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Theropod teeth from the upper Barremian (Lower Cretaceous) of Vadillos-1, Spain

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A B S T R A C T

The upper Barremian (Lower Cretaceous) palaeontological site of Vadillos-1 is located in the North of the Cuenca Province, Spain. It includes a sedimentary succession in "Weald" facies of brown and grey mudstones and red clays, corresponding to an alluvial-palustrine muddy floodplain. Among the collected fossils, there are several vertebrate remains belonging to theropod dinosaurs, including some teeth (VD1-197, VD1-178, VD1-179, and VD1-180) that are described and identified for the first time. The taxonomic assignment was approached following two methods beside the classical consideration of their overall morphology: a cladistic analysis performed on a tooth-based data matrix, and a discriminant analysis performed on a large dataset including measurements of non-avian theropod teeth. The DSDI > 1.2 and the braided enamel present seen in VD1-197 suggest that the specimen belongs to a Dromaeosauridae or a non-tyrannosaurid Tyrannosauroidea, but the cladistics analysis classifies this tooth in the latest. The analysis showed that VD1-178, VD1-179 and VD1-180 can be ascribed to Dromaeosauridae. The dental features characteristic of this clade and present in our specimens include a DSDI > 1.2, labial and lingual depressions, and a braided enamel surface texture, which allows to place these teeth more specifically within the Eudromaeosauria. The results show, for the first time, the presence of dromaeosaurids and possibly non-Tyrannosaurid Tyrannosauroidea at Vadillos-1, thus providing new data to the European Barremian record, and contributing to the updating the geographic distribution of these dinosaurs.

1. Introduction

The theropod record from the Barremian of Europe is relatively well-known, with occurrences in England (Milner, 2002; Sweetman, 2004), France (Allain et al., 2014) and Portugal (Figueiredo et al., 2021). Except for those in Alonso et al. (2017, 2018), most records of Spanish Barremian theropod teeth are imprecise, the majority of the papers reporting isolated theropod teeth having been published more than twenty years ago (e.g., Canudo et al., 1997; Ruiz-Omeñaca and Canudo, 2003), when taxonomic tools such as cladistics or complex morphometrics were not of common use as today, and the taxonomic assignments relied mainly on the overall morphology of the teeth.

Here we describe several newly discovered theropod teeth from the upper Barremian (Lower Cretaceous) vertebrate site of Vadillos-1 (Cuenca, Spain), presenting a first approach to their taxonomic assignment. For this purpose, the teeth were studied using modern techniques applied to this type of fossils, with the aim of obtaining the most precise taxonomic identification possible and thus, providing new data to the poorly known theropod record from this interval. The theropod teeth described here come from sediments collected at Vadillos-1, which have also yielded a rich assemblage consisting of other microfossils such as

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charophytes, palynomorphs, ostracods and a variety of vertebrate small remains belonging to fish (scales and teeth), amphibians and crocodilians (teeth, scute and eggshells) (e.g., Barroso-Barcenilla et al., 2017; Ruiz-Galván et al., 2017; Bravo et al., 2018; Barrón et al., 2019). The presence of theropod dinosaurs as well as other reptile fossils, such as crocodiles, ornithopod and ankylosaur dinosaurs is not new for the palaeontological site of Vadillos-1 since they were known from larger-sized fossils (Barroso-Barcenilla et al., 2017). However, to date no detailed description of the theropod remains from this site had been carried out. This paper aims to provide a description and taxonomic assignment of these theropod teeth, as well as to consider the relevance of these new records.

Anatomical abbreviations. AL: apical length, the basoapical extent of the mesial margin of the crown. CBL: crown base length, the mesiodistal length of the crown at the level of the cervix. CBW: crown base width, the labiolingual width of the crown at the cervix level, perpendicular to CBL. CBR: crown base ratio (CBW/CBL), a measure of the lingual compression. CH: crown height, the basoapical extent of the distal margin of the crown from the most distal point of the cervix to the most apical point of the apex. CHR: crown height ratio (CH/CBL), a measure of the crown elongation. MC: mesiocentral denticle density, the number of per 5 mm on the mesial carina at mid-crown. DC: distocentral denticle density, the number of per 5 mm on the distal carina at mid-crown. MA: mesioapical denticle density. DA: distoapical denticle density. CA: crown angle. MSL: mesial serrated carina length. MCL: mid-crown length. MCR: mid-crown ratio. MCW: mid-crown width. DDH: distal denticle height. DDL: distal denticle length. DSDI: denticle size density index (MC/DC), expressing the difference in size between the mesial and distal denticles. DSL: distal serrated carina length. MCAL: mesial carina length. DCAL: distal carina length. lri: longitudinal ridges. lad: labial depression. lid: lingual depression. tun: transverse undulation. ids: interdenticular sulci.

2. Geographical and geological context

The Barremian vertebrate site of Vadillos-1 (European Datum 1950: Lat. 40º 32' 20.2700'' , Long. 2º 8' 31.21''; UTM 30 X 572663, Y 4488011 N) is located in the Beteta Municipality, at the northern part of Cuenca Province, Central-eastern Spain. It is situated in the area known as the Beteta Georges, close to the village of Puente de Vadillos that gives its name to the site (Fig. 1A). The Lower Cretaceous in the region is represented mainly by continental strata without direct marine influence (Poyato-Ariza et al., 1998), although reworked marine fossils coming from the underlying Jurassic sandy limestones are occasionally found. In the area of Vadillos-1, the upper Barremian is widely exposed as an anticline fold, consisting mainly of mudstones rich in vertebrate remains (Barroso-Barcenilla et al., 2017, fig. 1[1-6]; Bravo et al., 2018).

The section of Vadillos-1 outcrops in “Weald” facies materials belonging to El Collado Sandstone and Clay Formation. It consists, from base to top, of a succession of 15 m of brown mudstones (B level), 7.5 m of grey mudstones (G level), and >4 m of red clays (R level). These three levels are separated by gradual boundaries and include interbedded gypsum, carbonate nodules (in B and G levels) and channels with oncolite sandstones (in R level) (Fig. 1B). The teeth described here paper were recovered after sieve-washing of sediments from the upper part of the grey mudstones (G level) of Vadillos-1. The sedimentary palaeoenvironment in which this succession was deposited has been interpreted by Barroso-Barcenilla et al. (2017) as an alluvial-palustrine floodplain.

3. Material and methods

The teeth here described were found in the last fieldwork season conducted in Vadillos-1 in 2018. 200 kg of clayish sediment from G level was sieve-washed in the lab to recover any small-sized fossils, mainly vertebrates, contained in the sediments. The procedure followed the standard methods used to retrieve this type of fossil remains (see for instance, Eaton, 2004). The sediment, once perfectly dry, was introduced in buckets with water for 24 h to obtain a disaggregate material that was subsequently screen-washed with pressurized water through sieves of 0.5 mm mesh size. Several washing cycles were needed until the silty-clay fraction was completely removed and a loose residue that could be picked for fossils obtained. The residue was divided into two size fractions using a 2 mm sieve; the fossils in the larger fraction (>2 mm) were picked directly with the naked eye, whereas for those in the smaller fraction (2–0.5 mm) a Motic SMZ-168 stereomicroscope and a Leica MZ16A were used. The fossils described here are temporarily stored at the University of Alcalá and will eventually be housed in the Paleontological Museum of Castilla-La Mancha (MUPA) once their study is conducted.

The terminology followed in this paper is based on the work of Hendrickx et al. (2015). Both qualitative and quantitative morphological features were considered to assign the teeth to the most inclusive clade. To this aim, a cladistic analysis based on tooth-based data matrix was performed as well as a discriminant analysis using a dataset of theropod teeth measurement.

Cladistic analysis. A cladistic analysis based on qualitative characters was carried out to determine the phylogenetic affinities of the four isolated theropod teeth from Hoces de Beteta. This analysis was performed using the tooth-crown-only data matrix of non-avian theropods created by Hendrickx et al. (2015) and recent updates by Meso et al. (2021, 2022). This data matrix includes 91 tooth-based characters scored across 103 genus-level terminals, which are bracketed between the basal saurischian *Herrerasaurus* and the basal avialan *Archaeopteryx*. The four isolated teeth from Vadillos-1 were treated as floating operational taxonomic units (OTUs) and scored separately following the recommendations made by Hendrickx et al. (2020a) to identify isolated theropod teeth.

The cladistics analysis was performed following the methodology detailed in previous works (Young et al., 2019; Hendrickx et al., 2020a; Meso et al., 2021, 2022) using TNT 1.1 (Goloboff et al., 2008). The search strategy consisted of a combination of the tree-search algorithms Wagner trees (“Traditional search” with 1000 replications, keeping 10 trees per replication) and TBR branch swapping. Afterwards, sectorial searches, ratchet (perturbation phase stopped after 20) and tree fusing (5 rounds), until 100 hits of the same minimum tree length were obtained (“New Technology Search”). Besides, a final round of TBR branch swapping was subjected.

