



New teeth of a basal Macronarian (Sauropoda) from the Jurassic–Cretaceous transition of Spain

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Abstract

In this work, a dentary, and several teeth from the Valdepalazuelos-Tenadas del Carrascal site (Burgos, Spain) are studied. Geologically, this site is situated at the base of the Rupelo Formation (Cuenca de Cameros), of Tithonian–Berriasian age. This formation has been interpreted as lacustrine–palustrine deposits with low gradient margins and with periodic changes in the water level. MDS-VPCR, 851 is a fragment of the rostral symphyseal zone of a right dentary, a robust bone with a rostral ridge on its lingual surface, large diameter foramina on the lingual surface, a wide Meckelian canal extending from the rostroventral margin, semicircular symphysis arranged rostrolingually, and with two alveoli preserving two erupting teeth each. Although the functional teeth have not been preserved, each alveolus could contain one active tooth and at least two replacement teeth. Eight maxillary and mandibular teeth are described, with a spatulate crown, a rough enamel surface, a D-shaped cross-section, and a very marked cingulum. The dentary and teeth from this site have evident differences with those of other taxa and specimens described in the Kimmeridgian–Berriasian of the Iberian Peninsula. Its greatest similarities are with *Camarasaurus*, but in the specimens from Valdepalazuelos there are characters that seem to be unique and differ from that taxon. Consequently, the specimens described here are identified as belonging to a basal macronarian, close to *Camarasaurus*. This work points to the existence of two macronarian sauropods in the Tithonian–Berriasian transit of the Cameros Basin, and increases the diversity of the Iberian record of that time period.

Keywords Dinosauria · Sauropoda · Camerosbasin · Rupelo Fm. · Tithonian · Jurassic-Cretaceous transition · Dentary · Tooth · Sauropoda · Macronaria · Paleobiodiversity · Spain

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Nuevos dientes de un macronario basal (Sauropoda) del Tránsito Jurásico-Cretácico de España

Resumen

En este trabajo se estudian un dentario y varios dientes procedentes del yacimiento Valdepalazuelos-Tenadas del Carrascal (Burgos, Spain), situado geológicamente en la base de la Formación Rupelo (Cuenca de Cameros), de edad Titoniense–Berriasiense. Esta formación se ha interpretado como depósitos lacustres-palustres con márgenes de gradiente bajo y con modificaciones periódicas del nivel del agua. MDS-VPCR,851 es un fragmento de la zona rostral sinfisial de un dentario derecho, es un hueso robusto con una cresta rostral en su superficie labial, forámenes de gran diámetro en la superficie lingual, un canal meckeliano amplio y extendido desde el margen rostroventral, sínfisis semicircular y dispuesta rostrolingualmente, y con dos alveolos que contienen dos dientes en erupción cada uno. Aunque los dientes funcionales no se han conservado, cada alvéolo podría contener un diente activo y al menos dos dientes de reemplazo. Se describen ocho dientes maxilares y mandibulares, de corona espatulada, superficie del esmalte rugosa, corona de sección transversal con forma en D y cingulo muy marcado. El dentario y los dientes de este yacimiento tienen diferencias evidentes con los de otros taxones y especímenes descritos en el Kimmeridgiense–Berriasiense de la península ibérica. Sus mayores similitudes se dan con *Camarasaurus*, pero en los especímenes de Valdepalazuelos hay caracteres que parecen ser únicos y le diferencian de ese taxón. Por consiguiente los especímenes descritos aquí se identifican como pertenecientes a un macronario basal, próximo a *Camarasaurus*. Este trabajo apunta a la existencia de dos saurópodos macronarios en el tránsito Titoniense–Berriasiense de la cuenca de Cameros, y aumenta la diversidad del registro ibérico de ese periodo temporal.

Palabras Clave Tránsito Jurásico · Cretácico · Dentario · Dientes · Sauropoda · Macronaria · Paleobiodiversidad · España

1 Introduction

The cranial remains of sauropods from the Kimmeridgian to the Berriasian of the Iberian Peninsula are scarce and correspond mostly to isolated teeth. The known Iberian sauropod record includes basal Macronaria (*Lourinhasaurus*, *Oceanotitan*), Titanosauriformes (*Galvesaurus*, *Lusotitan*, *Aragosaurus*), Diplodocoidea (*Dinheirosaurus* (= *Supersaurus*)) and Turiasauria (*Losillasaurus*, *Turiasaurus*, *Zby*) (Antunes & Mateus, 2003; Barco et al., 2005; Bonaparte & Mateus, 1999; Canudo et al., 2012; Casanovas et al., 2001; Dantas et al., 1998; Mateus et al., 2014; Mocho et al., 2019; Royo-Torres et al., 2006, 2014; Sanz et al., 1987). However, in most of them the type-specimen lacks cranial remains. So far, the scarce cranial material described corresponds to a partial basicranium of *Losillasaurus* from the Kimmeridgian of Valencia (Spain) (Casanovas et al., 2001), maxilla and dentaries of *Losillasaurus* from the Kimmeridgian-Tithonian of Teruel (Spain) (Royo-Torres et al., 2021); a dentary fragment with teeth attributed to Turiasauria from the Kimmeridgian of Asturias (Spain) (Canudo et al., 2010b); cranial material and teeth of *Turiasaurus* from Teruel (Spain) (Royo-Torres & Upchurch, 2012; Royo-Torres et al., 2006) and Asturias (Spain) (Canudo et al., 2010b) and isolated teeth included at *Aragosaurus* (Sanz et al., 1987). Nevertheless, Kimmeridgian–Tithonian sauropod teeth from the Iberian Peninsula show great morphological diversity (Mocho et al., 2017a, b; Royo-Torres et al., 2009), which is consistent with the large number of taxa described in this time interval. Turiasaurs, basal macronarians, titanosauriforms (including

brachiosaurids) and diplodocoids, and have been identified isolated teeth, showing practically the same diversity observed with postcranial remains (Canudo et al., 2010b; Dantas et al., 1998; Martínez et al., 2000; Mocho et al., 2019; Royo-Torres et al., 2009; Torcida Fernández-Baldor et al., 2020).

