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## NEW MATERIAL AND PHYLOGENETIC POSITION OF *ARENYSOSAURUS ARDEVOLI*, A LAMBEOSAURINE DINOSAUR FROM THE LATE MAASTRICHTIAN OF ARÉN (NORTHERN SPAIN)

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**ABSTRACT**—*Arenysaurus ardevoli* is a lambeosaurine hadrosaurid from the late Maastrichtian of Arén (Huesca, northern Spain) that has recently been described. The holotype is the first and the most complete lambeosaurine with a braincase from Europe. In this paper, we present a complete description of the postcranial skeleton, which was poorly described when the taxon was named because it was partially unprepared, and new information on several cranial bones (jugal, maxilla, and dentition). A new phylogenetic analysis of *Arenysaurus* and the closely related *Blasisaurus canudo*, also from the late Maastrichtian of Arén, places them inside the Parasaurolophini in a dichotomy with *Parasaurolophus* spp. Paleobiogeographically, the presence of *Arenysaurus* and its relationships with other lambeosaurines suggest at least one geodispersal event from Asia to Europe no later than the middle–late Campanian.

**SUPPLEMENTAL DATA**—Supplemental materials are available for this article for free at [www.tandfonline.com/UJVP](http://www.tandfonline.com/UJVP)

### INTRODUCTION

Hadrosaurids were common herbivorous dinosaurs during the Late Cretaceous in Laurasia (Horner et al., 2004). Their distribution was nearly worldwide, but the best-known fossil record comes from North America and Asia (Lund and Gates, 2006). In the last 15 years, numerous new remains have been discovered in Europe, which, together with the basal hadrosaurid *Telmatosaurus* Nopcsa, 1903, show the rich paleobiodiversity of the Campanian–Maastrichtian interval (Dalla Vecchia, 2009a, 2009b; Pereda-Suberbiola et al., 2009; Prieto-Márquez and Wagner, 2009; Cruzado-Caballero et al., 2010a, 2010b).

In Europe, the most abundant fossil record of hadrosaurids is from the Maastrichtian of Spain. Remains from the Tremp Basin (south-central Pyrenees) have made possible the description of three lambeosaurine taxa (*Pararhabdodon isonensis* Casanovas-Cladellas, Santafé-Llopis, and Isidro-Llorens, 1993 [including *Koutalisaurus kohlerorum* Prieto-Márquez, Gaete, Rivas, Galobart, and Boada, 2006]; *Arenysaurus ardevoli* Pereda-Suberbiola, Canudo, Cruzado-Caballero, Barco, López-Martínez, Oms, and Ruiz-Omeñaca, 2009; and *Blasisaurus canudo* Cruzado-Caballero, Pereda-Suberbiola, and Ruiz-Omeñaca, 2010a) and an indeterminate hadrosaurine (Pereda-Suberbiola et al., 2009; Prieto-Márquez and Wagner, 2009; Cruzado-Caballero et al., 2010a, 2010b). The European hadrosaurid record thus provides proof of high and previously unknown vertebrate paleodiversity in this continent during the latest Cretaceous. This fauna has affinities with North American and Asian taxa (Pereda-Suberbiola, 2009) as a result of several geodispersal events that occurred in the course of the latest Cretaceous. Here we present a complete

description of several new cranial remains and the postcranial skeleton of *Arenysaurus ardevoli* from the late Maastrichtian site of Blasi 3. In a previous paper, Pereda-Suberbiola et al. (2009) erected the taxon, described part of the cranial material, and reported briefly on the postcranial remains. New remains, which were unprepared in 2009, are here described for the first time (i.e., jugal, caudal vertebrae, ribs, hemal arches, and pubis). Thus, *Arenysaurus* (Fig. 1) is the best-represented and most complete lambeosaurine from the Ibero-Armorican Island. This taxon fills a gap in our understanding of the phylogeny of European lambeosaurines and has provided new data about geodispersal events with the rest of Laurasia.

**Institutional Abbreviations**—**MDE**, Musée des Dinosaures, Esperanza, France; **MPZ**, Museo Paleontológico de la Universidad de Zaragoza, Zaragoza, Spain.

### GEOLOGIC AND CHRONOLOGIC FRAMEWORK

The Late Cretaceous vertebrate-bearing localities of Blasi are located 2 km to the west of the town of Arén (or Areny de Noguera, Huesca Province) in northeastern Spain. Several publications have given an account of the vertebrate assemblages at these localities (López-Martínez et al., 2001; Pereda-Suberbiola et al., 2009; Blain et al., 2010; Cruzado-Caballero et al., 2010a, 2010b).

Seven of the localities have produced hadrosaurid remains (Blasi 1, Blasi 2a, Blasi 2b, Blasi 3, Blasi 3.4, Blasi 4, and Blasi 5). These are located stratigraphically in the Arén Formation (Blasi 1), the La Posa Formation (Blasi 2a, Blasi 2b, Blasi 3, and Blasi 3.4), and the Conques Formation (Blasi 4 and Blasi 5). In terms of the regional geology, they are located in the Tremp Basin of the south-central Pyrenees (Riera et al., 2009), or the Tremp-Graus Basin (Pujalte and Schmidt, 2005). It should be

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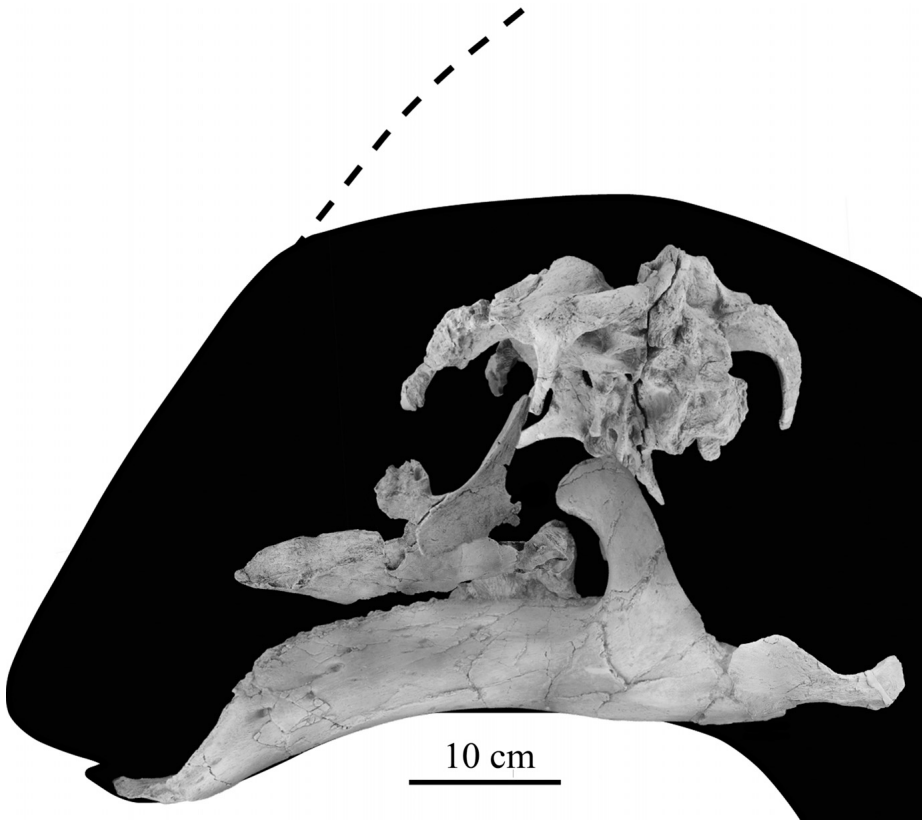


FIGURE 1. *Arenysaurus ardevoli*. Composite cranial reconstruction in left lateral view, with the following elements: MPZ2008/1, skull; MPZ2008/256, left maxilla; MPZ2011/01, left jugal; MPZ2008/258, left dentary; MPZ2008/259, right surangular (reversed).

noted that in previous papers the sites Blasi 2a to Blasi 5 were placed in the Tremp Formation following López-Martínez et al. (2001). Nevertheless, according to Pujalte and Schmidt (2005:79), “the term Tremp Group reflects more appropriately than the former Tremp Formation the stratigraphic complexity of the so-called <Garumnian> of the south Pyrenean Tremp-Graus basin.” The age of the ‘Garumnian’ in the south-central Pyrenees ranges from Maastrichtian (and probably latest Campanian; see Lopez-Martínez et al., 2001:55) to lower Eocene (Claret Formation in Pujalte and Schmidt [2005]; ‘fluvial upper red unit’ of the Tremp Formation in Riera et al. [2009]).

In accordance with the lithostratigraphic diagram of the Tremp Group including the Arén/Areny section (Pujalte and Schmidt, 2005:fig. 1B; see also Riera et al., 2009:fig. 3), in this paper we place Blasi 2a, Blasi 2b, Blasi 3, and Blasi 3.4 in the lower gray part of the Tremp Group, in the La Posa Formation (‘marine-to-continental transitional gray unit’ of the Tremp Formation, sensu Riera et al., 2009), and Blasi 4 and Blasi 5 in the lower red part of the Tremp Group, in the Conques Formation (‘fluvial lower red unit’ of the Tremp Formation, sensu Riera et al., 2009).

Using magnetostratigraphy, the Blasi sites have been placed in the upper part of a normal polarity chron correlated with chron C30n (Oms and Canudo, 2004; Pereda-Suberbiola et al., 2009:fig. 2), i.e., they are younger than 67.7 Ma and slightly older than 65.8 Ma (Ogg et al., 2008).

Besides hadrosaurids, remains of other vertebrates have been found at these sites: fishes, amphibians, lizards, turtles, crocodylians, and theropod and sauropod dinosaurs (Table 1). Recently, Puértolas et al. (2011) described a new crocodylian named *Arenysuchus gascabadiolorum*. This crocodylian comes from a

new site (the Elías site in the Conques Formation) discovered in 2008, very close to the sites of Blasi 1–3.

The Blasi 3 site, from which the *Arenysaurus* material was recovered, has provided remains of at least two other hadrosaurid individuals, an indeterminate juvenile lambeosaurine and a small adult hadrosaurid (Cruzado-Caballero and Canudo, 2005; Cruzado-Caballero et al., 2005; Cruzado-Caballero, 2012).

#### SYSTEMATIC PALEONTOLOGY

- DINOSAURIA Owen, 1842  
 ORNITHISCHIA Seeley, 1887  
 ORNITHOPODA Marsh, 1881  
 HADROSAURIDAE Cope, 1870  
 LAMBEOSAURINAE Parks, 1923  
*ARENYSAURUS* Pereda-Suberbiola, Canudo,  
 Cruzado-Caballero, Barco, López-Martínez, Oms, and  
 Ruiz-Omeñaca, 2009  
*ARENYSAURUS ARDEVOLI* Pereda-Suberbiola, Canudo,  
 Cruzado-Caballero, Barco, López-Martínez, Oms, and  
 Ruiz-Omeñaca, 2009  
 (Figs. 1–11)

**Original Diagnosis**—Lambeosaurine hadrosaurid characterized by a very prominent frontal dome, more developed than in other adult specimens; nearly vertical prequadrate process of the squamosal and jugal process of the postorbital; deltopectoral crest of the humerus oriented anteriorly. It differs from other lambeosaurines in having a unique combination of characters: short frontal, with a posterior length/maximal width ratio estimated at 0.5; midline ridge of parietal approximately at the level of the

TABLE 1. Faunal list from the Blasi sites.

Fauna	Blasi site					
	1	2 (2a and 2b)	3	3.4	4	5
Actinopterygii						
Lepisosteidae indet.		X				
Pycnodontiformes indet.		X				
Teleostei indet.		X				
Amphibia						
Albanerpetontidae						
<i>Albanerpeton</i> aff. <i>nexuosum</i>		X				
Anura						
Discoglossidae aff. <i>Paradiscoglossus</i> sp.		X				
Palaeobatrachidae indet.		X				
Squamata						
Indeterminate lizard 1 (Iguania or Scleroglossa)		X				
Indeterminate lizard 2 (Scleroglossa, Scincomorpha)		X				
Anguidae indet.		X				
Alethinophidia indet.		X				
Chelonii						
<i>Solemydidae</i> sp.		X				
Bothremydidae indet.		X	X		X	X
Crocodyliformes						
Crocodyliformes indet.		X			X	X
‘Trematochampsidae’ indet.		X	X			
Eusuchia indet.			X			
cf. <i>Arenysuchus gascabadiolorum</i>		X				
Alligatoroidea indet.	X		X			
<i>Acynodon</i> sp.		X				
Dinosauria						
Theropoda						
Theropoda indet.	X	X	X			
Coelurosauria indet.		X				
cf. <i>Euronychodon</i> sp.		X				
cf. Dromaeosauridae indet.		X	X			
Maniraptora indet.		X				
Ornithopoda						
Hadrosauridae indet.	X	X	X		X	X
Euhadrosauria indet.	X	X		X		
Hadrosaurinae indet.						
Lambeosaurinae indet.			X		X	
Lambeosaurinae						
<i>Arenysaurus ardevoli</i>			X			
<i>Blasisaurus canudo</i>	X					

Modified from López-Martínez et al. (2001), with data from Torices et al. (2004), Murelaga and Canudo (2005), Pereda-Suberbiola et al. (2009), Blain et al. (2010), Cruzado-Caballero et al. (2010a, 2010b, 2013), and Puértolas et al. (2011).

postorbital-squamosal bar; parietal not interposed between the squamosals in the occipital surface of the skull; lateral side of squamosal relatively low above the cotyloid cavity.