Discriminant analysis. In order to classify and predict the optimal classifications of the here studied theropod teeth, and if is possible to discriminate them from those of other theropods (i.e., family-level) based on quantitative data, a discriminant function analysis (DFA) has been carried out using the data set compiled by Meso et al. (2022). This dataset includes fifteen measurements, of which only eleven could be used for this study due to the incompleteness of the material (i.e., CBL, CBW, CH, AL, MCL, MCW, MSL, LAF, LIF, MDL, DCL), taken in 1374 teeth belonging to 91 taxa (i.e., 86 species and five indeterminate family-based taxa) separated into 21 monophyletic or paraphyletic groups. This dataset includes the measurements compiled by Hendrickx et al. (2015), modified by Young et al. (2019) and Hendrickx et al. (2020a,b), and recently updated by Meso et al. (2022).

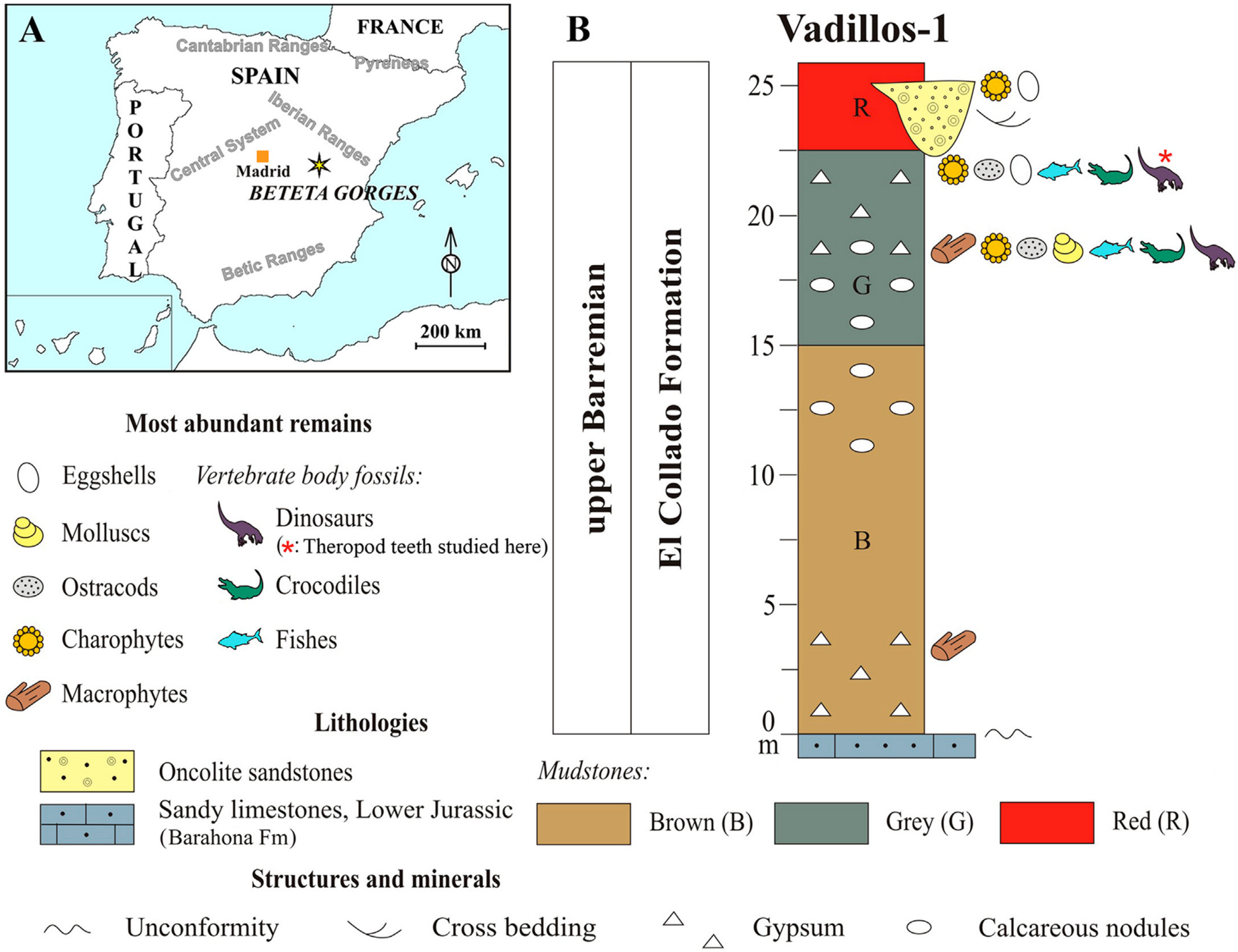


Fig. 1. A) General geographic location of the upper Barremian fossil site of Vadillos-1 (Cuenca, Spain) in the context of the Iberian Peninsula. B) Simplified biostratigraphic section of Vadillos-1, showing the main lithological characteristics and the most abundant remains, including the theropod teeth studied here (asterisk).

The discriminant function analysis (DFA) has been performed according to the recommendations of Young et al. (2019), in which all variables were log-transformed to normalize the quantitative variables. Finally, the DFA was run in Past version 4.10 (Hammer et al., 2001) using the discriminant analysis function, and treating each tooth as unknown taxa.

4. Description of the material

Dinosauria Owen, 1842
Saurischia Seeley, 1887
Theropoda Marsh, 1881
Coelurosauria von Huene, 1914

Material. VD1-197 (Fig. 2, Table 1)
Specimen VD1-197 (Fig. 2) includes the apical portion of the crown. This crown is triangular in outline, with a ziphodont morphology, with the distal part of the crown not curved distally (Fig. 2A1–A10). The apex is rounded. The mesial and distal profiles are straight (Fig. 2A1–A6). The lingual and labial surfaces remain convex from the base to the apex. The crown shows well-developed denticulated mesial and distal carinae. The extension of the preserved mesial carina (mcal) on the crown is 11.8 mm and distal carina length (dcal) is 10 mm. In mesial view, the carina is centrally positioned on the crown (Fig. 2A3). In distal view, the carina extends to the cervix and is also centrally positioned (Fig. 2A4). The denticles of the mesial carina are less developed compared to those from the distal carina (Fig. 2A7–A8), with a DSDI of 1.23 (Table 1). The mesial carina possesses 20 denticles per 5 mm at mid-crown, density gradually increasing apically and basally. The distal denticle density is 16.25 per 5 mm at mid-crown. In the two carinae, 34 denticles are present, being those from the mesial carina worst preserved. Morphologically, the denticles are slightly sub-rectangular in shape and the apicobasal axis of the denticles is larger than the mesiodistal length, giving them a sub-rectangular to subrounded outline (Fig. 2A9, A11). The interdenticular space is well defined. The enamel surface is badly preserved, although in a better state on the labial area, close to the apex and the carinae. Nevertheless, it is possible to observe that the enamel surface texture is braided, i.e., the enamel surface texture is made of alternating and interweaving grooves and sinuous very long ridges apicobasally oriented on the crown (Fig. 2A10).

Dromaeosauridae Matthew and Brown, 1922
Eudromaeosauria Longrich and Currie, 2009

