synonym of *Pararhabdodon* (Prieto-Márquez and Wagner, 2009).

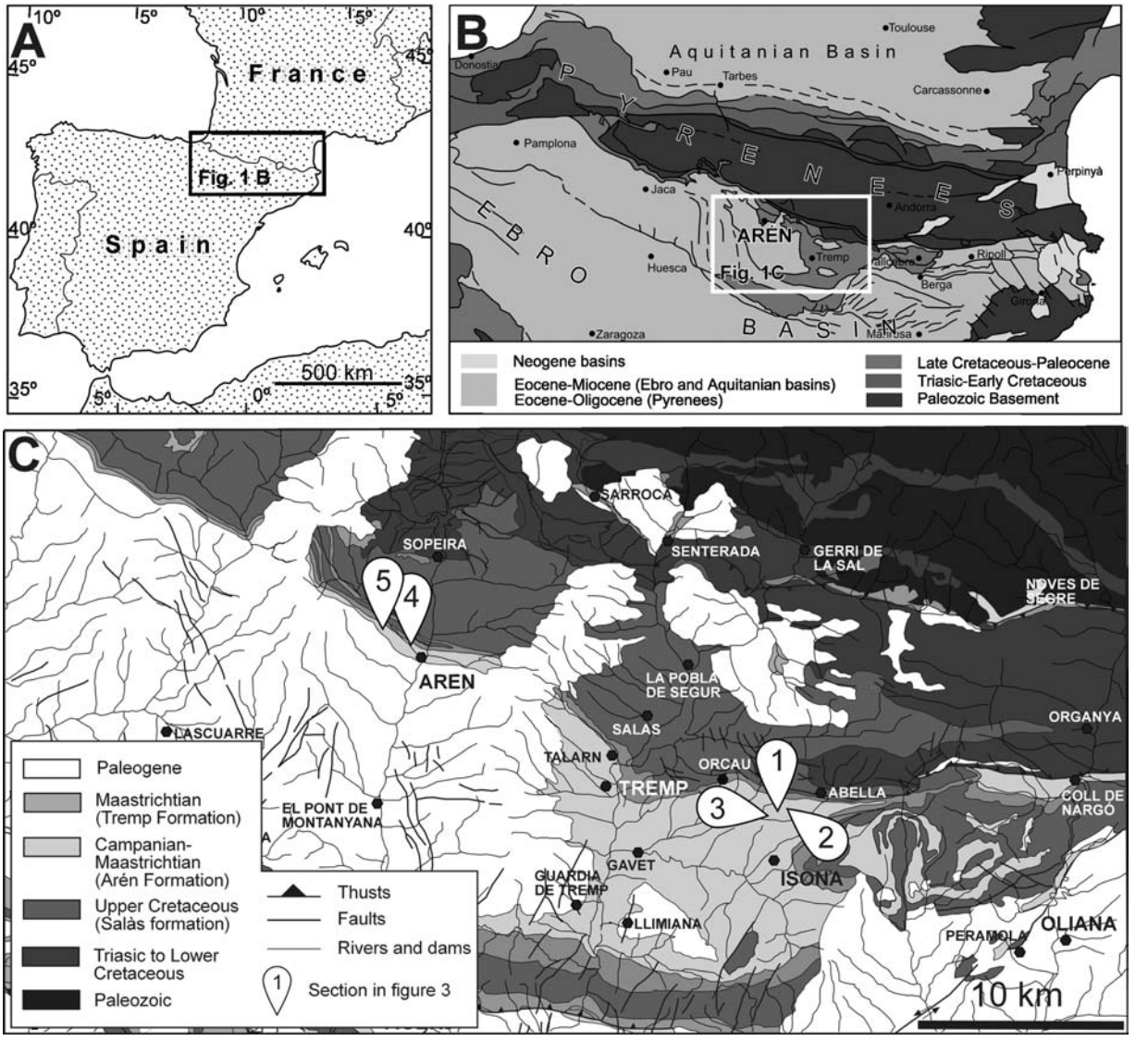


Figure 2. Setting of the studied site and sections with a general geographic location (A) and indication of the sketched geological map of the Pyrenees (B). The latter also indicates the map with the precise location of the sections (C) that can be found in Figure 3.

MDE-Cas2-248 is made up of 21 tooth positions with two preserved replacement teeth, and MDE-Cas2-02 has 21 tooth positions but no teeth are preserved. The teeth of MDE-Cas2-248 have a single prominent median carina that is straight and slightly caudally placed, and they do not have secondary ridges. Laurent et al. (2002) proposed that MDE-Cas2-248 is very similar to *Blasisaurus* (as Euhadrosauria indet. in López-Martínez et al. 2001, fig. 5(C),(D)), sharing a gracile form, the absence of secondary ridges and a coronoid process that is slightly projected anteriorly.

