

THE COMPLEX FAUNA OF EUROPEAN MAASTRICHTIAN HADROSAURIDS: CONTRIBUTIONS OF THE LAMBEOSAURINES FROM THE IBERIAN PENINSULA

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Introduction

The Iberian hadrosauroid fauna was very diverse and complex during the latest Cretaceous. It was composed of non-hadrosaurid hadrosauroids, hadrosaurines and lambeosaurines (Dalla Vecchia, 2009; Pereda-Suberbiola et al., 2009a, 2009b; Cruzado-Caballero et al., 2010a, 2010b). Up to four new genera and species of lambeosaurines have been described in the provinces of Lleida and Huesca (northeastern Spain, Fig. 1): *Pararhabdodon isonensis* Casanovas-Cladellas, Santafé-Llopis and Isidro-Llorens 1993 in the Sant Romà d'Abella site (Lleida); *Koutalisaurus kohlerorum* Prieto-Márquez, Gaete, Rivas, Galobart and Boada, 2006 in the Les Llaus site (Lleida); and *Arenysaurus ardevoli* Pereda-Suberbiola, Canudo, Cruzado-Caballero, Barco, López-Martínez, Oms and Ruiz-Omeñaca, 2009b and *Blasisaurus canudo* Cruzado-Caballero, Pereda-Suberbiola and Ruiz-Omeñaca, 2010a in Arén (Huesca; the Blasi 3 and Blasi 1 sites, respectively). The objective of this work is to introduce these lambeosaurines and try to establish their phylogeny and paleobiogeographical implications.

Geological frame

The Tremp Basin is located in the South-Central Pyrenees in the provinces of Huesca and Lleida (in the autonomous regions of Aragón and Catalonia, respectively). It has some excellent continuous outcrops with numerous hadrosaurid dinosaur sites. Stratigraphically, the sites of Sant Romà d'Abella and Les Llaus are in the Lower Red Unit of the Tremp Formation (or the Conques Formation of the Tremp Group). Biostratigraphic data (based on rudists, ostracods, charophytes and palynomorphs) give a Maastrichtian age to this unit (see references in Riera et al., 2009). Both sites are probably late Maastrichtian (Prieto-Márquez and Wagner, 2009). The Blasi sites are in the Arén Formation (Blasi 1) and the Grey Unit of the Tremp Formation (Blasi 3) (or La Posa Formation of the Tremp Group). Magnetostratigraphically, the Blasi sites are located in the upper part of a normal polarity chron correlated to chron C30n (late Maastrichtian, Oms and Canudo, 2004; Pereda-Suberbiola et al., 2009b: fig. 2), i.e. they are considerably younger than 67.7 Ma and slightly older than 65.8 Ma (Ogg et al., 2008). These rocks are transitionally overlain by lagoonal/marsh marls and red beds of the Lower Red Unit of the Tremp Formation, which is slightly younger in the Arén section (see references in López-Martínez et al., 2001).

Catalonian taxa

The first Catalonian taxon, *Pararhabdodon*, was initially classified as an iguanodontid, subsequently as a lambeosaurine and finally as a basal hadrosaurid (Casanovas-Cladellas et al., 1993; Casanovas et al., 1999; Prieto-Márquez et al., 2006). Its phylogenetic position is very problematic. Nowadays, it is considered to be a basal lambeosaurine on the basis of the following characters: the maxilla forms an acute embayment extending ventral to the jugal process between the jugal facet and the ectopterygoid shelf; the jugal facet of the maxilla is anteroposteriorly foreshortened, likely with a correspondingly anteroposteriorly narrow anterior jugal; the anterior dentary has a symphyseal process projecting medially such that the distance between the symphysis and the lateral surface of the dentary is three times the labiolingual thickness of the alveolar chamber. Moreover, *Pararhabdodon* shares with the Chinese hadrosaurid *Tsintaosaurus* an

elevation of the jugal facet of the maxilla that extends well above the level of the lateral margin of the ectopterygoid shelf, though they differ in the broader, subrectangular anterodorsal region of the maxilla (Prieto-Márquez and Wagner, 2009).

The second Catalanian taxon, *Koutalisaurus*, was described with a dentary that had previously been assigned to *Pararhabdodon* (Casanovas et al, 1999; Prieto-Márquez et al, 2006). Recently, Prieto-Márquez and Wagner (2009) have reviewed *Pararhabdodon*, *Koutalisaurus* and *Tsintaosaurus* remains and concluded that *Koutalisaurus* is most probably the junior synonym of *Pararhabdodon*. These authors argue that the dentaries of *Koutalisaurus* and *Tsintaosaurus* are indistinguishable, despite the posterodorsal orientation of the coronoid process, which appears to be an artifact of preparation (Prieto-Márquez et al., 2006).

