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New theropod remains from the late Barremian (Early Cretaceous) of Eastern Iberian Peninsula

Adrian Montealegre[a], Oscar Castillo-Visa[a,b] and Albert Sellés[a,b*]

[a] Institut Català de Paleontologia Miquel Crusafont – ICTA-ICP, Edifici Z, C/ de les Columnes s/n. Campus Universitat Autònoma de Barcelona, 08193 Cerdanyola del Vallès, Spain

[b] Museu de la Conca Dellà, c/Museu 4, E-25650 Isona, Lleida, Spain

*corresponding author: albert.garcia@icp.cat

ABSTRACT

In the last decade, the Iberian Peninsula has become a hot spot in the understanding of the early evolutionary history of large-bodied theropods from the Early Cretaceous, especially for the Spinosauridae and Carcharodontosauridae families. To date, at least five species of spinosaurids and one species of carcharodontosaurid inhabited the Iberian region during the Barremian. However, the discovery of new fossil remains suggests that such diversity of medium to large-sized theropods could be even higher. Here, we describe an unpublished large theropod tooth and two caudal vertebrae collected in the late 70s in the upper Barremian strata of the Arcillas de Morella Formation (Morella, eastern Spain). The tooth element displays a series of features that allow its identification as cf. *Protathlitis*, while the vertebral elements are tentatively attributed to an indeterminate carcharodontosaurid. Interestingly, these last remains are different from those of *Concavenator*, allowing speculating about the occurrence of another species of carcharodontosaurid allosauroids in the Iberian Peninsula during the Early Cretaceous apart of the famed humpbacked dinosaurs, and with some reminiscence to *Acrocanthosaurus*. Therefore, the new findings clearly illustrate the significance of any new theropod remains in depicting the theropod diversity before the final beak-up of Pangea in the Iberian Peninsula.

Keywords: Spinosauridae, Carcharodontosauridae, Early Cretaceous, Barremian.

1 Introduction

Recently, the Iberian Peninsula has become a hot spot in our understanding of the early diversification of spinosaurid and carcharodontosaurid theropods during the Early Cretaceous. On one hand, the discoveries of the basal spinosaurines *Vallibonavenatrix cani* (Malafaia et al. 2020a), *Camarillasaurus cirugedae* (Sánchez-Hernández and Benton, 2014; Smathi et al. 2021), and *Iberospinus natarioi* (Mateus and Estraviz-López, 2022), and the basal baryonychine *Protathlitis cinctorrensis* (Santos-Cubedo et al. 2023), along with abundant remains attributed to *Baryonyx* or close related taxa (see Buffetaut, 2007; Torcida et al. 1997; Viera and Torres 1995; Mateus et al. 2011, Ruiz-Omeñaca et al. 2005; Canudo et al. 2010; Gasulla et al. 2013; Alonso and Canudo, 2016; Malafaia et al. 2018; Malafaia et al. 2020c; Isasmendi et al. 2023; among many others), illustrate the high diversity of spinosaurids inhabiting the same region at that time. This abundant and diverse record questions the previous hypothesis postulating a vicariate divergence between Spinosaurinae and Baryonychinae linked to the fragmentation of Pangea (Sereno et al. 1998). On the other hand, the reports of the basal carcharodontosaurids *Lusovenator santosi* (Malafaia et al. 2020b) and *Concavenator corcovado* (Ortega et al. 2010) have allowed establishing the body bauplan of the more derived members of the clade. In addition, the discovery of isolated teeth (Canudo and Ruiz-Omeñaca, 2003; Canudo et al. 2010; Torcida Fernández-Balor 2005; Alonso et al. 2018) and fragmentary bone remains (Gasca et al. 2014) referred to carcharodontosaurids in the Barremian deposits of the extant Iberian region suggest a relatively high abundance of this group (Fig. 1A). Consequently, any new spinosaurid or carcharodontosaurid finding may provide valuable information about the early evolutionary stages of those two groups of carnosaurian theropods and their role in the Early Cretaceous ecosystems.