An incomplete right dentary (MDE-Fo1-10, Hadrosauridae indet.; Figure 4(A)) from the site of Le Bexen (Marnes Rouges de Roquelongue Formation; upper Maastrichtian) was described by Laurent et al. (1997). It is the largest French dentary (it is 210 mm long) but it does not preserve the anterior and posterior ends and the coronoid process. The Meckelian canal is large, and the suprameckelian foramen is oblique, at 45° to the alveolar medial surface. This dentary preserves 24 tooth positions without teeth. The other two dentaries described from Le Bexen (MDE-Fo1-01, MDE-Fo1-03) are very fragmentary (see Laurent et al. 1997). One additional dentary from the French record (MNHNP-sma 1 from the locality of Le Jadet) is too fragmentary for comparisons to be drawn. This is late Maastrichtian in age and is assigned to Hadrosauridae indet. (See Table 1).

### *The Spanish record*

In the Iberian Peninsula, the paleobiodiversity of hadrosaurids can be said to be high on the basis of the preserved dentaries. All the localities but one (La Solana in

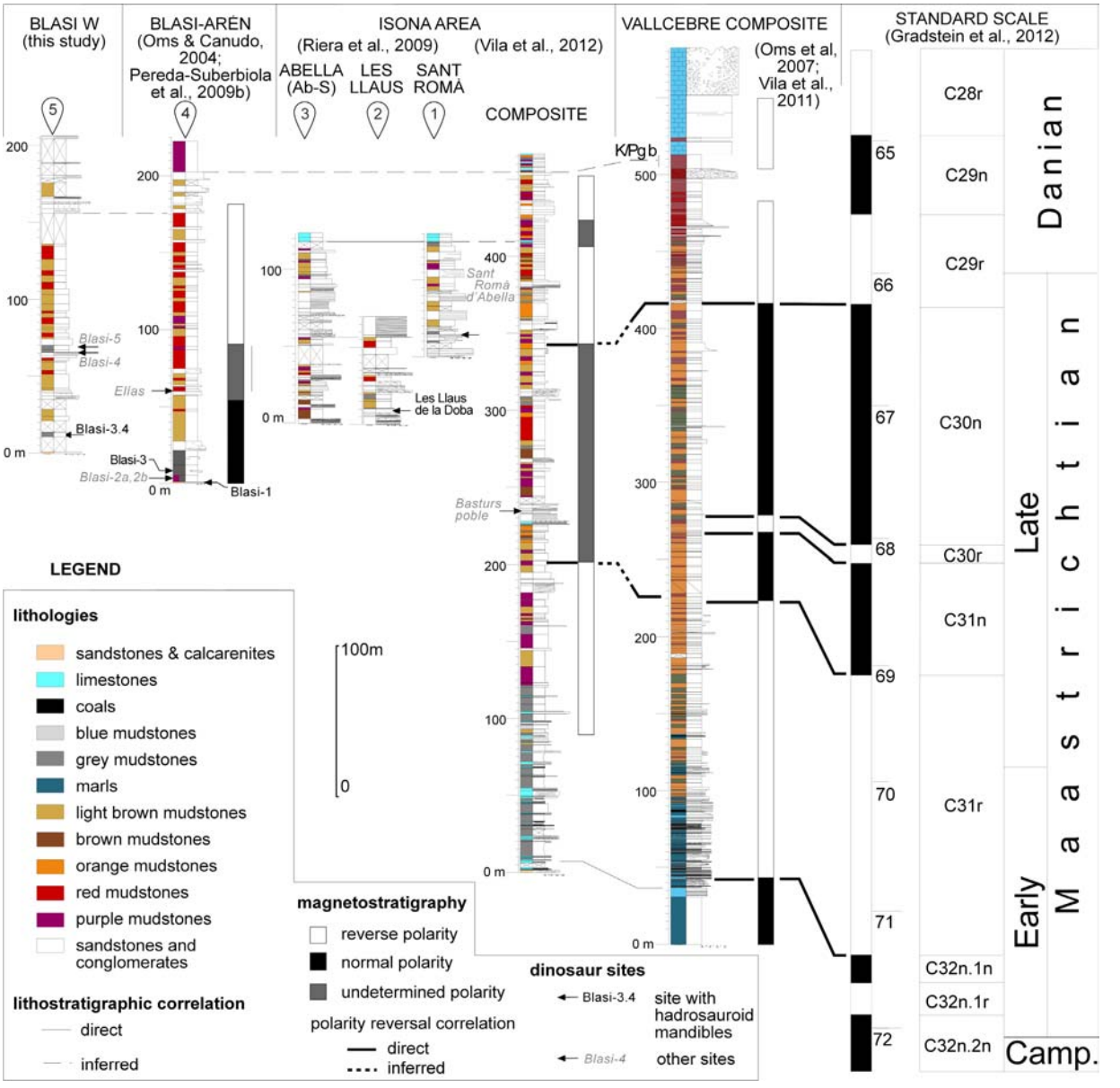


Figure 3. (Colour online) Location of the studied mandible (Blasi 3.4 site), in the west area of Blasi (section 5) and correlation with sections 4 to 1 (Blasi-Arén and Isona areas). See location of the sections in Figure 2(C). Lithostratigraphic correlations combined with magnetostratigraphic data from section 1, and Isona and Vallcebre, clearly indicate the correlation of Blasi 3.4 with the upper part of chron C30n (late Maastrichtian).