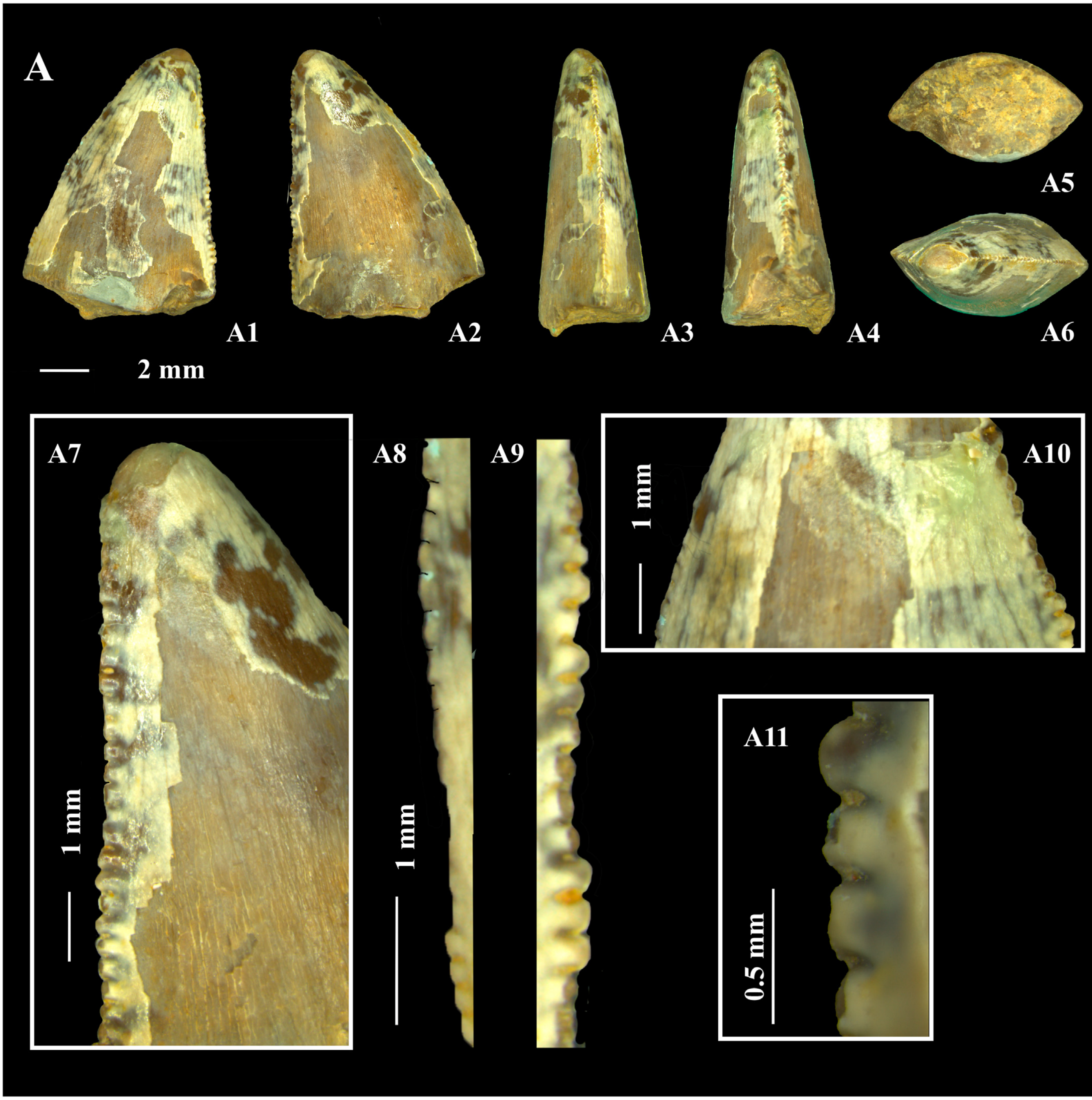


Fig. 2. Theropod tooth from the upper Barremian of Vadillos-1 (Cuenca, Spain). A) Specimen VD1-197 assigned to Coelurosauria with affinities to non-tyrannosaurid Tyrannosauroidea, in A1) labial, A2) lingual, A3) mesial, A4) distal, A5) basal, and A6) apical views, and details of A7) enamel texture, A8) denticles of mesial carina, A9) denticles of distal carina, A10) ornamentation of the tooth close to the apex, and A11) denticles of the distal carina.

Table 1
Dimensions of the theropod teeth studied here from the upper Barremian of Vadillos-1 (Cuenca, Spain). Abbreviations: AL, apical length, mm; CBL crown base length, mm; CBW, crown base width, mm; CBR, crown base ratio; CH, crown height, mm; CHR, crown height radio; MC, mesial carina count per 5 mm unit length; DC, distrocentral denticle density count per 5 mm unit length; MA, mesioapical denticle density; DA, distoapical denticle density; CA, crown angle; MSL, mesial serrated carina length, mm; MCL, mid-crown length, mm; MCR, mid-crown ratio; MCW, mid-crown width, mm; DDL, distal denticle length, mm; MDL, mesial denticle length, mm, and DSDI, denticle size density index.

Specimen	AL	CBL	CBW	CBR	CH	CHR	MC	DC	MA	DA	CA	MSL	MCL	MCR	MCW	DDL	MDL	DSDI
VD1-178	1.66	0.92	0.33	0.359	1.35	1.8043	?	50	?	?	54.41	?	0,55	0,4727	0,26	0.08	?	?
VD1-179	4.79	1.7	1.5	0.94	4.3	2.5	45	35	80	65	69.93	2.9	1.1	0.69	0.96	0.1315	0.09	1.28
VD1-180	8.7	4.6	1.96	0.4261	7.12	1.5478	40	26.25	?	30	58.98	6.18	3.33	0.4227	1.4	0.22	0.1052	1.52
VD1-197	?	?	?	?	?	?	20	16.25	16.25	20	?	?	?	?	?	0.26	0.24	1.23

Material. VD1-178 (Fig. 3A1–A7, Table 1)
Description. The specimen VD1-178 is most likely a shed tooth (Fig. 3A1–A7). It is ziphodont in morphology, showing a blade-like, slightly distally recurved, strongly labiolingually narrow (CBR < 0.4; Table 1) and moderately elongated crown (CHR = 1.8; Table 1). The labial face of the tooth shows a labial depression (lad), i.e., a wide concavity centrally positioned on the labial side of the tooth, occupying more than one-half of the width of the tooth and enclosed by two well-marked longitudinal ridges (lri). This depression extends from the base of the crown to the apex, where it narrows (Fig. 3A1). The lingual face of the tooth similarly displays a lingual depression (lid) which also extends from the base of the crown to the apex, also becoming narrower (Fig. 3A2). The extension of the mesial carina (mcal) on the crown is 1.66 mm and distal carina length (dcal) is 1.37 mm. In distal view, the carina is centrally positioned (Fig. 3A3). In mesial view, the mesial margin is slightly labiolingually convex (Fig. 3A4) and the absence of denticulated mesial carina stands out. The absence of denticles on the mesial carina and in the apical part of the distal carina may be the result of wear. The crown presents a cross-section with a 8-shaped outline (Fig. 3A5–A6). The distal carina shows 10 denticles from the base to the distocentral area (its lowermost 0.8 mm), absent towards the apex of the tooth due to damage located on the last 0.5 mm to the crown apex. VD1-178 presents subquadrangular hooked denticles, apically oriented, with 0.08 mm in size (Fig. 3A7). The interdenticular sulci are straight and slightly inclined basally. The enamel surface texture is braided, being clearly visible with or without light (Fig. 3A1–A7). Other forms of crown ornamentation are absent.

Material. VD1-179 (Fig. 3B1–B3, Table 1)
Description. Specimen VD1-179 (Fig. 3B1–B3) corresponds to a tooth that was shed. This crown shows ziphodont morphology, only slightly recurved in shape (Fig. 3B1), subcircular (CBR > 0.94) and strongly elongated (CHR = 2.5; Table 1). No description of the lingual side is possible due to bad preservation. On its labial side, the tooth displays a depression (lad) bounded by two mesiodistal convexities (Fig. 3B1). The outline of the crown in cross-section at the cervix is reniform or eight-shaped (Fig. 3B2). The crown shows well-developed mesial and distal carinae. The mesial carina (mcal) extends 5 mm and length of the distal carina (dcal) is 4.5 mm. Denticulation in the former is restricted to the apical half of the crown, extending 2.9 mm. Denticle density increases gradually apically and basally. On the distal carina, denticle density (DC) is 35 denticles per 5 mm at mid-crown. The denticles on the distal carina are comparatively larger than those on the mesial carina, with a DSDI of 1.28 (Table 1) to the point that the denticles of the mesial carina are less perceptible, and only better differentiated from the middle to the apical area of the crown. The distal denticles are subrectangular to subrounded in shape (Fig. 3B3), and thirty denticles have been counted, decreasing in size towards to the crown apex. Distoapical denticle density (DA) is 8 per mm. The interdenticular sulci are present, short and poorly developed. A well-visible braided enamel surface texture can be observed (Fig. 3B3). Transverse or marginal undulations, flutes and basal striations are absent.

Material. VD1-180 (Fig. 3C1–C7, Table 1)
Specimen VD1-180 (Fig. 3C1–C7) includes a fragmented crown. This tooth has a ziphodont morphology and is slightly recurved distally. It is labiolingually narrow (CBR = 0.426; Table 1) and moderately elongated (CHR = 1.54; Table 1). The distal carina is sharp and labiolingually compressed (Fig. 3C1). The labial face of the tooth shows a broad labial depression (lad) that extends from the base of the crown to the apex, where it becomes narrow. The lingual face of the tooth similarly includes a lingual depression (lid) (Fig. 3C1, C2). Each depression (lad and lid) is bounded by two mesiodistal convexities. Both labial and lingual sides show transverse undulations (tun), but their better observation depends on the light, being better observed with grazing light (Fig. 2C2). The crown shows well-developed and denticulated mesial and distal carinae (Fig. 2C3–C4). The extension of the mesial carina (mcal) on the crown is 8.7 mm and distal carina length (dcal) is 8.4 mm. The mesial carina possesses 40 denticles per 5 mm at mid-crown whereas the distal denticle density is 30 per 5 mm at mid-crown. The distal denticles are considerably larger than the mesial ones (which are poorly developed and eroded), with a DSDI of 1.52 (Table 1), along the whole length of the carina. In the mesial carina, the denticles are less perceptible, being better differentiated along the apical half of the crown (Fig. 2C1). The cross-section shows figure eight-shaped due to the labial and lingual depressions (Fig. 2C5). Distoapical denticle density (DA) is 30; unfortunately, the mesioapical denticle density (MA) cannot be observed since the tooth is broken at this level. On the distal carina, close to apical region, longer interdenticular sulci (ids) can be observed, a feature that is absent on the mesial carina. The denticles from the mesial carina are subquadrangular, while the denticles from the distal carina are subquadrangular to subrounded in shape, with well-defined interdenticular spaces (Fig. 2C6–C7). The enamel texture is braided (Fig. 2C7).

