

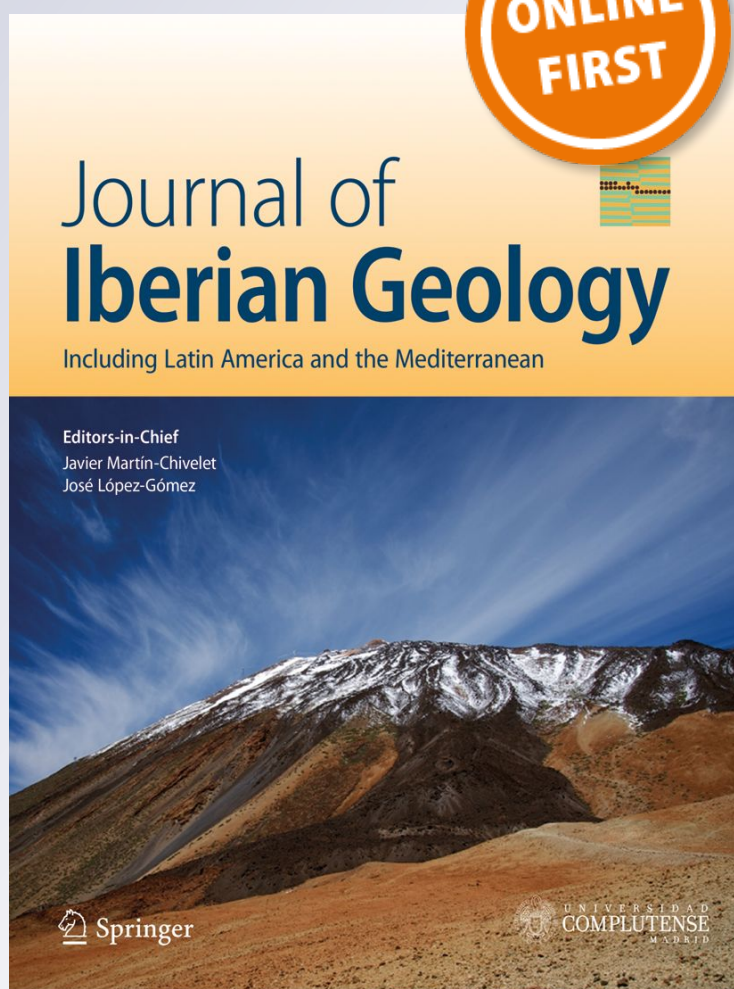
*A new contribution to our knowledge of the large-bodied theropods from the Barremian of the Iberian Peninsula: the “Barranco del Hocino” site (Spain)*

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# A new contribution to our knowledge of the large-bodied theropods from the Barremian of the Iberian Peninsula: the “Barranco del Hocino” site (Spain)

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## Abstract

**Introduction** Barranco del Hocino-1 is a new fossil site located near Estercuel, Teruel province, Spain. The fossil site is located geologically within the Oliete sub-basin, in the Blesa Formation (Barremian in age). Barranco del Hocino-1 shows a diverse assemblage of tetrapod vertebrates similar to other sites in the Blesa Formation.

**Materials and methods** Six isolated teeth belonging to Theropoda have been found. A study of their qualitative and quantitative characters, along with statistical (DFA) and cladistic analyses, enable us to identify four different dental morphotypes.

**Results** These morphotypes belong to separate tetanuran theropod taxa. One is related to Spinosauridae. The other morphotypes show affinities with non-spinosaurid tetanurans, probably related to Carcharodontosauria.

**Conclusions** The results are congruent with the known theropod record of the Iberian Peninsula and western Europe. This work is a new contribution to what is known of the palaeobiodiversity and distribution of large-bodied theropods from the Barremian of the Iberian Peninsula.

**Keywords** Lower Cretaceous · Blesa Formation · Theropoda · Dinosaur teeth · Spain

## Resumen

**Introducción** Barranco del Hocino-1 es un nuevo yacimiento localizado en el entorno de Estercuel, provincial de Teruel (España). Geológicamente se sitúa en la Formación Blesa (subcuenca de Oliete) de edad Barremiense. El yacimiento presenta una asociación diversa de vertebrados similar a otros de la misma formación.

**Materiales y métodos** Se han encontrado seis dientes aislados de dinosaurios terópodos. Mediante el estudio de los caracteres cualitativos y cuantitativos junto con el uso de análisis estadístico multivariante (DFA) y análisis cladístico se han podido identificar cuatro morfotipos diferentes.

**Resultados** Los morfotipos identificados pertenecen a diferentes grupos de tetanuros basales. Uno de los morfotipos está relacionado con Spinosauridae, mientras que el resto presentan afinidades con tetanuros no espinosáuridos, posiblemente relacionados con el clado Carcharodontosauria.

**Conclusiones** Los resultados son coherentes con el registro de terópodos conocido tanto en la península ibérica y Europa Occidental durante el Cretácico Inferior. El hallazgo supone una nueva contribución al conocimiento de la paleobiodiversidad y distribución de grandes terópodos del Barremiense de la península ibérica.

**Palabras clave** Cretácico Inferior · Formación Blesa · Theropoda · Dientes de dinosaurio · España

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## 1 Introduction

The presence of dinosaur remains is well-known in the Early Cretaceous sediments of the Iberian Peninsula (e.g., Pereda-Suberbiola et al. 2012). These include theropods, sauropods (basal macronarians, titanosauriforms and rebbachisaurid diplodocoids), thyreophorans and ornithopods

(iguanodontoids, dryosaurids and basal euornithopods). The Cretaceous Maestrazgo Basin, located in the Iberian Range, has yielded some of the most remarkable examples of these faunas. Particularly noteworthy within this record are dinosaurs such as the sauropods *Aragosaurus* and *Tastavinsaurus* (Sanz et al. 1987; Canudo et al. 2008b) and the ornithopods *Gideonmantellia*, *Delapparentia* (which has been recently proposed as belonging to *Iguanodon* sp.) and *Morelladon* (Ruiz-Omeñaca 2011; Ruiz-Omeñaca et al. 2012; Gasulla et al. 2015; Verdú et al. 2017), as well as a single theropod taxon, *Camarillasaurus* from the Barremian of Teruel (Sánchez-Hernández and Benton 2014). However, isolated tetanuran theropod teeth and theropod eggshells are also relatively abundant (Ruiz-Omeñaca et al. 1996; Infante et al. 2005; Sánchez-Hernández et al. 2007; Moreno-Azanza et al. 2014).

The Oliete sub-basin, situated in the northwestern part of the Maestrazgo Basin, presents a Wealden facies where just a few vertebrate fossil localities are known. The geological formations of this sub-basin have an enormous potential to add to what is known of the Barremian vertebrate faunas of the Iberian Peninsula. A good example is La Cantalera 1 (= La Cantalera) site, which has provided the most diverse assemblage of tetrapods (amphibians, squamates, mammals, crocodylomorphs and dinosaurs) from the early Barremian of the Iberian Peninsula (Badiola et al. 2008; Canudo et al. 2010; Puértolas-Pascual et al. 2015; Alonso and Canudo 2016). So far, isolated vertebrate remains (ornithopod dinosaurs, plesiosaurs) have also been found in other parts of the sub-basin (fossiliferous sites from Obón and Josa, Gasca et al. 2014a; Parrilla-Bel and Canudo 2015).

Recently, the amateur palaeontologist Juan Rubio found a new Wealden outcrop in the sub-basin. No vertebrate remains were reported here until the discovery of the locality of Barranco del Hocino-1 (Alonso et al. 2016). Three fieldwork campaigns (in 2015, 2016 and 2017) enabled us to recover roughly 250 bone remains, revealing the vertebrate palaeodiversity of the site. The fossil locality of Barranco del Hocino-1 is a bonebed composed of disarticulated elements with a notable degree of breakage and incompleteness. The fossil association is dominated by isolated macroremains of ornithopod dinosaurs. In addition, ankylosaur bones, theropod teeth, scarce microvertebrate remains (crocodylomorph and osteichthyan teeth), turtle shell fragments, coprolites and eggshells are also present (Alonso et al. 2016). The aim of the current paper is to give first insights into the theropod fauna from this site.

### 1.1 Geographical and geological setting

The Barranco del Hocino-1 fossil site is located within the municipality of Estercuel, Teruel province, Spain. Geologically, this fossil locality (Fig. 1) is situated in the

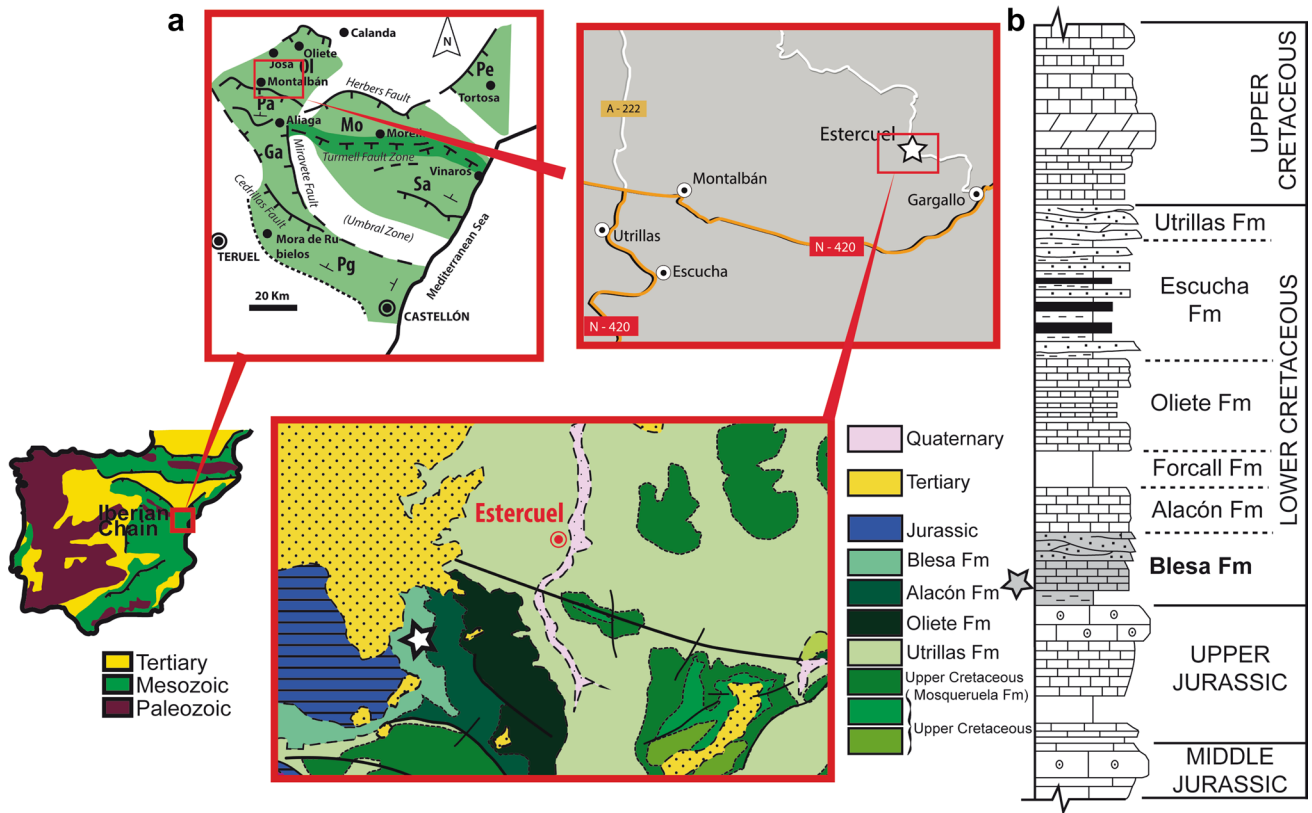
middle part of the Blesa Formation. The Early Cretaceous of the Iberian Range in the eastern part of the province of Teruel forms part of the Maestrazgo Basin, which is further divided into seven sub-basins (Salas et al. 2001). One of these is the Oliete sub-basin, where the Barranco del Hocino-1 site is located. This site is an outcrop of the continental facies from the middle part of the Blesa Formation. This geological unit comprises a lower part with alluvial to lacustrine sedimentation, followed by an upper part with two episodes of coastal lagoonal influence in the Josa area (Canudo et al. 2010). In the Estercuel area, it has not yet been possible to recognize the level that separates these two episodes.