**Holotype**—MPZ2008/1, a partial, articulated skull comprising the skull roof and braincase.

**Paratypes**—Cranial material: MPZ2008/256, fragmentary left maxilla; MPZ2008/257, fragmentary right maxilla; MPZ2008/258, left dentary with 12 teeth; MPZ2008/259, right surangular; MPZ2008/260–263, four isolated teeth. Postcranial skeleton: MPZ2007/706, MPZ2007/954–955, MPZ2008/264–267, seven cervical vertebrae; MPZ2008/268, a dorsal vertebra; MPZ2008/269–270, two dorsal ribs; MPZ2008/271, partial sacrum with ossified tendons; MPZ2004/480, pathological caudal vertebra; MPZ2006/20, 14 articulated caudal vertebrae and hemal arches; MPZ2008/272, MPZ2008/313, two caudal vertebrae; MPZ2008/314, MPZ2008/330, two hemal arches; MPZ2008/331–332, two ossified tendons; MPZ2008/333a–333b, right scapula (two fragments); MPZ2008/334, right coracoid; MPZ2008/336, right humerus; MPZ2008/335, fragmentary right

ilium; MPZ2007/707, right pubis; MPZ2007/711, right femur; MPZ2008/337, left femur.

**Referred Specimens**—MPZ2011/1, left jugal; MPZ2012/767, cervical vertebrae; MPZ2012/746–747, MPZ2012/767, three cervical ribs; MPZ2012/748–753, six dorsal ribs; MPZ2008/275–276, MPZ2008/281, MPZ2008/286, MPZ2008/288, MPZ2008/290–292, MPZ2008/296, MPZ2008/298–300, MPZ2008/302, MPZ2008/304, MPZ2008/306, MPZ2008/309–312, MPZ2012/754–758, 24 caudal vertebra; MPZ2008/315–317, MPZ2008/319, MPZ2008/321–323, MPZ2008/325–326, MPZ2008/328–329, 11 hemal arches.

**Comment**—Given their association and size, it is assumed that all the paratypes from the original publication (Pereda-Suberbiola et al., 2009) and the newly referred specimens (topotypes) come from a single hadrosaurid skeleton, from which the holotype derives. However, because all the material is partially disarticulated and comes from a locality that preserves two other small hadrosaurid individuals (i.e., an indeterminate juvenile lambeosaurine and a small adult hadrosaurid; Cruzado-Caballero and Canudo, 2005; Cruzado-Caballero et al., 2005, Cruzado-Caballero,

2012), it is preferable to designate a holotype and not convert all the material (paratypes and topotypes) assigned to *Arenysaurus* into a single holotype.

#### DESCRIPTION

For the skull and dentary descriptions, see Pereda-Suberbiola et al. (2009:546–567, figs. 2–3). Other cranial remains are described and figured below for the first time.

#### New Cranial Material

**Jugal**—MPZ2011/1 is a fragmentary left jugal (Fig. 2A, B). Its morphology is similar to those of *Blasisaurus* and an indeterminate lambeosaurine from Blasi 4 (MPZ2008/1884; Cruzado-Caballero et al., 2010b). The jugal includes the preserved dorsal half of the anterior process, which is expanded dorsally, unlike the elongated and slender anterior processes of *Telmatosaurus* and *Tethyshadros* Dalla Vecchia, 2009b (Weishampel et al., 1993; Dalla Vecchia, 2009b). The posterodorsal side of the anterior process is less inclined anteriorly than that in *Blasisaurus*, MPZ2008/1884, and MPZ2008/1885 (Hadrosaurine indet. from the Blasi 5 site; Cruzado-Caballero et al., 2010b). This form of the anterior process is similar to *Velafrons* Gates, Sampson, Delgado de Jesús, Zanno, Eberth, Hernandez-Rivera, Aguillón Martínez, and Kirkland, 2007, and *Lambeosaurus* Parks, 1923 (Evans and Reisz, 2007; Gates et al., 2007). A medially and slightly anteriorly projecting maxillary process is present on the anterior process of the jugal, unlike *Blasisaurus*. The postorbital process is triangular in cross-section, robust, and oriented posterodorsally, forming an angle of 58° with the long axis of the jugal, similar to those in *Blasisaurus*, *Parasaurolophus* sp., and *Velafrons*, with an angle of 60°; and unlike *Amurosaurus* Godefroit, Bolotsky, and Van Itterbeeck, 2004, with an angle of 45°; *Corythosaurus* Brown, 1914, with an angle of 75°; and *Lambeosaurus* and MPZ2008/1885, with an angle of 80° (Ostrom, 1961; Godefroit et al., 2004; Evans

and Reisz, 2007; Evans et al., 2007; Gates et al., 2007; Cruzado-Caballero et al., 2010a, 2010b). The orbital fenestra is 'V'-shaped, unlike *Blasisaurus* and MPZ2008/1884 (Cruzado-Caballero et al., 2010a, 2010b).

**Maxilla**—Two maxillary fragments (MPZ2008/256–257, left and right respectively; Fig. 3A–D) have been found in close association with the skull and are here referred to *Arenysaurus*. MPZ2008/256 is a left maxillary fragment. It is very long anteroposteriorly (227 mm) and narrow lateromedially. The premaxillary shelf is wide, concave, and rough. Posterior to this shelf, on the dorsal surface, there is a maxillary foramen. In medial view, there are almost 15 special foramina interconnected by a gently curving horizontal groove, along the entire length of the bone as preserved.

MPZ2008/257 is a right maxillary fragment with an anteroposterior length of 176 mm. The maxilla is broken medially, and the tooth positions can be observed. There are 14 tooth positions preserved, and these are slightly concave anteriorly. In medial view, there are 14 special foramina interconnected by a gently curving horizontal groove. The ectopterygoid ridge seems very prominent on the lateral side of the maxilla. This ectopterygoid ridge turns ventrally, unlike in *Pararhabdodon*, in which it is horizontal (Prieto-Márquez et al., 2006). The maxillary foramen is present close to the posterior border of the premaxillary shelf.

**Surangular**—MPZ2008/259 is a right surangular (Fig. 4A–D). It is anteroposteriorly longer and dorsoventrally wider than that of *Blasisaurus* (Cruzado-Caballero et al., 2010a). The surangular lacks a foramen on the lateral body of the bone, as is typical in hadrosaurids. In dorsal view, it is laterally very convex. The surangular portion of the mandibular glenoid is cup-shaped and is shallow and expanded both anteroposteriorly and mediolaterally. A deep groove for the *M. pterygoideus dorsalis* is located under the glenoid and near a prominent ridge that separates it from the angular facet (Ostrom, 1961). The lateral lip is robust. The retroarticular process is elongate and strong, it is compressed

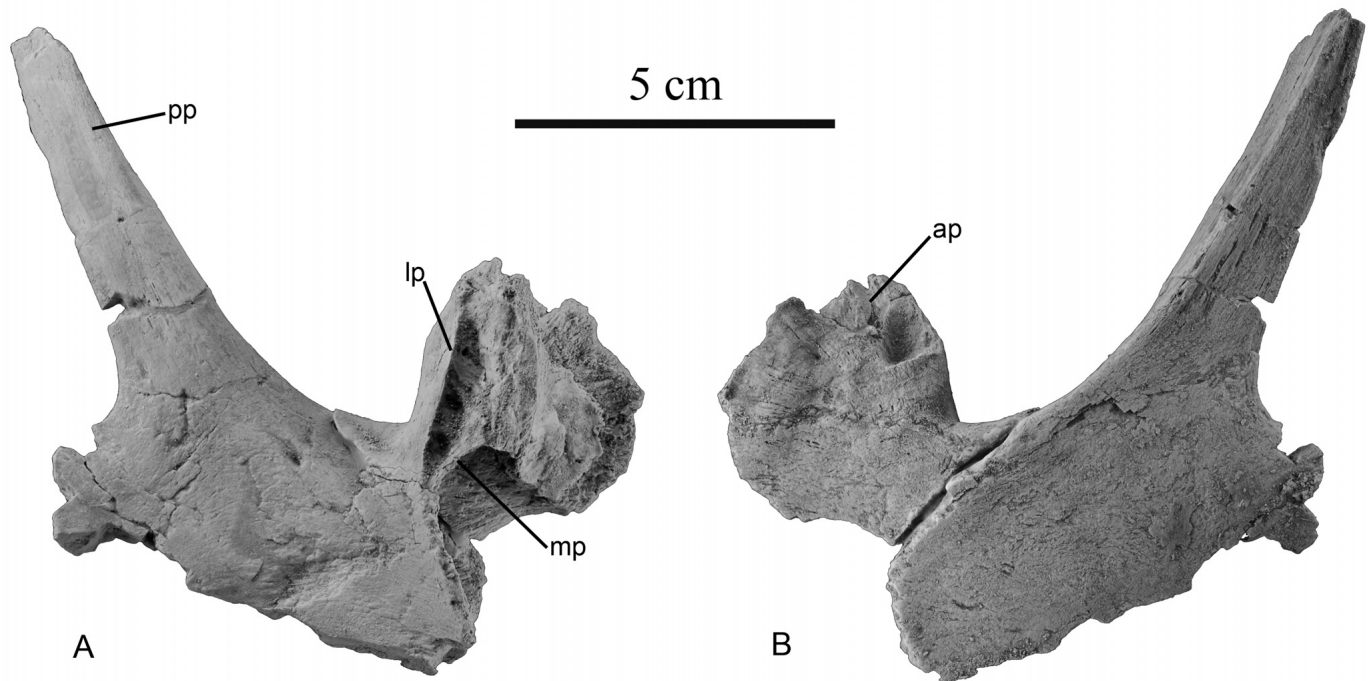


FIGURE 2. *Arenysaurus ardevoli* left jugal (MPZ2011/1) in medial (A) and lateral (B) views. **Abbreviations:** ap, anterior process; lp, lacrimal process; mp, maxillary process; pp, postorbital process.

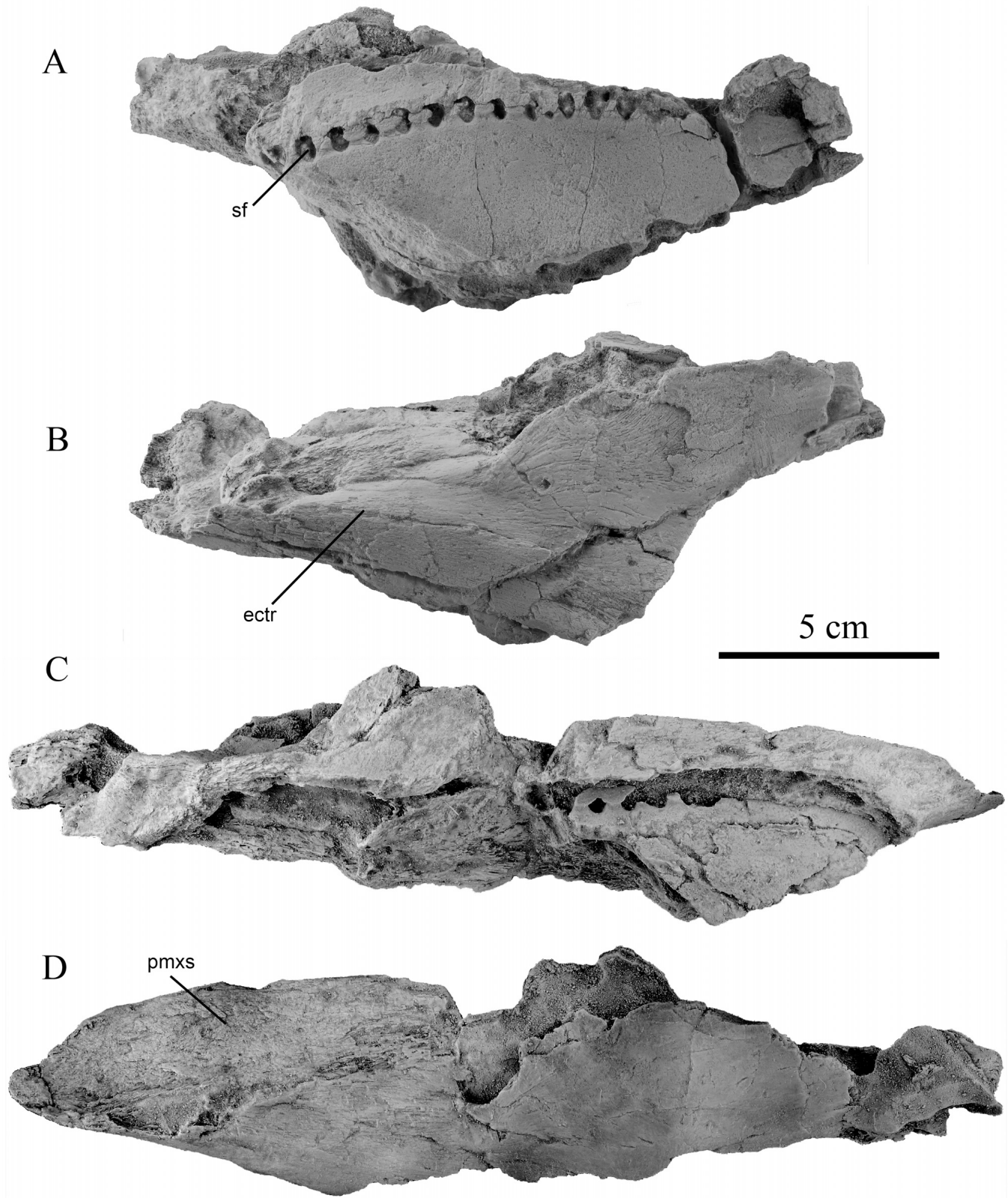


FIGURE 3. *Arenysaurus ardevoli* maxillae in medial (A, C) and lateral (B, D) views. A, B, right maxilla (MPZ2008/257); C, D, left maxilla (MPZ2008/256). **Abbreviations:** **ectr**, ectopterygoid ridge; **pmxs**, premaxillary shelf; **sf**, special foramina.