Most of the Kimmeridgian–Berriasian sauropod remains from the Iberian Peninsula have been recovered in the Lusitanian Basin (Portugal) and in the Maestrazgo Basin (Valencia and Teruel, Spain). Although two taxa, *Europatitan* and *Demandasaurus*, have been described from the late Barremian–early Aptian (Torcida Fernández-Baldor et al., 2011, 2017) of the Cameros Basin, however no sauropod taxa have been described during the Jurassic–Cretaceous transition of this latter basin. This contrasts with other parts of the Iberian Peninsula where several different taxa have been erected from the Kimmeridgian–Berriasian interval, as previously mentioned. Until the end of the 2010s, only scarce isolated sauropod remains from the Jurassic–Cretaceous transition of the Cameros Basin have been published (Canudo et al., 2010a).

In 2017, the excavations of the Valdepalazuelos-Tenadas del Carrascal site at the Burgos province (Spain) began (Online Resource). Since then, six digging campaigns (2017–2021, 2023) organized by the Museo de Dinosaurios de Salas de los Infantes (Salas de los Infantes, Burgos, Spain) have been developed. The site is a rich vertebrate fossil bonebed, especially in sauropod dinosaur remains, some of them semi-articulated but pending preparation. So far, only one isolated sauropod humerus, provisionally assigned

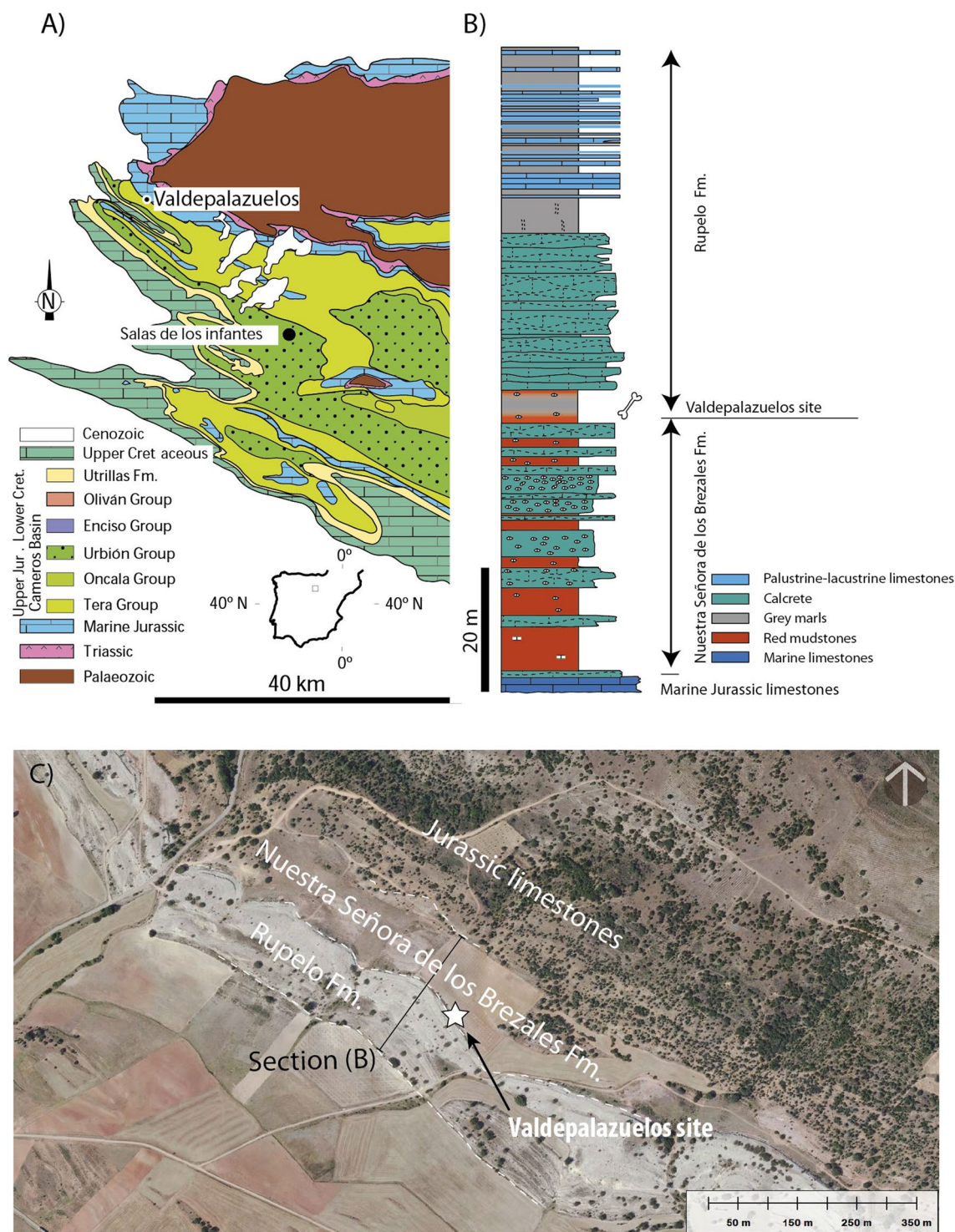


Fig. 1 Geological setting of the Valdepalazuelos site. **A** Geological map based on the groups proposed by Beuther, 1966. **B** Stratigraphic section of the Valdepalazuelos site. See location in **C**. **C** Aerial photograph indicating the position of the site and the stratigraphic section (**B**)

to a brachiosaurid titanosauriform close to *Duriantitan* (Barret et al., 2010), has been published (Torcida Fernández-Baldor et al., 2020). The aim of this paper is to describe the cranial material and isolated sauropod teeth found in the Valdepalazuelos site.