Of special interest is the fossil record from the Arcillas de Morella Formation (late Barremian, Early Cretaceous; Santos-Cubedo et al. 2023) that outcrops in the Morella sub-basin (Maestrazgo Basin, Valencia, Eastern Spain, Fig. 1B) because of its abundance, its historical significance (see Gasulla et al. 2009), and its role in the understanding the composition and evolution of the Early Cretaceous dinosaur communities from Iberia before the complete break-up of Pangea during the Aptian (Schettino and Turco 2010; Canérot 2016; Causer et al. 2020).

Between 1978 and 1979, palaeontologists of the former Institut de Paleontologia de Sabadell –current Institut Català de Paleontologia Miquel Crusafont (ICP-CERCA), Sabadell, Spain – performed a series of excavations along the red clays of the Arcillas de Morella Formation surrounding the village of Morella, discovering abundant remains attributed to brachiosaurid sauropods, *Iguanodon*, polacantid ankylosaurs, and tetanuran theropods. Although most of the fossils attributed to phytophagous dinosaurs were published (see Santafé et al. 1978; 1982), several theropod elements remained unstudied in the collections of the ICP Museum. Here, we describe an unpublished large theropod tooth and two caudal vertebrae from the upper Barremian Arcillas de Morella Formation unearthed close to Morella village, and we discuss their taxonomic affinity and implications.

2 Materials and methods

IPS919 is a large conical tooth initially identified as belonging to an indeterminate spinosaurid theropod, while IPS137683 and IPS137684 are two caudal centres originally laveled as "Theropoda indet.". All these remains are housed in the paleontological collection of the Museum of the Institut Català de Paleontologia Miquel Crusafont (ICP-CERCA; Sabadell, Spain).

The dental element (IPS919) was donated to Josep Vicente Santafé and Lourdes Casanovas by the Piarists of Morella (Valencia, Spain) in the late '70s, who originally discovered the fossils in the red clay of the Arcillas de Morella Formation outcropping south to the Morella village (L. Casanovas, per. com., February 2021). Unfortunately, the exact geographic and stratigraphic position of IPS919 is unknown (Fig. 1B).

No precise information is available for the original location of the two vertebral elements described in the present study (IPS137683 and IPS137684), but that they were for sure collected during the paleontological fieldworks conducted by J.V. Santafé and L. Casanovas in 1979. Nevertheless, the scarcity of theropod remains from the Arcillas de Morella Formation (see Gasulla et al. 2009) coupled with the additional information provided by the fossils associated with the studied specimens may provide some clues about their original location. First, of the ten localities explored by the aforementioned palaeontologists in 1979 (see Santafé et al. 1982), only two of them yielded theropod remains: El Beltrán and Mas de Romeu, both located close to the Morella village (see Gasulla et al. 2009: Fig. 1). A megalosaurid tooth and an ungual phalanx were unearthed from El Beltrán site, while the Mas de Romeu site yielded abundant theropod remains, including a vertebral fragment described by Santafé et al. (1982). Second, the vertebral elements studied here were originally stored in a single box at the ICP collections together with a middle caudal vertebra of a large ornithopod (IPS37403; cf. *Iguanodon*, per. obs.), and a posterior dorsal vertebra of a small neosuchid (IPS924; cf. *Goniopholis*, per. obs.), indicating that all the remains came from the same locality. Such association of taxa is consistent with the fossil record recovered from the Mas de Romeu site, which includes abundant remains of *Iguanodon bernissartensis*, thyreophors, theropods, and crocodiles (see Santafé et al. 1982). Because of that, it is most likely that the studied specimens could come from the Mas de Romeu site (see Fig. 1B).

The descriptive terminology of the dental element follows the anatomical nomenclature of Smith and Dodson (2003) and Hendrickx et al. (2015, 2016, 2019). The naming of the vertebral lamination and fossae follows the nomenclatural proposal of Wilson (1999) and Wilson et al. (2011).