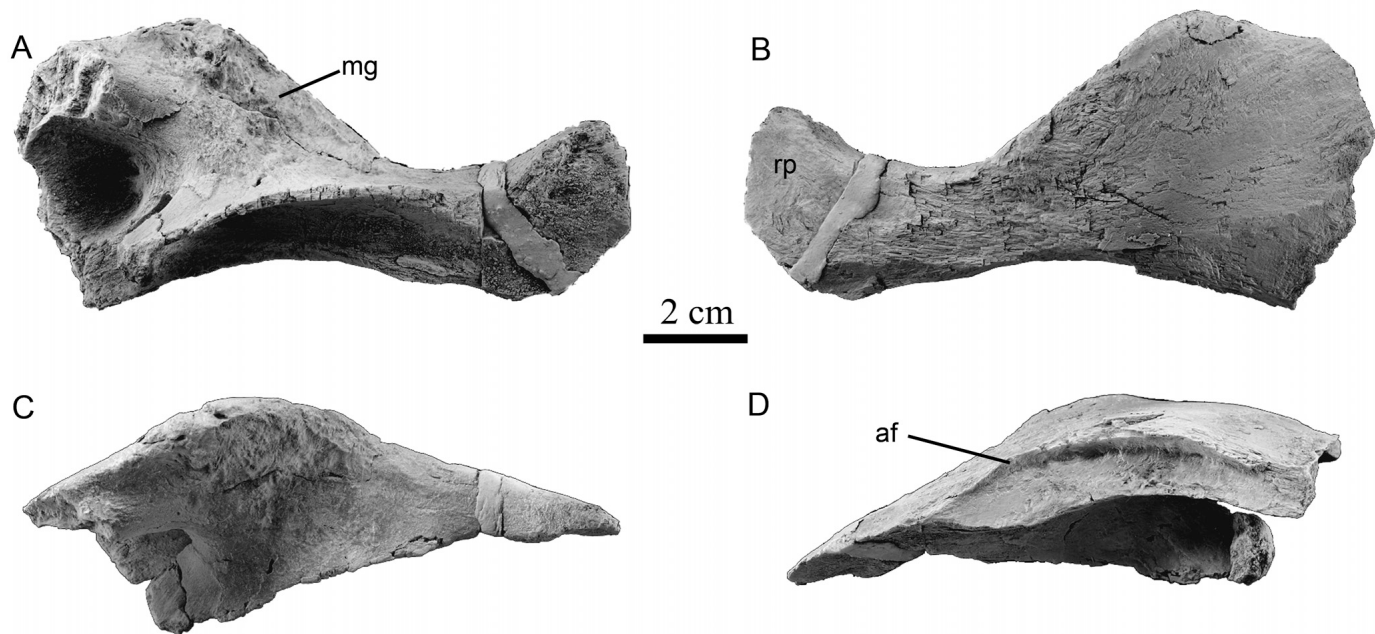


FIGURE 4. *Arenysaurus ardevoli* right surangular (MPZ2008/259) in medial (A), lateral (B), dorsal (C), and ventral (D) views. **Abbreviations:** af, angular facet; mg, mandibular glenoid; rp, retroarticular process.

mediolaterally, and on the ventral side there is an insertion area for the *M. pterygoideus ventralis* (Ostrom, 1961).

**Isolated Teeth**—The maxillary teeth are narrower than the dentary tooth. One isolated right dentary tooth (MPZ2008/263), two right maxillary teeth (MPZ2008/260, MPZ2008/262), and one fragmentary tooth (MPZ2008/261) have been collected (Fig. 5A–C). The crowns have the typical lanceolate shape of hadrosaurids (Horner et al., 2004). In both types of teeth there is a strong and straight median primary ridge on the enameled side of the crown, and the mesial and distal edges are not denticulate, as in *Blasisaurus* and unlike *Telmatosaurus* and *Tethyshadros* (Weishampel et al., 1993; Dalla Vecchia, 2009b; Cruzado-Caballero et al., 2010a). The height/width ratio is about 3.2 in the dentary tooth and 3.1 in the maxillary teeth. The dentary and maxillary teeth possess a faint secondary ridge mesial to the primary ridge.

#### Axial Skeleton

Pereda-Suberbiola et al. (2009:567) provided only short descriptions of the cervical, dorsal, sacral, and caudal vertebrae, and none of them were figured. Below, the vertebral series is described and figured for the first time in its entirety.

**Cervical Vertebrae and Ribs**—Eight partial to complete cervical vertebrae have been found (MPZ2007/706, MPZ2007/954–955, MPZ2008/264–267, MPZ2012/767; Fig. 6A–C, Table 2). These vertebral elements are indistinguishable from those of all other hadrosaurids. The centra are strongly opisthocoelous and particularly wide and short, with the following proportions: width > height = length, and with the heart-shaped anterior and posterior ends typical of the hadrosaurids (Horner et al., 2004). The anterior articular surface is globular, and the posterior surface is wider and cup-shaped. On the ventral side there is a prominent longitudinal keel. Few nutritional foramina are present on the lateral surfaces of the centra. The parapophyses are located at midheight on the depressed lateral surfaces. These are short and are linked to

the cervical ribs. The cervical ribs are dorsoventrally narrow and curved backwards. The neural arch surrounds a large neural canal. The lateral transverse processes are not very long, and are robust and curved backwards with a triangular cross-section. Near to the base of the transverse process there is a wide prezygapophysis with a flat surface facing upwards and inwards. The postzygapophyseal processes are long, have a triangular cross-section, and are curved backwards and outwards. They extend well above the level of the neural canal. The width between the postzygapophyseal processes decreases posteriorly in the cervical series. On the top of the postzygapophyseal process in ventral view there is a large circular postzygapophysis with flat surface face.

Three of the cervical vertebrae (MPZ2007/954, MPZ2007/955, MPZ2008/265) lack the neural spine. MPZ2007/706 has a neural spine that is curved backwards, mediolaterally compressed, anteroposteriorly wide, and dorsoventrally short, and that does not extend beyond the postzygapophyseal processes.

Several fragmentary cervical ribs have been recovered with the typical morphology of hadrosaurids (Horner et al., 2004). They are dorsoventrally flat and curved backwards. The tuberculum is expanded dorsoventrally at the joint with the cervical vertebrae. It is shorter than the capitulum, and MPZ2012/767 preserves an anteriorly projecting spine.

**Dorsal Vertebrae and Ribs**—A single dorsal vertebra has been found (MPZ2008/268; Fig. 6D–F, Table 3). As with the cervical vertebrae, this vertebra is indistinguishable from those of all other hadrosaurids. This vertebra is slightly deformed obliquely and eroded, so nutritional foramina cannot be observed. The transverse processes are long, have a cross-section that is triangular at the base and ellipsoidal at the end, and curve backwards and outwards. Near to the base of the transverse process there is a wide prezygapophysis with flat surface face. The location of the prezygapophysis indicates an anterior position in the dorsal vertebra series. In the neural spine, the postzygapophyseal processes are near the base in ventral view. They are long, ellipsoidal, and

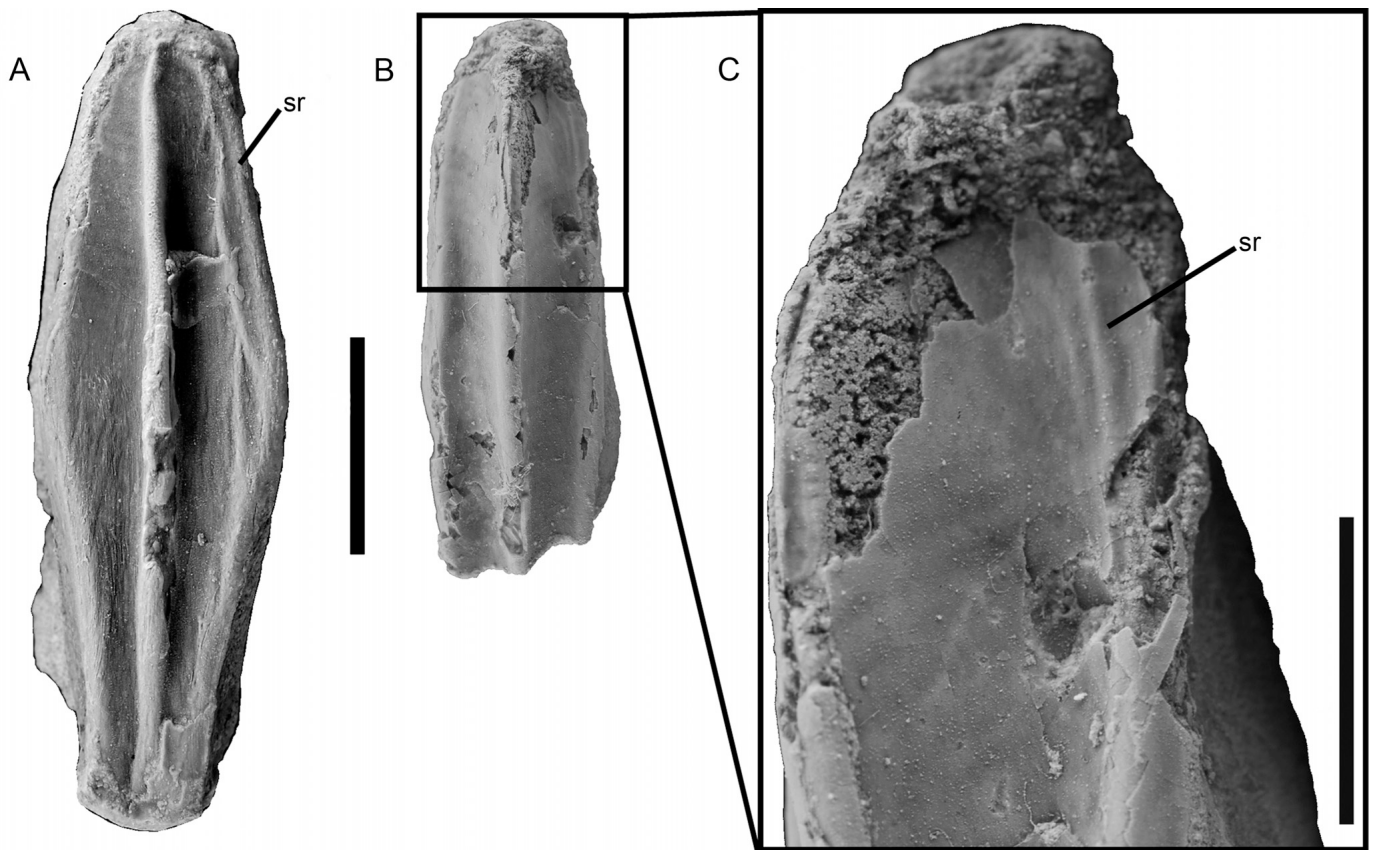


FIGURE 5. *Arenysaurus ardevoli* teeth. **A**, right dentary tooth (MPZ2008/263) in lingual view; **B**, right maxillary tooth (MPZ2008/260) in labial view; **C**, detail of the secondary ridge in labial view. **Abbreviation:** sr, secondary ridge. **A, B**, scale bar equals 1 cm. **C**, scale bar equals 0.5 cm.

have a flat surface that faces upwards and inwards. Between the postzygapophyseal processes there is a deep groove.

The neural spine is elongated, mediolaterally compressed, acute dorsally, and approximately 3.5 times the height of the centrum. It is inclined backwards, with the anterior border convex and the posterior slightly concave in lateral view.

The dorsal ribs (MPZ2008/269–270, MPZ2012/748–753) are fragmentary and, like the cervical ribs, have the typical hadrosaurid morphology (Horner et al., 2004). The lengths of the shafts are variable, and the cross-section is dorsoventrally flat.

**Sacral Vertebrae**—MPZ2008/271 is a partial sacrum formed from five fused centra, whose dorsal part is completely destroyed. An isolated element is identified as the last sacral vertebra

(Fig. 6G, H). The articular surfaces are elliptical in outline, wider than high, and concave. In ventral view, a broad and shallow sulcus is present in the sacrum, as in *Amurosaurus*, *Bactrosaurus* Gilmore, 1933, and *Pararhabdodon* (Godefroit et al., 1998, 2004; Casanovas-Cladellas et al., 1999). In *Arenysaurus*, the groove is not present in the first and last vertebrae. The neural spines are broken, except for the neural spine of the last centrum, which has a height that is more than three times that of the centrum, as in lambeosaurines (Horner et al., 2004).

**Caudal Vertebrae**—About two-thirds of the caudal series is preserved. Fifty-four vertebrae, including 14 that are articulated (MPZ2006/20), have been found, all of them indistinguishable from those of all other hadrosaurids. These vertebrae represent

TABLE 2. Measurements of cervical vertebrae, in mm.

Specimen	A-P length	D-V height	Lt-M width	Angle between postzygapophyseal processes	Length transverse processes (R/L)
MPZ2007/706	75.54	58.46	65.81	105°	74.5/73.85
MPZ2007/955	58.39*	49.39	78.97	90°	46.81*/43.88*
MPZ2008/267	X	X	X	90°	21.74*/28.57*
MPZ2008/266	X	X	X	X	27.94*/X
MPZ2007/954	68.41*	43.26*	50.72*	85°	31.67*/39.85*
MPZ2008/264	54.87*	55.41	55.46	X	X
MPZ2008/265	80.04*	48.33*	47.51	65°	39.88/16.92*
MPZ2012/767	X	X	X	91°	50/X

**Abbreviations:** A-P, anteroposterior; D-V, dorsoventral; L, left; Lt-M, lateromedial; R, right; \*, estimated; X, not preserved.