2 Geological setting

The Valdepalazuelos site is located on the Upper Jurassic–Lower Cretaceous non marine infill of the western Cameros basin (Fig. 1a). This basin was a rift during

this period and locally records a sedimentary succession mainly composed by siliciclastics (red mudstones, sandstones and conglomerates) and non-marine limestones. The stratigraphy of this basin has been established by different authors, who have proposed different stratigraphic frameworks, with lithostratigraphic units and depositional sequences (Clemente, 2010; Clemente & Pérez Arlucea, 1993; Platt, 1986; Salas & Casas, 1993). In the area, the pre-rift succession comprises Jurassic marine limestones. The first syn-rift unit is constituted by limestone-clast conglomerates at the base, which crops out discontinuously and show metric thickness in Valdepalazuelos area. In the places where the conglomerates are not present, a meter-scale laminar calcrete covers the marine limestones. The conglomerates are followed up by 45 m of red mudstones with intercalated calcretes that becomes more frequent and more mature upwards. This succession is the Nuestra Señora de los Brezales Formation (Platt, 1986). At the top of Nuestra Señora de los Brezales Fm. appears a 60 m thick limestone succession that corresponds with the Rupelo Fm. (Platt, 1986, 1989). The first 30 m of the limestones are constituted mainly by calcretes, except for a 4 m thick bed of marls at the base of the limestones. The Valdepalazuelos site is hosted within this marls bed (Fig. 1b, c). The upper 30 m of the limestone succession (Rupelo Formation) are constituted by palustrine – lacustrine limestones and marls with gastropod fragments, ostracods, charophytes, and a wide set of exposition features. Valdepalazuelos site locates in the transition between Las Viñas and Ladera members, within the Rupelo Formation, following the stratigraphic framework of Platt (1986); but following the stratigraphy of Clemente and Pérez Arlucea (1993), the site is located in the transition between Señora de los Brezales Formation and Boleras Formation. The age of the site is Tithonian–Berriasian following the biostratigraphic works in these units (Martín-Closas & Alonso Millán, 1998; Schudack & Schudack, 2009) although Sacristán-Horrajada et al. (2015) indicates that Boleras Formation is Tithonian in age based on the same references.

The site is located in a 2-m-thick grey marls bed that contains large sauropod bones (Torcida Fernández-Baldor et al., 2020), sauropod and theropod dinosaur teeth, coalified plant remains, gastropod molds, scattered carbonate nodules, and Jurassic limestone clasts. Some bones appear in anatomic connection and show good preservation; others are disconnected, and randomly scattered in the marls. Attached to some bones there are sandstone and conglomerate patches with millimetric or centimetric (0.5–2 cm) limestone clasts.

The palaeoenvironmental setting of this site corresponds to a shallow lacustrine carbonate precipitating lake or pond with an important clastic contribution. This pond probably developed on the transition between the alluvial systems and

the main lakes of the area, in zones dominated by pedogenic processes and calcrete formation. The coalified plant remains and the intense grey colour of the marls suggest anoxic sediment conditions facilitated the preservation of the organic matter. Despite the anatomic connection and good preservation of some bones, the patches of sandstone and conglomerate that are attached to the bones suggest the existence of floods that were able to move centimetric clast sizes.

3 Material and methods

3.1 Institutional abbreviations

MDS: Museo de Dinosaurios (Salas de los Infantes, Burgos, Spain).

VPCR: Yacimiento de Valdepalazuelos-Tenadas del Carrascal (Burgos, Spain).

CENIEH: Centro Nacional de Investigación sobre Evolución Humana (Burgos, Spain).

The material studied here is deposited in the “Museo de Dinosaurios de Salas de los Infantes” (Salas de los Infantes, Burgos, Spain): a dentary fragment MDS-VPCR,851 (2019 campaign); teeth MDS-VPCR,349 y MDS-VPCR,416 (2019 campaign); teeth MDS-VPCR,476, MDS-VPCR,560, MDS-VPCR,606 and MDS-VPCR,648 (2020 campaign).

In general, we use the standardized anatomical nomenclature based on the *Nomina Anatomica Avium* and *Nomina Anatomica Veterinaria* (see Harris, 2004). The morphological description of the dentition is at the macroscopic level. Measurements: length of the crown = the distance between the apex of the tooth and the base of the enamel cover, measured on the lingual side of the crown; tooth widths = the widest expansions of the tooth -mesiodistal, labiolingual—or root; Slenderness Index (SI) of Upchurch (1998) = ratio between length and mesiodistal width of the crown.

The types and terminology for wear facets are based in Janensch (1935–1936), Chatterjee & Zheng (2005) and Saegusa and Tomida (2011).

Five abrasion stages (Table 3) of functional teeth (F1–F5) were recognized based in Chatterjee & Zheng (2005).

Photos were taken with a photo camera Samsung ST200F. The dentary MDS-VPCR,851 (Figs. 2, 3) was analysed by micro-CT scan (VITomelX s 240 of GE Sensing & Inspections Technologies) at the “Centro Nacional de Investigación sobre Evolución Humana” (CENIEH) (Burgos, Spain). The resulting scan yielded 1672 images with 0.055 mm voxel size and image resolution of 1483 × 875 pixels. Raw data from the scan were imported, processed, and segmented with Avizo Software 2020.3 (Thermo Fisher Scientific). The 3D

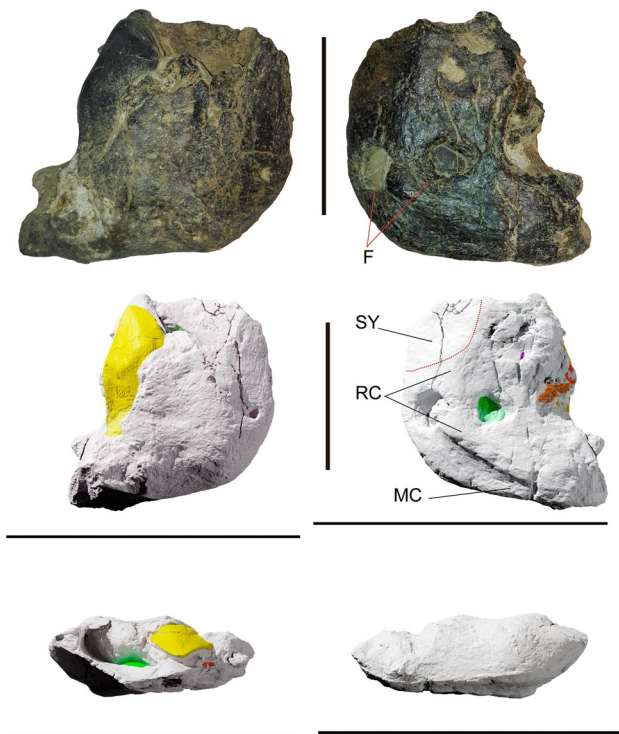


Fig. 2 MDS-VPCR,851 dentary of *Macronaria* indet., Valdepalazuelos-Tenadas del Carrascal site in views: **a** labial; **b** lingual. Images made from the scanning process, in views: **c** labial; **d** lingual; **e** dorsal; **f** ventral. In **c**, **d** and **f**, the replacement teeth that the piece retains have been highlighted in colour. *F*, foramina, *MC* Meckelian canal, *RC* rostral crest, *SY* symphysis. Red dashed line: limit of symphysis. Scale: 5 cm