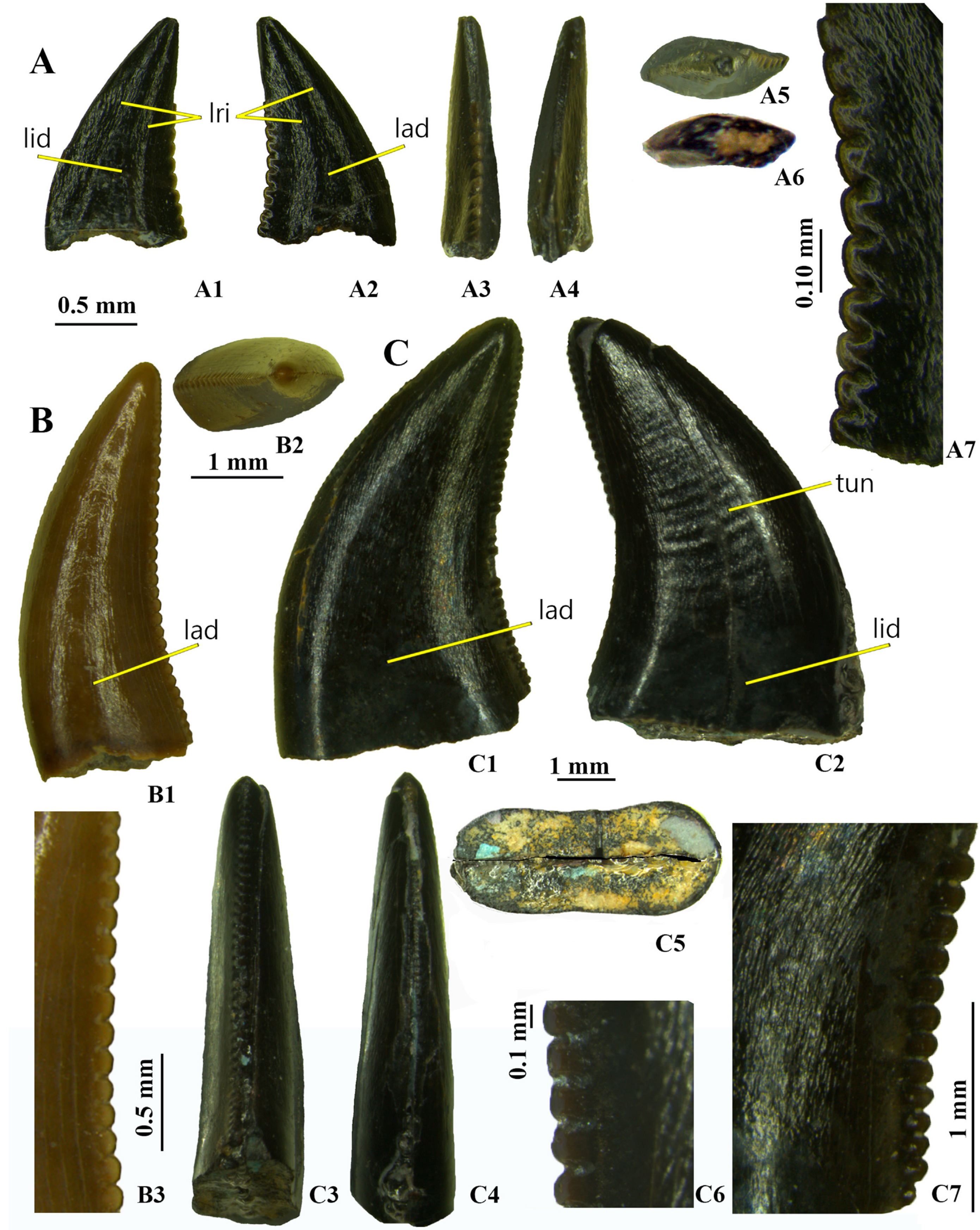
5. Results

5.1. Cladistic analysis

The cladistics analysis of the tooth-based data matrix (see Fig. 4 and supplementary material-1) yielded a different number of most parsimonious trees (MPTs). The specimen VD-1-197 is placed within Tyrannosauroidea while VD-1-178, VD-1-179 and VD-1-180 are found within Dromaeosauridae. VD-1-197 provided a single MPT (tree length = 669 steps; CI = 0.239; RI = 0.617). This tooth is classified as a coelurosaur and has been recovered with *Zuolong* as sister group and next to *Dilong* (4A). This tooth lacks some parts of the tooth, so one should be cautious with its cladistics position. The outcomes with VD-1-178 as the floating OTU provided three MPTs (tree length = 666 steps; CI = 0.240; RI = 0.617). The specimen VD1-178 has been recovered in a clade with *Atrociraptor*. The sister taxon of this clade is *Saurornitholestes* and basalmost *Deinonychus* (Fig. 4B). VD-1-179 yielded a single tree (tree length = 668 steps; CI = 0.240; RI = 0.617). *Bambiraptor* is recovered as the sister taxon of this tooth within other Dromaeosauridae (*Graciliraptor* and *Sinornithosaurus* in a polytomy as basal groups of the clade) (Fig. 4C). The results with VD-1-180 as the floating group yielded two MPTs (tree length = 674 steps; CI = 0.239; RI = 0.615) where this tooth was placed as de basal-most taxon of sister group *Saurornitholestes* and *Atrociraptor*, and in a polytomy with *Deinonychus* (Fig. 4D).

5.2. Morphometric analysis

In the DFA carried out from the using a dataset (Supplementary material-2; the dataset includes these material added to Meso et al., 2022 dataset) at the “clade-level” (Clade-level, PC1 and PC2 of account for 46.545% and 13.796% of the total variance respectively, Fig. 5), the specimen VD1-178 appears separated, but close to Dromaeosauridae and Megaraptora, while VD1-179 is among Dromaeosauridae and non-averostran Neotheropoda, and VD1-180 is among Dromaeosauridae, non-


A
lid
lri
lri
lad
A1
A2
A3
A4
A5
A6
A7
0.5 mm
0.10 mm
B
lad
B1
B2
1 mm
B3
0.5 mm
C
lad
tun
lid
C1
C2
1 mm
C3
C4
C5
C6
C7
0.1 mm
1 mm

tyrannosaurid Tyrannosauroidea, Megaraptora and Troodontidae (Fig. 5A).

The DFA carried out from the same dataset at the “taxon level” classified these teeth from Vadillos-1 (PC1 and PC2 account of 37.987% and 19.307% of the total variance respectively) as follows: VD1-178 is classified as *Eoraptor*, a basalmost theropod, while VD1-179 is classified related to VD1-180, and VD1-180 is classified as *Deinonychus*. The reclassification rate is relatively high, being 57.85% at the genus-level, and 58.65% at the clade-level. Showing the point-cloud at taxon level, VD1-179 is close to *Bambiraptor* (related also with VD1-179 in the cladogram), while VD1-180 is close to *Deinonychus* (Fig. 5B and Supplementary material-2).

6. Discussion

The different consensus trees obtained with the four isolated teeth from Hoces de Beteta were not entirely consistent with the general theropod phylogeny (Hendrickx et al., 2020a), so these conclusions remain uncertain until new material is found. Nevertheless, the cladistics analysis applied to these isolated teeth are reliable (Hendrickx and Mateus, 2014) when considering teeth separately as floating operational taxonomic units (Hendrickx et al., 2020a) and useful information can be extracted from them when comparing the results with other quantitative analyses.