2.1 Morphometric analysis

The morphometric analyses were performed using R-Studio software for R (R Core Team, 2021). The morphometric database used in this study, which includes 109 specimens, was constructed by gathering literature information on theropod –primarily spinosaurid– dentition (see Table S1), following similar criteria than those of Alonso and Canudo (2016). Prior to the analyses, the dataset was pruned of those elements lacking substantial information of selected morphometric parameters, this are: crown height (CH), crown base length (CBL), crown base wide (CBW), crown height ratio (CHR), crown wide ratio (CWR), apical length (AL), denticle mesial density (DMD), denticle distal density (DDD), and number of flutes (NF). As a result, 103 specimens were analysed. Missing values were replaced by null values in order to not affect the final result. All data were log transformed with Log (xþ1) in order to avoid data with zero values. All indeterminate Baryonychinae teeth from literature were re-named as Baryonychinae indet. Finally, a principal component analysis (PCA) was conducted to establish morphological similarity between analysed specimens.

3 Results

3.1 Systematic Palaeontology

Theropoda Marsh 1881

Carnosauria von Huene 1920

Spinosauridae Sromer 1915

Baryonychinae Charig & Milner 1986

cf. *Protathlitis* sp.

Description: IPS919 corresponds to a well-preserved almost complete tooth that preserves part of the root (Fig. 2, Table 1), and only minor cracking is observed along the crown. The element is straight, laterally compressed (Figs. 2B, D), and apico-distally curved (about 65º; Figs. 2A, C). The crown is elliptical in cross section, while the base is ovate (Figs. 1E-F). As preserved, the crown is 33.64 mm in TCH, 17.67 mm in CBL, and 6.6 mm in CBW. The crown surface is covered with distinctive striations, which runs along almost the entire length of the crown on both labial and lingual sides. The labial surface of the crown accounts with five of those flutes, while they are six for the lingual one. Under magnification, the enamel appears as wrinkled (Fig. 2G). Very fine carinae are present in both mesial and distal margins. Only the distal carina shows distinctive serration (density of 6-7 denticles per each millimeter), while the mesial one is smooth. A small wear facet is present at the apex of the crown, which extends straight down from the apex through the mesial carina until the midpoint of the crown, with a maximum length of 37.5 mm (Fig. 2E). Additionally, the wear facet is briefly present on the distal carina (Fig. 2B').

Allosauroidea Marsh 1878

Carcharodontosauridae Stromer 1931

cf. Carcharodontosauridae indet.

Description: IPS137683 is interpreted as an anterior caudal centrum on the base of the proportions of the centrum (w/h ratio of 0.9; see Table 2), the lack of transversal processes within the vertebral body, and the presence of articular surface for hemal archs only in the posterior side of the element (Fig. 3). The suture surface for the neural arch is completely visible in dorsal view, informing that the neural arch and the centrum were not fused at the time of death, and therefore of the immature ontogenetic stage of the specimen.

The anterior articular surface is largely damaged, only preserving small portions of its half dorsal part and the ventrolateral edge (Fig. 3A). Despite the shape of the anterior facet cannot be assessed, the preserved surface indicates that the articular surface was concave. By contrast, the distal articular facet is nearly complete and shows a sub-circular outline, almost as width as height (w/h 0.9) (Fig. 3B). This facet is just slightly concave, almost flat, suggesting an amphy-platycoelous condition for IPS137683. Only the articular facet for the right chevron is preserved on the ventral margin of the posterior articular facets. In lateral view, the posterior articular surface seems slightly ventrally offset regarding the anterior part of the vertebra (Fig. 3C-D). The lateral surfaces of the centrum are medially constrained, bestowing a characteristic hourglass-shaped to the vertebral element in both dorsal and ventral view (Fig. 3E-F). A shallow pleurocoel depression is present ventrally to the neural arch suture, which occupies most of the antero-posterior vertebral length. The neural canal is well exposed in dorsal view. It is strongly constrained in its middle part, while its distal end is more expanded than the anterior one (Fig. 3E). The ventral surface is transversally concave and flat, lacking any evidence of ventral groove. Two elliptical-shaped, very shallow concavities are located at each side of the anterior half of the ventral surface, which are separated from each other by very low ridge that fades near the mid-length of the centrum. Two small foramina are located at the end of the ventral ridge (Fig. 3F).