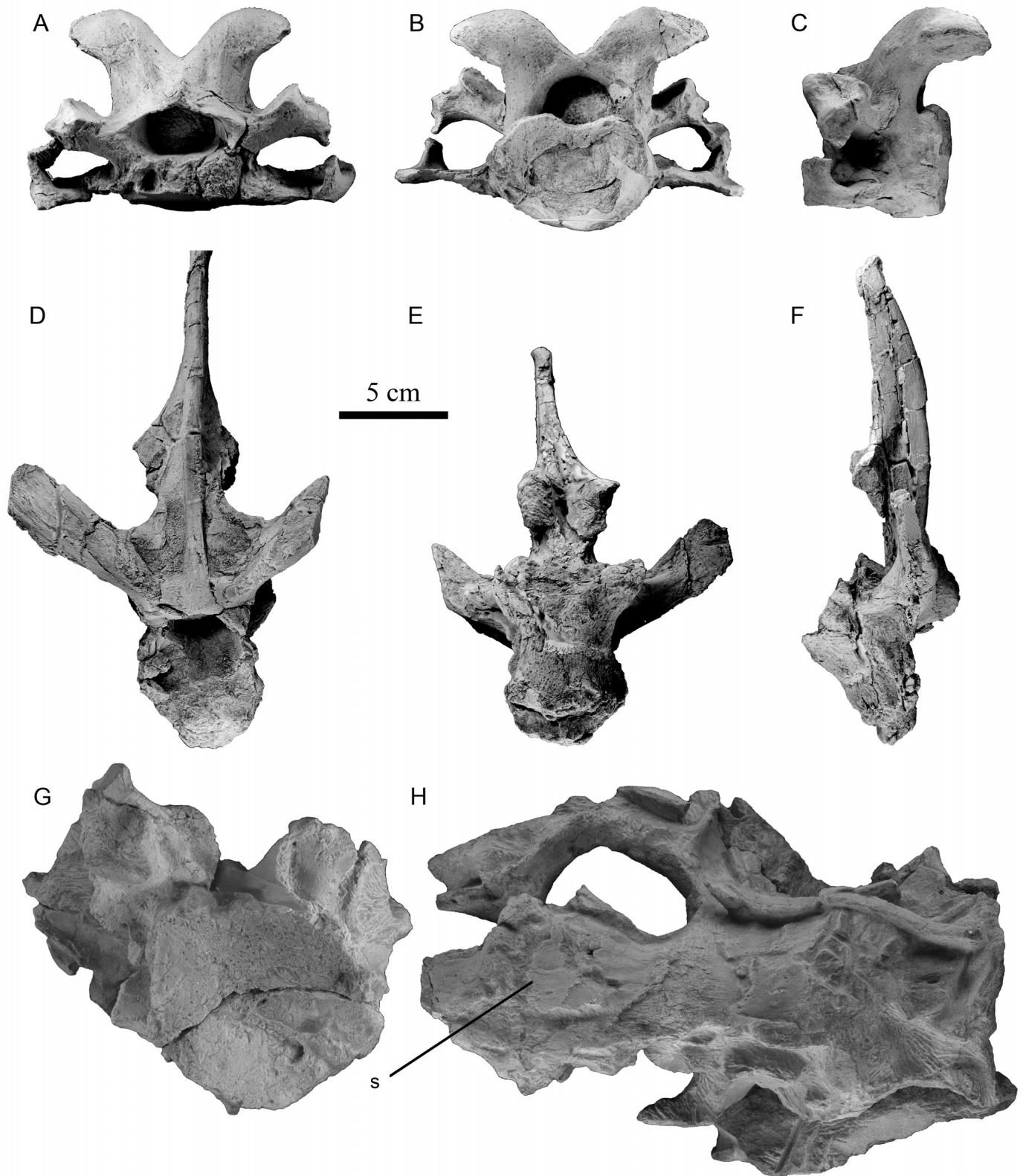


FIGURE 6. *Arenysaurus ardevoli* vertebrae in anterior (A, D, G), posterior (B), lateral (C and F), and ventral (G and E) views. A–C, cervical vertebrae (MPZ2007/955); E–G, dorsal vertebrae (MPZ2008/268); G, H, sacral vertebrae 1–5 (MPZ2008/271). **Abbreviation:** s, sulcus.

TABLE 3. Measurements of dorsal vertebrae, in mm.

Specimen	A-P length	D-V height	Lt-M width	Length spine	Angle spine	Length transverse processes (R/L)	Angle transverse processes (R/L)
MPZ2008/268	69.13*	40.43*	41.46	172*	71°	95.99/67.83*	84°/X

**Abbreviations:** **A-P**, anteroposterior; **D-V**, dorsoventral; **L**, left; **Lt-M**, lateromedial; **R**, right; \*, estimated; **X**, not preserved. Angle spine, angle between the neural spine and the vertical axis; Angle transverse processes, angle between the transverse process and the sagittal plane.

almost all of the anterior and middle sections of the tail. The anterior-most centra are typically amphiplatyan, anteroposteriorly narrow, with hexagonal articular surfaces, a transverse process, and hemapophyseal facets in the ventral side. Posteriorly, they present a sequence of dorsoventral reduction and anteroposterior increase in the dimensions of the centra; the mid-posterior vertebrae lack hemapophyseal facets. In lateral view, the sides of the mid-posterior centra are slightly depressed, lack transverse processes, and are pierced by irregularly distributed nutritional foramina of variable size.

The neural spines are very long (more than three times the height of the centrum), robust, and subvertical (with an angle to the vertical axis of almost 90°) in the anterior-most vertebrae. In the posterior-most vertebrae, the neural spines are slender, steeply inclined backwards (angle between 34° and 45°), and their end is slightly curved dorsally. The tip of the neural spine in the anterior-most vertebrae is broken, and we do not know if these were slightly expanded transversally as in *Barsboldia* Maryanska and Osmólska, 1981, and *Amurosaurus* (Maryanska and Osmólska, 1981; Godefroit et al., 2004).

In the middle caudal series, five vertebrae in the block MPZ2006/20 show marks parallel to the posterodorsal axis that are probably due to predation. These marks coincide in position with the pathological vertebra MPZ2004/480 (Canudo et al., 2005).

The neural spine of MPZ2004/480 presents a swelling and deviation near to the tip that produces a distinctive convexity on the right side and concavity on the left side (Fig. 7A–D). In anterior view, the anomalous bone growth creates an oval hole in the central section. The left side exhibits at least two parallel fractures partially covered by anomalous bone growth. These fractures have an anteroposterior orientation, and one is located at the base of the anomalous bone development, whereas the second is located above the hole. Canudo et al. (2005) explained these pathologies as being the result of a probable attack by a theropod dinosaur and the subsequent infection of the injury.

**Hemal Arches**—The hemal arches have the typical hadrosaurid ‘Y’ shape, are long and mediolaterally flat, and the articular facets are separated by an open hemal canal (Horner et al., 2004). The angle between the hemal arches and the centra cannot be measured because the hemal arches were discovered disarticulated from the caudal series.

#### Appendicular Skeleton

Pereda-Suberbiola et al. (2009) and Cruzado-Caballero et al. (2009) provided short descriptions of the right scapula, humerus, and pubis, and the femora. Only one of these bones, the right humerus, was figured (Pereda-Suberbiola et al., 2009:fig. 5). All

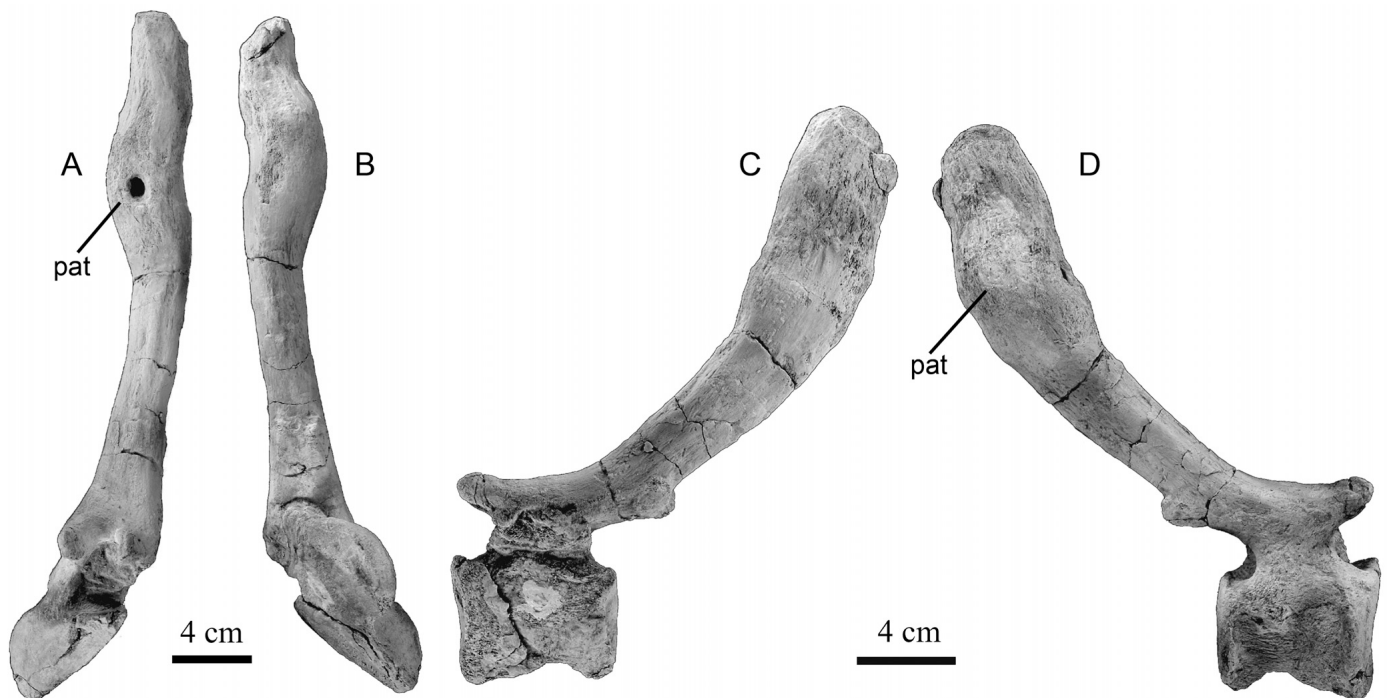


FIGURE 7. *Arenysaurus ardevoli* pathology caudal vertebra (MPZ204/480) in anterior (A), posterior (B), left lateral (C), and right lateral (D) views. **Abbreviations:** **pat**, pathology.

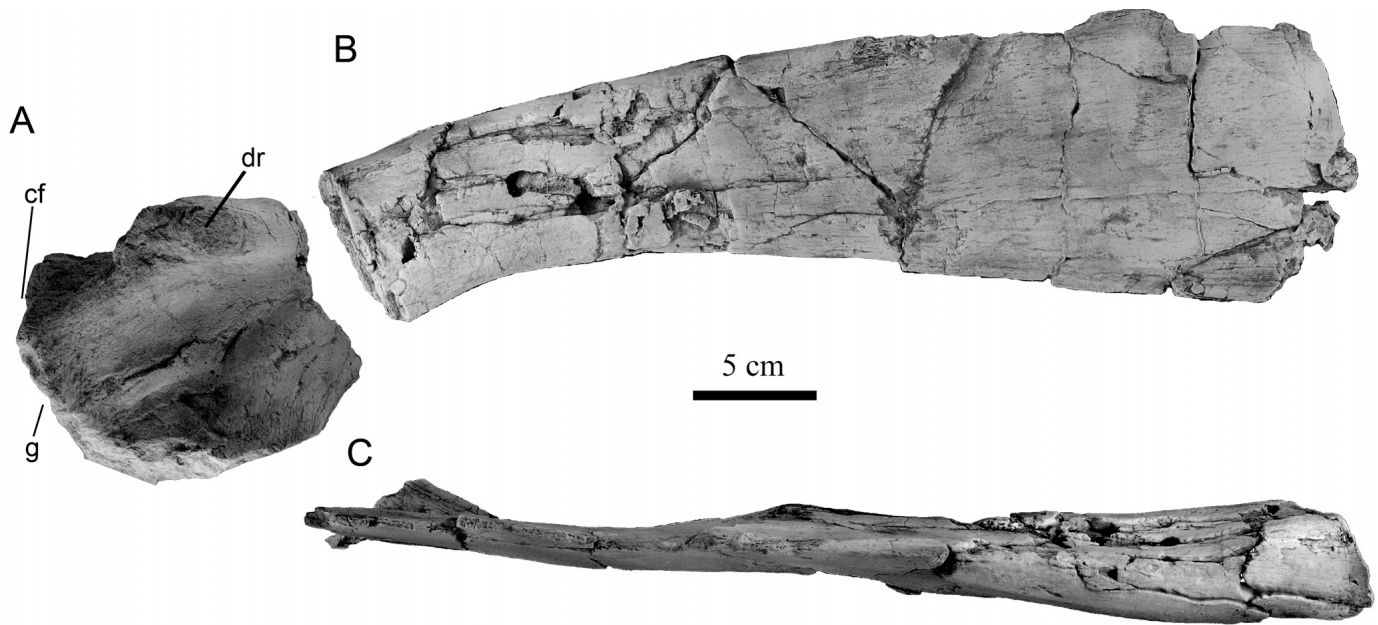


FIGURE 8. *Arenysaurus ardevoli* right scapula in medial (A and B) and dorsal (C) views. A, proximal fragment (MPZ2008/333a); B, C, distal fragment (MPZ2008/333b). **Abbreviations:** cf, coracoid facet; dr, deltoid ridge; g, glenoid.

of these bones and new unpublished appendicular remains are described and figured below.