the South-western Iberian Range; Company Rodríguez 2004; Pereda-Suberbiola, Canudo, Company, et al. 2009) are in the South Central Pyrenees. According to the dentary remains, the Spanish Maastrichtian record consists of at least five different taxa: (1) an indeterminate non-hadrosaurid hadrosauroid from Fontllonga site (IPS 36338, Figure 4(C); Camarasa municipality, Lleida province), (2) an indeterminate hadrosaurid from La Solana site (MGUV 2200 and MPV 181, Figure 4(E),(F); Tous municipality, Valencia province), (3) *Koutalisaurus* Prieto-Márquez, Gaete, Rivas, Galobart and Boada, 2006 from Les Llaus site (IPS SRA 27, Figure 4(D); Abella de la Conca municipality, Lleida province; junior synonym of *Pararhabdodon* Casanovas-Cladellas, Santafé-Llopis and Isidro-Llorens 1993 after Prieto-Márquez and Wagner (2009)), (4) *Arenysaurus* Pereda-Suberbiola, Canudo, Cruzado-Caballero, Barco, López-Martínez, Oms and Ruiz-Omeñaca, 2009 from Blasi 3 site (MPZ2008/258; Figure 4(H); Arén municipality, Huesca province) and (5) *Blasisaurus* Cruzado-Caballero, Pereda-Suberbiola and Ruiz-Omeñaca, 2010 from Blasi 1 site (MPZ99/664, Figure 4(G); Arén municipality) (see Pereda-Suberbiola,