The presence of charophyte oogonia attributed to *Atopochara trivolvris triquetra* in the lower part of the Blesa Formation indicates an early Barremian age (Riveline et al. 1996; Canudo et al. 2010; see discussion in Canudo et al. 2012). For the present, we date Barranco del Hocino-1 (upper part of the Blesa Formation) as Barremian in age, pending a more precise evaluation of the age.

The layer of Barranco del Hocino-1 lies within a stratigraphic succession of marly/lutitic levels, where palaeosols alternate with burrowed grey limestone beds. The fossiliferous bed consists of grey lutites with red, green and yellowish mottling, with the presence of bioturbation (invertebrate traces), carbonate nodules and calcrete. The fossil content consists of vertebrates, bivalves and gastropods, along with microfossil remains. Among the microfossils, ostracods and charophytes form the major bioclastic part of the residue from the 50- $\mu$ m sieve. The depositional environment is interpreted as an alluvial plain with evidence of shallow freshwater/palustrine episodes and the development of palaeosols. Fossil remains are found dispersed over an area that extends laterally about ten metres. The bones have undergone intense breakage, abrasion and weathering; some of them bear tooth traces on the bone surface as well.

## 2 Materials and methods

The fossils were recovered during the fieldwork campaign of 2015 carried out by the *Aragosaurus*-IUCA research team (University of Zaragoza). The material recovered is provisionally housed in the Natural History Museum of the University of Zaragoza (“Museo de Ciencias Naturales de la Universidad de Zaragoza”, Spain). Observations were made with a stereomicroscope. The teeth were measured with a Mitutoyo Digimatic Digital Calliper, Series No. 500. Six theropod teeth (Supplementary appendix A) from Barranco del Hocino-1 were analysed during the course of this research.



**Fig. 1** **a** Geographical and geological setting of Barranco del Hocino-1 site. **b** Stratigraphical setting of the Blesa Formation, from Canudo et al. (2010)

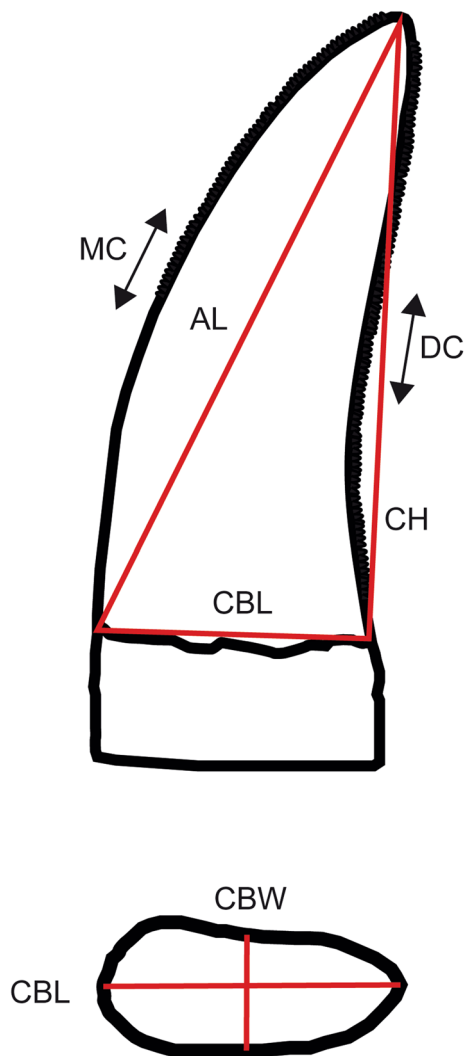
### 2.1 Anatomical nomenclature

The anatomical nomenclature used in this work follows the recommendations provided by Smith and Dodson (2003) and Hendrickx et al. (2015a). Each tooth includes a crown made of a layer of dentine covered by a layer of enamel, and a root consisting of dentine only. The cervix marks the transition between the crown and root. The top of the crown and root are called the crown or root apices, respectively. The mesial and distal edges of the tooth crown are commonly marked by apicobasally extended crests called carinae. The carinae may bear elaborate serrations known as denticles. Dental ornamentations, such as enamel undulations, flutes, grooves, ridges and depressions are often present on the crown surface. The pattern of the enamel surface is called the enamel texture (Hendrickx et al. 2015a).

The surface of the tooth facing outwards towards the lips is referred to as labial; the opposite surface facing the sagittal midline of the skull is called lingual. The surface closer to the jaw symphysis is called mesial, and the surface facing the jaw articulation is called distal. Basal refers to the direction from the apex to the cervix. Apical refers to the direction from the cervix to the apex.

### 2.2 Morphometric nomenclature

The morphometric terminology used in this work (Fig. 2) follows the terminology and abbreviations used in Smith et al. (2005) and Hendrickx et al. (2015a). 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. CBR: crown base ratio (CBW/CBL), a measure of the lingual compression. CBW: crown base width, the labiolingual width of the crown at the cervix level, perpendicular to CBL. 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. DC: distocentral denticle density, the number of denticles per 5 mm on the distal carina at mid-crown. DSDI: denticle size density index (MC/DC), introduced by Rauhut and Werner (1995), expressing the difference in size between the mesial and distal denticles. MC: mesiocentral denticle density, the number of denticles per 5 mm on the mesial carina at mid-crown.



**Fig. 2** DFA variables. *AL* apical length, *CBL* crown base length, *CBW* crown base width, *CH* crown height, *DC* disto-central denticle density, *MC* mesio-central denticle density

### 2.3 Qualitative and other features

Qualitative features of the teeth were studied in order to complement the morphometric information provided by measurements. These dental features include the shape of the tooth (Torices et al. 2015), the presence and characteristics of the mesial and distal carinae (Currie and Sloan 1990; Hendrickx 2015), the morphology of the denticles (Currie and Sloan 1990; Torices et al. 2015; Hendrickx et al. 2015a), the crown cross-section at the crown base, the crown ornamentations (Hendrickx 2015) and the preservation of the tooth.

### 2.4 Statistical analysis

A discriminant function analysis (DFA) was carried out using PAST3 (Hammer et al. 2001) on the dataset of Hendrickx et al. (2015b); data from White et al. (2015) and Csiki-Sava et al. (2016) were also included. The dataset contains 1015 teeth from different theropod clades and taxa, as well as the Barranco del Hocino-1 teeth: basal saurischians (*Eoraptor*), basal theropods (*Ischisaurus* = *Herrerasaurus*, *Eodromaeus*), non-averostran neotheropods (*Coelophysis*, *Liliensternus*, *Dilophosaurus*), Ceratosauridae (*Genyodectes*, *Ceratosaurus*), Noasauridae (*Noasaurus*, *Masiakasaurus*), Abelisauridae (*Abelisaurus*, *Rugops*, *Indosuchus*, *Majungasaurus*, *Aucasaurus*, *Skorpiovenator*, *Carnotaurus*), the possible metriacanthosaurid *Erectopus*, Piatnitzkysauridae (*Piatnitzkysaurus*), Megalosauridae (*Afrovenator*, *Duriavenator*, *Megalosaurus*, *Dubreuillosaurus*, *Torvosaurus*), Baryonychinae (*Baryonyx*, *Sucho-mimus*), Spinosaurinae (*Irritator*, *Spinosaurus*), Allosauridae (*Allosaurus*), Neovenatoridae (*Neovenator*), Carcharodontosauridae (*Acrocanthosaurus*, *Eocarcharia*, *Carcharodontosaurus*, *Giganotosaurus*, *Mapusaurus*), Megaraptora (*Australovenator*, *Fukuiraptor*, *Aerosteon*), non-tyrannosaurid Tyrannosauoidea (*Eotyrannus*, *Raptorex*), Tyrannosauridae (*Alioramus*, *Gorgosaurus*, *Daspletosaurus*, *Albertosaurus*, *Tyrannosaurus*), the possible dromaeosaurid *Nuthetes*, Dromaeosauridae (*Bambiraptor*, *Deinonychus*, *Dromaeosaurus*, *Velociraptor*, *Saurornitholestes*, *Atrociraptor*, *Zapsalis*), Troodontidae (*Troodon*, *Zanabazar*, *Pectinodon*), and *Richardoestesia*. The analysis performed was a discriminant function analysis (DFA). DFA is an ordination technique applied to previously identified data in order to find the best discriminant variables. It also has predictive power and is able to classify unknown data in the previously known groups (Hammer and Harper 2006).

The variables used are CBL, CBW, CH, AL, MC and DC. Absent data were coded as a question mark and missing values were estimated with a mean value for that measurement from across the sample. To better reflect a normal distribution, all the data were log-transformed (see Samman et al. 2005). In order to avoid interference and overlapping between groups, and given the absence of mesial teeth from Barranco del Hocino 1 site, the mesial teeth were removed from the dataset.

The presence of small groups affects the accuracy of the analysis; in this case we maintained low number groups due to the relevance of some of them from comparison with Barranco del Hocino 1 morphotypes, even though this was at the expense of an improved analysis.

Also, we maintained isolated teeth that have been identified on generic level, for the same reason as above. Ideally, the dataset would consist of non-isolated teeth. Nonetheless,

some taxa include isolated teeth; the relevance of those groups leads us to do not exclude the specimens.

The DFA of the 860 remaining teeth returned 70.99% correctly classified teeth (Supplementary appendix A).

The functions obtained explain the variance of the dataset. The first and the second functions explain 80.58% of the variance (Supplementary appendix A). These canonical functions can be used to create a plot showing the graphical representation of the morphospace occupied by the teeth in a dispersion graph (Fig. 3). The weight of each variable in the canonical functions can be found in Supplementary appendix A.