Description: IPS137684 is a slightly amphicoelus centrum lacking most of the neural arch, only preserving the base of the neural arch pedicels and the base of the postzygapophisal processes (Fig. 4). The centrum is longer than taller (elongation index of 2.97; see Table 2), and it is constrained laterally in its middle length (Fig. 4A-B), which bestows a markedly hourglass-shape morphology in both dorsal and ventral view (Fig. 4C-D). The articular facets are offset. The anterior articular surface is sub-circular in morphology, while the posterior one is sub-trapezoidal-shaped (Fig. 4E), with the dorsal region more expanded laterally than the ventral one (Fig. 4F). No pleurocoels are present in the lateral surface of the centrum (Fig. 4A-B).

Despite incomplete, a dorsoventrally shallow, sub-horizontally oriented, elliptical-shaped transversal process is located on the posterior half of the lateral side of the vertebral body (Fig. 4A-B). The transversal process links to the anterior part of the vertebral body by a well-develops anterocentrodiapophisial lamina (acdl). A thin accessory lamina is located ventrally to acdl, both separated by a small and shallow fossa (Fig. 4G-H). It extends posteriorly to the anteroventral site of the transversal process but it not connects to the process. Anteriorly, this accessory lamina merge into a triangular rough surface located in the anterior half of the centrum (Figs. 4A, G). Due to is location; it is likely that such rugosity would be related to the attachment of the *M. caudofemoralis longus.* The junction between the acdl and the accessory lamina produces an anteroposteriorly elongated, shallow fossa (Fig. 4G-H). The transversal process connects to the posterior region of the centrum by a short and thin posterocentodiapophisial lamina (pcdl). A posterodorsally directed shallow ridge emerges from the dorsal surface of the transversal process, which may correspond to the postzigapophyseal-diapophisial lamina (podl) (Fig. 4A-C). The ventral surface shows a well-developed longitudinal groove that expanded posteriorly, but fades anteriorly. It is enclosed between two low ventral ridges (Fig. 4D). The articular surfaces of the chevrons are located on the posterior end of the ventral surface of the vertebral body, just posteriorly to the most expanded part of the ventral groove (Fig. 4D).

3.2 Morphometric Principal Component Analysis Results

The principal component analysis shows that the two first principal components can explain about the 97.4% of the variance. The main loading of the PC1, which describes the 95.318% of total variance, is defined by the positive correlation to CH, CBW, CB – this is the general crown size and robustness base size – and a negative correlation with DD. On the other hand, The PC2 loading, which explains the 2.065% of the variance, is described by a strong positive correlation to DD and moderate relationship with CBW and CH.

The selected out-group, here represented by the carcharodontosaurid teeth, is primarily plotted in the quadrate IV in a clear distinctive morphospace from the other groups (Fig. 5). By contrast, baryonychine spinosaurids encompass a large morphospace that extends across the quadrants I, II, and III. Such morphological variation might reflect either intraspecific or interspecific variability, as the results for *Baryonyx* and *Suchomimus* suggest. However, and despite the evident overlapping, it is worth noting that in detail each sampling group – defined by its geographic and temporal distribution– seems to occupy a distinctive morphospace (see Fig. 5). Finally, spinosaurine spinosaurids are mainly restricted to the quadrant 3, in a separate morphospace from baryonychines. However, it is noteworthy that the spinosaurine teeth from Thailand (cf. *Siamosaurus*) falls far from the other spinosaurine specimens and overlap the morphospace occupied by baryonychines (Fig. 5). Despite it is out of the scope of the present study to analyse in detail the aforementioned results, current data suggest the existence of some degree of homoplasy regarding tooth morphology between the two subfamilies of spinosaurids, especially in basal members of the clades.