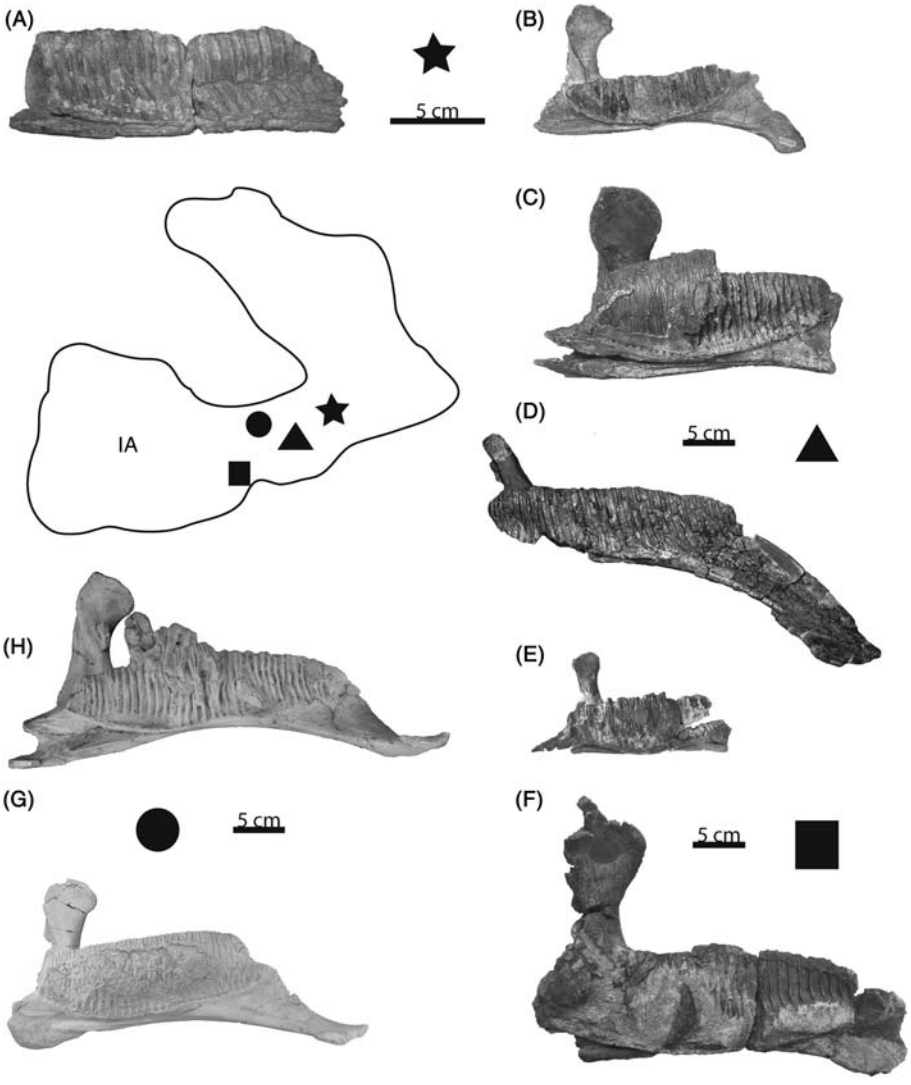


Figure 4. Silhouette of the Late Cretaceous Ibero-Armorican island (see Figure 1) with the location of the best-preserved hadrosauroid dentaries; star: Le Bexen (Aude department) and Cassagnau 2 (Haute-Garonne department); circle: Blasi sites (Huesca province); triangle: Fontllonga and Les Llaus (Lleida province); square: La Solana (Valencia province). A–H: dentaries in medial view; all are left dentaries except A, D and F, which are right dentaries that have been turned around for better comparison. A: MDE-Fo1-10, Hadrosauridae indet. from Le Bexen; B: MDE-Cas2-248, Euhadrosauria indet. from Cassagnau 2; C: IPS-36338, Hadrosauroidea indet. from Fontllonga; D: IPS-SRA-27, *Pararhabdodon isonensis* from Les Llaus; E: MGUV-2200, Hadrosauridae indet. from La Solana; F: MPV-181, Hadrosauridae indet. from La Solana; G: MPZ99/664 *Blasisaurus canudoi* from Blasi 1; H: MPZ2008/258, *Arenysaurus ardevoli* from Blasi 3. C, E, F taken from Pereda-Suberbiola, Canudo, Company et al. (2009, fig. 1(E)–(G)); D taken from Prieto-Márquez et al. (2006, fig. 7(A)); G taken from Cruzado-Caballero, Pereda-Suberbiola and Ruiz-Omeñaca (2010, fig. 3.1); H taken from Pereda-Suberbiola, Canudo, Cruzado-Caballero et al. (2009, fig. 4(A)). Scale bar: 5 cm.

Canudo, Company, et al. 2009; Pereda-Suberbiola, Canudo, Cruzado-Caballero, et al. 2009; Prieto-Márquez and Wagner 2009; Cruzado-Caballero, Pereda-Suberbiola et al. 2010 and references therein).

Several additional dentaries have been discovered, all of them currently indeterminate hadrosaurids. These are from the sites of Basturs Poble (Isona i Conca Dellà municipality, Lleida province; Prieto-Márquez et al. 2007), Amor-2 (Beranuy municipality, Huesca province; Cruzado-Caballero et al. 2012) and Barranco Serraduy-1 (Isábena municipality, Huesca province; Puértolas-Pascual et al. 2012).

IPS 36338 (Figure 4(C)) is a fragmentary left dentary from Fontllonga site (upper Maastrichtian; Conques Formation, Tremp Group). It is robust, with a very strong sub-vertical coronoid process, whose posterodorsal side is large and protruding. In posterior view, the suprameckelian foramen is oblique. The dental battery does not extend posteriorly to the coronoid process. In medial view, it is possible to make out 30–31 tooth positions, and each

position has two functional teeth and two replacement teeth. The ventral deflection of the dentary (*sensu* Horner et al. 2004) is located at about the 12th most anterior tooth position. The teeth present a faint secondary ridge that, according to Casanovas-Cladellas et al. (1999b), could be bifid in the basal part of the crown. Also, these teeth have neither papillae nor denticles.

MGUV 2200 and MPV 181 (Figure 4(E),(F)) are two fragmentary dentaries from juvenile and adult individuals, respectively. These dentaries were found in the site of La Solana (upper Maastrichtian; Villalba de la Sierra Formation). In both dentaries the dental battery terminates posterior to the apex of the coronoid process. Also in both dentaries the deflection is located at about the 11–12th most anterior tooth position. The coronoid process is slender, sub-vertical, and in posterior view an oval and oblique suprameckelian foramen can be seen.

MGUV 2200 has 29 tooth positions with some teeth preserved. The teeth have a faint secondary ridge and bear small marginal denticles not supported by ridges. MPV 181 has 36–37 tooth positions and preserves some shifted teeth.

IPS SRA 27 is the only known dentary currently assigned to *Pararhabdodon.* It comes from the site of Les Llaus (upper Maastrichtian; Conques Formation, Tremp Group), 750 m west of the site of Sant Roma d'Abella (Isona and Conca Dellà municipality), the type locality of *Pararhabdodon* (Prieto-Márquez et al. 2006). It is a complete right dentary with a contact surface for the predentary that is extremely long and strongly deflected (Figure 4(D)). The coronoid process is broken, so it does not fit with the mandibular ramus and its current backward inclination is an artefact; nevertheless it is complete and has a height of 104 mm from its base to its apex. The dental battery has a length of 243 mm and shows 35 tooth positions but does not preserve any teeth (Casanovas-Cladellas et al. 1999a; Prieto-Márquez et al. 2006; Prieto-Márquez and Wagner 2009). In occlusal view, the dental battery is straight but it turns slightly inwards in the last positions, i.e. those adjacent to the coronoid process. The deflection point of the dentary is located between the 10–11th tooth positions.

Two lambeosaurines have been described from the upper Maastrichtian Blasi sites in Arén: *Blasisaurus* from the Blasi 1 site (Arén Formation) and *Arenysaurus* from the Blasi 3 site (La Posa Formation, Tremp Group). Both specimens preserve the left dentary. The dentary of *Blasisaurus* (MPZ99/664, Figure 4(G)) is slightly less robust than that of *Arenysaurus* (MPZ2008/258, Figure 4(H)). In both dentaries the coronoid process is anteriorly projecting. In *Blasisaurus* the dorsal side of the coronoid process is convex, and in *Arenysaurus* it is tip-like with the posterodorsal border higher than the anterodorsal border. Also, in these dentaries the anteriormost portion is modestly deflected ventrally. The dental battery of *Blasisaurus* has a length of 170 mm and 35 tooth positions, and that of *Arenysaurus* has a length of 275 mm and 37 tooth positions. In the *Arenysaurus* dentary the starting point of the deflection is located at the 9–10th tooth position, whereas in the *Blasisaurus* dentary it starts at the 10–11th tooth position. The teeth of both taxa have a slightly sinuous primary ridge and do not have papillae. The *Arenysaurus* teeth have a posterior secondary ridge that is absent in *Blasisarus*.