### 2.5 Cladistic analysis

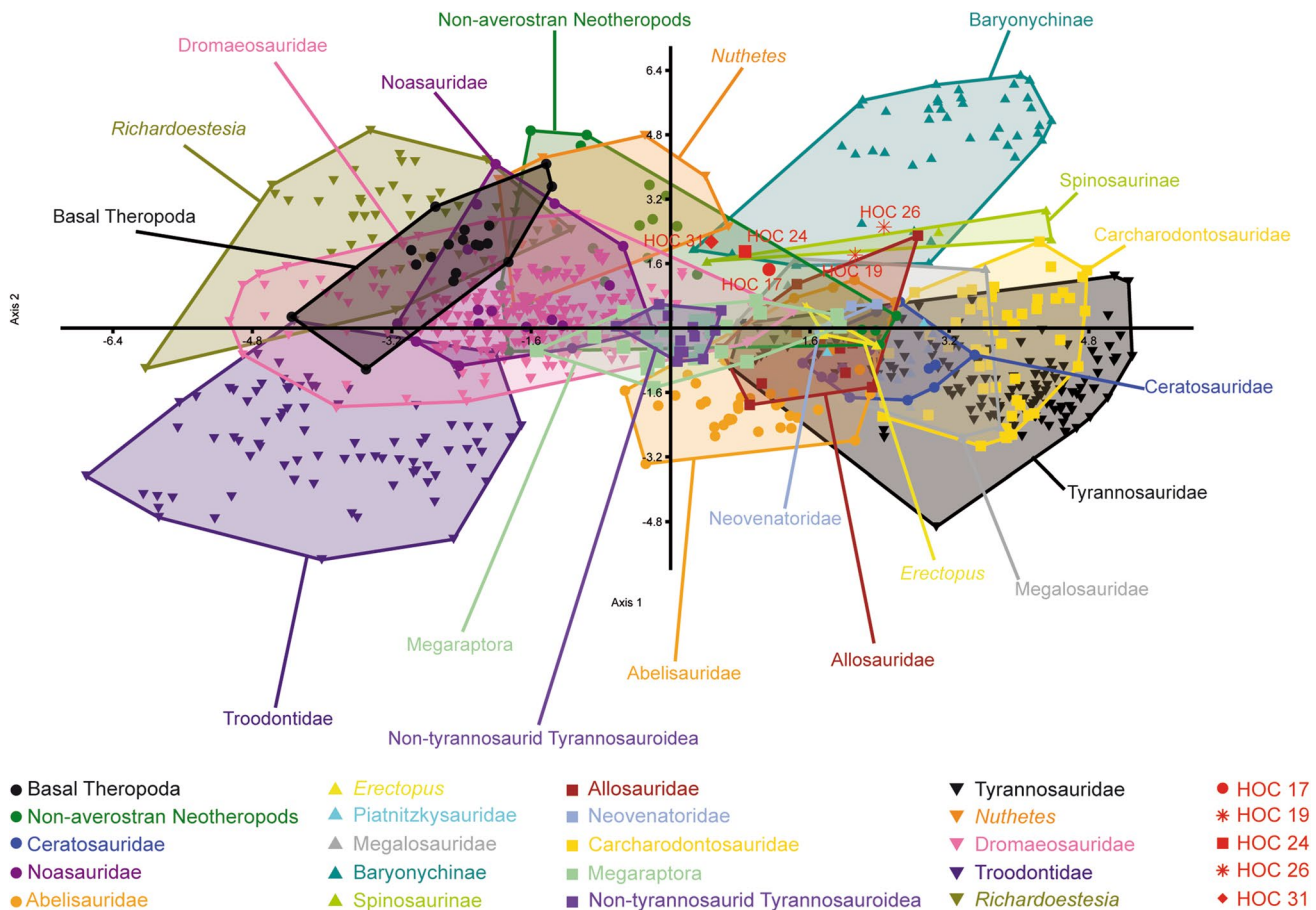
Cladistic analyses have been used by some authors to evaluate the phylogenetic position of isolated theropod teeth. The teeth from Barranco del Hocino-1 were analysed using the supermatrix of Hendrickx and Mateus (2014b), with the modifications proposed by Gerke and Wings (2016). The supermatrix includes 60 theropod taxa with 1972

characters. Of these 1972 characters, 141 characters are dentition-based features. The analysis was carried with TNT 1.5 (Goloboff and Catalano 2016) using the “Traditional search” with 1000 replications, keeping 10 trees per replication. The protocol of Hendrickx and Mateus (2014b) and Gerke and Wings (2016) was performed as well, using the “New Technology Search”, selecting “Sectorial Search”, “Ratchet”, “Drift” and “Tree fusing”, and stabilizing the consensus trees twice with a factor of 75, followed an additional round of TBR using. Both analyses produced the same results.

## 3 Results

### 3.1 Systematic palaeontology

TETANURAE Gauthier, 1986



**Fig. 3** Results of the DFA conducted on a dataset of 1015 teeth, including Barranco del Hocino-1 teeth. The first function explains the 56.86% of variance; the second canonical function explains the 23.72% of the variance

### 3.1.1 Tetanurae indet. 1

Material: One shed tooth (HOC 24).

**3.1.1.1 Description** This morphotype includes one tooth lacking the apex and a small part of the base (Fig. 4). The enamel surface is worn, show microstratches and the lingual area has some white marks on its apical and central regions that were caused by the roots of modern plants. The tooth is ziphodont, with a labiolingually compressed and a distally curved crown. The tooth crown also bears serrations but lacks a few denticles on the mesial and distal carina.

A transverse break is located at the mid-crown. Another break affects the lowermost part of the lingual surface, where a small fragment was detached from the crown. In basal view the tooth crown reveals the pulp cavity.

HOC 24 is a medium-sized theropod tooth, with a crown base length (CBL) of 9.43 mm, crown base width (CBW) of 5.63, and preserved crown height (CH) of 14.32 mm. The estimated value of the crown height (CH) is 20.2 mm. With a CBR and a CHR of 0.6 and 2.15 respectively, the crown is moderately labiolingually flattened and moderately elongated, with an ovoid cross-section at its base.

The mesial and distal profiles are convex and concave, respectively. The mesial margin of the tooth crown is more recurved than the distal margin; the crown has carinae on

both mesial and distal margins. The mesial carina extends from the apex to the basal third of the crown, finishing well above the cervix. On the other hand, the distal carina extends along the entire distal margin. In addition, the labial surface adjacent to the distal carina is flattened.

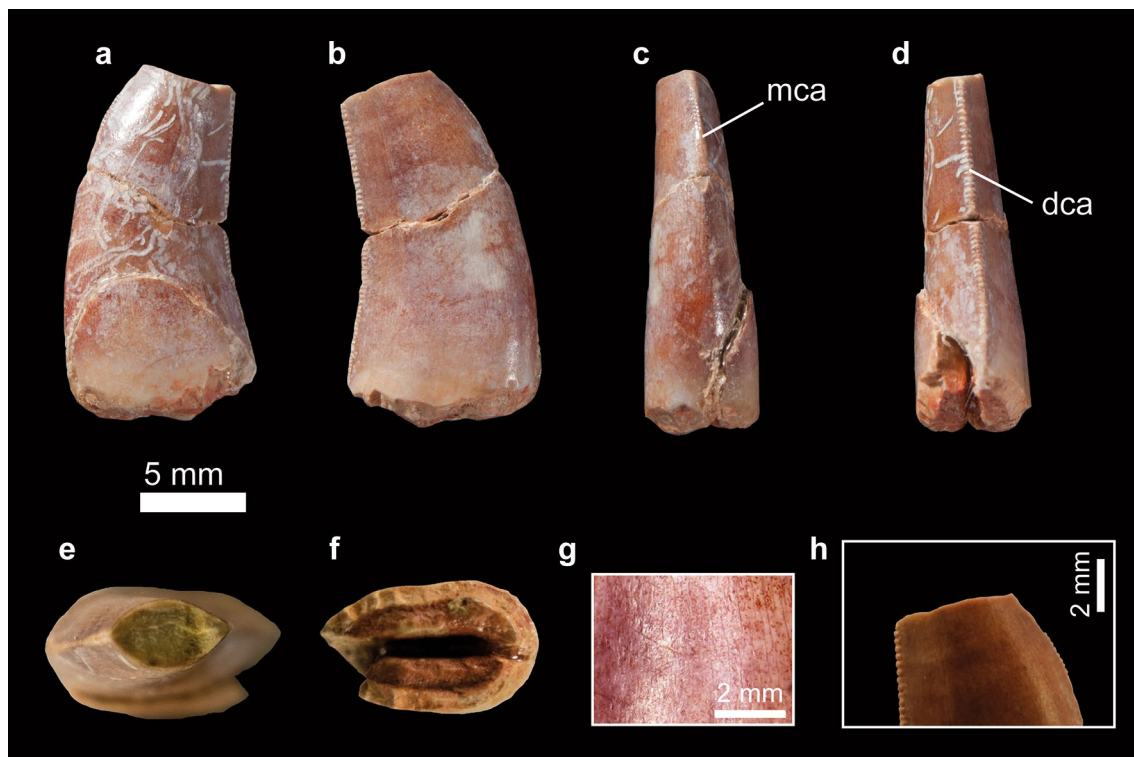
The mesial carina bears denticles and is centrally positioned. The labial surface is slightly basoapically sigmoid with the basal part of the crown convex and the apical part concave. The lingual surface, however, seems to remain basoapically convex.

In distal view, the distal carina is displaced labially and bears denticles all along the edge. The labial and lingual surfaces are mesiodistally convex, with the lingual side more convex than the labial side.

In apical view, the tooth crown has a lenticular cross-section and both the mesial and distal carinae are acute. In basal view, the cross-section of the crown is oval and slightly lanceolate whereas the cross-section at the level of the mid-crown is lenticular.

The mesial carina preserves nine denticles per 2 mm (around 22.5 denticles per 5 mm). In lateral view, the apicobasal axis of the denticles is greater than the mesiodistal axis, giving them an apicobasally subrectangular outline. The external margin of the denticles is parabolic.

The distal carina has around 20 denticles per 5 mm at the mid-crown. The denticles gradually decrease in size towards



**Fig. 4** Tetanurae indet. 1. HOC 24. **a** Lingual, **b** labial, **c** mesial, **d** distal, **e** apical, **f** basal views. **g**, **h** Enamel surface and denticles. *dca* distal carina, *mca* mesial carina



its base. Morphologically, they are chisel-shaped and the mesiodistal axis of the denticles is greater than the apico-basal length, which give them a subrectangular outline. The denticles are positioned perpendicularly to the carina and the external margin is parabolic to semicircular. In addition, the outline of the denticles is either symmetrically or asymmetrically convex. The interdenticular space between denticles is narrow and deeper in the distal denticles. The distal carina shows interdenticular sulci diagonally oriented basally towards the base of the tooth crown. They are short and are better seen at low light angle.

The crown surface is covered with microscratches on both lingual and labial sides due to wear and erosion. The surface also displays marginal undulations, which are short and are better seen at certain angles. In addition there are transverse undulations covering the complete surface of the crown; they are apically concave and they curve towards the apex as they approach the carina. The enamel texture is braided (sensu Hendrickx et al. 2015a).

**3.1.1.2 Discussion** HOC 24 is a moderately compressed crown, suggesting that it is a lateral tooth. This tooth is different from other theropod clades. Coelophysids and compsognathids have small crowns bearing minute denticles (Buckley 2009; Hendrickx and Mateus 2014b). The dentition of abelisaurid theropods is usually squat, weakly recurved and some of them have hooked denticles and the mesial carina reaches the cervix (Hendrickx et al. 2015b) whereas non-abelisaurid ceratosaurs have a mesial carina that extends at a certain distance from the cervix. HOC 24 is also clearly different from the conodont teeth with apico-basal enamel flutes, minute denticles and deeply veined enamel texture of spinosaurids (Charig and Milner, 1997; Canudo et al. 2008a; Hendrickx and Mateus 2014b). In addition, it does not possess the thickened and incrassate crowns of derived tyrannosauroids (Brusatte et al. 2010; Csiki-Sava et al. 2016) and it is significantly different from troodontids, therizinosaurids, ornithomimosaurids, alvarezsaurids, oviraptorosaurs or avialans, which have small, conical, folioid and/or unserrated crowns. When serrated, the carinae bear either particularly large, often hooked denticles, or minute serrations (Pérez-Moreno et al. 1994; Norell et al. 2009; Hendrickx and Mateus 2014b; Hendrickx et al. 2015b; Csiki-Sava et al. 2016).