models obtained (Figs. 2, 3) were rendered with Blender v. 2.90.1 (Blender Foundation).

Images have been digitally processed with Microsoft Office Picture Manager, Adobe Illustrator 2019[®] and Adobe Photoshop CC 2019[®].

4 Systematic palaeontology

Sauropoda Marsh, 1878

Neosauropoda Bonaparte, 1986

Macronaria, Wilson & Sereno, 1998.

Macronaria indet.

Material

MDS-VPCR,851 is a fragment of the right dentary, which internally preserves some teeth in formation (Figs. 2,3) MDS-VPCR,416 is a right maxillary tooth, which preserves the dental crown and the proximal part of the root (Fig. 4a–d); MDS-VPCR,560 is an almost complete left maxillary tooth, with only the apical end of the root missing (Fig. 4e–h); MDS-VPCR, 349 is a right

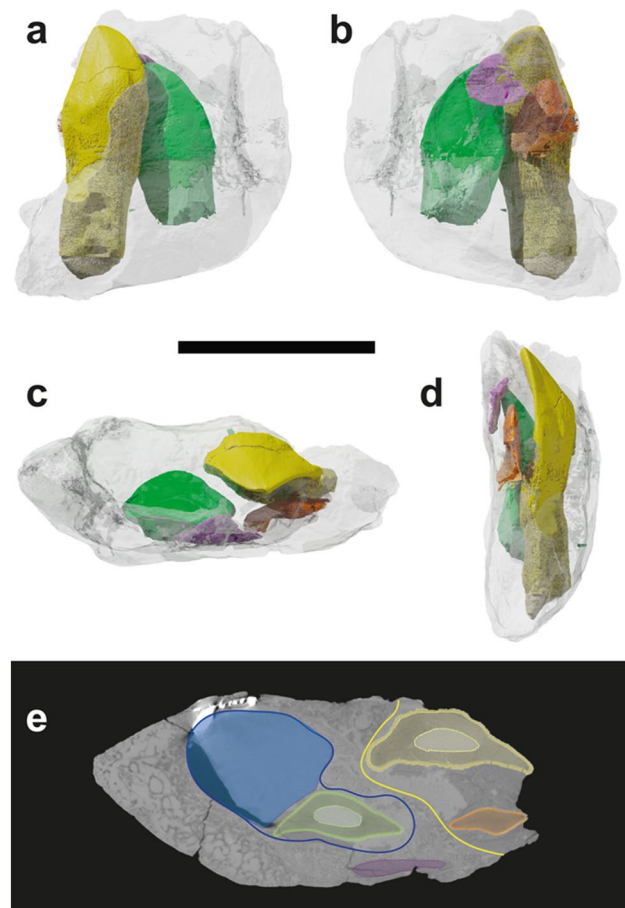


Fig. 3 MDS-VPCR,851 dentary of *Macronaria* indet., Valdepalazuelos-Tenadas del Carrascal site. Images processed from scans, with the replacement teeth highlighted in color, in views: **a** labial; **b** lingual; **c** dorsal; **d** caudal. Scan image, cross section of MDS-VPCR,851 in dorsal view, **e** with the position and extension of the dental alveoli; socket delimited with blue stripe: first dental socket, and with yellow stripe, second dental socket. Scale: 5 cm

dentary tooth, it preserves the dental crown, very worn at the apex, and the proximal part of the root (Fig. 4k, l); MDS-VPCR,606 is a dental crown, probably from the dentary, sectioned apicobasally and with pronounced wear due to use (Fig. 4m, n).

4.1 Dentary

MDS-VPCR,851 is a fragment of the rostral symphyseal zone of a right dentary (Figs. 2, 3). It is a robust bone, with a dorsoventral height of 76 mm, a labiolingual width of 29 mm, and a preserved rostrocaudal length of 84 mm. In medial view, the rostral margin is gently convex, producing a semicircular edge in the rostroventral corner, without developing a chin-like shape that diplodocoids present (Holland, 1924; Janensch, 1935–36; Salgado & Bonaparte, 1991). The lingual surface is flat, forming a thick ridge