In the bonebed of Basturs Poble (upper Maastrichtian, Conques Formation, Tremp Group), there are disarticulated cranial and postcranial remains of at least five hadrosaurid individuals. These have been cited in an abstract but have not been described in detail or figured (Prieto-Márquez et al. 2007). The dentaries have a rostral end that is elongated medially and nearly as long as that of *Pararhabdodon*. Some teeth have secondary ridges. There are at least three dentaries (unpublished data) but unfortunately there are no adult dentaries in the sample; Prieto-Márquez et al. (2007) say that 'these specimens may represent *Pararhabdodon*; however, the discovery of an adult dentary is required to test the hypothesis'.

MPZ2013/72 is a fragmentary right dentary probably from a juvenile individual from the site of Amor-2 (upper Maastrichtian, Conques Formation, Tremp Group) near the village of Beranuy (figured erroneously as AM3-15 (from the Amor-3 site) by Cruzado-Caballero et al. (2012, fig. 2(A)). This dentary only preserves eight tooth positions without teeth and the base of the coronoid process. The Meckelian canal has an ellipsoidal form and is oblique to the alveolar medial surface.

Another dentary from the Beranuy area (Barranco Serraduy-1 site, upper Maastrichtian, La Posa Formation, Tremp Group) has been cited in a faunal list for the Beranuy/Serraduy sites (Puértolas-Pascual et al. 2012, table 1). BS1-13 is a left dentary, but it remains unprepared so it is not possible to ascertain its characteristics at present.

Recently, a new site has been found in the Blasi area (Arén; Blasi 3.4), and from its surface a new hadrosaurid dentary has been collected (MPZ2010/952; Cruzado-Caballero, Ruiz-Omeñaca, Gaete et al. 2010, fig. 3). This is described in this paper.

## Systematic paleontology

Superorder **Dinosauria** Owen, 1842

Order **Ornithischia** Seeley, 1887

Infraorder **Ornithopoda** Marsh, 1881

Family **Hadrosauridae** Cope, 1870

**Euhadrosauria** Weishampel et al., 1993

**Euhadrosauria indet**

(Figure 5)

*Material.* A left dentary (MPZ2010/952) from the Blasi 3.4 site (Arén, Huesca province), upper Maastrichtian, La Posa Formation (Tremp Group).