One of the most striking features of this morphotype is a mesial carina that does not reach the cervix. This trait is seen in basal theropods such as *Eoraptor*, non-spinosaurid megalosauroids and most piatnitzkysaurid mesial and lateral teeth (Hendrickx et al. 2015b), neovenatorids (Hutt et al. 1996), carcharodontosaurids such as *Acrocanthosaurus*, megaraptorans (White et al. 2015), therizinosaurids, dromaeosaurids and microraptorans (Hendrickx 2015). The presence of transverse and marginal undulations is common among

non-neocoelurosaur averostrans (Brusatte et al. 2007, Hendrickx and Mateus 2014b).

A slightly concave or planar surface adjacent to the distal carina is seen among non-neocoelurosaur theropods. The slightly concave or planar surface is observable in *Skorpiovenator*, *Erectopus*, *Piatnitzkysaurus*, *Afrovenator*, *Sinraptor*, *Neovenator*, *Fukuiraptor* and *Australovenator*, as well as *Coelophysis*, *Dilophosaurus* and *Ceratops* (Hendrickx 2015).

DFA (Supplementary appendix A) classifies HOC 24 as a member of the group Neovenatoridae. The cladistic analysis (Supplementary appendix B) recovers HOC 24 as a tyrannosauroid.

This tooth shows some differences with respect to Tetanurae indet. 2 and Tetanurae cf. Carcharodontosauria indet. (see below). The tooth has a thicker cross-section and the general shape of the crown is more squat. It also possesses a planar surface adjacent to the distal carina. Despite this, they share some common features, including the presence of transverse and marginal undulations, a relatively similar denticle density, a mesial carina that does not reach the cervix and a distal carina that is displaced labially. The differences between the morphotypes could be explained by ontogenetic variation, different tooth positions, or the presence of two different taxa.

Given the incompleteness of the tooth crown here we prefer to be cautious and consider this morphotype as Tetanurae indet.

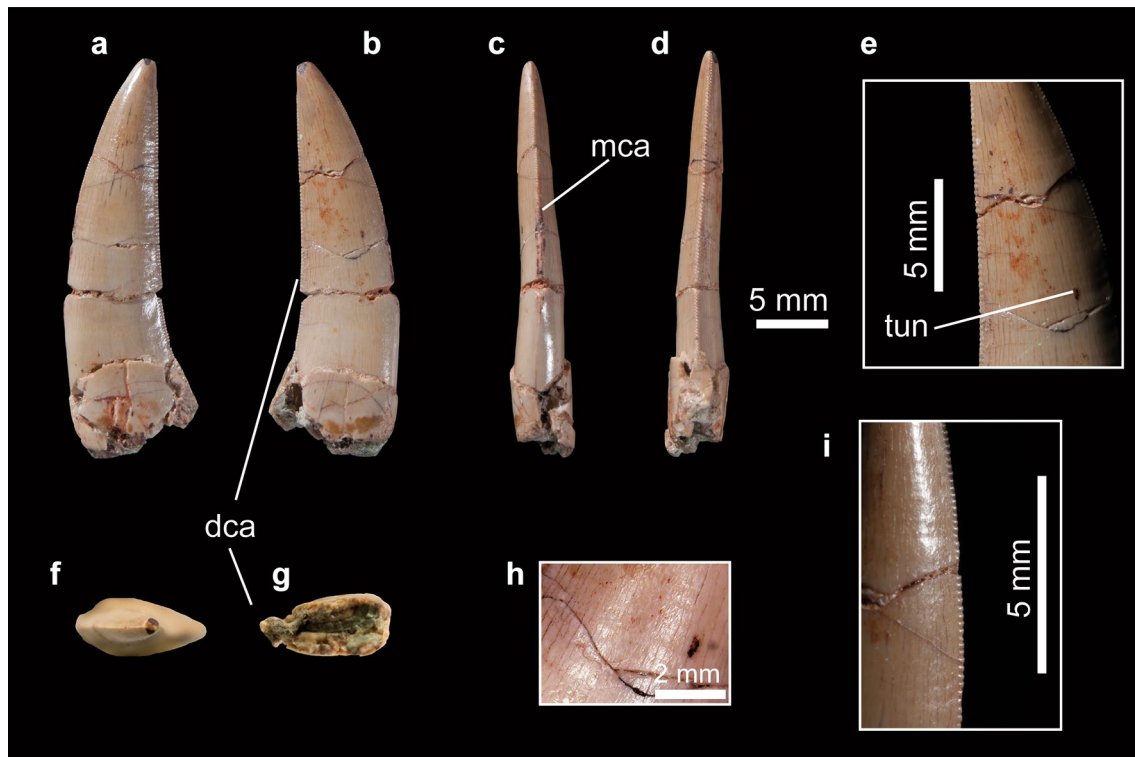
### 3.1.2 Tetanurae indet. 2

Material: HOC 31, a shed tooth.

**3.1.2.1 Description** The morphotype comprises one tooth lacking the root and part of the base (Fig. 5). The enamel surface is worn and shows microscratches. The tooth is ziphodont, with a labiolingually compressed and curved crown. The tooth crown has transverse breaks and the basal-most part is broken; this is the most damaged area. In basal view, it reveals a pulp cavity filled with sediment.

HOC 31 is a medium-sized theropod tooth, with a preserved crown base length (CBL) of 8.75 mm, a preserved crown base width (CBW) of 4.2 mm, and preserved crown height (CH) of 25.2 mm. The tooth crown is strongly labiolingually compressed (CBR around 0.4) and elongated (CHR around 2.8).

In lateral view, the mesial margin of the tooth crown is convex, while the distal margin is concave. The mesial margin is more recurved than the distal margin. The apex is acute and has spalled surfaces both on labial and lingual sides. The tooth crown has mesial and distal carinae, and the mesial carina terminates well above the cervix whereas the distal carina extends on the whole crown.



**Fig. 5** Tetanurae indet. 2. HOC 31 in **a** labial, **b** lingual, **c** mesial, **d** distal view. **e** Detail of undulations, mesial and distal carinae. **f** Apical, **g** basal views. **h** Enamel surface, **i** mesial carina

In mesial view, the mesial carina bears denticles and is located on the mesiodistal axis of the crown. The labial surface of HOC 31 is slightly sigmoid basoapically, with the basalmost part of the crown convex whereas the apical part is concave.

In distal view, the distal carina bears serrations as well and is very slightly displaced labially. The labial and lingual surfaces of the tooth crown are weakly mesiodistally convex.

In apical view, the tip is distally positioned on the crown. In basal view, the cross-section of the crown is lanceolate at the level of the cervix with the mesial surface being broader than the distal surface. The cross section at the level of the mid-crown is lenticular with the mesial and distal margins both acute.

The mesial carina has 24 denticles per 5 mm at the mid-crown. The denticles display a gradual variation in size towards the basalmost part of the crown. The mesial denticles have the same basoapical and mesiodistal length which give them a subquadrangular shape. The external margin of the denticles is parabolic.

The distal carina has 20 denticles per 5 mm at the mid-crown, and the denticle size density index (DSDI) is 1.2. The denticles are perpendicular to the distal margin of the tooth. The denticles decrease in size towards the base, displaying a gradual variation. The distocentral denticles are subquadrangular. There is, however, variation in shape: the distobasal

denticles are proximodistally subrectangular. The main axis of the denticles is perpendicular to the mesial carina and the external margin of the denticles is parabolic to semicircular; they are either symmetrically or asymmetrically convex. The space between denticles is narrow and deeper in the distal denticles. There are interdenticular sulci; they are short, basally inclined and they are present on the distal margin.

The crown surface is worn and is covered with micro-scratches probably due to wear and erosion. The enamel surface displays horizontally oriented marginal undulations which bend towards the tip of the crown near the mesial and distal carinae. In addition, there are horizontally oriented transverse undulations, which are apically concave, and they curve apically as they approach the carinae. The transverse undulations completely cover the enamel surface of the tooth crown.

The original enamel texture appears to be braided (sensu Hendrickx et al. 2015a).

**3.1.2.2 Discussion** This tooth share traits commonly found in non-maniraptoriform tetanurans. HOC 31 is strongly labiolingually compressed, the mesial carina does not reach the cervix, the distal carina is slightly displaced labially, and it also has transverse and marginal undulations, interdenticular sulci, a braided enamel texture and a lenticular cross-section. However, the tooth crown shows some differences

with respect to Tetanurae cf. Carcharodontosauria indet. (see below). The DSDI is 1.2 and the distocentral denticles are subquadrangular instead of proximodistally subrectangular. The labial and lingual surfaces are similarly mesiodistally convex instead of a lingual surface more mesiodistally convex in shape.

DFA analysis (Supplementary appendix A) classifies this tooth as *Erectopus*. The cladistic analysis (Supplementary appendix B) recovers a polytomy at the base of Averostra. A reduced strict consensus was calculated using the pruning trees option in TNT (Supplementary appendix B), resulting in the pruning of HOC 31. It is recovered either as the sister taxon of Averostra, as the sister taxon of *Dubreuillosaurus*, as the sister taxon of *Piatnitzkysaurus* or as the sister taxon of Spinosauridae.

The difference in size between the mesial and distal denticles in this morphotype is remarkable. This character is present in the lateral dentition of noasaurids such as *Noasaurus* and *Masiakasaurus*, piatnitzkysaurids such as *Marshosaurus* and *Piatnitzkysaurus*, non-tyrannosaurid Tyrannosauroida such as *Proceratosaurus* (Rauhut et al. 2010), *Dilong*, *Guanlong*, *Eotyrannus* and *Xiongguanlong*, Dromaeosaurids such as *Velociraptor* and *Deinonychus* show this condition as well (Hendrickx 2015).

Despite the similarity between Tetanurae cf. Carcharodontosauria indet. (see below) and this tooth, the high

denticle size index (DSDI) and the absence of this feature in allosauroids leads us to consider this morphotype as another morphotype of Tetanurae indet. However, we do not exclude that the differences between this morphotype and Tetanurae cf. Carcharodontosauria indet. could be explained by ontogenetic variation, different tooth positions, or the presence of two different taxa. New discoveries are required to resolve this issue.