Regarding IPS919, it is placed within the baryonychine morphospace. Furthermore, it fits well within the morphospace defined by the contemporary fossil record recovered from the Arcillas de Morella Formation, and close to the tooth referred to *Protathlitis cinctorrensis* (Fig. 5).

4 Discussions

4.1 Taxonomic affinity

4.1.1. Dental element

The tooth IPS919 presents a series of characteristics that allows its inclusion within the Spinosauridae, such as possessing a subcircular outline of the basal cross-section, mesial carina extending well-beneath the cervix and to the base of crown, flutes on both lingual and labial sides of the tooth, distal margin of lateral teeth convex, with apex centrally positioned, root strongly tapered apically and oval to subcircular in cross-section at mid-root, and veined enamel texture (see Hendrickx et al. 2019 for more details). Within the family, spinosaurines primarily differ from baryonychines by the loss of mesial and distal serration, the well-pronounced carinae, the non-curved profile of the crown, and the smoothly enamel texture (see Table 3). In this regard, IPS919 shows more similitude with baryonychines, given that they have curved conical crowns with wrinkled enamel texture, and minute denticles in poorly defined carinae. These morphological observations are consistent with the PCA results based on morphological characters, in which IPS919 is recovered as a member of Baryonychinae. Despite it is difficult to establish its low taxonomic range only based on multivariate data, the results suggest close affinity with the baryonychines from the Arcillas de Morella Fm. (see Fig. 5).

On recent years, several new taxa have been ascribed to Baryonychinae, but most of them preserve very few dental remains. For instance, very little is known about the dentition of the controversial taxon *Suchosaurus cultridens*, especially because the holotype, a worn tooth

(NHM R36536) lacks diagnostic features (Mateus et al. 2011). It has eight flutes on the lingual side and four in the labial one, while IP919 has at least five to six flutes in each side. However, this character has to be taken with caution, because the number of fluting in Baryonychinae teeth is highly variable (Ruiz-Omeñaca et al. 1998).

Only poorly preserved premaxillary dentition is known for the UK spinosaurids *Riparovenator milnerae* and *Ceratosuchops inferiodios* (Barker et al. 2021). Both taxa show typical baryonychine characteristics, such as conidont tooth with minor labiolingual compression, flutes in both labial and lingual surfaces, and veined enamel texture. *Riparovenator* is further characterized by having fine serration with a density of 5-8 denticles/mm (Barker et al. 2021). It is difficult to establish any detailed comparison between the aforementioned taxa and IPS919, since the two of them show similar synapomorphic characters of the Baryonychidae subfamily. However, IPS919 seems to be more curved than those of *Riparovenator* and *Ceratosuchops*, but this difference may reflect a distinct dental position of the teeth.

Despite preserving fragments of the dentary, most of the dentition of the Portuguese *Iberospinus natarioi* is missing (Mateus and Estraviz-López 2022). The only two partially preserved teeth of this taxon show some worth noting features: no-presence of transverse undulations in the crown, nine flutes in both lateral and lingual faces of the crown, both mesial and distal carinae bearing denticles all over their preserved lengths, although mesial denticles may disappears just before reaching the cervix. Therefore, IPS919 differs, at least, from *Iberospinus* in the density and distribution of denticles in the carinae, and in the number of flutes.

IPS919 shares several features with the African *Suchomimus tenerensis* (Sereno et al. 1998), but also showing some differences (see Table 3). Both specimens have serration in the distal carina with a density of about 6 denticles per each millimeter, but while they are uniformly distributed in *Suchomimus*, denticles are not so in IPS919. Despite the two of them shows strongly textured enamel, the base of the crowns of *Suchomimus* teeth are smooth while in IPS919 the textured enamel extends well within the base of the tooth. The teeth of *Baryonyx walkeri* are characterized by having serration in both carinae (only in the distal one in IPS919), and four faint flutes on the labial side (about 5 to 6 in both sides in IPS919). Some specimens (i.e. ML1190; Charig and Milner 1986; 1997) show weak linguolabial compression, which contrast with the oval condition of the IPS919 tooth.