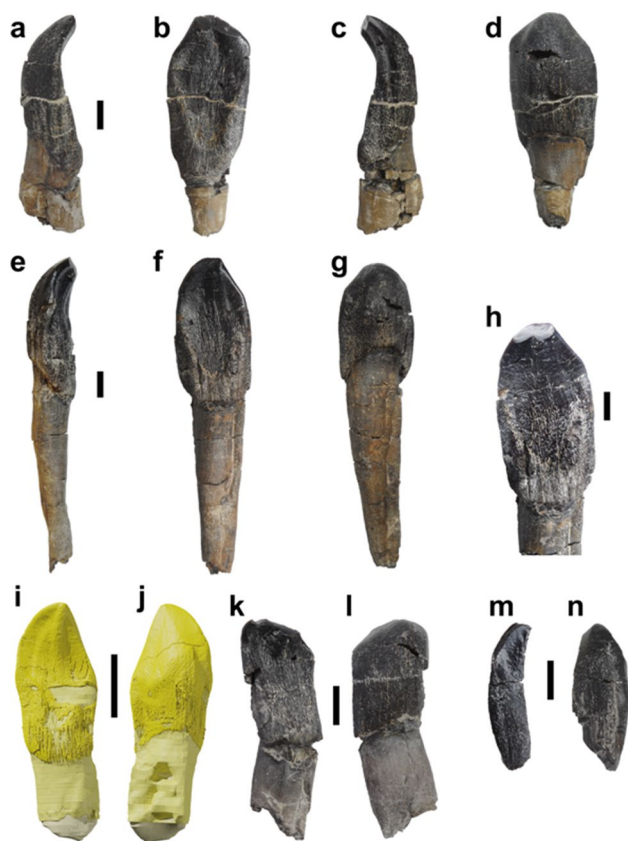


Fig. 4 Macronaria teeth indet., Valdepalazuelos-Tenadas del Carrascal site. MDS-VPCR,416 in views: **a** mesial; **b** lingual; **c** distal; **d** labial. MDS-VPCR,560 in views: **e** distal; **f** lingual; **g** labial; **h** lingual with detail of enamel roughness and apical wear facet. Replacement tooth in the MDS-VPCR,851 dentary in views: **i** lingual; **j** labial. MDS-VPCR,349 in views: **k** lingual; **h** labial. MDS-VPCR, 606 in views: **m** distal; **n** labial. Scale: 1 cm

rostrally (rostral crest), more developed in its ventral part (Figs. 2b,d and 3). The rostral crest is delimited ventrally and rostrally by a depressed area that runs parallel to the rostral and ventral border of the dentary. The ventral part of this depressed area is narrower, forming a groove which would correspond to the Meckelian canal, such as in specimens of *Camarasaurus lentus* Marsh, 1898, *Camarasaurus grandis* Marsh, 1877 and *Camarasaurus* sp. (Madsen et al., 1995). Wilson (2005) also interpreted this depressed zone as a continuation of the Meckelian canal in the titanosaur *Nemegtosaurus*, in the same way as interpreted by Poropat et al. (2023) in the dentary of *Diamantinasaurus*. In the dorsal part of the depressed area, the articular symphysis is located (Fig. 2b,d). The symphysis is semicircular in outline, slightly concave in its central part, arranged obliquely with respect to the lingual surface, and delimited caudally by the rostral crest.

On the lingual surface, there are three very large foramina in the ventral half of the dentary that communicate with the

dental alveoli (Fig. 2b,d): one subcircular near anterior border; another more posterior, subtriangular in shape, with the longest axis in the rostrocaudal direction, and which reveals part of a replacement tooth of the first alveolus; and a more caudally located third large foramen, fractured, apparently subcircular, that reveals a small part of a replacement tooth in the second preserved alveolus. Rostrocaudally, their respective diameters are: 15/15/17 mm (estimated).

The labial surface preserves a small anterior foramen 3 mm in diameter (Fig. 2a,c). The face is flat, with two dorsoventrally ridges that coincide with the position of the teeth inserted in the first and second dental alveoli. In the caudal area, part of the bony wall has been lost, revealing a large replacement tooth which is inserted into the second socket (Figs. 2, 3). The dorsal border has been largely lost, enabling observation in dorsal view the more developed replacement teeth of the first and second alveoli (Fig. 2e). In the rostral-most part of the first socket there is a large hole that corresponds to the place where the functional tooth would be located. In lateral view the ventral border is straight, and in ventral view it is protruding and narrow, like a crest displaced towards the medial aspect and running obliquely with respect to the rostrocaudal axis of the bone (Fig. 2a,c,f).

Several authors have studied the processes of formation and continuous replacement of teeth or polyphyodontia in vertebrates, with special interest in reptiles and dinosaurs (Woerdeman, 1921; Edmund, 1960; Osborn, 1970; D’Emic et al., 2013; Whitlock & Richman, 2013). The replacement of teeth in reptiles occurs in an alternating sequence that could have a sequence in “waves” that Woerdeman (1921) named with the term *Zahnreihen*. In this model there are simultaneously erupted and functional teeth, others in various degrees of formation, some of these prepared to replace those that are being detached. Various hypotheses have been put forward to explain how this dental replacement model would be produced (Edmund, 1960; Osborn, 1970; Whitlock & Richman, 2013). D’Emic et al. (2013) studied tooth replacement rates, formation time, and other factors that affect tooth replacement in sauropods. In the Valdepalazuelos dentary, the alternating dental replacement process can be partially observed, although limited to the first two positions of the dental series. The micro-CT scan of this dentary allowed us to see that in each of the two preserved dental alveoli of MDS-VPCR,851 there are two replacement teeth (Fig. 3). A similar situation occurs in *Camarasaurus*, with one functional tooth and two replacement teeth in the dentary, or up to three replacement teeth in the premaxilla (D’Emic et al., 2013; Wiersma & Sander, 2017). In diplodocoids there may be five replacement teeth, or even up to nine in the extreme case *Nigersaurus* (D’Emic et al., 2013; Sereno et al., 2007). The first alveolus has a deep hole in its rostral-most part, filled with matrix and close to the lateral face of the dentary, that would correspond to the place

of a functional tooth that has become detached (Figs. 2e and 3c,e). In addition, the alveolus has two replacement teeth, one with the crown fully formed and part of the root arranged in the middle region of the alveolus; and another smaller and flatter tooth, more caudally located and close to the medial surface of the dentary, which only consists of the apical half of the dental crown (Fig. 3b,c,e). The second alveolus preserves two teeth, the first tooth is located more rostrally, next to the lateral surface of the dentary, which has the complete dental crown and root, the latter approximately slightly less than 50% of its total length. The second tooth is more caudally located in the middle part of the alveolus, and only preserves the apex of the dental crown, either because it is in an early phase of formation or because of a preservation problem, since that part of the dentary is eroded and somewhat distorted (Fig. 3b,c,e).

The complete conservation of the first dental socket of MDS-VPCR,851 allows us to estimate that each socket would house up to three teeth: one functional and two replacement teeth. In their ontogenetic process, the teeth would begin to form in the most caudal part of the alveolus and next to the medial face of the dental tooth. The tooth development would start with the crown from its apex to its base, and then the root would progressively form in an apicobasal direction. The tooth in formation would migrate inside the alveolus from its caudal position to a more rostral position, and finally occupying a medial area within the dental cavity, where the maximum development of the crown would be reached before erupting. The final root development would occur when the tooth already has a functional character. The arrangement of teeth in dental series in MDS-VPCR, 851 is similar to that described for Eusauropoda, including *Camarasaurus* (D’Emic et al., 2013), and the dental replacement process described is consistent with the Zahnreihen model (Woerdeman, 1921). Therefore, throughout the dentary there are erupted and functional teeth, others detached, and other teeth about to erupt to replace the latter.