**Scapula**—MPZ2008/333a and MPZ2008/333b are two fragments of a broken right scapula: the proximal fragment and an almost complete blade, respectively (estimated length 525 mm; Fig. 8A–C). MPZ2008/333a is narrow and has a rectangular shape, unlike the triangular shape of *Telmatosaurus* (Weishampel et al., 1993). The deltoid fossa is broad and bears numerous longitudinal striations and a prominent knob, probably an extensive attachment site for a powerful *M. supracoracoideus* (Dilkes, 2000). This knob and the anterior orientation of the deltopectoral crest would have increased the power of the animal's arm. The acromion process is horizontally projecting, similar to *Wulagasaurus* Godefroit, Hai, Yu, and Lauters, 2008, and *Secernosaurus* Brett-Surman, 1979 (Godefroit et al., 2008; Prieto-Márquez and Salinas, 2010). It is less robust than in *Pararhabdodon* (Prieto-Marquez et al., 2006) and parallel to the dorsal side, unlike in *Tethyshadros* (Dalla Vecchia, 2009b). The acromion process bears striations for the attachment of the *M. trapezius* (Godefroit et al., 2004). The coracoid facet is large, rough, and cup-shaped, as in *Charonosaurus* Godefroit, Zan, and Jin, 2000, and *Amurosaurus* (Godefroit et al., 2001, 2004). The glenoid facet is smaller, straight, and oriented backwards. These two facets form an angle of approximately 135°, similar to the condition in *Wulagasaurus* and unlike MDE-Les-25 (*Euhadrosauria* indet. from Lestaillats, France), which has an angle of 90°, and *Pararhabdodon*, which has an angle of 100° (Laurent et al., 1999; Prieto-Márquez et al., 2006; Godefroit et al., 2008).

MPZ2005/333b possesses a narrow scapular neck, as in lambeosaurines and in contrast to more primitive hadrosaurids (Horner et al., 2004), so that the blade is approximately 60% wider than the proximal neck. The scapular blade is narrow and in lateral view it is anteriorly convex. The dorsal and ventral margins of the scapula are curved slightly downward and diverge, with the maximum width on the symmetrical posterior side, as

in *Amurosaurus*, *Lambeosaurus*, *Nipponosaurus* Nagao, 1936, *Sahaliyana* Godefroit, Hai, Yu, and Lauters, 2008, and an indeterminate lambeosaurine from New Mexico (Nagao, 1936; Williamson, 2000; Godefroit et al., 2004, 2008; Suzuki et al., 2004; Evans and Reisz, 2007). According to Godefroit et al. (2001, 2004), the elongation and ventral curvature of the scapular blade may be related to a general increase in the power of the forelimb, because this lengthens the in-lever arms of the *M. teres major*, which inserted along the posteroventral side of the scapular blade.

**Coracoid**—MPZ2008/334 is a right coracoid (Fig. 9). As is common in hadrosaurids, the hook-shaped ventral process is prominent and points anteroventrally (Horner et al., 2004; Godefroit et al., 2008). The coracoid foramen is large and elliptical; it is completely surrounded by the coracoid. It is anteroposteriorly wider than dorsoventrally high, but less so than in *Charonosaurus* (Godefroit et al., 2001). The anterior edge of the coracoid is thinner than the posterior one. The ventral edge forms a small glenoid fossa. On the posterior side, the scapular articular surface and the glenoid have a similar length, but the scapular articulation is thicker than the glenoid. This surface is thicker dorsoventrally than mediolaterally, unlike in *Hadrosaurus* Leidy, 1858, *Brachylophosaurus* Sternberg, 1953, *Edmontosaurus*, *Saurolophus* Brown, 1912, and *Gryposaurus* Lambe, 1914 (Prieto-Márquez et al., 2006). The two articular surfaces form an angle of about 135°, this angle being greater than those of the *Pararhabdodon* (100°), *Brachylophosaurus* (115°), *Bactrosaurus* and *Amurosaurus* (120°), and *Secernosaurus* (126°), and less than those of *Charonosaurus* and *Nipponosaurus* (150°) (Godefroit et al., 1998, 2001, 2004; Suzuki et al., 2004; Prieto-Márquez et al., 2006; Prieto-Márquez, 2007; Prieto-Márquez and Salinas, 2010). The biceps tubercle is large and projects laterally.

**Humerus**—MPZ2008/336 is an incomplete right humerus (see Pereda-Suberbiola et al., 2009:fig. 5). It is massive, the cross-section is rectangular, and the shaft is straight, unlike in *Telmatosaurus* (Weishampel et al., 1993) and *Tethyshadros* (Dalla

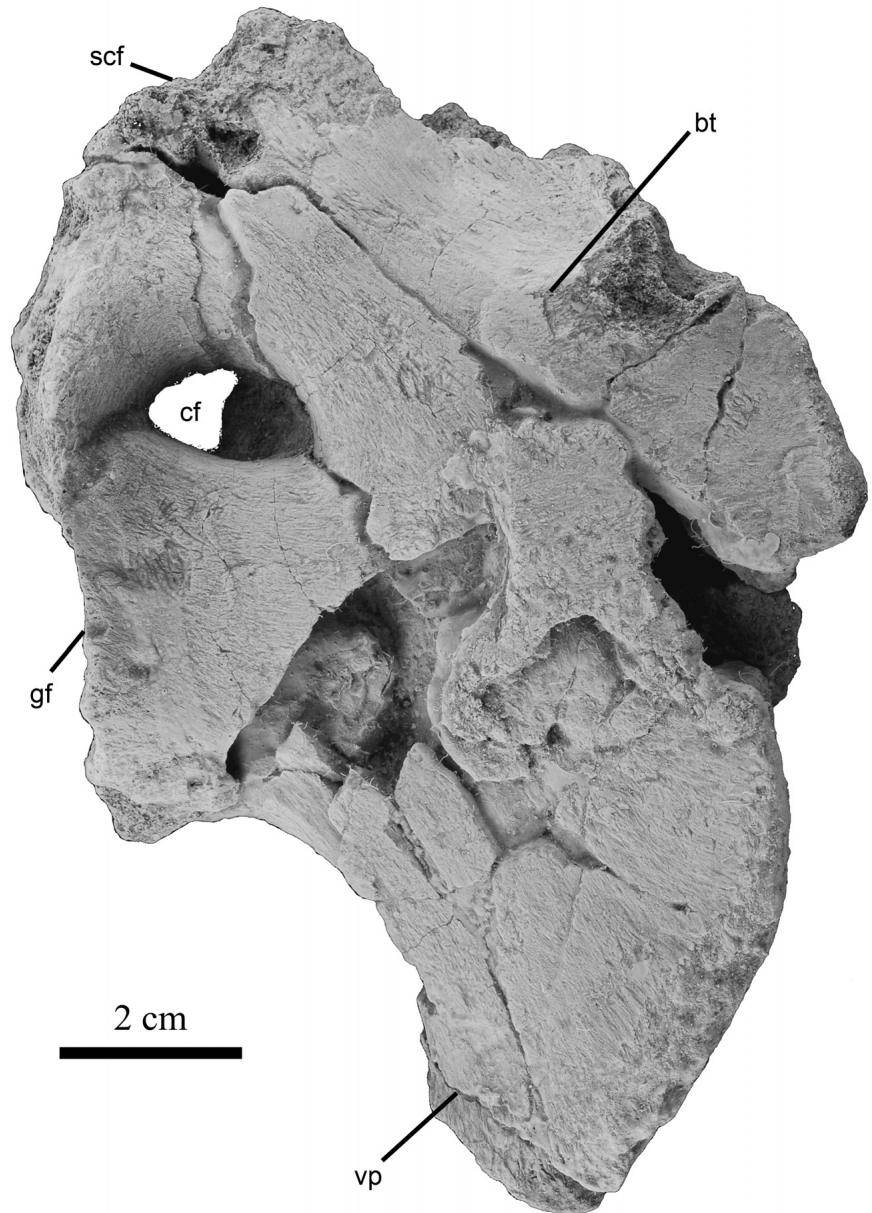


FIGURE 9. *Arenysaurus ardevoli* right coracoid (MPZ2008/334) in anterior view. **Abbreviations:** **bt**, biceps tubercle; **cf**, coracoid foramen; **gf**, glenoid fossa; **scf**, scapular facet; **vp**, ventral process.

Vecchia, 2009b). The deltopectoral crest is oriented anteriorly as in *Wulagasaurus*, so that the maximum width of the shaft is distal unlike in other lambeosaurines, where the maximum width is at the level of the deltopectoral crest (Godefroit et al., 2008). The bicipital groove is deep and narrow. The proximal portion of the humerus is broken, and the distal portion presents the ulnar and radial condyles. The ulnar condyle is more developed than the radial one. The intercondylar groove is slightly wider on the posterior side than on the anterior side. On the medial side, there is a prominent knob on the shaft.

**Ilium**—MPZ2008/335 is the preacetabular process of a right ilium (Fig. 10A, B). It is wide dorsoventrally, narrow mediolaterally, and ventrally directed. In medial view, near to the

dorsal side there is a groove between two ridges, and a slight scar for the *M. iliobtibialis* (Dilkes, 2000).

**Pubis**—MPZ2007/707 is the prepubic blade of a robust right pubis (Fig. 11A, B). It is anteroposteriorly short, dorsoventrally expanded, and is nearly symmetrical. It is similar to the type 5 pubis (*Parasaurolophus* Parks, 1922, and *Bactrosaurus*) of Brett-Surman and Wagner (2006) and to stage 1 (*Parasaurolophus*) of Prieto-Márquez (2010). In lateral view, it is slightly concave and has strong muscular marks that posteriorly are perpendicular to the neck and anteriorly are oblique to the blade. In medial view, there are also strong muscular marks, probably for the *M. ambiens* (Brett-Surman and Wagner, 2006). The neck is wide and strong, with the dorsal side nearly straight. The

## PHYLOGENETIC ANALYSIS

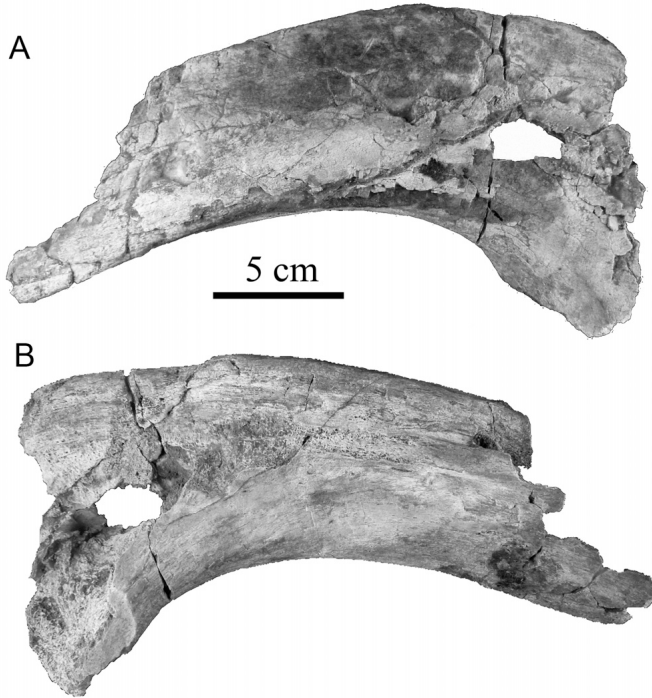


FIGURE 10. *Arenysaurus ardevoli* right ilium (MPZ2008/335) in lateral (A) and medial (B) views.

iliac peduncle is strong, anteriorly directed, and has a triangular cross-section.

**Femora**—Both femora (MPZ2007/711 and MPZ2008/337) were recovered from the site. MPZ2007/711 is a complete right femur with a typical hadrosaurid form and a length of 711 mm. It has a straight massive shaft, unlike *Telmatosaurus*, which has a distal portion that is medially inclined (Weishampel et al., 1993). The cross-section is rectangular and mediolaterally narrow. The femoral head and greater trochanter are separated by a wide groove. The greater trochanter is narrow anteroposteriorly and wider laterally than the femoral head. A groove separates the greater trochanter from the lesser trochanter, which is developed mediolaterally. Below the lesser trochanter there is a slight insertion mark for the M. puboischiofemoralis internus 2 (pars dorsalis) (Dilkes, 2000). The fourth trochanter is triangular in shape and mediolaterally narrow. In lateral view, the insertion area for the M. caudifemoralis brevis (Dilkes, 2000) is not separated into two areas, unlike the femora from Blasi 1 (Cruzado-Caballero et al., 2009). The distal condyles are expanded anteroposteriorly and proximodistally. They are lateromedially narrow due to diagenetic deformation; the intercondylar extensor groove is not closed, probably due to this deformation. MPZ2008/337 is an incomplete left femur. Only the distal part has been preserved, and its diaphysis is partially hollow. The distal condyles are bioturbated by invertebrate galleries, as is the case in MPZ2007/711. They are wide proximodistally and they are not complete anteroposteriorly. There is a well-developed intercondylar extensor groove that is closed, forming a tunnel (Horner et al., 2004).

Bioturbation has been observed in both femora and also in two other bones (MPZ2008/336, right humerus; MPZ2008/333a, right scapula). These are possibly traces produced by necrophagous insects (Cruzado-Caballero et al., in preparation).

In this paper, we follow the definition of Sereno (1998:62) for the clade Hadrosaurinae, which is “all hadrosaurids closer to *Saurolophus* than to *Parasaurolophus*,” and for Lambeosaurinae, which is “all hadrosaurids closer to *Parasaurolophus* than to *Saurolophus*.” Within Lambeosaurinae there are two widely recognized lineages, which were defined by Evans and Reisz (2007:385) as Parasaurolophini: “taxa more closely related to *Parasaurolophus walkeri* than to *Corythosaurus casuarius*”; and Corythosaurini: “taxa more closely related to *C. casuarius* than to *P. walkeri*.”