As a result of these revisions, both Catalanian taxa are closer to *Tsintaosaurus*, forming a clade of basal lambeosaurines defined by three synapomorphies: the long medial projection of the symphyseal region of the dentary; the nearly straight anterior edentulous region of the dentary for articulation with the prementary; and a dorsally elevated maxilla-jugal joint; as well as one ambiguous synapomorphy: the ventral deflection of the anterior edentulous region of the dentary greater than 25°.

Aragonian taxa

In the province of Huesca the genera *Arenysaurus* and *Blasisaurus* have recently been described as basal lambeosaurines. Of these, *Arenysaurus ardevoli* preserves the most complete skeleton, which includes the first articulated partial skull of a European lambeosaurine. This skull is characterized by a very prominent frontal dome, more developed than in other adult specimens, and by the nearly vertical prequadratic process of the squamosal and jugal process of the postorbital. It differs from other lambeosaurines in having a unique combination of characters: a short frontal, with a posterior length/width ratio estimated at 0.5; the midline ridge of the parietal approximately at the level of the postorbital-squamosal bar; the parietal not interposed between the squamosals in the occipital surface of the skull; and the lateral side of the squamosal relatively low above the cotyloid cavity. Other characters of the cranial and post-cranial remains are: a robust jugal with the anterior process expanded dorsally, a straight dorsoposterior end of the jugal; maxilla with the ectopterygoid ridge ventrally turned; dentary with its anterior portion modestly deflected ventrally, a moderate diastema, and the presence of a mesial secondary ridge in maxillary and dentary teeth; glenoid and coracoid facets of the scapula forming an angle of 135°; straight humerus with deltopectoral crest oriented anteriorly, and pubis of type 5 *sensu* Brett-Surman and Wagner (2006; i.e. *Parasaurolophus* and *Bactrosaurus*; Pereda-Suberbiola et al., 2009b).

Blasisaurus canudo is characterized by a jugal with an autapomorphy resulting from the combination of a hook-like dorsal posterior process and a relatively narrow and D-shaped infratemporal fenestra. This jugal also presents a unique combination of characters: the posterior edge of the anterior process well-projected ventrally in a straight line (as in *Parasaurolophus*), a concave posteroventral edge beneath the infratemporal fenestra (as in *Sahaliyana* and hadrosaurines), and a very short jugal: the length/height ratio lower than 1.2 [only *Olorotitan*, *Velafrons* and *Tsintaosaurus* have such a low ratio, in these genera due to the height of the postorbital process (see Cruzado-Caballero et al., 2010a)].

According to Cruzado-Caballero et al. (2010a), *Blasisaurus* and *Arenysaurus* are closely related and are united by two synapomorphies: 1) a short dentary diastema, whose length between the first dentary tooth and the prementary is less than one-fifth the total length of the tooth row (the diastema is even shorter in *Arenysaurus* than in *Blasisaurus*, character 80 of Sues and Averianov, 2009); and 2) the dentary portion anterior to the tooth row in lateral view is approximately straight (character 79 of Sues and Averianov, 2009). On the other hand, these taxa differ in the dentary in several characters: in dorsal view, the dentary of *Blasisaurus* is rather straight, while that of *Arenysaurus* is concave lateromedially; the distance between the first dentary tooth and the inflection point of the symphysis is approximately 15.5% of the total length of the dental battery in *Blasisaurus*, while in *Arenysaurus* it is only 4.5%; the dorsal side of the coronoid process is convex in *Blasisaurus* and tip-like in *Arenysaurus*; the coronoid process of *Blasisaurus* extends anteriorly but not so much as in *Arenysaurus*; the dental battery of *Blasisaurus* is made up of 35 tooth

positions, as opposed to the 37 tooth positions of *Arenysaurus* (Pereda-Suberbiola et al., 2009b). Several characters in the dentary teeth are also different: in *Blasisaurus* they have no secondary ridges, unlike in *Arenysaurus* (Pereda-Suberbiola et al., 2009b); the height/length ratio of the dentary teeth in the anterior positions is greater in *Blasisaurus* (3.65) than in *Arenysaurus* (3.15). Finally, they differ in several characters in the jugal: the dorsoposterior side of the anterior process in *Arenysaurus* is straight unlike in *Blasisaurus*; the maxillary process of *Blasisaurus* is projected less laterally and more anteriorly than in *Arenysaurus*; the postorbital process of *Blasisaurus* is more posterodorsally oriented with regard to the long axis of the jugal (60°) than that of *Arenysaurus* (45°); the orbital fenestra is V-shaped in *Arenysaurus* unlike in *Blasisaurus*.