6.1. Identification and comparison

Material. VD1-197

The result of the cladistics analysis classifies the tooth VD1-197 as a coelurosaur with affinity to non-tyrannosaurid Tyrannosauroidea (Fig. 4A and Supplementary material-1). It shows two different dental features worth highlighting: 1) a DSDI > 1.2, a condition common in Dromaeosauridae, Tyrannosauroidea, Non-averostran Neotheropoda (*Dracovenator* and *Dilophosaurus*), Noasaurinae and Piatnitzkysauridae; and 2) Braided enamel texture, a condition present in non-tyrannosaurid Tyrannosauroidea, Eudromaeosauria, non-abelisaurid Ceratosauria, non-spinosaurid Megalosauroidea, Carcharodontosauria, *Aorun*, most non-averostran Theropoda and non-neocoelurosaur Coelurosauria (Hendrickx et al., 2019). Dilophosauridae are restricted to the Upper Triassic to the Lower Jurassic, and have never been recorded in Europe, as well as the Jurassic Piatnitzkysauridae and *Aorum*. Having in mind the considerations related to these two features, comparisons of VD1-197 with other taxa should be restricted to Dromaeosauridae and non-tyrannosaurid Tyrannosauroidea. The cladistics analysis supports more affinity to non-tyrannosaurid Tyrannosauroidea (Fig. 4A). However, since this tooth only preserves the apical portion of the crown, it could not be included in the morphometric analysis. Therefore, is more cautious classify it as Coelurosauria, but pointing its proximity with non-tyrannosaurid Tyrannosauroidea.

Compared to Coelurosauria teeth from the Lower Cretaceous of Spain, VD1-197 shows affinities with the tooth MAP-7598 from the Barremian of El Castellar, Teruel (Torrente et al., 2018, fig. 1) both in its overall shape (considering the tip of the crown) and surface texture, but MAP-7598 shows chisel-shaped denticles, while they are subquadrangular to subrounded in VD1-197. The specimen MDS-OTII, 82 classified as Coelurosaria indet., but pointing affinities with basal tyrannosauroids, from the Lower Cretaceous of Salas de los Infantes, Burgos, Spain differs from VD1-197 in the presence of abundant transversal and marginal undulations, although in the first tooth the tip of the crown is not preserved (see Alonso et al., 2017, fig. 7).

Compared to Barremian theropod teeth outside Spain, VD1-197 shows affinities with the tooth of the tyrannosauroid *Eotyrannus lengi* from the Wealden Supergroup of southern England figured by Naish and Cau (2022; figs. 4 and 14f) both in the general morphology and enamel texture.

Material. VD1-178

The results of the cladistics analysis support a dromaeosaurian affinity to the shed tooth VD1-178 (Fig. 4B and Supplementary material-1). The morphometric analyses (i.e., discriminant analysis), indicate that VD1-178 appears separated, but close to Dromaeosauridae and Megaraptora, while the DFA carried out from the same dataset at the “taxon level” classified the tooth as *Eoraptor*, a basal theropod (Fig. 5 and Supplementary material-2). This can be explained by: 1) the limited information available as sample size due to preservation issues of the specimen, the mesial carina incomplete for observation because of being worn (MSL and MDL not available); and 2) Megaraptora and Dromaeosauridae show some similar dimensions (CBL, CBW and CBR; see Supplementary material-2 and the dataset uploaded by Meso et al., 2022).

The specimen VD1-178 is inferred as lateral in position based on the lingual and labial depressions (Hendrickx et al., 2015). The features to highlight in this tooth are the following: 1) crowns with 8-shaped cross-section, a feature present in most Dromaeosauridae, but also in *Berberosaurus*, Metriacanthosauridae, some Megaraptora, Tyrannosauroidea and Troodontidae; 2) braided enamel texture (see discussion above); 3) hooked denticles, a condition common in *Eoraptor*, *Gojirasaurus*, Abelisauroidea, Therizinosauroidea, Eudromaeosauria and Troodontidae (including Anchiornithinae); and 4) presence of interdenticular sulci, feature also present in *Tawa*, non-neocoelurosaur Averostra, *Falcarius*, many eudromaeosaurians and a few derived troodontids. The mentioned features are relatively common dental features in many groups of theropods (see Hendrickx et al., 2019). However, when these 4 features appear together, the attribution of the tooth is limited to Eudromaeosauria. Although VD1-178 shows certain affinities with Megaraptora in the quantitative and qualitative analyses, hooked denticles have not been described to date in the latest group. The hooked denticles of Troodontidae tend to be particularly large, bulbous, and widely separated, being strongly different from the denticles of Dromaeosauridae. According to Hendrickx et al. (2019), between dromaeosaurids, hooked denticles are present in the eudromaeosaurians *Atrociraptor* (TMP 1995.166.01; Currie and Varricchio, 2004; fig. 14.7) and *Saurornitholestes* (Currie et al., 1990; Sankey, 2001). This observation agrees with the result obtained in the cladistic analysis, in which the specimen VD1-178 was recovered in a clade with *Atrociraptor*, appearing *Saurornitholestes*as as the sister taxon of this clade (see Fig. 4B).

Material. VD1-179

The analyses performed from the tooth-based data matrix support the specimen VD1-179 as a Dromaeosauridae (Fig. 4C and Supplementary material-1). Also, the morphometric analysis (see Fig. 5 and Supplementary material-2) shows that this tooth presents strong affinities to Dromaeosauridae. As indicated before,

Fig. 3. Theropod teeth from the upper Barremian of Vadillos-1 (Cuenca, Spain). Specimens assigned to Eudromaeosauria. A) Specimen VD1-178 in A1) lingual, A2) labial, A3) distal, A4) mesial, A5) apical and A6) basal views, and A7) detail of the denticles of distal carina. B) Specimen VD1-179, in B1) lingual, B2) apical views and B3) detail of the denticles of distal carinae. C) Specimen VD1-180, in C1) lingual, C2) labial, C3) distal, C4) mesial, C5) basal views, C6) and C7) detail of the denticles of distal carina. lad: labial depression; lid: lingual depression; lri: longitudinal ridge; est: estriation; tun: transverse undulation.

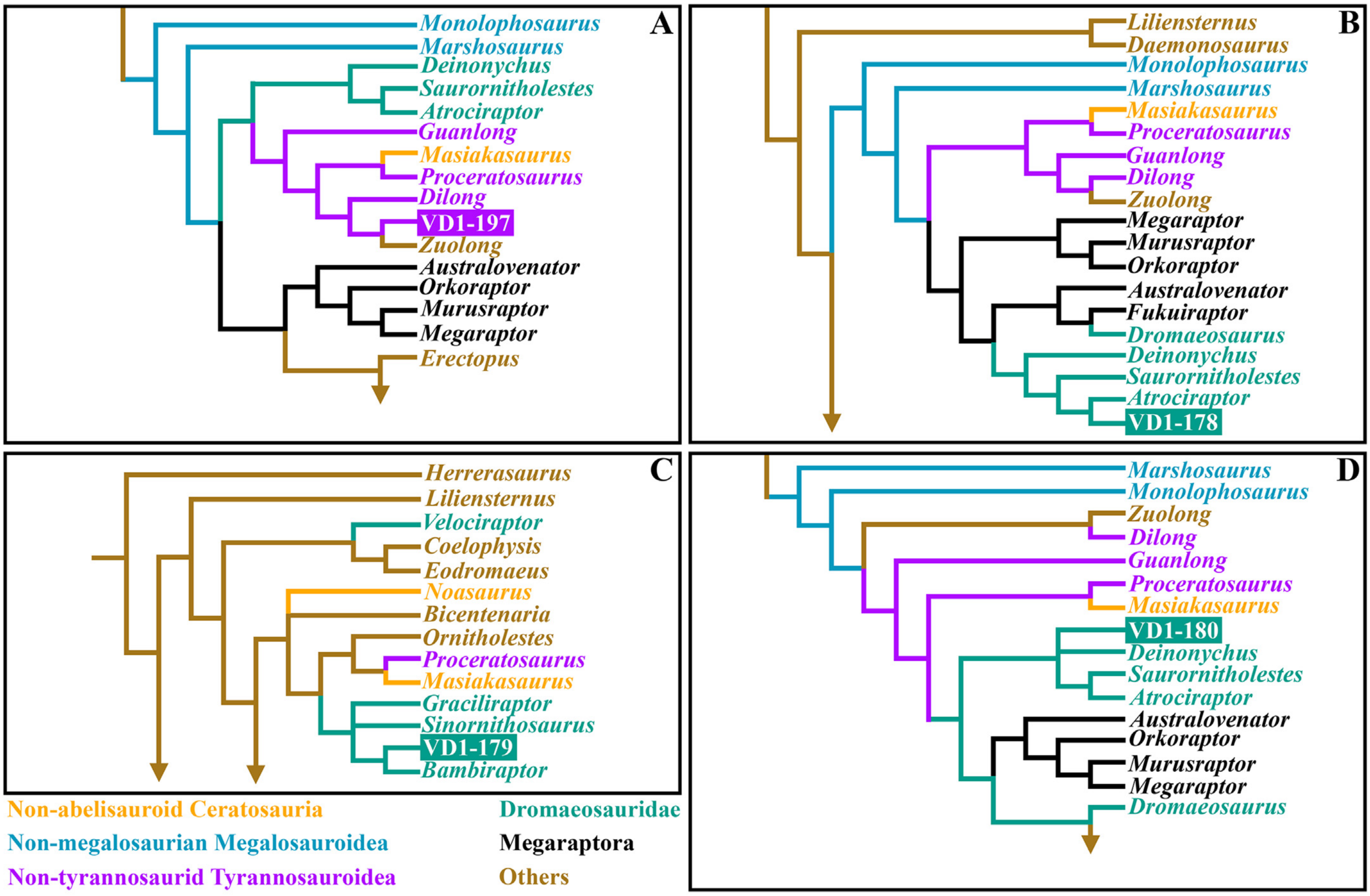


Fig. 4. Details of the results of the cladistic analysis based on qualitative characters from the dentition-based data matrix of non-avian theropods created by Hendrickx et al. (2015) and updated by Meso et al. (2021, 2022). A) VD1-197. B) VD1-178. C) VD1-179. D) VD1-180.

showing the point-cloud at taxon level, VD1-179 is close to *Bambiraptor* (recovered as the sister taxon of VD1-179 in the cladogram, see Figs. 4 and 5), giving additional support to the result obtained by the cladistic analysis.