To assess the phylogenetic relationships of the Spanish lambeosaurines, we have included these taxa in the matrix proposed by Godefroit et al. (2012), to which we have added one more character from Prieto-Márquez (2010, character 82), which scores important information for differentiating *Arenysaurus* and *Blasisaurus*. In this data set, we have corrected some typos related to the Spanish hadrosaurids (see Appendix 1) and included new material described in the present work. Character distributions were analyzed with Mesquite 2.74 (Maddison and Maddison, 2010). The resulting matrix included 22 taxa coded for 119 characters and was run with TNT version 1.1 (Goloboff et al., 2008). All characters were unordered and equally weighted. A heuristic search with 1000 replications, retaining 10 trees per replication, was carried out using *Probactrosaurus* Rozhdestvensky, 1966, as the outgroup. Five most parsimonious trees were obtained (tree length = 188 steps, consistency index = 0.713, retention index = 0.805, rescaled consistency index = 0.574). Bremer supports and bootstrap values were calculated for each branch to assess its robustness.

The strict consensus tree is presented in Figure 12. In contrast to Godefroit et al. (2012), we have not deleted *Sahaliyana* a posteriori, because its position remained stable in all trees, forming a trichotomy with the tribes Parasaurolophini and Lambeosaurini in the consensus. We also considered the deletion of *Velafrons*, because its variable position within Lambeosaurini has been reported in previous studies (Godefroit et al., 2012). If *Velafrons* is removed, only one tree of 186 steps is recovered. Nevertheless, we have chosen not to remove it, because its position is not relevant for the current study. The resulting topology resembles previously published hypotheses, with the exceptions of the polytomy within Lambeosaurini attributable to *Velafrons* and, more significantly, the position of *Arenysaurus* and *Blasisaurus*, which has turned out to be more derived than previously stated.

Previous analyses reported *Arenysaurus* as the sister taxon to *Amurosaurus* and all more derived lambeosaurines (Pereda-Suberbiola et al., 2009; Godefroit et al., 2012). Cruzado-Caballero et al. (2010a) found the clade formed by *Arenysaurus* and *Blasisaurus* to be placed in a trichotomy with *Amurosaurus* and the node that includes Lambeosaurini and Parasaurolophini. With the inclusion of the new postcranial data we have recovered a more derived position for the *Arenysaurus* + *Blasisaurus* clade, nested within the tribe Parasaurolophini. Although the three synapomorphies of Parasaurolophini cannot be coded for either *Arenysaurus* or *Blasisaurus*, *Arenysaurus* shares the following characters with the genus *Parasaurolophus*: (1) a caudal process of the postorbital elongated above the infratemporal fenestra (character 36:1); (2) a short diastema between the first dentary tooth and the pre-dentary, also shared with *Blasisaurus* (character 58:0); (3) mediolaterally broad distal condyles of the humerus (character 78:1); and (4) a deltoid ridge of the scapula that is dorsoventrally deep and craniocaudally long, with a well-demarcated ventral margin (character 109:1). Nevertheless, both taxa are well differentiated from all other Parasaurolophini in having a wide lingual projection of the symphyseal region of the dentary (character 105:0). It is of

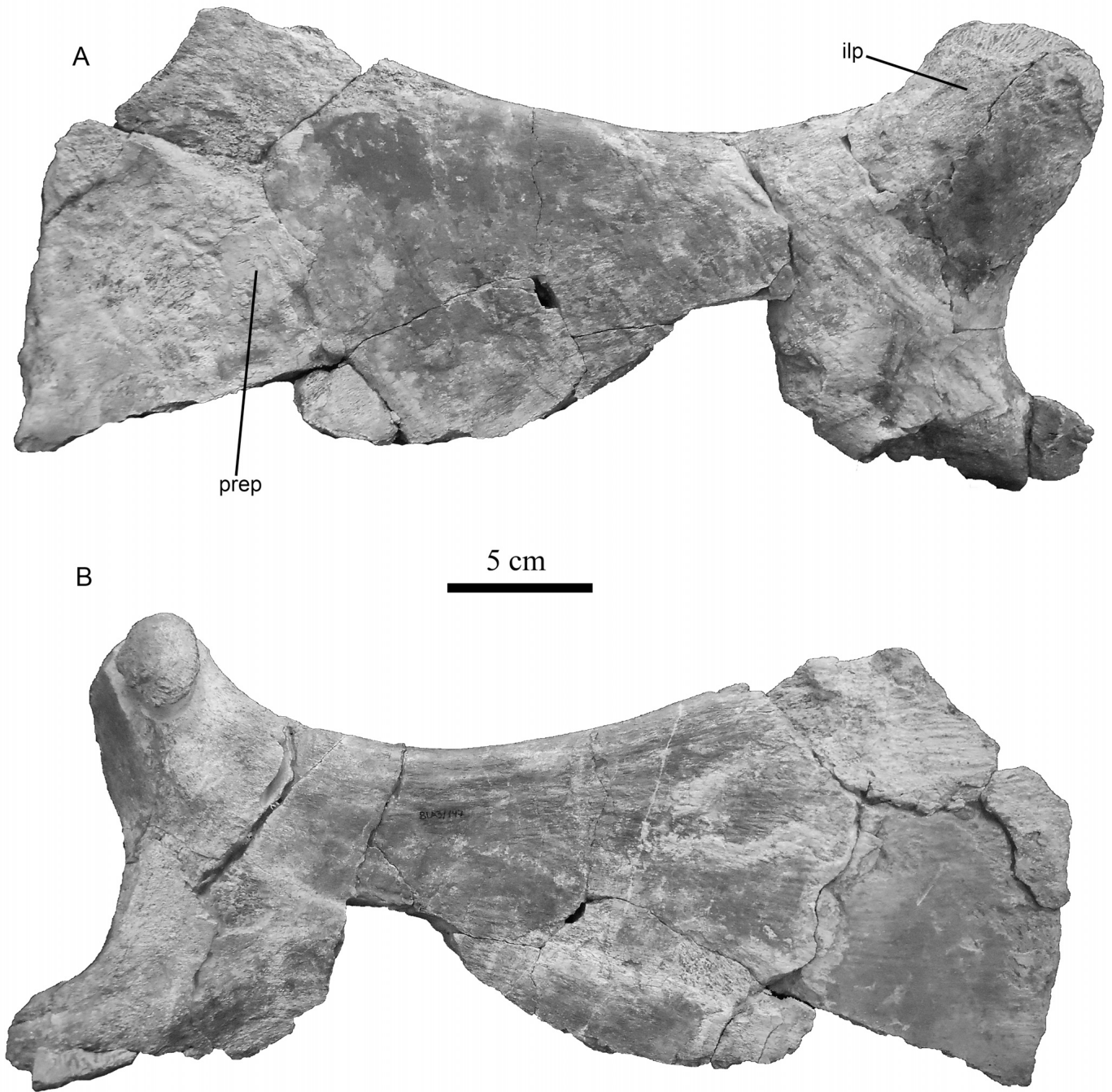


FIGURE 11. *Arenysaurus ardevoli* right pubis (MPZ2007/707) in medial (A) and lateral (B) views. **Abbreviations:** **ilp**, iliac peduncle; **prep**, prepubic blade.

interest to compare *Arenysaurus* and *Blasisaurus* with *Pararhabdodon*, the only other Spanish lambeosaurine. *Arenysaurus* differs in that it has (1) sacral neural spines elongated, approximately three times the height of the centrum or greater (character 68:1); (2) humeral distal condyles mediolaterally broad, which flare moderately from the shaft of the humerus (character 78:1); (3) a lingual projection of the symphyseal region of the dentary, with a ratio between the labiolingual extension of the symphyseal region and

the maximum labiolingual width of the dentary that reaches 1.65 (character 105:0); and (4) a concave medial or lateral profile of the dorsal margin of the rostral edentulous region of the dentary for articulation with the prementary (character 106:0). Of these characters, *Blasisaurus* shares with *Arenysaurus* its differences from *Pararhabdodon* in the characters 58, 105, and 106.

*Blasisaurus* also shares with all other derived lambeosaurids a straight dentary tooth row (character 119:1), a derived state not

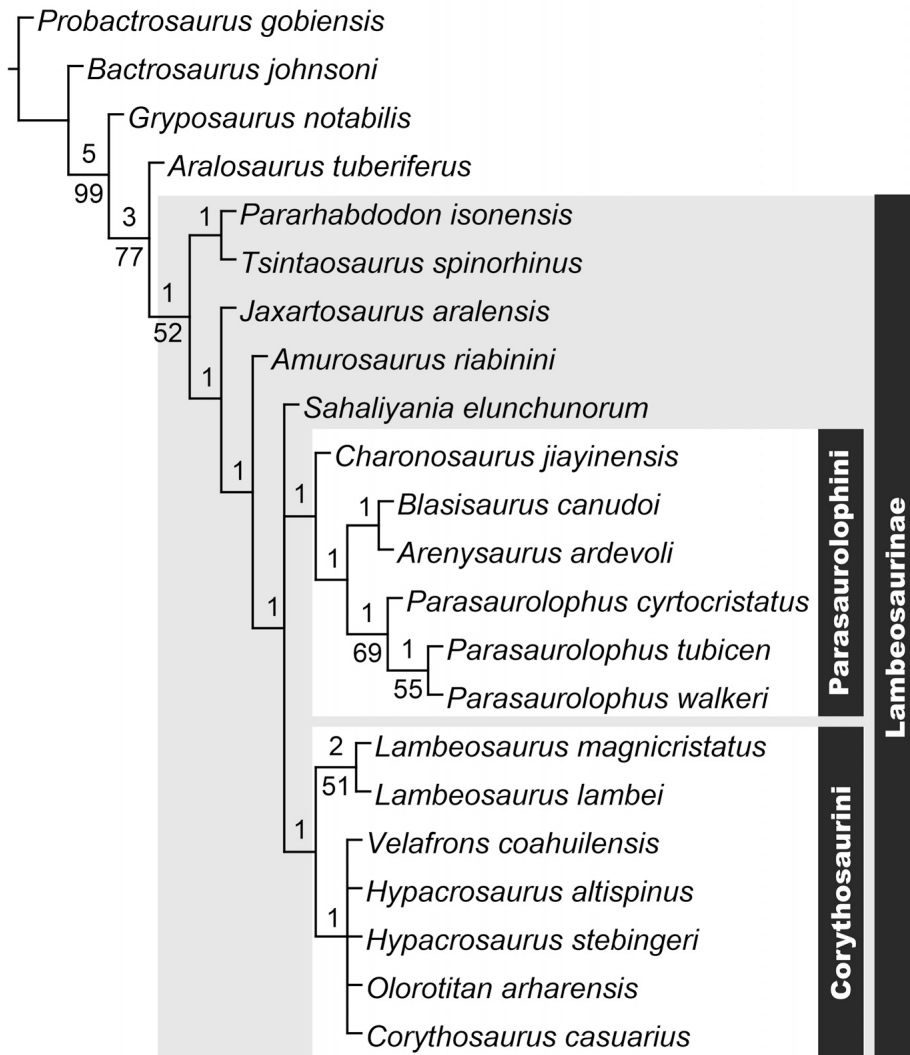


FIGURE 12. Strict consensus of five most parsimonious trees (tree length = 188 steps, consistency index = 0.713, retention index = 0.805, rescaled consistency index = 0.574). Data set based on the matrix of Godefroit et al. (2012), with the addition of character 48 from Prieto-Marquez (2010), and the correction of several typos with respect to the Spanish taxa. See Appendix 1 and Supplementary Materials for character scores and data matrix. Note the position of *Arenysaurus* and *Blasisaurus* as members of Lambeosaurini, instead of the more basal position recovered in previous studies, as sister taxa of *Amurosaurus* (Pereda Suberbiola et al., 2009; Cruzado-Caballero et al., 2010a; Godefroit et al., 2012). Numbers over the branches are Bremer support values and numbers under the branches represent bootstrap values after 1000 replicates.

shared with *Arenysaurus*, which possesses the ancestral condition of a dentary tooth row that is bowed lingually.

#### PALEOBIOGEOGRAPHIC IMPLICATIONS

The geodispersal events of hadrosaurids between western North America and eastern Asia, in both directions, have been amply proved in previous works (Head, 1998, 2001; Godefroit et al., 2003, 2004, 2008; Horner et al., 2004; Fiorillo, 2008; Sues and Averianov, 2009; Prieto-Márquez, 2010). Similarly, a connection between Asia and Europe during the second half of the Late Cretaceous has been discussed (Pereda-Suberbiola et al., 2009; Prieto-Márquez and Wagner, 2009; Cruzado-Caballero et al., 2010b).

According to Pereda-Suberbiola et al. (2009) and Prieto-Márquez and Wagner (2009), among other authors, the connection between Asia and Europe was probably interrupted prior to the Maastrichtian. Before that, there were 'semipermeable' barriers as a result of land bridges that emerged or were submerged depending on climatic and sea-level changes. These bridges allowed several dinosaur taxa to use the European archipelago as a refuge; among these were the lambeosaurines (Pereda-Suberbiola, 2009).

Conversely, several tetrapod taxa from the Late Cretaceous of Europe are considered to have Euramerican affinities: paleobatrachid frogs, batrachosauroidid salamanders, solemydid turtles, basal crocodyloids, and, tentatively, chelydroid turtles, alligatoroid crocodyliforms, and nodosaurid dinosaurs (see references in Pereda-Suberbiola, 2009; Puértolas et al., 2011). These taxa probably used bridges that sporadically opened high-latitude routes from eastern North America into Europe and allowed faunal exchange between the two areas (see Puértolas et al., 2011, and references therein). Our phylogenetic hypotheses suggest that these geodispersal events also affected the European fauna of lambeosaurine hadrosaurids.