Among the isolated teeth found in Valdepalazuelos site, the most developed ones (MDS-VPCR,416 and 560) show a great degree of coincidence with those of MDS-VPCR,851.

Therefore, we assume that they all belong to individuals of the same taxon, and it cannot be ruled out that they belong to the same individual.

4.2 Teeth

The general morphology of the teeth from Valdepalazuelos site is spatulate. The mesial and distal edges are parallel up to two thirds of the crown, and in the apical third they curve towards the apex, gently on the mesial edge and somewhat concave at the distal edge. In the apical zone, the convergence of the mesial and distal edges of the crown forms an apex that is slightly distally deflected (Fig. 4i,j).

The enamel of the dental crowns exhibits a roughness (wrinkled surface). The presence of wrinkled tooth enamel was considered to be a synapomorphy of Eusauropoda by Wilson and Sereno (1998), but other works extend this derived state back into more basal sauropodomorphs such as *Chinshakiangosaurus* and melanorosaurids (Upchurch et al., 2007; Yates, 2007). This enamel ornamentation is formed by wavy apicobasal sulci and anastomosed ridges; the ridges slope towards the edges of the tooth (Fig. 4b,d,f,g,h). In the apical part of the crown, grooves and ridges are more widely spaced and their density is less than in the basal half of the crown. The root also presents a less pronounced rough surface formed by pits, grooves, and ridges.

MDS-VPCR,560 and MDS-VPCR,416 are large teeth (Table 1) from the rostral zone of the maxillary dental series (Janensch, 1935–36; Chure et al., 2010; Allain & Aquesbi, 2008). They show facets of lingual wear, which indicates their maxillary position (Carballido & Pol, 2010). In its middle part, the section of the dental crown is D-shaped. Its labial face has a very marked convexity in the mesiodistal direction, with a well-developed basiapically bulb that reaches the apex of the crown, and bordered on its flanks by two broad and shallow grooves, more pronounced at the base, that run along the entire crown from the base to the apex (Fig. 4d,g). The contact between the crown and the root develops a symmetrical contour that

Table 1 Parameters and indices of the teeth studied in this work

Pieza	L	MDCW	LLCW:	ABCL	BCW	ABRL	SI
MDS-VPCR,560	102	26	14	47/496*	18	14	18/19*
MDS-VPCR,416	66	25	14	45/5*	18	(18)	18/2*
MDS-VPCR,349	48	(17)	(09)	(28)	13	2	(28)
MDS-VPCR, 606	(31)	–	(09)	–	–	–	–
MDS-VPCR,648	–	–	–	–	–	–	–
MDS-VPCR, 476	–	–	–	–	–	–	–

L Total length apicobasal, *MDCW* mesiodistal width of the crown, *LLCW* labiolingual crown width, *ABCL* apicobasal length of the crown, *BCW* Width of the crown at its base, *ABRL* apicobasal length of the root, *SI* slenderness index, *LCW/AMDW* (Upchurch, 1998). All measurements in mm. Values in parentheses: incomplete measurement. Values with an asterisk: estimates

is convex towards apex. In the dental crowns of MDS-VPCR,560 and MDS-VPCR,416 the lingual face is concave mesiodistally and apicobasally, reaching its greatest depth in the axial area, and developing a ridge from the apex to the base of the crown. This happens in the anterior-most teeth of the dental series, as seen in an unerupted tooth from the dentary MDS-VPCR,851 (Fig. 4i,j). On the lingual side, there is a mesial and distal facet. These facets have a shallow concavity from the base to two-thirds of the height of the crown and separated from the lingual side by two pronounced ridges. These ridges laterally reach the cingulum which appears at the base of the crown as a broad thickening. In the contact area with the cingulum, the lingual face reaches its maximum depth, a character that could be unique of the teeth from this site. In lingual view, and unlike what occurs on the labial face, the contact between the crown and the root has a rectilinear path.

MDS-VPCR,560 preserves a large part of an elongated root tapering towards its basal tip (Fig. 4e–g). The root has a sub-elliptic section, with the major axis in a mesiodistal direction. The lingual and labial surfaces of the root are convex, with a more depressed and flattened area basiapically developed, which is parallel to the distal border on the lingual surface, and parallel to the mesial border on the labial surface. These depressed areas of the dental root have been described in other sauropod taxa, such as the titanosauriform *Sibirotitan* (Averianov & Sues, 2017); in both cases the depressed areas widen towards the root apex.

MDS-VPCR,349 is a smaller tooth, so it is considered from a caudal position within the dental series (Fig. 4k,l). The contact zone between the crown and the root is fractured and displaced, but the basal part of the root is preserved. The crown exhibits very marked apical wear, so the degree of deviation of the apex with respect to the apicobasal axis of the crown is not clearly observed. It has several morphological differences with respect to the teeth MDS-VPCR,560 and MDS-VPCR,416: greater enamel wear is observed on the labial surface of MDS-VPCR,349, although the apical wear facet is oriented towards the lingual side, which would indicate its maxillary position. It is also a slenderer tooth, with an estimated SI (Upchurch, 1998) around 2.8, higher if compared to the SI values between 1.9 and 2 of MDS-VPCR 560 and 416 (Table 1). On the labial side, the apicobasal bulb is less pronounced and can only be seen flanked in its distal area by a shallow groove that does not reach the apex of the crown. On the lingual side, the crest develops from the apex to practically the base of the crown, not very pronounced but delimiting two concave mesial and distal zones on the crown. The lateral ridges on the lingual surface are less pronounced and delimit narrow mesial and distal facets;

the cingulum is incomplete, but it is less thickened than in the maxillary teeth MDS-VPCR,560 and MDS-VPCR,416.