TETANURAE Gauthier, 1986

MEGALOSAUROIDEA Fitzinger, 1843

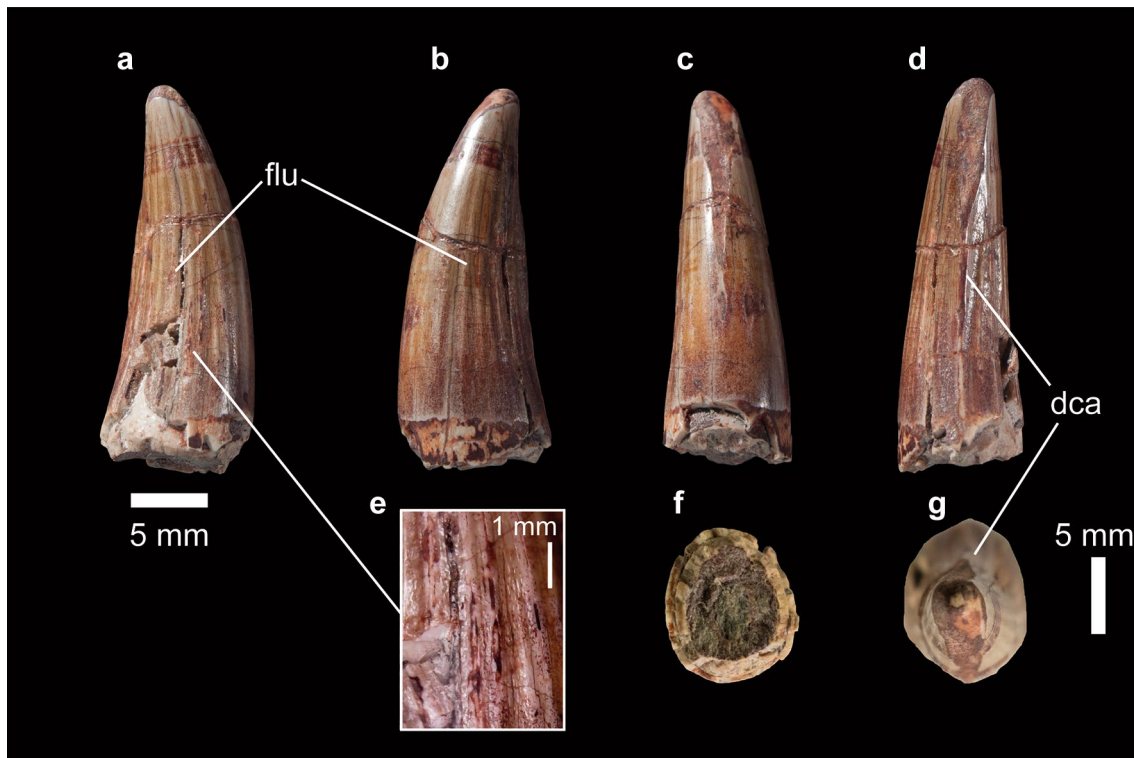
Spinosauridae Stromer, 1915

Spinosaurinae Sereno, Beck, Dutheil, Gado, Larsson, Lyon, Marcot, Rauhut, Sadleir, Sidor, Varricchio, Wilson and Wilson, 1998

### 3.1.3 Spinosaurinae indet.

Material: HOC 17, HOC 28, two shed teeth.

**3.1.3.1 Description** HOC 17 is a conical tooth from a theropod dinosaur preserving most of the crown and a small part of the root (Fig. 6). The enamel shows small fractures, and some parts are missing. A transverse break is located at the end of the apical third. The lingual surface has a damaged area in its basal region, which is lacking



**Fig. 6** Spinosaurinae indet. HOC 17: **a** lingual, **b** labial, **c** mesial, **d** distal view. **e** Enamel surface and ornamentation. **f** Basal view. **g** Apical views. *dca* distal carina, *flu* flutes

fragments of the crown. The surface is also covered with microscratches, and some parts of the original enamel texture are worn, possibly due to abrasion. HOC 28 is a poorly preserved theropod tooth fragment but here it is considered to represent the same morphotype as HOC 17 because of its general similarity and the presence of longitudinal flutes along the crown. Therefore, the description of this morphotype is based on the better-preserved tooth, HOC 17.

HOC 17 is a medium-sized tooth from a theropod dinosaur, with a crown base length (CBL) of 10.27 mm, crown base width (CBW) of 8.61 mm, and crown height (CH) of 23.25 mm. The tooth is conodont (sensu Hendrickx et al. 2015a). With a CBR and a CHR of 0.8 and 2.26 respectively, the crown is weakly labiolingually compressed and moderately elongated, with a broad and rounded cross-section at its base.

In lateral view, the mesial and distal profiles are convex and concave, respectively. The crown is moderately recurved and its curvature is greater mesially than distally. The base of the crown is longer than the mid-crown mesiodistally.

In distal view, the mesial and distal profiles are curved towards the lingual side of the crown. The labial and lingual surfaces are mesiodistally convex with the enamel extending to the same level basally. The distal carina is centrally positioned on the distal margin of the crown and reaches the cervix. It does not show any serrations.

In mesial view, the mesial surface is worn, and this precludes the recognition of a possible mesial carina. The mesial carina, if it was originally present, extended significantly (5.5 mm) above the cervix and was medially positioned. In apical view, the tip is slightly lingually oriented.

The cross-sections at the level of the cervix and the mid-crown are elliptical to subcircular; the mesial margin is wider than the distal margin. Both labial and lingual surfaces are mesiodistally convex along the crown; mesial and distal margins are convex as well.

The distal carina is partially eroded, but the central part, which is better preserved, lacks denticles, suggesting that the distal carina is unserrated.

The apex of the crown has a spalled surface extending along the apical third of the crown on both the mesial and distal surfaces. Numerous flutes running apicobasally are visible on the lingual and labial sides of the crown. Five and eight flutes are present on the labial and lingual sides, respectively.

Some parts of the enamel are smooth due to erosion and wear. The preserved enamel surface texture corresponds to the veined texture described by Hendrickx et al. (2015a). The texture is basoapically oriented in the middle of the crown but curves towards the carina at the distal margin. The enamel texture is best preserved between the apicobasal ridges delimiting each flute.

**3.1.3.2 Discussion** The tooth has a combination of features seen in spinosaurid teeth such as a slight distal curvature, a subcircular cross-section, fluted enamel on both labial and lingual sides of the crown and a veined enamel texture. Spinosaurid teeth either have minute denticles or unserrated carinae (Charig and Milner 1997; Sereno et al. 1998; Ruiz-Omeñaca et al. 2005; Canudo et al. 2008a; Gasca et al. 2008).

Some authors have pointed out the presence of a morphotype of spinosaurid tooth from the Barremian of Teruel Province with an unserrated mesial carina (Artoles Formation, Ruiz-Omeñaca et al. 1998; El Castellar Formation, Gasca et al. 2008). However, this cannot be established in the case of this tooth. The mesial carina, if present, was not reaching the cervix.

The presence of flutes is characteristic of spinosaurid teeth, although they are present in other taxa as well (e.g., *Coelophysis*, *Ceratosaurus*, *Masiakasaurus*, *Scipionyx*, and some dromaeosaurids; Hendrickx 2015). HOC 17 has flutes on both sides as in *Suchomimus*, *Spinosaurus* and *Siamosaurus* whereas *Baryonyx* tends to have flutes restricted to one side of the crown (Charig and Milner 1997; Hendrickx 2015). The veined enamel texture (sensu Hendrickx et al. 2015a) of the tooth characterizes spinosaurid teeth. It has been found in *Baryonyx*, *Suchomimus*, *Spinosaurus* and other spinosaurids (Canudo et al. 2008a; Serrano-Martínez et al. 2016; Hendrickx 2015).

Spinosaurids are divided traditionally into two subfamilies, Baryonychinae and Spinosaurinae. There are various morphological differences between their teeth. Baryonychine teeth have serrated carinae with minute denticles, more labiolingually compressed teeth than spinosaurines and a more pronounced distal curvature of the crown (Charig and Milner 1997; Canudo et al. 2008a; Alonso and Canudo 2016). Also, spinosaurine teeth have unserrated carinae, as exemplified by *Irritator*, *Angaturama* and *Spinosaurus* (Stromer, 1915; Kellner and Campos 1996; Sues et al. 2002). In general, all these differences are plesiomorphies in baryonychine teeth, or apomorphies in spinosaurine teeth.

The DFA analysis classifies HOC 17 as belonging to a member of Spinosaurinae (Supplementary appendix A). Likewise, the cladistic analysis considers this morphotype as the sister taxon of the group formed by *Spinosaurus* and *Irritator* (Supplementary appendix B). The possible presence of spinosaurine spinosaurids in the Lower Cretaceous of the Iberian Peninsula has been proposed before (Sánchez-Hernández et al. 2007; Alonso and Canudo 2016), but the most common spinosaurid material belongs to Baryonychinae (Infante et al. 2005; Canudo et al. 2008a; Gasca et al. 2008; Mateus et al. 2011; Alonso and Canudo 2016).

Given the combination of features and the results of the analyses here we consider this morphotype as Spinosaurinae indet.

## TETANURAE Gauthier, 1986

**3.1.4 Tetanurae cf. Carcharodontosauria indet.**

Material: HOC 19 and HOC 26, two shed teeth.

**3.1.4.1 Description** The morphotype comprises two teeth lacking the root and the basalmost part of the tooth. The enamel surface is worn and shows microscratches. The shape of the teeth is the common blade-like morphology, with labiolingually compressed and distally curved crowns bearing serrated carinae (Fig. 7). The crown HOC 19 is the best-preserved tooth; it lacks the basal part, and the break reveals the dentine and a narrow pulp cavity filled with sediment. The apex and some areas of the labial and lingual surfaces lack the enamel cover, especially the lingual surface, which shows a longitudinal area from the basal part to the mid-crown where the enamel is missing.

The crown HOC 26 exhibits transverse breaks over its entire height: at least four large breaks plus minor fractures. The base is the most damaged region of the crown and some parts are missing. It also has a series of white marks which are more evident on the lingual surface of the crown. These marks were caused by the roots of modern plants that damaged the enamel.

HOC 19 and HOC 26 are medium-sized theropod teeth, with a preserved crown base length (CBL) of 14.8 and 16.2 mm respectively; a preserved crown base width (CBW) of 6.8 and 7.5 mm respectively; and preserved crown height (CH) of 39.1 and 50.6 mm respectively. All the crowns are strongly to moderately labiolingually compressed (CBR value around 0.4) and elongated (CHR around 2.6–3). The teeth have a narrow, teardrop-shaped cross-section at their bases.

In lateral view, the mesial and distal profiles are convex and concave, respectively. The mesial margins of the crowns are more recurved than the distal margins. The apices are acute, pointed and have spalled surfaces. The crowns have carinae on both mesial and distal margins, and the extension of these carinae varies: the mesial carina extends along two-thirds of the preserved crown height whereas the distal carina seems to reach the cervix.

In distal view, the distal carina is slightly displaced labially and bears serrations all along the crown. The labial and lingual surfaces are mesiodistally convex, with the lingual side more convex than the labial side, which is weakly mesiodistally convex, almost flattened.

In mesial view, the mesial carina bears serrations and extends significantly above the cervix. The mesial carina of HOC 19 is placed slightly labially. On the other hand, the mesial carina of HOC 26 is placed labially at the tip but curves slightly towards the base, becoming centrally positioned. The labial surfaces of HOC 19 and HOC 26 are

slightly sigmoid, with the basalmost part of the crowns and the apical part being convex and concave, respectively. The converse situation is found on the lingual surfaces, where the basal part is concave and the apical part is convex.

In apical view, the tip is distally positioned on the crown and slightly lingually oriented. Both the mesial and distal carinae are acute. In basal view, the cross-section of the crowns is lanceolate at the level of the cervix with a rounded and wide labial margin whereas the lingual margin is acute. The cross-section at the level of the mid-crown is lenticular with the mesial and distal margins both acute.

The mesial carinae of HOC 19 and HOC 26 have around 21–22 denticles per 5 mm at the mid-crown, respectively. The size of the denticles decreases towards the basalmost part of the crown and they display a regular variation in size, i.e. not sporadic or sudden. In lateral view, the denticles possess a subquadrangular outline, with the same basoapical and mesiodistal length. They are positioned perpendicularly to the carina.