The specimen VD1-179 is inferred as lateral in position based on the presence of a labial depression. It shows the following characters common in Dromaeosauridae: 1) reniform to 8-shaped crown in cross-section; 2) braided enamel texture surface; 3) a DSDI > 1.2, and 4) presence of interdenticular sulci (see discussion above). These features are relatively common dental features in many groups of theropods, as previously discussed (see Hendrickx et al., 2019). Nevertheless, when these four features appear combined, the attribution of the tooth is restricted to Eudromaeosauria.

Compared to other Lower Cretaceous teeth from Spain, the specimen VD1-179 (Fig. 2B) is similar to that described by Rauhut (2002, fig. 2A) from the Barremian of Uña, initially classified as cf. *Richardoestesia*, and later reclassified as Velociraptorinae indet. by Ruiz-Omeñaca (2006, p. 292) due to the general shape of the tooth, its strongly elongate and only slightly recurved shape, and the denticulation of the carinae. Moreover, the DSDI ranges from 1.08 to 1.5 in both teeth. In addition, the tooth from the Barremian of Uña presents, according to Rauhut (2002), a shallow longitudinal groove on the antapical part of its labial and lingual sides, that seem to be homologous structures to those described in specimen VD1-179 as labial (lad) and lingual (lid) depressions.

Material. VD1-180

According to the cladistic analysis, VD1-180 falls within the Dromaeosauridae (Fig. 4D and Supplementary material-1). The morphometric analysis at clade level (see Fig. 5 and Supplementary material-2) places this tooth among the Dromaeosauridae, non-tyrannosaurid Tyrannosauroidea, non-averostran Neotheropoda, Megaraptora, Troodontidae and some basalmost theropod (Fig. 5A). This result is understood considering the fact that all these dinosaurs possess teeth of similar dimensions (e.g., CBL, CBW, CH, AL, CBR). Showing the point-cloud at taxon level, VD1-180 is classified as *Deinonychus*, being coherent with the results of the cladistic analysis (Fig. 4), which includes this tooth in the Dromaeosauridae (more specifically among eudromaeosaurians).

Tooth VD1-180 is again inferred as lateral in position based on the lingual and labial depressions. VD1-180 shows a variety of dental features found among Eudromaeosauria: 1) crowns with 8-shaped cross-section; 2) a DSDI > 1.2; 3) braided enamel texture, and 4) transverse undulations. The crown with 8-shaped cross-section, the DSDI > 1.2 and the braided enamel texture are common features found in other theropod groups as well, as previously mentioned. Transverse undulations appear in many eudromaeosaurians, but are also common in *Eodromaeus*, *Dracovenator*, non-neocoelurosaur Averostra, *Falcarius*, and a few derived troodontids as *Troodon* (Hendrickx et al., 2019). Although these features are relatively common dental features in several groups of

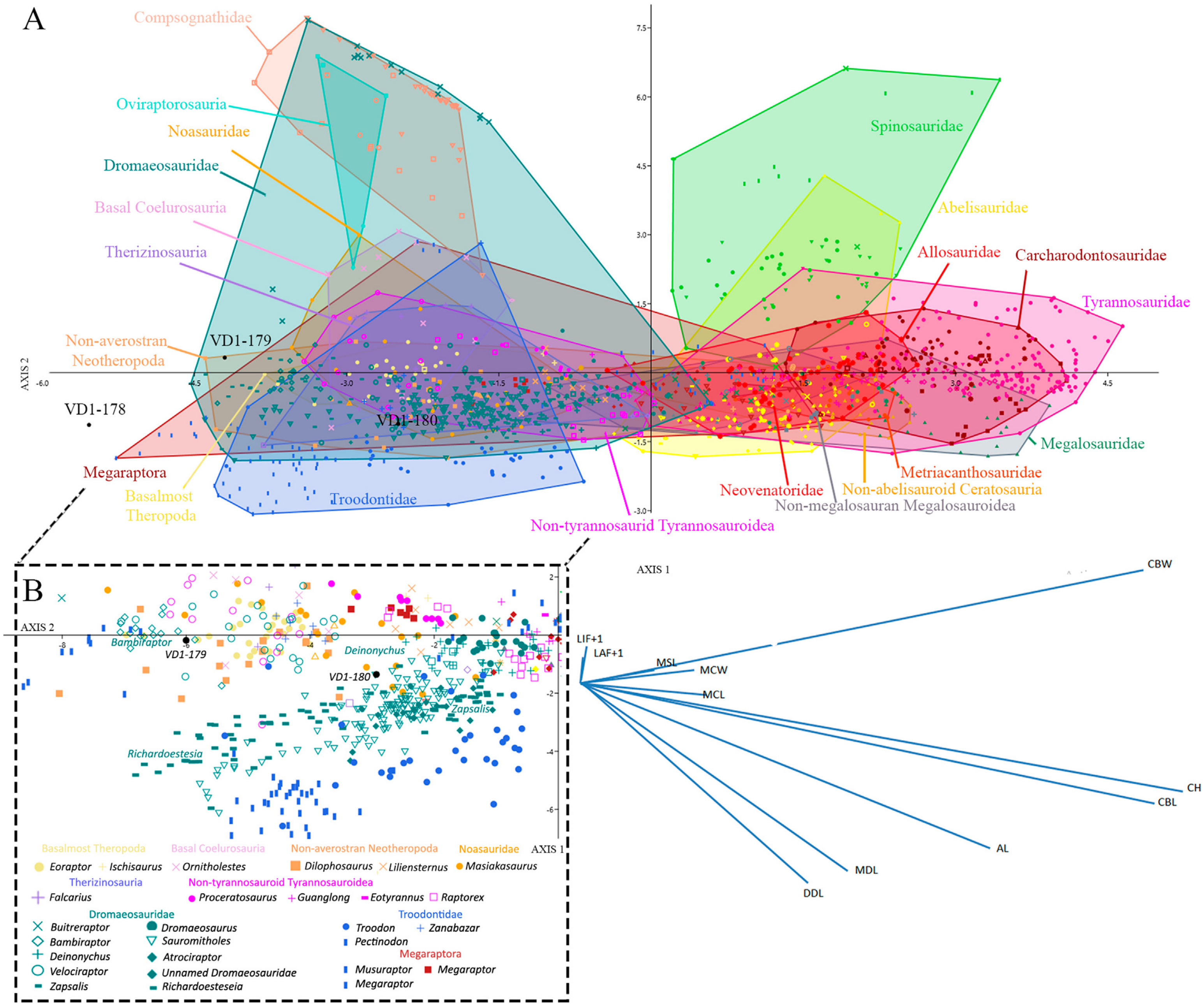


Fig. 5. A) Results of the discriminant analysis performed at the "group"-level on the whole dataset along the first two canonical axes of maximum discrimination in the whole dataset, excluding non-ziphodont teeth and some basal forms (specimens from the Meso et al., 2022 dataset adding VD1-178, VD1-179 and VD1-180 from the present study (PC1 and PC2 account for 46.545% and 13.796% of the total variance, respectively). B) Results of the discriminant analysis performed at the "taxon-level" on the whole dataset showing only the area in which the teeth VD1-179 and VD1-180 appear (PC1 and PC2 account of 37.987% and 19.307% of the total variance respectively). Abbreviations: AL, apical length; CBL, crown base; CBW, crown base width; CH, crown height; MCL, mid crown length; MCW, mid-crown width; MSL, mesial serrated carina length.

theropods, when found together they are exclusive of the Eudromaeosauria (see Hendrickx et al., 2019).