The distribution of lambeosaurines in a simplified phylogenetic tree shows three hypothetical geodispersal episodes (see Fig. 13): (1) *Pararhabdodon* or its ancestors migrated from Asia to the Iberian island of the European archipelago (Prieto-Márquez and Wagner, 2009); (2) *Arenysaurus*, *Blasisaurus*, or their ancestors migrated from Asia to the Iberian island; and (3) *Parasaurolophus* spp. or their ancestors migrated probably from Asia to North America.

Geodispersal events 1 and 2 (from Asia to Europe) could have occurred at the same time, no later than the middle-late

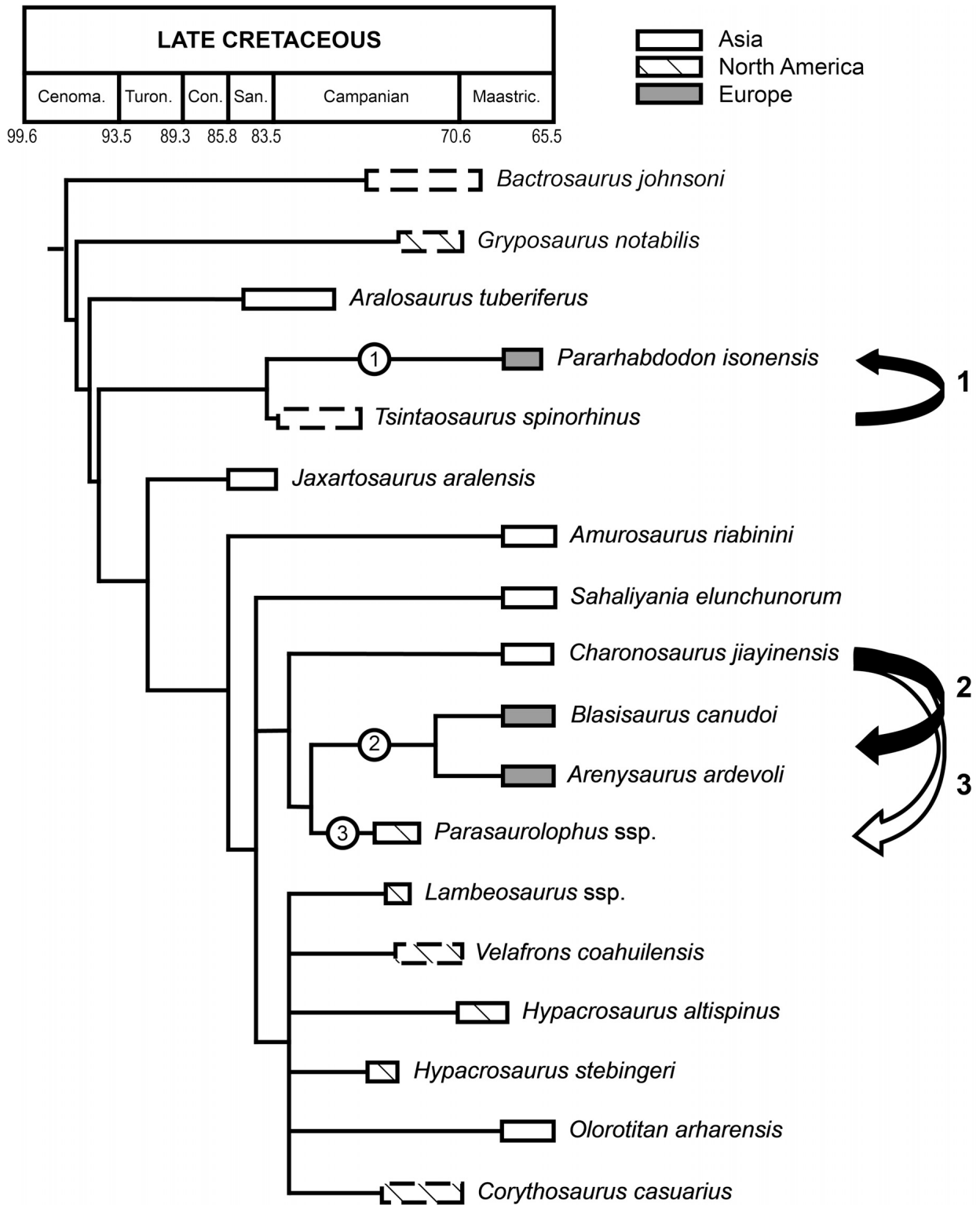


FIGURE 13. Biogeographic implications of the lambeosaurine phylogenetic analysis carried out in this paper. Geodispersal events are marked with numbers: 1, 2, from Asia to Europe; 3 from Asia to North America. Dashed-line boxes represent uncertain ranges of presence of species. Boundaries (Ma) after Walker and Geissman (2009), and the age of the represented species is based on Prieto-Márquez (2010).



Campanian according to Prieto-Márquez and Wagner (2009). Geodispersal event 3 (from Asia to North America) probably occurred prior to or during the early–middle Campanian.

Two additional geodispersal events have been recognized in a previous paper by the present authors (Cruzado-Caballero et al., 2011:fig. 2), based on the phylogenetic analyses of Evans and Reisz (2007) and Gates et al. (2007) with the addition of *Arenysaurus* and *Blasisaurus*: (4) *Velafrons* and *Lambeosaurus* spp. or their ancestors migrated from Asia to North America before or during the early Campanian; and (5) *Olorotitan* or its ancestors migrated from North America to Asia in the middle–late Campanian. Nevertheless, the phylogeny of corythosaurines is not resolved in the present phylogenetic analysis, and these two geodispersal cannot be tested.

Hypothetical geodispersal episodes 3–5 are for the moment tentative. It is thus necessary to reach a greater consensus on the phylogeny of hadrosaurids and a greater knowledge of the European taxa to test them.

### CONCLUSIONS

*Arenysaurus ardevoli* is the most complete lambeosaurine from the Iberian Peninsula, indeed from anywhere in Europe. It possesses several cranial characters that differentiate it from *Pararhabdodon*: jugal with anterior process expanded dorsally, straight posterodorsal end, postorbital process forming an angle of 58° with the long axis of the jugal, and ‘V’-shaped orbital fenestra; maxilla with ectopterygoid ridge ventrally turned; dentary with anterior portion modestly deflected ventrally, a moderate diastema, and a lingual projection of the symphyseal region of the dentary with a ratio between the labiolingual extension of the symphyseal region and the maximum labiolingual width of the dentary that reaches 1.65; the presence of a mesial secondary ridge in maxillary and dentary teeth (Pereda-Suberbiola et al., 2009). Additional postcranial characters that differentiate *Arenysaurus* from *Pararhabdodon* are rectangular scapula with glenoid and coracoid facets forming an angle of 135°; straight humerus with deltopectoral crest oriented anteriorly; sacral neural spines elongated, approximately three times the height of the centrum or greater; humeral distal condyles mediolaterally broad and flaring moderately from the shaft of the humerus; and pubis of type 5 (*Parasaurolophus* and *Bactrosaurus*) sensu Brett-Surman and Wagner (2006) and stage 1 (*Parasaurolophus*) sensu Prieto-Márquez (2010).

*Arenysaurus* and *Blasisaurus* form a clade that is placed inside the Parasaurolophini tribe in a dichotomy with *Parasaurolophus* spp. The presence of *Arenysaurus*, *Blasisaurus*, and *Pararhabdodon* in Europe and *Parasaurolophus* spp. in North America suggests the occurrence of at least two geodispersal events of Asian lambeosaurines from Asia to Europe and North America. These geodispersal events probably involved the use of ‘semipermeable’ barriers that served as temporary connections between Asia and Europe from the middle–late Campanian. Moreover, the European fauna of lambeosaurine hadrosaurids could have been affected by geodispersal events of other tetrapod faunas from eastern North America.

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### LITERATURE CITED

- Blain, H. A., J. I. Canudo, G. Cuenca-Bescós, and N. López-Martínez. 2010. Amphibians and squamates from the latest Maastrichtian (Upper Cretaceous) of Blasi 2 (Huesca, Spain). *Cretaceous Research* 31:433–446.
- Brett-Surman, M. K. 1979. Phylogeny and paleobiogeography of hadrosaurian dinosaurs. *Nature* 277:560–562.
- Brett-Surman, M. K., and J. R. Wagner. 2006. Discussion of character analysis of the appendicular anatomy in Campanian and Maastrichtian North American hadrosaurids—variation and ontogeny; pp. 125–169 in K. Carpenter (ed.), *Horns and Beaks: Ceratopsian and Ornithomimid Dinosaurs*. Indiana University Press, Bloomington and Indianapolis, Indiana.
- Brown, B. 1912. A crested dinosaur from the Edmonton Cretaceous. *Bulletin of the American Museum of Natural History* 31:131–136.
- Brown, B. 1914. *Corythosaurus casuarius*, a new crested dinosaur from the Belly River Cretaceous, with provisional classification of the family Trachodontidae. *Bulletin of the American Museum of Natural History* 33:559–565.
- Canudo, J. I., P. Cruzado-Caballero, and M. Moreno-Azanza. 2005. Possible theropod predation evidence in hadrosaurid dinosaurs from the upper Maastrichtian (Upper Cretaceous) of Arén (Huesca, Spain). *Kaupia. Darmstädter Beiträge zur Naturgeschichte* 14:9–13.
- Casnovas-Cladellas, M. L., J. V. Santafé-Llopis, and A. Isidro-Llorens. 1993. *Pararhabdodon isonense* n. gen. n. sp. (Dinosauria). *Estudio morfológico, radio-tomográfico y consideraciones biomecánicas*. *Paleontología i Evolució* 26–27:121–131.
- Casnovas-Cladellas, M. L., X. Pereda-Suberbiola, J. V. Santafé, and D.B. Weishampel. 1999. First lambeosaurine hadrosaurid from Europe: palaeobiogeographical implications. *Geological Magazine* 136:205–211.
- Cope, E. D. 1870. Synopsis of the extinct Batrachia, Reptilia, and Aves of North America. *Transactions of the American Philosophical Society* 14:1–252.
- Cruzado-Caballero, P. 2012. Restos directos de dinosaurios hadrosáuridos (Ornithopoda, Hadrosauridae) del Maastrichtense superior (Cretácico Superior) de Arén (Huesca). Ph. D. thesis, University of Zaragoza, Zaragoza, Spain, 411 pp.
- Cruzado-Caballero, P. and J. I. Canudo. 2005. Sobre la diversidad de los hadrosaurios en el Maastrichtense superior (Cretácico superior) de Arén (Huesca); pp. 115–116 in E. Bernáldez, E. Mayoral and A. Guerreiro dos Santos (eds.), XXI Jornadas de la Sociedad Española de Paleontología. Gestión e Investigación de la Paleontología en el Siglo XXI, Program and Abstracts, October 4–8, 2005, Sevilla.
- Cruzado-Caballero, P., J. I. Canudo, and J. I. Ruiz-Omeñaca. 2005. Nuevas evidencias de la presencia de hadrosaurios lambeosaurinos (Dinosauria) en el Maastrichtense superior de la Península Ibérica (Arén, Huesca). *Geogaceta* 38:47–50.
- Cruzado-Caballero, P., J. I. Canudo, and J. I. Ruiz-Omeñaca. 2009. Los fémures de Blasi (Arén, Huesca, Spain): una contribución a los hadrosauroides europeos del Maastrichtense superior; pp. 197–205 in P. Huerta Hurtado and F. Torcida Fernández-Baldor (eds.), *Actas de las IV Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno*. Colectivo Arqueológico y Paleontológico de Salas, Salas de los Infantes, Burgos, Spain.
- Cruzado-Caballero, P., X. Pereda-Suberbiola, and J. I. Ruiz-Omeñaca. 2010a. *Blasisaurus canudo* gen. et sp. nov., a new lambeosaurine dinosaur (Hadrosauridae) from the latest Cretaceous of Arén (Huesca, Spain). *Canadian Journal of Earth Sciences* 47:1507–1517.
- Cruzado-Caballero, P., J. I. Ruiz-Omeñaca, and J. I. Canudo. 2010b. Evidencias de la coexistencia de dinosaurios hadrosaurinos y lambeosaurinos en el Maastrichtiano superior de la Península Ibérica (Arén, Huesca, España). *Ameghiniana* 47:153–164.
- Cruzado-Caballero, P., J. I. Canudo, M. Moreno-Azanza, and J. I. Ruiz-Omeñaca. 2011. The complex fauna of European Maastrichtian