Phylogeny and paleobiogeographical implications

A cladistic study of the Aragonian taxa has been conducted. This followed the Evans and Reisz (2007) matrix and included character 82 from Sues and Averianov (2009) and the addition of *Arenysaurus*, *Blasisaurus* (this study) and *Velafrons* (data from Gates et al., 2007). We have not included the Catalonian taxa (*Pararhabdodon* and *Koutalisaurus*) due to the problematic assignation of the referred material of both species. *Arenysaurus* and *Blasisaurus* are placed within the tribe Parasaurolophini, and are more derived than *Charonosaurus* and basal to the node that includes the three *Parasaurolophus* species. In contrast to what is suggested by the previous analysis (Cruzado-Caballero et al., 2010a), *Arenysaurus* and *Blasisaurus* do not form a clade together, but are successive outgroups to the genus *Parasaurolophus*, *Blasisaurus* being more derived than *Arenysaurus*.

Paleobiogeographically, the presence of *Arenysaurus* and *Blasisaurus* and their relationships with other lambeosaurines, with the addition of *Pararhabdodon* and *Tsintaosaurus* as “tsintaosaurs” following Prieto-Márquez and Wagner (2009), suggest several geodispersal events (Fig. 2): 1) a dispersal event from Asia to Europe (*Pararhabdodon* or its ancestors), no later than the middle to late Campanian; 2) a second dispersal event from Asia to Europe (*Arenysaurus* or its ancestors) no later than the middle to late Campanian, as in the case of event 1; 3) a dispersal event from Europe to North America (*Parasaurolophus* spp. or its ancestors), probably beforehand or in the early Campanian; 4) a dispersal event from Asia to North America (*Velafrons* and *Lambeosaurus* spp. or their ancestors), beforehand or in the early Campanian, as in the case of event 3; and 5) a last dispersal event from North America to Asia (*Olorotitan* or its ancestors), in the mid- late Campanian-early Maastrichtian.

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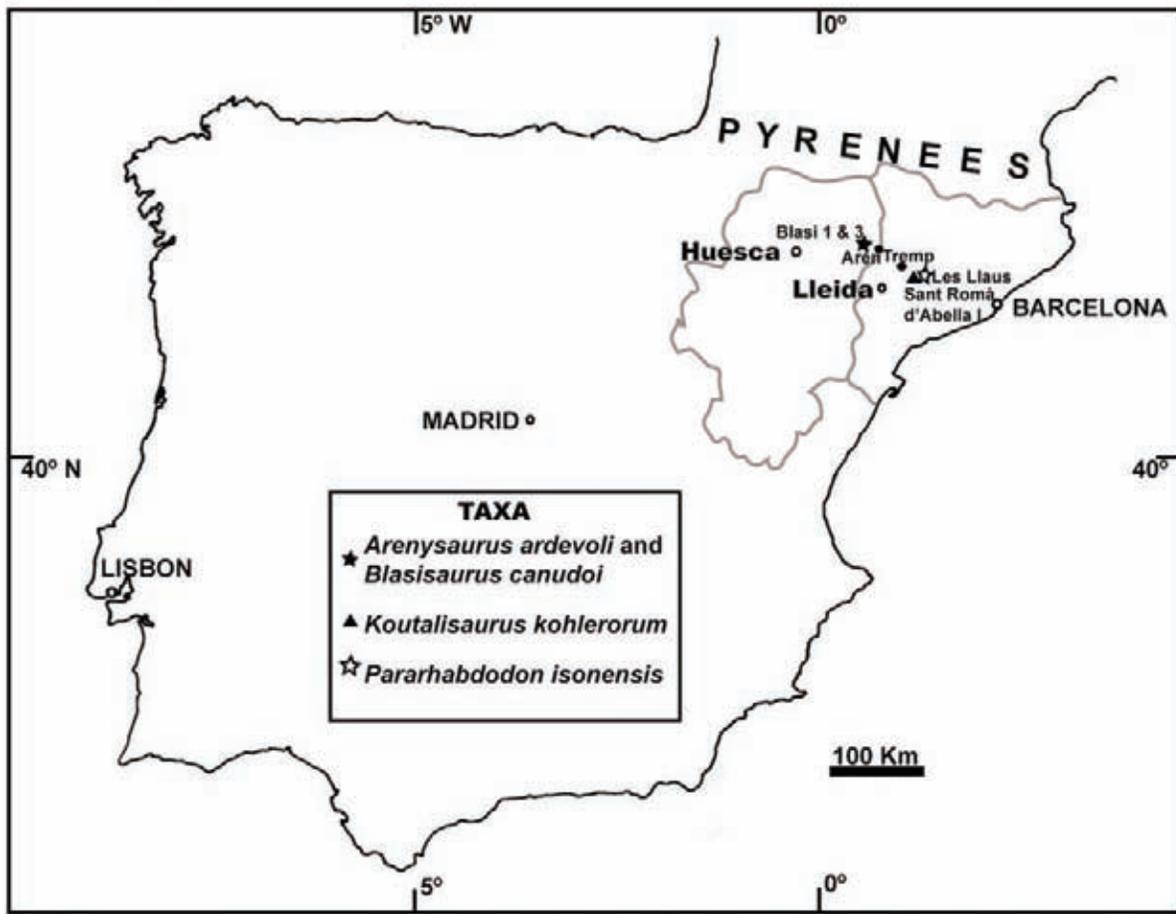