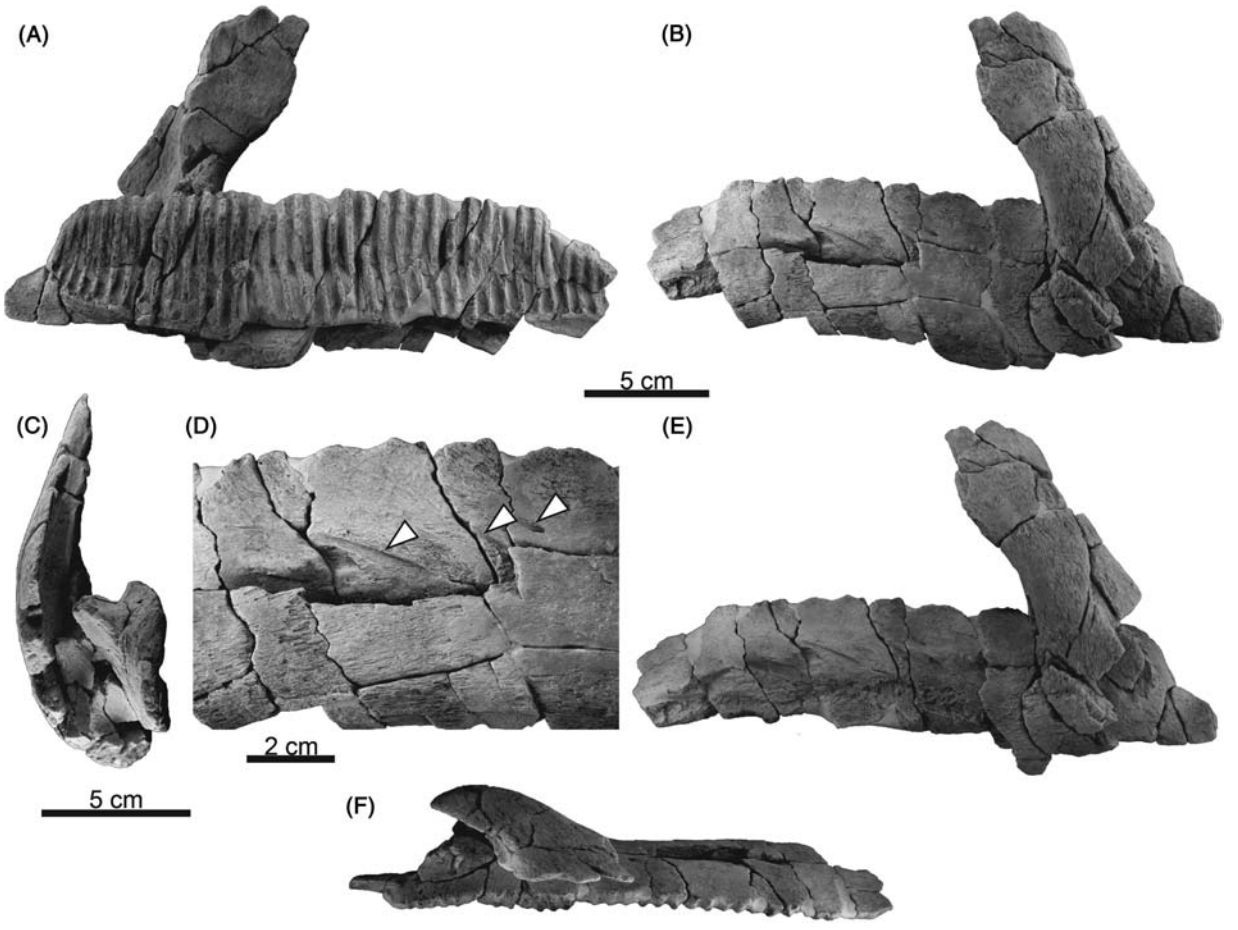


Figure 5. Euhadrosauria indet. from Blasi 3.4. MPZ2010/952 left dentary in medial (A), lateral (B, D, E), posterior (C) and dorsal (F) views. B, D and E show different details of the nutritional foramina, with the external mandibular artery covered (B, D) and exposed (E). White arrows in D indicate the blood vessels that end in the nutritional foramina.

*Description*

MPZ2010/952 is an incomplete left dentary (Figure 5(A)–(F)) that does not preserve the symphyseal zone. It has several diagnostic characters of Hadrosauridae *sensu* Horner et al. (2004), such as a distal extension of the dentary tooth row caudal to the apex of the coronoid process, the dental battery inclined downwards in its anterior part and the caudalmost end of the dentary well behind the coronoid process, which is inclined slightly forwards (Figure 5(A)).

MPZ2010/952 has parallel dorsal and ventral borders. In medial view the angular facet is broken, and the suprameckelian foramen forms an angle of about 30° with the alveolar medial surface, similar to IPS 36338 and MGUV 2200, and unlike MDE-Fo1-10 and *Telmatosaurus* with 90° (Figure 5(C), Casanovas-Cladellas et al. 1999b; Laurent et al. 2002). Through this foramen passes the external mandibular artery that covers the whole lateral side of the dentary and ends in the large foramen of the symphyseal zone. From this artery at least five small blood vessels issue that end in the nutritional foramina that perforate the lateral side (Figure 5(B),(D),(E)). The external mandibular artery runs parallel to the internal mandibular artery, which covers the Meckelian canal. In dorsal view, the longitudinal axis of the dentary is parallel to the lateral side and is slightly arched lingually (Figure 5(F)).

The dental battery does not have any teeth; it is complete, with an anteroposterior length of 225 mm and 36 dental positions (Figure 5(A)). The dental battery is shorter than that of *Arenysaurus* (275 mm) and longer than that of *Blasisaurus* (170 mm). The number of tooth positions is similar to MPV 181 with 36–37 positions, less than *Arenysaurus* with 37, and greater than *Blasisaurus* and *Pararhabdodon* with 35, IPS 36338 with less than 34 and MGUV 2200 with 29 (Company Rodríguez 2004; Pereda-Suberbiola, Canudo, Company, et al. 2009; Pereda-Suberbiola, Canudo, Cruzado-Caballero, et al. 2009; Cruzado-Caballero, Pereda-Suberbiola and Ruiz-Omeñaca 2010). In dorsal view, the dental battery is straight with its posteriormost part deflected medially, similar to *Pararhabdodon*. The tooth positions have a width of 6 mm, and are straight except in the proximal half, where they incline anteriorly. These positions end posterior to the apex

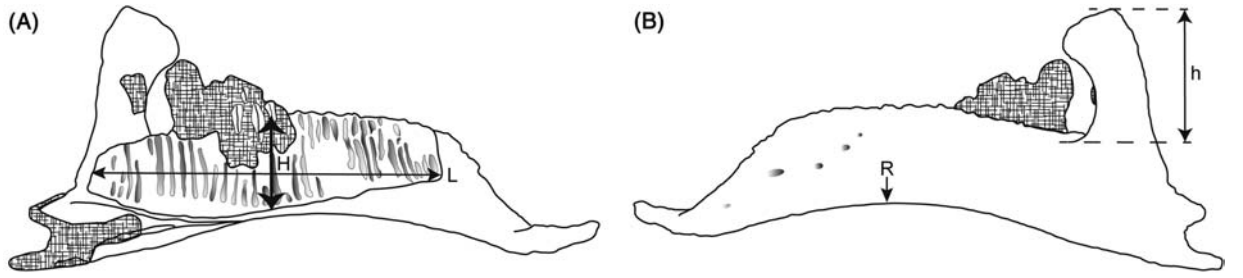


Figure 6. Schematic drawings of left dentary in medial (A) and lateral (B) views, showing the measurements taken for Table 2. *H*, height of the dental battery at its midpoint, taken from the base of the dental battery to the uppermost dorsal border of the dentary, without measuring the functional crowns; *L*, length of the dental battery; *h*, height of coronoid process, measured in lateral view from its base to its dorsalmost expansion. The arrow marks the relative position of the inflexion point where the ventral margin of the dentary originates (*R*). The dentary represented, as a model, in this figure is that of *A. ardevoli*, drawn by the authors (see Figure 4(H) for a picture). Scratched areas represent matrix.