IPS919 shows very similitudes with the Portuguese "*Suchosaurus girardi"*, currently referred to *Baryonyx* sp. (Mateus et al. 2011). Beyond the overall tooth crown morphology, they both show similar denticle density (7 denticles/mm), and similar number of flutes in both lingual and labial surfaces, accounting with a total of 12 flutes in "*Suchosaurus"* and around 11-14 in IPS919; though the distribution of these flutes is somehow different in each specimen (4-8 in "*S. girardi*", and 5-6 in IPS919).

The teeth of the recently described baryonychine *Protathlitis cinctorrensis* from the Arcillas de Morella Formation of Cinctorres (Valencia, Spain; Santos-Cubedo et al. 2023) are characterized by sculptured crowns, with a distal carina with 6 denticles/mm, no denticles on the mesial side, and between 9 to 12 of total flutes (Suñer and Santos-Cubedo 2006). These features are almost identical to that of IPS919, but slightly differing in the total number of flutes (see Table 3). Nevertheless, this feature can vary even within the same specimen (e.g. *Baryonyx walkeri*).

Finally, Canudo et al. (2008) described several teeth from Arcillas de Morella Formation recovered in the Mas de la Parreta site. They are characterized by having small denticles in both mesial and distal sides (average of 8 denticles/mm), fine granulated enamel, and 13-16 total flutes, features that clearly differ from the penecontemporary IPS919. In this regard it is worth noting that Ruiz-Omeñaca (2006) and Gasca et al. (2008) postulated the presence of at least two distinctive species of baryonychines in the Iberian Peninsula: one having both mesial and distal denticles– as those reported by Canudo et al. (2008)–, and another having denticles only in the distal side of the crown, such as *Protathlitis cinctorrensis* (Suñer and Santos-Cubedo 2006; Santos-Cubedo et al. 2023). In sum, and by considering all the mentioned above, we tentatively refer IPS919 to *Protathlitis sp.*

4.1.2. Vertebral elements

The anterior caudal centrum IPS137683 is characteristic for its apparent simplicity, especially because of the absence of pleurocoels and almost flat ventral surface. The overall morphology of IPS137683, this is an amphy-platycoelus, hourglass-shaped centrum with slightly offset sub-circular articular facets, resemble the anterior caudal elements of several medium to large size theropods, like abelisaurids (Méndez 2014), allosaurids like *Allosaurus* (Madsen 1976; Britt

1991; Rauhut, 1999; Chure 2000), and carcharodontosaurids like *Acrocanthosaurus* (Harris 1998).

The presence/absence of well-developed pleurocoels in caudal vertebras is highly variable in theropod dinosaurs, even within the same taxonomic group. However, the absence of pleurocoelic fossae in the anterior caudal vertebral have been primarily reported in basal non-coelurosaurian tetanurans (i.e. *Xuanhanosaurus*, *Shidaisaurus*, *Ornitholestes* or *Monolophosaurus*), some derived spinosaurids (i.e. *Suchomimus*, *Spinosaurus*, *Baryonyx*), megalosaurids (i.e. *Eustreptospondylus*, *Strptopondylus*, *Megalosaurus*, *Afrovenator*), abelisaurids, basal allosauroids (i.e. *Saurophaganax*, *Poekilopleuron*, *Lourighnanosaurus),* as well as in some carcharodontosaurids (i.e. *Acrocanthosaurus*, *Mapusaurus*, *Concavenator*, *Giganotosaurus*, *Tyrannotitan*, *Meraxes*, and *Neovenator)* and metriacanthosaurids (i.e. *Yungchuanosaurus*, *Siamotyrannus*, *Sinraptor*, and *Metriacanthosaurus*) (Delcourt 2017; Carrano et al. 2012; Coria and Currie 2006). Nevertheless, the generalized absence of pneumatic openings on the lateral sides of the caudal centrums is considered a synapomorphic feature for both Carcharodontosauridae (Canale et al. 2022) and Abelisauridae (Novas et al. 2013). With all the previously mentioned in mind and by considering the current Early Cretaceous theropod fossil record from the Iberian Peninsula, IPS137683 could either belong to a derived spinosaurid, to a basal allosauroid or to a carcharodontosaurid.