The studied teeth represent different stages of wear. The unerupted tooth of the dentary lacks wear or F1 phase (Chatterjee & Zheng, 2005; Wiersma & Sander, 2017). MDS-VPCR,560 shows lingually oriented wear facets: one apical, which coincides with the position of the lingual crest; and another facet developed towards the mesial edge on the carina (“drop-shaped” facet sensu Wiersma & Sander, 2017). In both mesial and distal margins of the apical area, the polished carinae can be seen due to wear, which extends slightly towards the labial and lingual surfaces, causing the removal of enamel ornamentation in those areas. In MDS-VPCR,416 the wear of the mesial carinae is poorly spread and more elongated than what is observed in MDS-VPCR,560. These two teeth would be in the F3 phase of tooth wear (Chatterjee & Zheng, 2005; Wiersma & Sander, 2017).

MDS-VPCR,349 would be located in a posterior position of the dental series. It has suffered a more pronounced wear process, with the distal carina much lowered, as well as an intense wear on the entire labial surface from the mesial to the distal margins of the apical area. There is a large loss of the enamel layer in the middle part of the apex of the labial face, due to a semicircular contour fracture, which was functional as it retains scratches due to dental friction. This tooth would be in an F4 wear phase (Chatterjee & Zheng, 2005; Wiersma & Sander, 2017). The greatest wear on the labial surface would place it on the dentary, but the orientation of the apical facet is lingual, which could imply its maxillary position. It could be that the tooth was originally arranged in an anomalous way within the maxilla, or because some trauma caused the apicobasal fracture; this disposition could explain its lingual and labial wear.

MDS-VPCR,606 is a small dental crown with an oblique apicobasal fracture, from which a distal position in the dental series can be inferred. The lingual face preserves the mesial half, but a large part of the labial face is also preserved at the distal zone (Fig. 4m,n). MDS-VPCR,606 shows a marked degree of wear due to use. The apex has an apical wear facet, oriented towards the labial margin, from which its location in the right dentary can be deduced (Carballido & Pol, 2010; Rauhut, 2003; Wiersma & Sander, 2017), and that it is continued with an elongated and narrow facet in the mesial carina. In labial view, the entire apical zone is worn and polished, with the roughness of the enamel totally disappeared. This wear continues near the mesial edge in a shallow groove lateral to the labial bulb, where the roughness of the enamel has completely disappeared. On the lingual side, the apical and mesial enamel roughness have been lost due to wear. MDS-VPCR,606 shows an advanced degree of wear, forming apical, mesial, and probably distal facets. In addition, there has been extensive polishing of the enamel of the dental crown, so it would be in an advanced F4 phase of

dental wear (Chatterjee & Zheng, 2005; Wiersma & Sander, 2017).

5 Discussion

The dentary and teeth from the Valdepalazuelos-Tenadas del Carrascal site have been compared with Iberian taxa and other specimens from the Kimmeridgian to the Berriasian of the Iberian Peninsula.

From the Kimmeridgian to the Berriasian of the Iberian Peninsula two sauropod dentaries have been described. Canudo et al. (2010b) described a sauropod dentary from the Kimmeridgian of Asturias and it was assigned to cf. *Turiasaurus*. The dentary of cf. *Turiasaurus* differs from MDS-VPCR,851 as it has several foramina on the labial side in a dorsal position (some located on a crest), and no Meckelian canal is observed. On the contrary, MDS-VPCR,851 has several large foramina on the lingual side in a ventral position, and only one small ventral foramen on the labial side is observed. MDS-VPCR,851 also has a well-developed Meckelian canal from the proximoventral side. Royo-Torres et al. (2021) described two dentaries of a *Losillasaurus* specimen from the San Lorenzo site (Teruel), Kimmeridgian to Tithonian in age. MDS-VPCR,851 differs from it as *Losillasaurus* dentary has an oblong symphysis section and a series of relatively small foramina aligned in a dorsal position, and MDS-VPCR,851 presents a semicircular symphysis with wide foramina in a ventral position of the lingual surface.

Comparing with Diplodocoidea dentaries, they have a subrectangular outline in dorsal view and develop a chin-like shape in their proximoventral part (Upchurch et al., 2004; Whitlock et al., 2011). On the contrary, MDS-VPCR,851 dentary does not have an U-contour, and lacks a chin-like shape.

A humerus assigned to Titanosauriformes brachiosaurid from the Valdepalazuelos site has been recovered (Torcida Fernández-Baldor et al., 2020) and, therefore, the dentary MDS-VPCR,851 will be compared with this clade of sauropods. Brachiosaurids such as *Giraffatitan* possess a dentary with a Meckelian canal that can develop from the proximal zone, as occurs in MDS-VPCR,851 (Janensch, 1935–36). The symphyseal zone in *Giraffatitan* develops basiapically and has a rectangular outline. Nevertheless, this area in MDS-VPCR,851 is more dorsally and is semicircular in appearance.

The dentaries of basal Macronarians, such as *Camarasaurus*, have relatively small foramina on the labial surface and their symphyseal area is similar in position and shape to that of brachiosaurids (Madsen et al., 1995; Marsh, 1898). These two characters differ from what is observed in MDS-VPCR,851, as it has large foramina on the lingual surface, and a semicircular symphyseal area in a mid-dorsal position.

Unlike the dentary, the comparative study of the teeth within MDS-VPCR,851 and the isolated teeth described in this work are more useful to compare and identify the specimens from Valdepalazuelos.

The teeth from Valdepalazuelos site differ from those assigned to Turiasauria. Teeth of turiasaurians have a heart shape, denticles on the mesial and distal edges, and a low slenderness value SI (Upchurch, 1998) of 1.3 to 1.4 approximately (Mateus et al., 2014; Royo-Torres et al., 2006). The teeth studied here are generally spatulate in shape, without marginal denticles, and relatively slender, SI value (Upchurch, 1998) of 1.8 to 2.