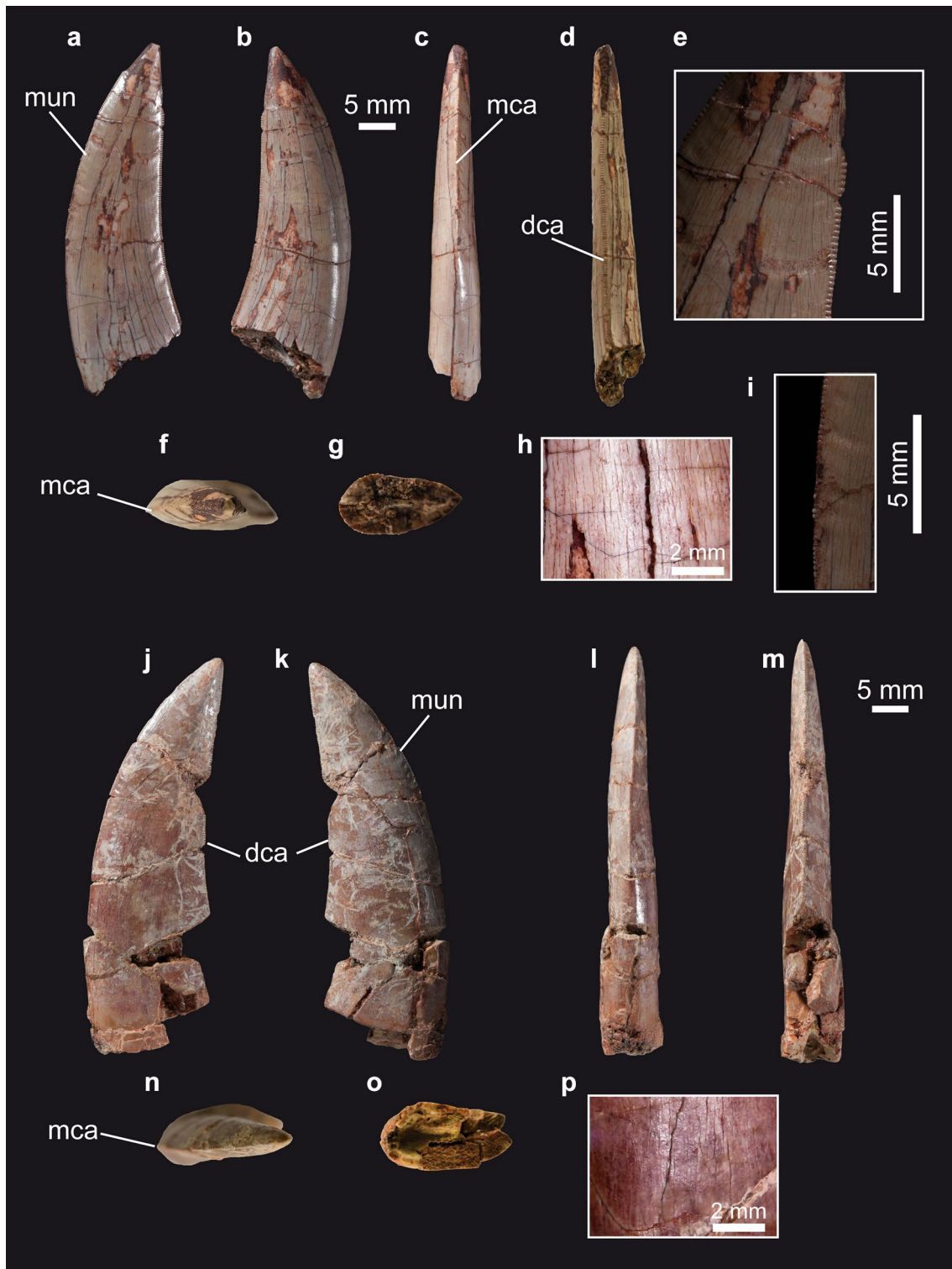
The distal carinae of HOC 19 and HOC 31 have 18–19 denticles per 5 mm at the mid-crown, respectively, and the denticle size difference index (DSDI) has a value of around 1. The denticles also decrease in size towards the base, displaying a gradual variation. They are chisel-shaped and proximodistally subrectangular, with a mesiodistal axis that is greater than the apicobasal axis except in the apical denticles, which are subquadrangular in shape. The main axis of the denticles is perpendicular to the distal carina.

The external margin of the mesial and distal denticles is parabolic to semicircular and either symmetrically or asymmetrically convex; they do not hook towards the tooth apex. The lingual and labial surfaces of the denticles are convex. The interdenticular space between denticles is narrow and deeper in the distal denticles. There are short and basally inclined interdenticular sulci between the distal denticles; they are better seen at a low light angle.

The crown surface is covered with microscratches due to erosion and wear. The external enamel shows diagonally oriented marginal undulations which bend towards the tip of the crown near the carinae. They are abundant, and they are restricted to the carina. Where the carina is not present (e.g. the mesial margin of the basalmost part of the crown), the marginal undulations are absent. These wrinkles are clearly visible whereas the transverse undulations are better seen at certain angles. The transverse undulations are apically concave, curving apically as they approach the carina, and they completely cover the enamel surface of the crowns.

The original enamel texture appears to be braided (sensu Hendrickx et al. 2015a).

**3.1.4.2 Discussion** The teeth of this morphotype share traits commonly found in non-maniraptoriform tetanurans. They are strongly labiolingually compressed, as seen in the lateral



**Fig. 7** Tetanurae cf. *Carcharodontosauria* indet. HOC 19 in **a** labial, **b** lingual, **c** mesial, **d** distal view. **e** Undulations and denticles on the distal carina. **f** Apical view, **g** basal views, **h** enamel surface, **i** mesial

carina. HOC 26 in **j** labial, **k** lingual, **l** mesial, **m** distal, **n** apical, **o** basal views, **p** enamel surface. *dca* distal carina, *mca* mesial carina, *mun* marginal undulations

dentition (Hendrickx et al. 2015b). The mesial carina does not reach the cervix, the distal carina is slightly displaced labially, and they also have marginal and transverse undulations, interdenticular sulci, a braided enamel texture and a lenticular cross-section. Megalosauroids and allosauroids share these characteristics (Hendrickx 2015; Hendrickx et al. 2015b). A mesial carina that does not reach the cervix is seen in megalosaurids (Hendrickx et al. 2015b), *Neovenator* (Hutt et al. 1996), *Australovenator* (Hocknull et al. 2009; White et al. 2015), *Alioramus* (Brusatte et al. 2012), Therizinosauria, and Microraptorinae, and is also seen in *Acrocanthosaurus* and *Dromaeosaurus* (Hendrickx 2015). The labial side of the teeth is weakly mesiodistally convex and comparatively flat. A surface centrally positioned on the crown roughly flattened on the labial side of lateral teeth is seen in non-abelisauroid ceratosaurs and neovenatorids (Hendrickx and Mateus 2014b; Hendrickx 2015); unlike non-abelisauroid ceratosaurs the mesial carina of this morphotype does not reach the cervix.

Teeth with a weak displacement of the distal carina are common in non-maniraptoriform theropods. Only a few clades such as Ceratosauridae, *Masiakasaurus*, *Allosaurus*, Tyrannosauroida and *Dromaeosaurus* show a distal carina strongly deflected labially (Hendrickx 2015). Another characteristic of HOC 19 and HOC 26 is the presence of transverse and marginal undulations, a widespread feature among theropods (Brusatte et al. 2007). The braided texture of the enamel is also widespread and can be observed in megalosauroids, allosauroids, tyrannosauroids and basal ceratosaurians (Hendrickx 2015).

DFA (Supplementary appendix A) classifies HOC 19 and HOC 26 as *Erectopus*. *Erectopus* is a basal allosauroid from the Albian of France (Allain et al. 2005). Some differences exist between this morphotype and the dentition of *Erectopus*: *Erectopus* has a concave surface on the lingual side adjacent to the distal carina (Hendrickx and Mateus 2014b), the mesial carina reaches the cervix (Allain et al. 2005) and the denticle density is slightly different. The cladistic analysis (Supplementary appendix B) places HOC 19 in a polytomy with *Piatnitzkysaurus* and *Erectopus*. On the other hand, the cladistics analysis of HOC 26 recovers a polytomy at the base of Averostira. A reduced strict consensus was calculated using the pruning trees option in TNT. The pruning of HOC 26 from the consensus tree increased the resolution of the consensus (Supplementary appendix B). HOC 26 is either recovered as the sister taxon of *Erectopus* or within Megalosauridae.

HOC 19 and HOC 26 share some traits with megalosaurids. The mesial carina does not reach the cervix, they are strongly to moderately labiolingually compressed, the enamel surface displays marginal and transverse undulations, and some of the denticle traits are relatively similar. In addition a flattened labial surface is seen on *Erectopus*.

Despite these similarities some differences exist: *Erectopus* has a planar surface adjacent to the distal carina on the lingual margin of the crown and the mesial carina reaches the cervix. Besides, the labial surface of megalosaurids is not flattened (Hendrickx 2015).

The presence of non-spinosaurid basal tetanurans is known for the deposits of the Lower Cretaceous of western Europe. Nevertheless, these are allosauroids related to Carcharodontosauria; if *Afrovenator* is of Jurassic age (Rauhut and López-Arbarelo 2009) then the youngest skeletal record of megalosaurids is *Torvosaurus* from the Kimmeridgian/Tithonian of Portugal and western USA (Hendrickx and Mateus 2014a). The only tetanuran described from the Early Cretaceous of Spain, *Concavenator corcovatus* from the upper Barremian of Las Hoyas (Cuenca province), is a basal carcharodontosaurid (Ortega et al. 2010). Another carcharodontosaurid specimen comes from other Barremian deposits in Teruel, where an isolated distal femur (Gasca et al. 2014b) has been found, sharing affinities with *Acrocanthosaurus*. Recently, a single carcharodontosaurid theropod tooth from the Valanginian of Romania (Csiki-Sava et al. 2016) has been proposed as the earliest evidence of Carcharodontosauridae in Europe. Carcharodontosaurid carcharodontosaurians are also found in Gondwanan deposits from the Early Cretaceous (Novas et al. 2005; Fanti et al. 2014), and in North America they are represented by the Albian genus *Acrocanthosaurus* (Serenio et al. 1996; Harris 1998; Brusatte and Sereno 2008; Csiki-Sava et al. 2016), becoming abundant and diverse in the course of the “Middle” and Late Cretaceous (Csiki-Sava et al. 2016). Non-carcharodontosaurid carcharodontosaurians are represented by *Neovenator* (Hutt et al. 1996) from the Barremian Wealden of England, which shares the features seen in this morphotype.

Given the absence of non-spinosaurid megalosauroid theropods from the Early Cretaceous of the Iberian Peninsula, these teeth are here considered as belonging to an indeterminate Carcharodontosauria, pending the discovery of additional skeletal material to support this hypothesis.

## 4 Discussion

The palaeobiodiversity of theropods from the Early Cretaceous of the Iberian Peninsula includes a broad set of neotheropods. The ceratosaur *Camarillasaurus cirugedae* (Sánchez-Hernández and Benton, 2014) has been described in the Barremian deposits of the Galve sub-basin. Among tetanurans there is a combination of basal and derived taxa. Basal tetanurans for which there is evidence include spinosaurids (Buffetaut 2007; Canudo et al. 2008a; Gasca et al. 2008; Mateus et al. 2011; Alonso and Canudo 2016) and carcharodontosaurians such as *Concavenator corcovatus* (Ortega et al. 2010), as well as other indeterminate

carcharodontosaurids (Gasca et al. 2014b). There is also evidence of derived tetanurans such as coelurosaurids, including ornithomimosaurids such as *Pelecanimimus* (Pérez-Moreno et al. 1994), maniraptorans such as dromaeosaurids (i.e., Ruiz-Omeñaca et al. 1996; Rauhut 2002; Canudo et al. 2010) as well as birds (i.e., Sanz et al. 1988). Thus the theropod fossil record from Barranco del Hocino-1 is congruent with the known record of theropods from the Early Cretaceous of the Iberian Peninsula. However, according to our phylogenetic analyses, these teeth would extend the non-spinosaurid megalosauroid lineage into the Early Cretaceous. HOC 19, HOC 24, HOC 26 and HOC 31 share some traits with some megalosauroids (e.g. a mesial carina that does not reach the cervix, they are strongly to moderately labiolingually compressed, the enamel surface displays marginal and transverse undulations, and some of the denticle traits are relatively similar).