Fig. 1. Map showing the location of sites in Huesca and Lleida provinces (Spain). Gray lines show the outlines of the autonomous regions of Aragón and Catalonia.

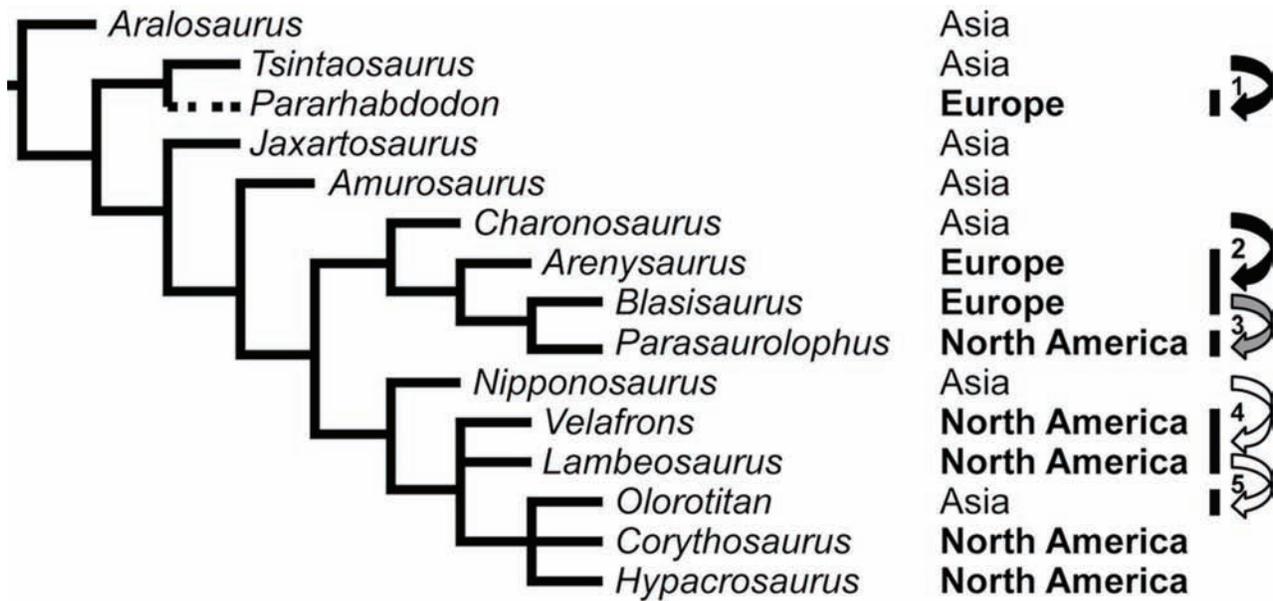


Fig. 2. Biogeographic implications of the lambeosaurine phylogenetic analysis ruled out in this paper. The relative position of *Pararhabdodon* is based on the phylogenetic analysis of Prieto-Márquez and Wagner (2009).