of the coronoid process as in *Pararhabdodon*. Although the ventral border is broken, it has been possible to estimate a midpoint depth of 65.36 mm in medial view (Figure 6). Due to the breakage of the ventral border, moreover, it is possible to see the internal tissue fibres, which are deflected ventrally in the 13–14th tooth positions of the dental battery. This arrangement of fibres marks the start of the anterior ventral deflection of the dentary.

The coronoid process is high (112 mm in length), slender, with a flat inner side as is usual in hadrosaurids; it is more anteriorly inclined than *Arenysaurus* and *Blasisaurus* (but not as strongly projected as shown in Figure 5(A) due to preservation problems) and slightly curved inwards (Figure 5(C)). Anterodorsally the coronoid process is broken and it is not possible to know whether it is expanded anteriorly. Like *Telmatosaurus*, the anterodorsal border seems to be higher than the posterodorsal border, unlike *Arenysaurus, Charonosaurus jiayinensis* Godefroit, Zan and Jin, 2000, *Amurosaurus riabinini* Bolotsky and Kurzanov, 1991 and MGUV 2200, where the posterodorsal side is higher than the anterodorsal side, and unlike *Blasisaurus* and *Sahaliyania elunchunorum* Godefroit, Hai, Yu and Lauters, 2008, where both borders are equal in height (Weishampel et al. 1993; Godefroit et al. 2001, 2004, 2008; Company Rodríguez 2004). The adductor fossa is narrow.

## Discussion

As we consider MPZ2010/952 to be the dentary of an adult individual, here it will only be compared with other adult dentaries from the Ibero-Armorican record (i.e. Spanish record, as all the well-preserved French dentaries are from juvenile individuals; see Laurent et al. 2002).

MPZ2010/952 has a relatively high number of dental positions in the dental battery (36 in 225 mm). In this respect it falls between *Blasisaurus* (35 in 170 mm) and *Pararhabdodon* (35 in 263 mm) and *Arenysaurus* (37 in 275 mm). All these three dentaries are considered to be non-juvenile lambeosaurine individuals. Although MPZ2010/952 has no diagnostic character that identifies it as a basal hadrosaurid, a lambeosaurine or a hadrosaurine, it has a greater number of dental positions than basal hadrosaurids [30 or less according to Godefroit et al. (2008, char. 41) and Prieto-Márquez (2010, char. 1); 32 or less according to Horner et al. (2004, char. 1), Suzuki et al. (2004, char. 46), Evans and Reisz (2007, char. 60) and Sues and Averianov (2009, char. 92)]. Moreover, its 36 dental positions are within the range of the adult individuals of hadrosaurines and lambeosaurines ((more than 32 according to Horner et al. (2004, char. 1), Suzuki et al. (2004, char. 46), Evans and Reisz (2007, char. 60) and Sues and Averianov (2009, char. 92)). On the other hand, the dentary tooth density (number of tooth positions per cm; Prieto-Márquez 2008, char. 2) of MPZ2010/952 is 1.68, which according to this author lies within the range of nearly all hadrosaurine and all lambeosaurine hadrosaurids (except *Charonosaurus*), which have a value $>1.1$ for this index. Moreover, it falls within the range of Iberian lambeosaurines, which extends from 1.34 in *Arenysaurus* to 2.06 in *Blasisaurus* (Table 2). In summary, the number of dental positions and their density indicate that MPZ2010/952 is the dentary of an adult hadrosaurid and probably a derived one.

According to Godefroit et al. (2008), although it is variable, a ventral deflection of the rostral part of the dentary is a usual character in lambeosaurines. The position of the internal tissue fibres in the first third of the dental battery of MPZ2010/952, together with the number and the density of dentary teeth, indicates that the dentary belongs to the lambeosaurine clade or at least affirms that this dentary is euhadrosaurian (*sensu* Weishampel et al. 1993).

In order to ascertain whether or not the new dentary from Blasi 3.4 belongs to one of the euhadrosaurian species already known from the Ibero-Armorican Realm,

Table 2. Measurements and indexes in selected dentaries of Late Cretaceous Ibero-Armorican euhadrosaurians, ordered by the length of the dental battery.

| Material | Taxon | *L* | *H* | *h* | *n* | Td (n/L) | *H*/*L* | *h*/*H* | *h*/*L* | *R* |
|---|---|---|---|---|---|---|---|---|---|---|
| MPZ99/664 | *Blasisaurus canudoi* | 170 | 57.17 | 151 | 35 | 2.06 | 0.34 | 2.64 | 0.89 | 0.66 |
| MPZ2010/952 | Euhadrosauria indet. | 225 | 65.36 e | 112 | 36 | 1.68 | 0.29 | 1.71 | 0.50 | 0.58 |
| IPS SRA 27 | *Pararhabdodon isonensis* | 243 | 74.57 | 104 | 35 | 1.44 | 0.31 | 1.39 | 0.43 | 0.54 |
| MPZ2008/258 | *Arenysaurus ardevoli* | 275 | 70.77 | 95.65 | 37 | 1.34 | 0.26 | 1.35 | 0.35 | 0.65 |