The absence of groove or keels in the ventral surface of anterior caudal vertebra –which bestow a flattened surface– seems to be an ancestral condition for non-avian theropods, being described in the coelophysids *Coelophysis* and *Liliensternus*. By contrast, this is a very uncommon treat in non-coelurosaurian tetanurans, where only the megalosaurid *Wiehenvenator* (Rauhut et al. 2016) and the metriacanthosaurid *Siamotyrannus* exhibit similar condition. Despite the basal carcharodontosaurid *Concavenator* has been codified as having flat ventral surface (Carrano et al. 2012; Benson et al. 2010), a recent review of its axial skeleton indicates that at least the anterior caudal vertebra have a ventral groove (Cuesta et al. 2019). In this regard the ventral surface of IPS137683 is almost flat but it possesses a very fine keel on the anterior half of the caudal centrum. This is clearly different from most of spinosaurids and basal allosauroids, which usually exhibit a ventral groove flanked by two ridges. Most carcharodontosaurids exhibit a well-developed ventral keel on the anterior caudal vertebra (*Acrocanthosaurus, Aerosteon, Giganotosaurus*, *Mapusaurus, Neovenator*), but some of them also have ventral groove, like *Acrocanthosaurus* and *Mapusaurus*, differing from the condition observed in the studies specimen. Therefore, with the current data IPS137683 cannot be tentatively identified beyond the family level, remaining here as a cf. carcharodontosauridae indet.

The location of the transversal process in the vertebral body informs of the position of IPS137684 within the caudal series, probably close to the "transition point" (between the 22nd to 26th in *Allosaurus fragilis*; Allain and Chure 2002). IPS137684 is characterized by showing (1) offset articular facets, (2) an hourglass shaped centrum with a (3) narrow longitudinal groove in the ventral surface flanked by ventral keels along, (4), lacking of lateral pleurocoels, and (5) well-developed laminae in the lateral surface of the vertebra.

The offset between articular facets is a feature observed in abelisaurids (Méndez 2014), *Allosaurus* (Madsen 1976), and in some carcharodontosaurian mid and posterior caudal vertebrae (e.g., Stovall and Langston 1950; Rauhut 1999; Coria and Currie 2006; Malafaia et al. 2019; 2020b; Carrano 2024). The hourglass shaped centrum is typical to the middle and posterior caudal centra of several allosauroid taxa (i.e. Madsen 1976; Britt 1991; Rauhut 1999; Chure 2000) but especially common in carcharodontosaurians (i.e., Malafaia et al. 2019; 2020b; Chokchaloemwong et al. 2019; Coria et al. 2020; Comes da Costa Pereira et al. 2020). The narrow longitudinal groove in the ventral surface, bounded by faint keels in the caudal centrum is also commonly found in Abelisauroidea, Allosauroidea –especially carcharodontosaurids–, and Megalosauroidea (Ezcurra and Méndez 2009; Benson et al. 2010; Mateus et al. 2011; Carrano et al. 2012; Rauhut et al. 2016; Malafaia et al. 2017; 2019; 2020b; Coria et al. 2020). Carrano (2024) mentioned a considerable dorsoventral reduction in the caudal transverse processes of Allosauroidea, a feature that seems alto exhibit IPS137684.