Previous studies have supported the reliability of cladistics analyses applied to isolated teeth (e.g. Hendrickx and Mateus 2014b; Csiki-Sava et al. 2016). Nevertheless, it is interesting to point out that the state of preservation of Barranco del Hocino 1 teeth is deficient; partially explaining the results. The absence of relevant information about the crown and root could input a considerable amount of noise in our analyses.

In addition, the dataset does not include theropods from the Barremian of the Iberian Peninsula. It would be interesting to draw a comparison between Barranco del Hocino-1 morphotypes and theropods such as *Concavenator* (Ortega et al. 2010). A comprehensive study of its dentition would probably improve the identification of isolated teeth from the Early Cretaceous of the Iberian Peninsula.

The association of spinosaurids and other basal tetanurans is also found in other places, such as the Wealden of England, which has *Baryonyx* (Charig and Milner 1997) and *Neovenator* (Hutt et al. 1996) and other indeterminate basal tetanurans (Benson et al. 2009; Gasca et al. 2014b). This association represents the megapredators of the epoch. These clades are also found in the north of Africa, where there are spinosaurine and baryonychine spinosaurids such as *Spinosaurus* from the Cenomanian of Egypt (Stromer, 1915) and *Suchomimus* from the Aptian/Albian of Niger (Serenó et al. 1998) and carcharodontosaurians such as *Carcharodontosaurus* from the Cenomanian of Morocco and *Eocarcharia* from the Aptian/Albian of Niger (Brusatte and Sereno 2007; Brusatte et al. 2007; Sereno and Brusatte 2008, Fanti et al. 2014).

The absence of other theropod taxa in the Barranco del Hocino-1 fossil assemblage, especially smaller theropods, is remarkable. In contrast, other fossil sites in the Blesa Formation, such as La Cantalera-1, have evidence of the presence of small theropods. This may be explained by the taphonomic characteristics of the remains. Another explanation

is the amount of sediment sampled. Small-sized teeth are usually recovered when screen-washing is carried out. Three tonnes of sediment have been screen-washed from the La Cantalera-1 site, whilst just a few kilograms have been screen-washed here at Barranco del Hocino-1. This bias could affect the palaeobiodiversity that comes to light.

## 5 Conclusions

Barranco del Hocino-1 is a new fossil site in the Oliete sub-basin within the Maestrazgo Basin. Among the vertebrate fossils recovered from the site are remains from large-sized theropods which consist of isolated teeth. Four different morphotypes of theropod tooth have been identified. One morphotype has been assigned to Spinosauridae. The other morphotypes have been assigned to Tetanurae and one has been tentatively attributed to Carcharodontosauria indet. in the light of the known record of basal tetanurans from the Barremian of the Iberian Peninsula and western Europe. These results represent a new contribution to our knowledge of the palaeobiodiversity and distribution of theropods from the Barremian of the Iberian Peninsula. They also provide further evidence of the palaeontological interest of this area.

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## References

- Allain, R. (2005). The enigmatic theropod dinosaur *Erectopus superbus* (Sauvage 1882) from the Lower Albian of Louppy-le-Chateau. In Carpenter, K. (Ed.), *The carnivorous dinosaurs* (pp. 72–86). Bloomington, Indiana: Indiana University Press.
- Alonso, A., & Canudo, J. I. (2016). On the spinosaurid theropod teeth from the early Barremian (Early Cretaceous) Blesa Formation (Spain). *Historical Biology*, 28(6), 823–834.
- Alonso, A., Gasca, J. M., Navarro-Lorbés, P., Núñez-Lahuerta, C., Galán, J., Parrilla-Bel, J., et al. (2016). La asociación faunística



- de Barranco del Hocino 1, un nuevo yacimiento de vertebrados del Barremiense (Cretácico Inferior) de Teruel. *Cuadernos del Museo Geominero*, 20, 303–307.
- Badiola, A., Canudo, J. I., & Cuenca-Bescós, C. (2008). New multituberculata mammals from the Hauterivian/Barremian transition of Europe (Iberian Peninsula). *Palaeontology*, 51(6), 1455–1469.
- Benson, R. B., Brusatte, S. L., Hutt, S., & Naish, D. (2009). A new large basal tetanuran (Dinosauria: Theropoda) from the Wessex Formation (Barremian) of the Isle of Wight, England. *Journal of Vertebrate Paleontology*, 29(2), 612–615.
- Brusatte, S. L., Benson, R. B., Carr, T. D., Williamson, T. E., & Sereno, P. C. (2007). The systematic utility of theropod enamel wrinkles. *Journal of Vertebrate Paleontology*, 27, 1052–1056.
- Brusatte, S. L., Carr, T. D., & Norell, M. A. (2012). The osteology of *Alioramus*, a gracile and long-snouted tyrannosaurid (Dinosauria: Theropoda) from the Late Cretaceous of Mongolia. *Bulletin of the American Museum of Natural History*, 366, 1–197.
- Brusatte, S. L., Norell, M. A., Carr, T. D., Erickson, G. M., Hutchinson, J. R., Balanoff, A. M., et al. (2010). Tyrannosaur paleobiology: New research on ancient exemplar organisms. *Science*, 329, 1481–1485.
- Brusatte, S. L., & Sereno, P. C. (2007). A new species of *Carcharodontosaurus* (Dinosauria: Theropoda) from the Cenomanian of Niger and a revision of the genus. *Journal of Vertebrate Paleontology*, 27(4), 902–916.
- Brusatte, S. L., & Sereno, P. C. (2008). Phylogeny of Allosauroidae (Dinosauria: Theropoda): Comparative analysis and resolution. *Journal of Systematic Palaeontology*, 6(2), 155–182.
- Buffetaut, E. (2007). The spinosaurid dinosaur *Baryonyx* (Saurischia, Theropoda) in the Early Cretaceous of Portugal. *Geological Magazine*, 144(6), 1021–1025.
- Buckley, L. G. (2009). *Individual and ontogenetic variation in theropod dinosaur teeth: A case study of Coelophysis bauri (Theropoda: Coelophysoidea) and implications for identifying isolated theropod teeth* (pp. 109). MSc. Dissertation, University of Alberta, Edmonton, Alberta, Canada.
- Canudo, J. I., Gasca, J. M., Aurell, M., Badiola, A., Blain, H.-A., Cruzado-Caballero, P., et al. (2010). La Cantalera: An exceptional window onto the vertebrate biodiversity of the Hauterivian–Barremian transition in the Iberian Peninsula. *Journal of Iberian Geology*, 36(2), 205–224.
- Canudo, J. I., Gasca, J. M., Moreno-Azanza, M., & Aurell, M. (2012). New information about the stratigraphic position and age of the sauropod *Aragosaurus ischiaticus* from the Early Cretaceous of the Iberian Peninsula. *Geological Magazine*, 149(2), 252–263.
- Canudo, J. I., Gasulla, J. M., Gómez-Fernández, D., Ortega, F., Sanz, J. L., & Yagüe, P. (2008a). Primera evidencia de dientes aislados atribuidos a Spinosauridae (Theropoda) en el Aptiano inferior (Cretácico Inferior) de Europa: Formación Arcillas de Morella (España). *Ameghiniana*, 45(3), 649–652.
- Canudo, J. I., Royo-Torres, R., & Cuenca-Bescós, G. (2008b). A new sauropod: *Tastavinsaurus sanzi* gen. et sp. nov. from the Early Cretaceous (Aptian) of Spain. *Journal of Vertebrate Paleontology*, 28(3), 712–731.
- Charig, A. J., & Milner, A. C. (1997). *Baryonyx walkeri*, a fish-eating dinosaur from the Wealden of Surrey. *Bulletin of the Natural History Museum of London*, 53, 11–70.
- Csiki-Sava, Z., Brusatte, S. L., & Vasile, S. (2016). “*Megalosaurus cf. superbus*” from southeastern Romania: The oldest known Cretaceous carcharodontosaurid (Dinosauria: Theropoda) and its implications for earliest Cretaceous Europe–Gondwana connections. *Cretaceous Research*, 60, 221–238.
- Currie, P. J., Rigby, J. K. J., & Sloan, R. E. (1990). Theropod teeth from the Judith River Formation of southern Alberta, Canada. In K. Carpenter & P. J. Currie (Eds.), *Dinosaur systematics: Approaches and perspectives* (pp. 107–125). New York: Cambridge University Press.
- Fanti, F., Cau, A., Martinelli, A., & Contessi, M. (2014). Integrating palaeoecology and morphology in theropod diversity estimation: A case from the Aptian–Albian of Tunisia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 410, 39–57.
- Gasca, J. M., Canudo, J. I., & Moreno-Azanza, M. (2014a). On the Iberian iguanodont dinosaur diversity: New fossils from the lower Barremian, Teruel province, Spain. *Cretaceous Research*, 50, 264–272.
- Gasca, J. M., Canudo, J. I., & Moreno-Azanza, M. (2014b). A large-bodied theropod (Tetanurae: Carcharodontosauria) from the Mirambel Formation (Barremian) of Spain. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 273(1), 13–23.
- Gasca, J. M., Moreno-Azanza, M., & Canudo, J. I. (2008). Dientes de dinosaurios terópodos espinosáuridos de la Formación El Castellar (Cretácico Inferior, Teruel). *Palaeontologica Nova SEPAZ*, 8, 233–234.
- Gasulla, J. M., Escaso, F., Narváez, I., Ortega, F., & Sanz, J. L. (2015). A new sail-backed styracosternan (Dinosauria: Ornithopoda) from the Early Cretaceous of Morella, Spain. *PLoS One*, 10(12), e0144167.
- Gauthier, J. A. (1986). Saurischian monophyly and the origin of birds. In K. Padian (Ed.), *The origin of birds and the evolution of flight. Memoirs of the California Academy of Sciences* (Vol. 8, pp. 1–55). San Francisco: California Academy of Sciences.
- Gerke, O., & Wings, O. (2016). Multivariate and cladistic analyses of isolated teeth reveal sympatry of theropod dinosaurs in the Late Jurassic of northern Germany. *PLoS One*, 11(7), e0158334.
- Goloboff, P. A., & Catalano, S. A. (2016). TNT versión 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics*, 32, 221–238. <https://doi.org/10.1111/cla.12160>.
- Hammer, Ø., & Harper, D. A. T. (2006). *Paleontological data analysis* (p. 351). Oxford: Blackwell.
- 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.
- Harris, J. D. (1998). A reanalysis of *Acrocanthosaurus atokensis*, its phylogenetic status, and paleobiogeographic implications, based on a new specimen from Texas. *New Mexico Museum of Natural History and Science Bulletin*, 13, 1–75.
- Hendrickx, C. (2015). Evolution of Teeth and Quadrate in Non-avian Theropoda (Dinosauria: Saurischia), with the Description of *Torvosaurus* Remains from Portugal. Ph.D. Dissertation. Universidade Nova de Lisboa, p. 646.
- Hendrickx, C., & Mateus, O. (2014a). *Torvosaurus gurneyi* n. sp., the largest terrestrial predator from Europe, and a proposed terminology of the maxilla anatomy in nonavian theropods. *PLoS One*, 9(3), e88905. <https://doi.org/10.1371/journal.pone.0088905>.
- Hendrickx, C., & Mateus, O. (2014b). 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. (2015a). A proposed terminology of theropod teeth (Dinosauria, Saurischia). *Journal of Vertebrate Paleontology*, 35(5), e982797.
- Hendrickx, C., Mateus, O., & Araújo, R. (2015b). The dentition of megalosaurid theropods. *Acta Palaeontologica Polonica*, 60(3), 627–642.
- Hocknull, S. A., White, M. A., Tischler, T. R., Cook, A. G., Calleja, N. D., Sloan, T., et al. (2009). New mid-Cretaceous (Latest Albian) dinosaurs from Winton, Queensland, Australia. *PLoS One*, 4(7), e6190.
- Hutt, S., Martill, D. M., & Barker, M. J. (1996). The first European allosauroid dinosaur (Lower Cretaceous, Wealden Group,