Comparing to other Spanish Lower Cretaceous theropod teeth, the tooth VD1-180 (Fig. 2C) is similar to the specimen CAN1-1029 from the Hauterivian–Barremian of La Cantalera site studied by Gasca et al. (2009) and Canudo et al. (2010) in the overall size of the tooth, but CAN1-1029 is more curved and shows apically oriented denticles. Moreover, in the crown of the specimen from La Cantalera, no labial or lingual depressions (lad and lid) are to be seen. The specimen VD1-180 is also similar to the teeth of Dromaeosauridae (possibly Velociraptorinae) described by Canudo et al. (1997, fig. 2) from the upper Barremian of the Vallipón site, coinciding with their overall shape. However, VD1-180 is larger and shows both a broad central longitudinal labial depression (lad) and a central longitudinal lingual depression (lid) absent in the teeth from Vallipón. VD1-180 also resembles the tooth of velociraptorine dromaeosaurid from the Barremian of Uña, described and figured by Rauhut (2002, fig. 2g). Both teeth show similar shape, they are strongly compressed laterally and slightly recurved and show rounded denticles. However, VD1-180 shows labiolingually compressed mesial and distal carinae, while the carinae of the tooth described by Rauhut (2002) does not show flattened carinae.

Compared to other Lower Cretaceous teeth from Europe, this tooth is also very similar to the genus *Nutheles* Owen, 1954, described and figured by Milner (2002, fig. 1a-g, pl.1-2) from the Berriasian of the Isle of Purbeck, England. Although Milner (2002) describes the enamel as smooth, it seems to be braided as in VD1-180 (Hendrickx; pers. communication).

6.2. Distribution

In Spain, isolated dromaeosaurid teeth have been reported from the Hauterivian–Barremian of La Cantalera (Teruel) in the Blesa Formation (Gasca et al., 2009; Canudo et al., 2010); the Barremian of Vallipón (Castellote, Teruel) in the Artoles Formation (Canudo et al., 1997); and of Uña (Cuenca) in La Huérguina Formation (Rauhut and Zinke, 1995; Rauhut, 2002; Ruiz-Omeñaca, 2006). Three theropod teeth (VD1-178, VD1-179 and VD1-180) confirm the partial coincidences previously observed by Barroso-Barcenilla et al. (2017) with the taxa recorded in the well-known nearby site of Uña, from the coeval La Huérguina Formation, and also show new coincidences with the Hauterivian–Barremian site of La Cantalera, from the Blesa Formation, and the upper Barremian dinosaur site of Vallipón, from the Artoles Formation.

Considering other teeth with eudromaeosaurian affinities outside of Spain, some isolated specimens have been reported from the Kimmeridgian (Upper Jurassic) of Guimarota, Portugal (Zinke, 1998) and of Langernberg, Germany (Lubbe et al., 2009), and from the Barremian of the Isle of Wight, United Kingdom (Sweetman, 2004). Compared to these specimens from Portugal and Germany, VD1-179, and VD1-180 are considerably smaller and are moderately recurved distally. The specimens from Germany described by Lubbe et al. (2009, fig. 5) show denticles slightly inclined apically, while no inclination has been observed in the specimens from Vadillos-1, except in VD1-178, that shows hooked denticles apically oriented. Compared to the teeth from the Barremian of the Isle of Wight (Sweetman, 2004), the teeth studied by the latest author show larger specimens compared to those here studied from Spain.

About the presence of tyrannosauroids in Spain, no records are clearly confirmed to date. However the presence of teeth possibly belonging to tyrannosauroids is suggested by Alonso et al. (2017, specimen MDS-OTII,82 from the Lower Cretaceous of Salas de los Infantes, Burgos, classified as Coelurosauria indet.), Alonso et al. (2018, specimen HOC 24 from the Barremian of Barranco del Hocino, Teruel, classified as Tetanurae indet., but situated among tyrannosauroids in the cladistics analyses carried out by the authors) and Torrente et al. (2018, specimen MAP-7598 from the Barremian of El Castelar, Teruel, classified as Coelurosaria indet., with affinities with dromaeosaurids and tyrannosauroids). In this sense, the affinity of VD1-197 from Vadillos-1 to non-Tyrannosaurid Tyranosauroidea is especially interesting in order to raise new questions about the distribution of this group.

About the record of tyrannosauroids out of Spain, the presence of basal tyrannosauroids has been described from the Middle to Upper Jurassic of Portugal (Zinke, 1998; Rauhut 2003), and southern England (e.g., Benson, 2008; Rauhut et al., 2010), and in the Lower Cretaceous of England (Naish and Cau, 2022).

7. Conclusions

New theropod remains from the upper Barremian of Vadillos-1 (Cuenca, Spain) have been described in this paper. Three isolated theropod teeth (VD1-178, VD1-179 and VD1-180) are referred to dromaeosaurids on the basis of the descriptions combined with the cladistic and discriminant analyses. More specifically, they can be classified as Eudromaeosauria because of their features (8-shaped cross section, with lingual and labial depressions, DSDI>1.2, braided enamel texture, hooked denticles (in the case of VD1-178) and transverse undulations (in the case of V1-180). A fourth isolated theropod tooth (VD1-197) presents morphological similarities with both dromaeosaurids and non-tyrannosaurid tyrannosauroids, but the cladistic analysis places this tooth among the latter group. The dromaeosaurid fossils identified in Vadillos-1 and described here confirm the similarities pointed out in previous papers between the vertebrate assemblage of this site and those of other sites in the province of Cuenca, as well as with several upper Barremian dinosaur sites of central Spain (Teruel). Additionally, the possible presence of tyrannosauroids in the assemblage as indicated by the cladistic analysis opens new possibilities regarding the distribution of these theropod groups and points to a greater palaeobiodiversity than previously thought.

Data availability

Data will be made available on request.

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References

Allain, R., Vullo, R., Le Loeuff, J., Tournepiche, J.F., 2014. European ornithomimosaurs (Dinosauria, Theropoda): an undetected record. Geológica Acta: An International Earth Science Journal 12 (2), 127–135.

Alonso, A., Canudo, J.I., Torcida, Fernández-Baldor, F., 2017. Isolated theropod teeth associated with sauropod remains from El Oterillo II (Early Cretaceous) site of Salas de los Infantes (Burgos, Spain). Journal of Iberian Geology 43, 193–215.

Alonso, A., Gasca, J.M., Navarro-Lorbés, P., Rubio, C., Canudo, J.I., 2018. A new contribution to our knowledge of the large-bodied theropods from the Barremian of the Iberian Peninsula: the "Barranco del Hocino" site (Spain). Journal of Iberian Geology 44 (1), 7–23.

Barrón, E., Barroso-Barcenilla, F., Sevilla, P., 2019. Estudio palinológico del Barremiense de las Hoces de Beteta (Cuenca, España). In: Libro de Resúmenes de la XXIII Bienal de la Real Sociedad Española de Historia Natural, pp. 119–120.

Barroso-Barcenilla, F., Berrocal-Casero, M., Blain, H.A., Callapez, P.M., Cambra-Moo, O., Escaso, F., Martín-Closas, C., Ortega, F., Pérez-García, A., Prieto, I., Rodríguez-Lázaro, J.M., Ruiz-Galván, A., Sanz, J.L., Segura, M., Sevilla, P., 2017. Geological and palaeontological context of three new Barremian (Lower Cretaceous) vertebrate sites in the Iberian Peninsula (Cuenca Province, Central Spain). Proceedings of the Geologists' Association 128, 256–270.

Bravo, A.M., Sevilla, P., Barroso-Barcenilla, F., 2018. Avian and crocodilian eggshells from the upper Barremian site of Vadillos-1 (Lower Cretaceous, Cuenca province, Spain). Cretaceous Research 85, 28–41.

Benson, R.B., 2008. New information on Stokesosaurus, a tyrannosauroid (Dinosauria: Theropoda) from North America and the United Kingdom. Journal of Vertebrate Paleontology 28 (3), 732–750.

Canudo, J.I., Cuenca-Bescós, G., Ruiz-Omeñaca, J.I., 1997. Dinosaurios dromeosaúridos (Saurischia: Theropoda) en el Barremiense Superior (Cretácico Inferior) de Castellote, Teruel. Geogaceta 22, 39–42.

Canudo, J.I., Aurell, M., Gasca, J.M., Badiola, A., Blain, H.A., Cruzado-Caballero, P., Gómez-Fernández, D., Moreno-Azanza, M., Parrilla, J., Rabal-Garcés, R., Ruiz-Omeñaca, J.I., 2010. La Cantalera: an exceptional window onto the vertebrate biodiversity of the Hauterivian-Barremian transition in the Iberian Peninsula. Journal of Iberian Geology 36, 205–224.

Currie, P.J., Varricchio, D.J., 2004. Canyon Formation (Upper Cretaceous) of Alberta, Canada. In: Feathered dragons: Studies on the Transition from Dinosaurs to Birds, p. 112.