Notes: French dentaries have not been taken into account, being fragmentary (preserving incomplete dental batteries) or juvenile (with only a small number of tooth positions). Abbreviations: e, estimated measure; *H*, height of the dental battery at its midpoint; *h*, height of coronoid process; *L*, length of the dental battery; *n*, number of tooth positions; *R*, relative position of the inflexion point where the ventral margin of the dentary originates (Prieto-Márquez 2010, char. 37); Td, tooth density. Every measurement is given in mm, except for tooth density, which is tooth positions per cm.



several measurements have been taken in the dentaries of these species (Table 2, see methods in Figure 6).

It is observed that the tooth density decreases when the length of the dental battery increases, so this is not discriminant as a specific character. Several features and ratios distinguish MPZ2010/952 from the morphology of both *Arenysaurus* and *Blasisaurus* dentaries, making it more similar to the dentary of *Pararhabdodon*: (1) the dental battery exceeds the posterior edge of the coronoid process (in *Arenysaurus* it does not reach the posterior edge, and in *Blasisaurus* it finishes just at the posterior edge of the coronoid process), (2) in dorsal view the dental battery is straight, with a small posterior zone that is inclined medially (in *Arenysaurus* it is laterally concave and in *Blasisaurus* it is straight but with a small anterior zone laterally inclined), (3) the ratio of the location of the origin of the ventral deflection of the dentary (Prieto-Márquez 2010, char. 37) is 0.58 (*Pararhabdodon* 0.54, *Arenysaurus* 0.65 and *Blasisaurus* 0.66), (4) the midpoint height/total length ratio of the dental battery is estimated at 0.29 (*Arenysaurus* 0.26, *Pararhabdodon* 0.31 and *Blasisaurus* 0.34).

MPZ2010/952 also differs from *Arenysaurus* and *Blasisaurus* in having a coronoid process that is more anteriorly sloping (in *Pararhabdodon* the orientation of the coronoid process is an artefact due to breakage and plaster reconstruction).

One of the ratios that best distinguishes MPZ2010/952 from *Pararhabdodon* is that between the height of the coronoid process and the height of the dental battery at its midpoint; in *Pararhabdodon* and *Arenysaurus* this ratio is $<1.4$, and in *Blasisaurus* it is $>2$, whereas in MPZ2010/952 its value is intermediate (1.71) (Table 2). To a lesser extent, the ratio between the height of the coronoid process and the length of the dental battery also distinguishes the taxa; in *Arenysaurus* and *Pararhabdodon* this ratio is $<0.43$; and in *Blasisaurus* it is $>0.85$, while in MPZ2010/952 it is 0.50 (Table 2). In the light of these ratios, together with the features and measures already discussed, it seems most plausible that MPZ2010/952 represents a fourth euhadrosaurian taxon in the Ibero-Armorican Realm, in addition to *Pararhabdodon*, *Arenysaurus* and *Blasisaurus*.

According to Prieto-Márquez (2010, char. 36), on the other hand, the ventral deflection of MPZ2010/952 lies within the range of lambeosaurine values (0.65 or less), with the exception of the hadrosaurines *Brachylophosaurus canadensis* Sternberg, 1953 and *Gryposaurus latidens* Horner, 1992. This being so, it is more probable that MPZ2010/952 belongs to a lambeosaurine than to a hadrosaurine. It should be noted, however, that an indeterminate hadrosaurine cranial bone has been described in the nearby Blasi 5 site [Conques Formation; a fragmentary right jugal (MPZ2007/1885) described by Cruzado-Caballero, Ruiz-Omeñaca and Canudo 2010], so a hadrosaurinae origin cannot be ruled out.

Given the fragmentary character of MPZ2010/952, it is not possible to assign it either to Lambeosaurinae or Hadrosaurinae, but it can be recognised as an indeterminate euhadrosaurian. It represents the fifth euhadrosaurian taxon in the South Central Pyrenees and in the Ibero-Armorican Realm.

## Conclusions

The Ibero-Armorican record of hadrosauroid dentaries from the Maastrichtian is the most complete and most diverse in Europe, with at least five different taxa, all from the Iberian Peninsula. This record presents dentaries of both basal and derived taxa, and different ontogenetic states. The high heterogeneity of the taxa recorded in the Latest Cretaceous of Europe is thus the most complex in Laurasia.

A new locality in the Tremp Basin of the South Central Pyrenees (Blasi 3.4; Arén municipality, Huesca province, Spain) has provided a new dentary that presents a mosaic of characters that allow it to be assigned to indeterminate euhadrosaurians. This dentary represents a different taxon from *Arenysaurus, Blasisaurus* and *Pararhabdodon*, the three euhadrosaurians already known in this basin.

This new dentary adds to the dentary record from Europe and increases the great diversity of hadrosauroids,

already seen in cranial and postcranial remains, in the Maastrichtian of the Ibero-Armorican Realm.

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