- England. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, 10, 635–644.
- Infante, P., Canudo, J. I., & Ruiz-Omeñaca, J. I. (2005). First evidence of theropod dinosaurs from the Mirambel Formation (Lower Barremian, Lower Cretaceous) from Castellote, Teruel. *Geogaceta*, 38, 31–34.
- Kellner, A. W. A., & Campos, D. A. (1996). First early Cretaceous theropod dinosaur from Brazil with comments on Spinosauridae. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 199(2), 151–166.
- Mateus, O., Araújo, R., Natário, C., & Castaninha, R. (2011). A new specimen of the theropod dinosaur *Baryonyx* from the early Cretaceous of Portugal and taxonomic validity of *Suchosaurus*. *Zootaxa*, 2827, 54–68.
- Moreno-Azanza, M., Canudo, J. I., & Gasca, J. M. (2014). Unusual theropod eggshells from the Early Cretaceous Blesa Formation of the Iberian Range, Spain. *Acta Paleontologica Polonica*, 59(4), 843–854.
- Norell, M. A., Makovicky, P. J., Bever, G. S., Balanoff, A. M., Clark, J. M., Barsbold, R., et al. (2009). A review of the Mongolian Cretaceous dinosaur *Saurornithoides* (Troodontidae: Theropoda). *American Museum Novitates*, 3654, 1–63.
- Novas, F. E., de Valais, S., Vickers-Rich, P. A., & Rich, T. H. (2005). A large Cretaceous theropod from Patagonia, Argentina, and the evolution of carcharodontosaurids. *Naturwissenschaften*, 92, 226–230.
- Ortega, F., Escaso, F., & Sanz, J. L. (2010). A bizarre, humped Carcharodontosauria (Theropoda) from the lower Cretaceous of Spain. *Nature*, 467(7312), 203–206.
- Parrilla-Bel, J., & Canudo, J. I. (2015). On the presence of plesiosaurs in the Blesa Formation (Barremian) in Teruel (Spain). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 278(2), 213–227.
- Pereda-Suberbiola, X., Ruiz-Omeñaca, J. I., Canudo, J. I., Torcida, F., & Sanz, J. L. (2012). Dinosaur faunas from the Early Cretaceous (Valanginian-Albian) of Spain. In P. Godefroit (Ed.), *Bernissart dinosaurs and early Cretaceous terrestrial ecosystem* (pp. 379–407). Bloomington: Indiana University Press.
- Pérez-Moreno, B. P., Sanz, J. L., Buscalioni, A. D., Moratalla, J. J., Ortega, F., & Rasskin-Gutman, D. (1994). A unique multitoothed ornithomimosaur dinosaur from the lower Cretaceous of Spain. *Nature*, 370, 363–367.
- Puértolas-Pascual, E., Rabal-Garcés, R., & Canudo, J. I. (2015). Exceptional crocodylomorph biodiversity of “La Cantalera” site (lower Barremian; Lower Cretaceous) in Teruel, Spain. *Palaeontologia Electronica*, 18(2), 1–16.
- Rauhut, O. W. M. (2002). Dinosaur teeth from the Barremian of Uña, Province of Cuenca, Spain. *Cretaceous Research*, 23(2), 255–263.
- Rauhut, O. W. M., & López-Arbarello, A. (2009). Considerations on the age of the Tiouaren Formation (Iullemeden Basin, Niger, Africa): Implications for Gondwanan Mesozoic terrestrial vertebrate faunas. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 271, 259–267.
- Rauhut, O. W. M., Milner, A. C., & Moore-Fay, S. (2010). Cranial osteology and phylogenetic position of the theropod dinosaur *Proceratosaurus bradleyi* (Woolward, 1910) from the Middle Jurassic of England. *Zoological Journal of the Linnean Society*, 158, 155–195.
- Rauhut, O. W. M., & Werner, C. (1995). First record of the family Dromaeosauridae (Dinosauria: Theropoda) in the Cretaceous of Gondwana (Wadi Milk Formation, northern Sudan). *Paläontologische Zeitschrift*, 69, 475–489.
- Riveline, J., Berger, J. P., Feist, M., Martín-Closas, C., Schudack, M., & Soulié-Marsche, I. (1996). European Mesozoic-Cenozoic charophyte biozonation. *Bulletin de la Société géologique de France*, 167(3), 453–468.
- Ruiz-Omeñaca, J. I. (2011). *Delapparentia turolensis* nov. gen et sp., un nuevo dinosaurio iguanodontoideo (Ornithischia: Ornithopoda) en el Cretácico Inferior de Galve. *Estudios Geológicos*, 67(1), 83–110.
- Ruiz-Omeñaca, J. I., Canudo, J. I., & Cuenca-Bescós, G. (1996). Dientes de dinosaurios (Ornithischia y Saurischia) del Barremiense superior (Cretácico inferior) de Vallipón (Castellote, Teruel). *Mas de las Matas*, 15, 59–103.
- Ruiz-Omeñaca, J. I., Canudo, J. I., & Cuenca-Bescós, G. (1998). Primera cita de dinosaurios barionícidos (Saurischia: Theropoda) en el Barremiense superior (Cretácico Inferior) de Vallipón (Castellote, Teruel). *Mas de las Matas*, 17, 201–223.
- Ruiz-Omeñaca, J. I., Canudo, J. I., Cuenca-Bescós, G., Cruzado-Caballero, P. L., Gasca, J. M., & Moreno-Azanza, M. (2012). A new basal ornithopod dinosaur from the Barremian of Galve, Spain. *Comptes Rendus Paleovol*, 11(6), 435–444.
- Ruiz-Omeñaca, J. I., Cruzado-Caballero, P., Infante, P., & Moreno-Azanza, M. (2005). Baryonychine teeth (Theropoda: Spinosauridae) from the lower Cretaceous of La Cantalera (Josa, NE Spain). *Kaupia*, 14, 59–63.
- Salas, R., Guimerà, J., Más, R., Martín-Closas, C., Meléndez, A., & Alonso, A. (2001). Evolution of the Mesozoic central Iberian Rift System and its Cainozoic inversion (Iberian Chain). *Mémoires du Muséum Nationale de l’Histoire Naturelle, Paris*, 186, 145–185.
- Samman, T., Powell, G. L., Currie, P. J., & Hills, L. V. (2005). Morphometry of the teeth of western North American tyrannosaurids and its applicability to quantitative classification. *Acta Palaeontologica Polonica*, 50, 757–776.
- Sánchez-Hernández, B. R., & Benton, M. (2014). Filling the ceratosaur gap: A new ceratosaurian theropod from the Early Cretaceous of Spain. *Acta Palaeontologica Polonica*, 59(3), 581–600.
- Sánchez-Hernández, B., Benton, M. J., & Naish, D. (2007). Dinosaurs and other fossil vertebrates from the Late Jurassic and Early Cretaceous of the Galve area, NE Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 249, 180–215.
- Sanz, J. L., Bonaparte, J. F., & Lacasa, A. (1988). Unusual Early Cretaceous birds from Spain. *Nature*, 331, 433–435.
- Sanz, J.L., Buscalioni, A.D., Casanovas, M.L., Santafé, J.V. (1987). Dinosaurios del Cretácico Inferior de Galve (Teruel, España). *Estudios geológicos*. Volumen extraordinario Galve-Tremp, pp. 45–64.
- Sereno, P. C., Beck, A. L., Dutheil, D. B., Larsson, H. C. E., Lyon, G. H., Marcot, J. D., et al. (1998). A long-snouted predatory dinosaur from Africa and the evolution of spinosaurids. *Science*, 282(5392), 1298–1302.
- Sereno, P. C., & Brusatte, S. L. (2008). Basal abelisaurid and carcharodontosaurid theropods from the lower Cretaceous Elrhaz Formation of Niger. *Acta Palaeontologica Polonica*, 53(1), 15–46.
- Sereno, P. C., Dutheil, D. B., Iarochene, M., Larsson, H. C. E., Lyon, G. H., Magwene, P. M., et al. (1996). Predatory dinosaurs from the Sahara and Late Cretaceous faunal differentiation. *Science*, 272, 986–991.
- Serrano-Martínez, A., Vidal, D., Sciscio, L., & Ortega, F. (2016). Isolated theropod teeth from the Middle Jurassic of Niger and the early dental evolution of Spinosauridae. *Acta Palaeontologica Polonica*, 61(2), 403–415.
- Smith, J. B., & Dodson, P. (2003). A proposal for a standard terminology of anatomical notation and orientation in fossil vertebrate dentitions. *Journal of Vertebrate Paleontology*, 23(1), 1–12.
- Smith, J. B., Vann, D. R., & Dodson, P. (2005). Dental morphology and variation in theropod dinosaurs: Implications for the taxonomic identification of isolated teeth. *The Anatomical Record*, 285A, 699–736.
- Stromer, E. (1915). Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltier-Reste der Baharijje-Stufe (unterstes Cenoman). 3. Das Original des Theropoden

- Spinosaurus aegyptiacus* nov. gen., nov. spec. *Abhandlungen der Königlich Bayerischen Akademie der Wissenschaften, Mathematisch-physikalische Klasse*, 28(3), 1–32.
- Sues, H. D., Frey, E., Martill, D. M., & Scott, D. M. (2002). *Irritator challengerii*, a spinosaurid (Dinosauria: Theropoda) from the Lower Cretaceous of Brazil. *Journal of Vertebrate Paleontology*, 22(3), 535–547.
- Torices, A., Currie, P., Canudo, J. I., & Pereda Suberbiola, X. (2015). Theropod dinosaurs from the Upper Cretaceous of the South Pyrenees Basin of Spain. *Acta Paleontologica Polonica*, 60(3), 611–626.
- Verdú, F. J., Godefroit, P., Royo-Torres, R., Cobos, A., & Alcalá, L. (2017). Individual variation in the postcranial skeleton of the Early Cretaceous *Iguanodon bernissartensis* (Dinosauria: Ornithomorphia). *Cretaceous Research*, 74, 65–86.
- White, M. A., Bell, P. R., Cook, A. G., Poropat, S. F., & Elliott, D. A. (2015). The dentary of *Australovenator wintonensis* (Theropoda, Megaraptoridae); implications for megaraptorid dentition. *PeerJ*, 3, e1512.

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