- hadrosaurids: contributions of the lambeosaurines from the Iberian Peninsula; pp. 33–37 in D. R. Braman, D. A. Eberth, D. C. Evans, and W. Taylor (eds.), International Hadrosaur Symposium at the Royal Tyrrell Museum of Palaeontology, September 22–23, 2011. Program and Abstracts. Royal Tyrrell Museum of Palaeontology, Drumheller.
- Cruzado-Caballero, P., J. I. Ruiz-Omeñaca, R. Gaete, V. Riera, O. Oms, and J. I. Canudo. 2013. 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. *Historical Biology*.
- Dalla Vecchia, F. M. 2009a. European hadrosauroids; pp. 45–74 in P. Huerta Hurtado and F. Torcida Fernández-Baldor (eds.), *Actas de las IV Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno*. Colectivo Arqueológico y Paleontológico de Salas, Salas de los Infantes, Burgos, Spain.
- Dalla Vecchia, F. M. 2009b. *Tethyshadros insularis*, a new hadrosauroid dinosaur (Ornithischia) from the Upper Cretaceous of Italy. *Journal of Vertebrate Paleontology* 29:1100–1116.
- Dilkes, D. W. 2000. Appendicular myology of the hadrosaurian dinosaur *Maiasaura peeblesorum* from the Late Cretaceous (Campanian) of Montana. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 90:87–125.
- Evans, D. C., and R. R. Reisz. 2007. Anatomy and relationships of *Lambeosaurus magnicristatus*, a crested hadrosaurid dinosaur (Ornithischia) from the Dinosaur Park Formation, Alberta. *Journal of Vertebrate Paleontology* 27:373–393.
- Evans, D. C., R. R. Reisz, and K. Dupuis. 2007. A juvenile *Parasaurolophus* (Ornithischia: Hadrosauridae) braincase from Dinosaur Provincial Park, Alberta, with comments on crest ontogeny in the genus. *Journal of Vertebrate Paleontology* 27:642–650.
- Fiorillo, A. R. 2008. Dinosaurs of Alaska: implications for the Cretaceous origin of Beringia; pp. 313–326 in R. B. Blodgett and G. D. Stanley Jr. (eds.), *The Terrane Puzzle: New Perspectives on Paleontology and Stratigraphy from the North American Cordillera*. Special Paper of the Geological Society of America 442.
- Gates, T. A., S. D. Sampson, C. R. Delgado de Jesús, L. E. Zanno, D. Eberth, R. Hernández-Rivera, M. C. Aguillón Martínez, and J. I. Kirkland. 2007. *Velafrons coahuilensis*, a new lambeosaurine hadrosaurid (Dinosauria: Ornithopoda) from the late Campanian Cerro del pueblo Formation, Coahuila, México. *Journal of Vertebrate Paleontology* 27:917–930.
- Gilmore, C. W. 1933. On the dinosaurian fauna of the Iren Dabasu Formation. *Bulletin of the American Museum of Natural History* 67:23–78.
- Godefroit, P., Y. Bolotsky, and V. Alifanov. 2003. A remarkable hollow-crested hadrosaur from Russia: an Asian origin for lambeosaurines. *Comptes Rendus Palevol* 2:143–151.
- Godefroit, P., Y. L. Bolotsky, and I. Y. Bolotsky. 2012. Osteology and relationships of *Oloroitian arharensis*, a hollow-crested hadrosaurid dinosaur from the latest Cretaceous of Far Eastern Russia. *Acta Palaeontologica Polonica* 57:527–560.
- Godefroit, P., Y. L. Bolotsky, and J. Van Itterbeeck. 2004. The lambeosaurine dinosaur *Amurosaurus riabinini*, from the Maastrichtian of Far Eastern Russia. *Acta Palaeontologica Polonica* 49:585–618.
- Godefroit, P., S. Zan, and L. Jin. 2000. *Charonosaurus jiyinensis* n. g., n. sp., a lambeosaurine dinosaur from the late Maastrichtian of north-eastern China. *Comptes Rendus de l'Académie des Sciences. Série IIa, Sciences de la Terre et des planètes* 330:875–882.
- Godefroit, P., S. Zan, and L. Jin. 2001. The Maastrichtian (Late Cretaceous) lambeosaurine dinosaur *Charonosaurus jiyinensis* from north-eastern China. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre* 71:119–168.
- Godefroit, P., S. Hai, T. Yu, and P. Lauters. 2008. New hadrosaurid dinosaurs from the uppermost Cretaceous of northeastern China. *Acta Palaeontologica Polonica* 53:47–74.
- Godefroit, P., Z.-M. Dong, P. Bultynck, H. Li, and L. Feng. 1998. Sino-Belgian Cooperation Program “Cretaceous dinosaurs and mammals from Inner Mongolia”; 1. New *Bactrosaurus* (Dinosauria, Hadrosauridae) material from Iren Dabasu (Inner Mongolia, P. R. China). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre* 68(Supplement):3–70.
- Goloboff, P., J. C. Farris, and K. C. Nixon. 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24:774–786.
- Head, J. J. 1998. A new species of basal hadrosaurid (Dinosauria, Ornithischia) from the Cenomanian of Texas. *Journal of Vertebrate Paleontology* 18:718–738.
- Head, J. J. 2001. A reanalysis of the phylogenetic position of *Eolambia caroljonesa* (Dinosauria, Iguanodontia). *Journal of Vertebrate Paleontology* 21:392–396.
- Horner, J. R., D. B. Weishampel, and C. A. Forster. 2004. Hadrosauridae; pp. 438–463 in D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*, second edition. University of California Press, Berkeley, California.
- Lambe, L. M. 1914. On *Gryposaurus notabilis*, a new genus and species of trachodont dinosaur from the Belly River Formation of Alberta, with a description of the skull of *Chasmosaurus belli*. *The Ottawa Naturalist* 27:145–155.
- Laurent, Y., L. Cavin, and M. Bilotte. 1999. Découverte d'un gisement à vertébrés dans le Maastrichtien supérieur des Petites-Pyrénées. *Comptes rendus de l'Académie des Sciences. Série IIa, Sciences de la Terre et des planètes* 328:781–787.
- Leidy, J. 1858. *Hadrosaurus foulkii*, a new saurian from the Cretaceous of New Jersey. *Proceedings of the Academy of Natural Sciences of Philadelphia* 10:215–218.
- López-Martínez, N., J. I. Canudo, L. Ardévol, X. Pereda-Suberbiola, X. Orue-Etxebarria, G. Cuenca-Bescós, J. I. Ruiz-Omeñaca, X. Murellaga, and M. Feist. 2001. New dinosaur sites correlated with Upper Maastrichtian pelagic deposits in the Spanish Pyrenees: implications for the dinosaur extinction pattern in Europe. *Cretaceous Research* 22:41–61.
- Lund, E. K., and T. A. Gates. 2006. A historical and biogeographical examination of hadrosaurian dinosaurs; pp. 263–276 in S. G. Lucas and R. M. Sullivan (eds.), *Late Cretaceous Vertebrates from the Western Interior*. New Mexico Museum of Natural History and Science Bulletin 35.
- Maddison, W. P., and D. R. Maddison. 2010. Mesquite: A Modular System for Evolutionary Analysis, version 2.73. Available at mesquiteproject.org. Accessed May 30, 2012.
- Marsh, O. C. 1881. Principal characters of American Jurassic dinosaurs. Part V. *American Journal of Science, Series 3* 21:417–423.
- Maryanska, T., and H. Osmólska. 1981. Postcranial anatomy of *Saurolophus angustirostris* with comments on other hadrosaurs. *Palaeontologica Polonica* 46:119–141.
- Nagao, T. 1936. *Nipponosaurus sachalinensis*, a new genus and species of trachodont dinosaur from Japanese Saghalien. *Journal of the Faculty of Science, Hokkaido Imperial University. Series 4, Geology and Mineralogy* 3:185–220.
- Nopcsa, F. 1903. *Telmatosaurus*, new name for the dinosaur *Limnosaurus*. *Geological Magazine, Series 4* 10:94–95.
- Ogg, J. G., G. Ogg, and F. M. Gradstein. 2008. *The Concise Geologic Time Scale*. Cambridge University Press, New York, vi + 177 pp.
- Oms, O., and J. I. Canudo. 2004. Datación magnetoestratigráfica de los dinosaurios del Cretácico terminal (Maastrichtense superior) de Arén (Huesca, Unidad Surpirenaica Central). *Geo-Temas* 6 5:51–54.
- Ostrom, J. H. 1961. Cranial morphology of the hadrosaurian dinosaurs of North America. *Bulletin of the American Museum of Natural History* 122:33–186.
- Owen, R. 1842. Report on British fossil reptiles. Part II. Reports of the British Association for the Advancement of Science 11:60–204.
- Parks, W. A. 1922. *Parasaurolophus walkeri*, a new genus and species of crested trachodont dinosaur. *University of Toronto Studies, Geological Series* 13:1–32.
- Parks, W. A. 1923. *Corythosaurus intermedius*, a new species of trachodont dinosaur. *University of Toronto Studies, Geological Series* 15:1–57.
- Pereda-Suberbiola, X. 2009. Biogeographical affinities of Late Cretaceous continental tetrapods of Europe: a review, affinités paléobiogéographiques des tétrapodes continentaux du Crétacé supérieur d'Europe: une mise au point. *Bulletin de la Société Géologique de France* 180:57–71.
- Pereda-Suberbiola, X., J. I. Canudo, P. Cruzado-Caballero, J. L. Barco, N. López-Martínez, O. Oms, and J. I. Ruiz-Omeñaca. 2009. The last hadrosaurid dinosaurs of Europe: a new lambeosaurine from the uppermost Cretaceous of Arén (Huesca, Spain). *Comptes Rendus Palevol* 8:559–572.
- Prieto-Marquez, A. 2007. Postcranial osteology of the hadrosaurid dinosaur *Brachylophosaurus canadensis* from the Late Cretaceous

- of Montana; pp. 91–116 in K. Carpenter (ed.), *Horns and Beaks: Ceratopsian and Ornithopod Dinosaurs*. Indiana University Press, Bloomington and Indianapolis, Indiana.
- Prieto-Marquez, A. 2010. Global phylogeny of Hadrosauridae (Dinosauria: Ornithopoda) using parsimony and Bayesian methods. *Zoological Journal of the Linnean Society* 159:435–502.
- Prieto-Marquez, A., and G. C. Salinas. 2010. A re-evaluation of *Secernosaurus koeneri* and *Kritosaurus australis* (Dinosauria, Hadrosauridae) from the Late Cretaceous of Argentina. *Journal of Vertebrate Paleontology* 30:813–837.
- Prieto-Marquez, A., and J. R. Wagner. 2009. *Pararhabdodon isonensis* and *Tsintaosaurus spinorhinus*: a new clade of lambeosaurine hadrosaurids from Eurasia. *Cretaceous Research* 30:1238–1246.
- Prieto-Márquez, A., R. Gaete, G. Rivas, A. Galobart, and M. Boada. 2006. Hadrosaurid dinosaurs from the Late Cretaceous of Spain: *Pararhabdodon isonensis* revisited and *Koutalisaurus kohlerorum*, gen. et sp. nov. *Journal of Vertebrate Paleontology* 26:929–943.
- Puértolas, E., J. I. Canudo, and P. Cruzado-Caballero. 2011. A new crocodylian from the Late Maastrichtian of Spain: implications for the initial radiation of crocodyloids. *PLoS ONE* 6:e20011.
- Pujalte, V., and B. Schmitz. 2005. Revisión de la estratigrafía del Grupo Tremp (“Garumniense”, Cuenca de Tremp-Graus, Pirineos meridionales). *Geogaceta* 38:79–82.
- Riera, V., O. Oms, R. Gaete, and A. Galobart. 2009. The end-Cretaceous dinosaur succession in Europe: the Tremp Basin record (Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology* 283:160–171.
- Rozhdestvensky, A. K. 1966. [New iguanodonts from Central Asia. Phylogenetic and taxonomic relationships between late Iguanodontidae and early Hadrosauridae]. *Palaeontologicheskii Zhurnal* 1966:103–116. [Russian; English translation: Rozhdestvensky, A. K. 1967. New iguanodonts from Central Asia. *International Geology Review* 9:556–566].
- Seeley, H. G. 1887. On the classification of the fossil animals commonly called Dinosauria. *Proceedings of the Royal Society of London* 43:165–171.
- Sereno, P. C. 1998. A rationale for phylogenetic definitions, with application to the higher-level taxonomy of Dinosauria. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 210:41–83.
- Sternberg, C. M. 1953. A new hadrosaur from the Oldman Formation of Alberta: discussion of nomenclature. *National Museum of Canada Natural History Papers* 128:1–12.
- Sues, H.-D., and A. Averianov. 2009. A new basal hadrosauroid dinosaur from the Late Cretaceous of Uzbekistan and the early radiation of duck-billed dinosaurs. *Proceedings of the Royal Society B* 267:2549–2555.
- Suzuki, D., D. B. Weishampel, and N. Minoura. 2004. *Nipponosaurus sachaliensis* (Dinosauria: Ornithopoda): anatomy and systematic position within Hadrosauridae. *Journal of Vertebrate Paleontology* 24:145–164.
- Walker, J. D., and J. W. Geissman (eds.). 2009. 2009 Geologic Time Scale. Geological Society of America. doi: 10.1130/2009.CTS004R2C.
- Weishampel, D. B., D. B. Norman, and D. Grigorescu. 1993. *Telmatosaurus transsylvanicus* from the Late Cretaceous of Romania: the most basal hadrosaurid dinosaur. *Palaeontology* 36:361–385.
- Williamson, T. E. 2000. Review of Hadrosauridae (Dinosauria, Ornithischia) from the San Juan Basin, New Mexico; pp. 191–213 in S. G. Lucas and A. B. Heckert (eds.), *Dinosaurs of New Mexico*. New Mexico Museum of Natural History and Science Bulletin 17.

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APPENDIX 1. Character coding scores for the 119 characters of Godefroit et al. (2012), to which we have added one more character from Prieto-Márquez (2010, character 82) in *Arenysaurus* and *Blasisaurus*.

*Arenysaurus*

????? ????? ????? ????1 ?1?1? ?1??? ?111 10111 01?01 1100?  
110?0 110?1 1111? ?1?1? 11111 ?1?1? ????? 101?? 1???? ?1?1?  
????0 0111? ????? ????0

*Blasisaurus*

????? ????? ????? ????? ????? ?1211 0???? ????? ????? ?????  
????0 11011 1111? ????? ????? ????? ????? ????? ????? ????1  
????0 01??? ????? ????1