The sauropod teeth from Valdepalazuelos also have evident differences with those assigned to diplodocoids that have very slender pencil-type teeth, with long straight dental crowns; mesiodistal and linguolabial low widths, SI values higher than 4; and facets of apical wear inclined lingually or labially according to their position (Calvo, 1994; Upchurch et al., 2004). On the contrary, the Valdepalazuelos teeth are spatulate, mesiodistally broad, labially concave and lingually convex, have SI values between 1.8 and 2, and have V-shaped enamel facets extending from the apex to the mesial and distal sides.

In the Iberian Peninsula, a tooth classified as Diplodocidae indet. has been described from the Late Jurassic of Asturias (Martínez et al., 2000). This tooth is cylindrical, with the distal part inclined lingually and some shallow grooves that run along the mesial and distal edges of the crown in labial view. These characters clearly differentiate it from the teeth of Valdepalazuelos as they are spatulate and regularly curved in a basiapical direction. In the Jurassic–Cretaceous transition of Teruel, a particular diplodocoid tooth assigned to Diplodocoidea? indet. has been described. It is cylindrical, with smooth enamel, with a lingually inclined wear facet and an expansion in the final part of the crown (Cuenca-Bescós et al., 1997). This tooth has not been related to any specific taxon and differs from the spatulate teeth with rough enamel studied in this work.

Differences with the teeth assigned to brachiosaurids are also observed as they have a pencil-shape, asymmetric in lingual view, with an inclination of the apical part of the crown towards the lingual face, without a cingulum, high slenderness SI values between 2 and 4, slightly expanded apices, and wear facets restricted to the apex of the crown (Janensch, 1935–36; Calvo, 1994; Upchurch & Barret, 2000; Rauhut, 2001; Chure et al., 2010; Mocho et al., 2017b). Unlike brachiosaurids, the teeth of Valdepalazuelos are spoon-shaped, maintain a symmetry in lingual view (except in their apical part), they have a cingulum between crown and root, they have a continuous basoapical curvature in mesial view, their slenderness SI value is lower between 1.8 and 2, the apical part is expanded, and the wear facets develop apically and on the mesial and distal carinae.

The teeth of Valdepalazuelos-Tenadas del Carrascal present a spatulate morphology that distinguishes them from other taxa of the Jurassic–Cretaceous transition of the Iberian Peninsula, such as turiasaurs, diplodocoids and brachiosaurids. Morphologically, the set of characters of the teeth from Valdepalazuelos are quite similar to *Camarasaurus* from the Late Jurassic of the United States (Madsen et al., 1995; Marsh, 1877, 1898; Ostrom & McIntosh, 1966), as well as to some isolated teeth described in Portugal from rocks of similar ages (Mocho et al., 2016, 2017b). The characters shared by the teeth of Valdepalazuelos and basal macronarians, such as *Camarasaurus*, are: spatulate, mesiodistally wide and linguolabially compressed crown, SI values between 1.8 and 2 (Chure et al., 2010), lingually curved apices, developed lingual crest, crown with D-shaped cross-section and rough enamel surface. A tooth from the Upper Jurassic of the “Costa de los dinosaurios” at Asturias (Spain) was described as *Camarasauridae* (Martínez et al., 2000), later related to *Neosodon* by Royo-Torres and Canudo (2003), a taxon that has been identified as a turiasaur (Royo-Torres, 2009). It has a rhombic shape, and rough enamel that on the lingual side it is only developed in the basal part of the crown. On the contrary, the Valdepalazuelos teeth are spatulate and have the enamel covering practically the entire surface of the dental crown.

The existence of wide foramina on the lingual side and the rostrolingual arrangement of the symphyseal area in the dentary MDS-VPCR,851 are characteristics that differentiate it from other sauropod taxa described from the Kimmeridgian to the Berriasian of the Iberian Peninsula. Likewise, the dental crowns from Valdepalazuelos have a basoapically concave lingual face with its greatest depth in the area of contact with the cingulum, a character that could be unique to these teeth. This could indicate the existence of a new unknown taxon in the Kimmeridgian–Berriasian of the Iberian record. New findings and studies on the fossils collected in Valdepalazuelos would be necessary to establish a more precise identification of the specimen described in this work. The current data we have, allow us to establish a tentative identification of the sauropod remains studied in this work as a basal macronarian aff. *Camarasaurus*. In the Iberian Peninsula, *Lourinhasaurus* (Dantas et al., 1998) is the only camarasaurid described from the Kimmeridgian–Berriasian age and shares many similarities with *Camarasaurus grandis* (Mocho et al., 2014). However, it is not possible to compare the sauropod from Torrelara studied here with *Lourinhasaurus*, since we do not know the teeth of the Portuguese taxon.

This is the first record of basal Macronaria in the western sector of the Cameros Basin, whose sauropod record of the Tithonian–Berriasian transition also contains evidence of brachiosaurids, non-titanosaurian titanosauriforms, and diplodocoids (Torcida Fernández-Baldor et al., 2020, 2021,

2022). In the Valdepalazuelos site, the works published so far point to the presence of two macronarian taxa, but there is a large number of fossils pending preparation and study, necessary to obtain more evidence for the identification of the sauropod specimens from the site. Recent work in the Cameros Basin is providing information on a high diversity of sauropods, which corresponds to what is found in the Kimmeridgian–Berriasian record of the Iberian Peninsula.

6 Conclusions

For the first time, sauropod teeth from the Jurassic–Cretaceous transition from the occidental sector of the Cameros Basin (North of Spain) are described. Until now, sauropod remains in this basin were scarce and fragmentary. The teeth studied here come from the Valdepalazuelos-Tenadas del Carrascal site (Burgos, Spain) of Tithonian–Berriasian age. Seven teeth and a jaw fragment have been described. Due to their similar morphology, are considered to be from the same taxon, and could even be from the same individual. These dentary and teeth have characters that could be indicative of a taxon not known in the sauropod record of that age. The morphology of these teeth is consistent with basal macronarians close to *Camarasaurus*. The only sauropod fossil described so far in Valdepalazuelos is a humerus morphologically close to the brachiosaurid *Duriatitan*. This would imply the presence of two different macronarian taxa in the Valdepalazuelos site, although future studies will be necessary to prove this. The new data we present here reinforces the evidence of the presence of basal macronarians during the Tithonian–Berriasian of the Cameros Basin that remain for the moment undescribed.

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Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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