Currie, P.J., Rigby, J.K.J., Sloan, R.E., 1990. Theropod teeth from the Judith River Formation of southern Alberta, Canada. In: Carpenter, K., Currie, P.J. (Eds.), Dinosaur Systematics: Approaches and Perspectives. Cambridge University Press, New York, pp. 107–125.

Eaton, J.G., 2004. New screen-washing approaches to biostratigraphy and paleoecology of nonmarine rocks, Cretaceous of Utah. Bulletin of Carnegie Museum of Natural History 36, 21–30.

Figueiredo, S.D., Carvalho, C.N.d., Cunha, P., Sousa Carvalho, I.d., 2021. New dinosaur tracks from the Lower Barremian of Portugal (Areia do Mastro Formation, Cape Espichel). Journal of Geoscience and Environment Protection 9 (1), 84–96.

Gasca, J.M., Gómez-Fernández, D., Moreno-Azanza, M., Canudo, J.I., 2009. Un paseo por los yacimientos de dinosaurios del tránsito Hauteriviense-Barremiense (Cretácico Inferior) de Aragón. Paleolusitana 1, 211–219.

Goloboff, P.A., Farris, J.S., Nixon, K.C., 2008. TNT, a free program for phylogenetic analysis. Cladistics 24 (5), 774–786.

Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4 (1), 1–9.

Hendrickx, C., Mateus, O., 2014. Abelisauridae (Dinosauria: Theropoda) from the Late Jurassic of Portugal and dentition-based phylogeny as a contribution for the identification of isolated theropod teeth. Zootaxa 3759 (1), 1–74.

Hendrickx, C., Mateus, O., Araújo, R., 2015. A proposed terminology of theropod teeth (Dinosauria, Saurischia). Journal of Vertebrate Paleontology 35, e982797.

Hendrickx, C., Mateus, O., Araujo, R., Choiniere, J., 2019. The distribution of dental features in non-avian theropod dinosaurs: Taxonomic potential, degree of homoplasy, and major evolutionary trends. Palaeontologia Electronica 22 (3), 1–110.

Hendrickx, C., Tschopp, E., Ezcurra, M., 2020a. Taxonomic identification of isolated theropod teeth: The case of the shed tooth crown associated with *Aerosteon* (Theropoda: Megaraptora) and the dentition of Abelisauridae. Cretaceous Research 108, 104312.

Hendrickx, C., Stiegler, J., Currie, P.J., Han, F., Xu, X., Choiniere, J., Wu, X.C., 2020b. Dental anatomy of the apex predator *Sinraptor dongi* (Theropoda: Allosauroidea) from the Late Jurassic of China. Canadian Journal of Earth Sciences 57 (9), 1127–1147.

Huene, F.v., 1914. Beiträge zur geschichte der Archosaurier. Geologie und Paläontologie Abhandlungen 13, 1–53.

Longrich, N.R., Currie, P.J., 2009. A microraptorine (Dinosauria–Dromaeosauridae) from the late Cretaceous of North America. Proceedings of the National Academy of Sciences 106 (13), 5002–5007.

Lubbe, T. van der, Richter, U., Knötschke, N., 2009. Velociraptorine dromaeosaurid teeth from the Kimmeridgian (Late Jurassic) of Germany. Acta Palaeontologica Polonica 54, 401–408.

Marsh, O.C., 1881. Principal characters of American Jurassic dinosaurs, V. American Journal of Science 21, 417–423.

Matthew, W.D., Brown, B., 1922. The family Deinodontidae, with notice of a new genus from the Cretaceous of Alberta. Bulletin of the American Museum of Natural History 46, 367–385.

Meso, J.G., Hendrickx, C., Baiano, M.A., Canale, J.I., Salgado, L., Díaz-Martínez, I., 2021. Isolated theropod teeth associated with a sauropod skeleton from the Late Cretaceous Allen Formation of Río Negro, Patagonia, Argentina. Acta Palaeontologica Polonica 66 (2), 409–423.

Meso, J.G., Gianechini, F.A., Valieri, R.J., Apesteguía, S., Correa, S.A.S., 2022. Theropods from the La Bonita site, Bajo de la Carpa Formation (Neuquén Group, Santonian), Río Negro, Argentina: analysis of dental evidence. Cretaceous Research 137, 105–250, 105250.

Milner, A.C., 2002. Theropod dinosaurs of the Purbeck limestone group, Southern England. Special Papers in Palaeontology 68, 191–202.

Naish, D., Cau, A., 2022. The osteology and affinities of *Eotyrannus lengi*, a tyrannosauroid theropod from the Wealden Supergroup of southern England. PeerJ 10, e12727.

Owen, R., 1842. Report on British Fossil Reptiles, II. In: Report of the Eleventh Meeting of the British Association for the Advancement of Science, pp. 60–204.

Owen, R., 1954. On some fossil reptilian and mammalian remains from the Purbecks. Quarterly Journal of the Geological Society of London 10, 420–433.

Poyato-Ariza, F.J., Talbot, M.R., Fregenal-Martínez, M.A., Meléndez, N., Wenz, S., 1998. First isotopic and multidisciplinary evidence for nonmarine coelacanths and pycnodontiform fishes: palaeoenvironmental implications. Palaeogeography, Palaeoclimatology, Palaeoecology 144, 65–84.

Rauhut, O.W.M., 2002. Dinosaur teeth from the Barremian of Uña, province of Cuenca, Spain. Cretaceous Research 23, 255–263.

Rauhut, O.W.M., 2003. A tyrannosauroid dinosaur from the Upper Jurassic of Portugal. Palaeontology 46 (5), 903–910.

Rauhut, O.W.M., Zinke, J., 1995. A description of the Barremian dinosaur fauna from Uña with a comparison to that of Las Hoyas. In: Extended Abstracts II International Symposium of Lithographic Limestones, pp. 123–126.

Rauhut, O.W.M., Milner, A.C., Moore-Fay, S., 2010. Cranial osteology and phylogenetic position of the theropod dinosaur *Proceratosaurus bradleyi* (Woodward, 1910) from the Middle Jurassic of England. Zoological Journal of the Linnean Society 158 (1), 155–195.

Ruiz-Galván, A., Barroso-Barcenilla, F., Ortega, F., Sevilla, P., 2017. Crocodyliform dental remains from the Lower Cretaceous sites of the Beteta Gorges (Cuenca, Spain). In: Barrios de Pedro, S., Blanco Moreno, C., de Celis, A., Colmenar, J., Cuesta, E., García-Martínez, D., Gascó, F., Jacinto, A., Malafaia, E., Martín Jiménez, M., de Miguel Chaves, C., Mocho, P., Pais, V., Páramo Blázquez, A., Pereira, S., Serrano Martínez, A., Vidal, D. (Eds.), A Glimpse of the Past, Abstract book of the XV Encuentro de Jóvenes Investigadores en Paleontología – XV Encontro de Jovens Investigadores em Paleontologia, Pombal, pp. 353–355.

Ruiz-Omeñaca, J.I., 2006. Restos directos de dinosaurios (Saurischia, Ornithischia) en el Barremiense (Cretácico inferior) de la cordillera Ibérica en Aragón (Unpubl. PhD thesis). Universidad de Zaragoza, p. 440.

Ruiz-Omeñaca, J.I., Canudo, J.I., 2003. Un nuevo dinosaurio terópodo ("*Prodeinodon*" sp.) en el Cretácico Inferior de La Cantalera (Teruel). Geogaceta 34, 111–114.

Sankey, J.T., 2001. Late Campanian southern dinosaurs, Aguja Formation, Big Bend, Texas. Journal of Paleontology 75 (1), 208–215.

Seeley, H., 1887. On a sacrum, apparently indicating a new type of Bird, *Ornithodesmus cluniculus* Seeley, from the Wealden of Brook. Quarterly Journal of the Geological Society of London 43, 206–211.

Sweetman, S.C., 2004. The first record of velociraptorine dinosaurs (Saurischia, Theropoda) from the Wealden (Early Cretaceous, Barremian) of southern England. Cretaceous Research 25, 353–364.

Torrente, M.Á., Verdú, F.J., Cobos, A., Alcalá, L., 2018. Diente de un coelurosaurio (Theropoda, Dinosauria) del Barremiense (Cretácico Inferior) de El Castellar (Teruel, España). Geogaceta 63, 79–82.

Young, C.M., Hendrickx, C., Challands, T.J., Foffa, D., Ross, D.A., Butler, I.B., Brusatte, S.L., 2019. New theropod dinosaur teeth from the Middle Jurassic of the Isle of Skye, Scotland. Scottish Journal of Geology 55 (1), 7–19.

Zinke, J., 1998. Small theropod teeth from the Upper Jurassic coal mine of Guimarota (Portugal). Paläontologische Zeitschrift 72, 179–189.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cretres.2022.105392.