Despite weakly developed vertebral ridges are present in *Allosaurus* (DMNH 2149) and *Neovenator* (Brusatte et al. 2008), well-developed lamination in the lateral surface of middle and posterior caudal vertebra, especially the acdl (Fig. 2A-D, G-H), is characteristic of the basal carcharodontosaurid (i.e. *Veterupristisaurus milneri*, *Lusovenator santosi* - SHN.036, SHN.19; Rauhut 2011; Malafaia et al. 2017; 2020b). This feature is absent in other basal members of the clade such as *Acrocanthosaurus atokensis* (Stoval and Langston 1950; Currie and Carpenter 2000; Carrano 2024) and *Concavenator corcovado* (Ortega et al. 2010; Cuesta et al. 2019), suggesting that the occurrence of lateral ridges could be a somewhat limited to basal carcharodontosaurians. Because all of the aforementioned, IPS137684 can be referred to Allosauroidea, and tentatively to a non-derived carcharodontosaurids (see Fig. 6A).

Among basal carcharodontosaurids, IPS137684 slightly resembles the isolated carcharodontosaurid caudal centrum MCT 2670-LE from the Jurassic of Brazil (Bandeira et al. 2021) in the general hourglass morphology of the centrum and the presence of a shallow ventral groove enclosed between low ridges. However, such groove is not expanded posteriorly in MCT 2670-LE as it occurs in IPS137684. In addition, they differ in the shape of the articular facets, being more rounded in the Brazilian specimens, and in the occurrence of pleurocoel in the lateral surface of the vertebral body, which is absent in the studied specimen.

Veterupristisaurus milneri (Rauhut 2011) from the Late Jurassic of Tanzania was described as having a narrow, very shallow longitudinal groove fading anteriorly, expanding just in front of the chevron facets, and laterally bordered by low but well-defined ridges. This is almost an identical condition observed in IPS137684. However, the *Veterupristisaurus* is autapomorphically distinctive by the presence of a thick acdl (Rauhut 2011), while this lamina is thinner in the studied element. Furthermore, IPS37403 possess a well-developed pcdl and a rugous surface on the anterior half of the lateral surface, features not present in *Veterupristisaurus* (Fig. 6C).

IPS137684 share several features with the type and referred caudal elements of *Lusovenator santosi*, (SHN.036, Malafaia et al. 2020b; SHN.019, Malafaia et al. 2019), such as the general shape of the centrum, the absence of pleurocoels, a longitudinal, shallow ventral groove bounded by low crests, and presence of acdl and pcdle (referred as posterior laminar ridge in Malafaia et al. 2020b). Both IPS137684 and the referred caudal vertebra of *Lusovenator* (SHN.19/4) also share a ventral groove expanded posteriorly (Malafaia et al. 2019). The morphology of the posterior articular facet of IPS137684 (sub-trapezoidal) is slightly different to that of *L. santosi* middle caudal vertebra (i.e. SHN.036/56; sub-circular), but similar to those of distal elements (i.e. SHN.036/59). Nevertheless, IPS-37403 (s/n) differs from *Lusovenator santosi* in the occurrence of an accessory lamina and a rough surface on the anterior half of the lateral surface of the vertebral body (Fig. 6B).

As a final observation, it is worth noting that *Acrocanthosaurus atokensis* was descried has having an “accessory transversal process” that can be traced along the middle caudal series (Harris 1998). Despite the nature of such feature is not explained in the original study, the location of this feature in the 29th caudal vertebra (SMU 74646K2; see Harris 1998: fig. 26) is almost identical to the rouge surface observed on the anterior half of IPS137684 (see Fig. 6E). Without more information, such structure may well represent a homoplasic character with

Acrocanthosaurus, given that “accessory transversal process” is also reported in the caudal vertebras of the compsognathid *Sinosauropteryx prima* (NIGP 127587 and NIGP 127586; Currie and Chen 2001). Anyhow, this feature is not observed in the penecontemporary *Concavenator* (Fig. 6D).

In sum, IPS137684 shares some characters commonly featured by basal carcharodontids, like *Veterupristisaurus* and *Lusovenator*. Despite the taxonomic affinity of the studied specimen cannot be assessed beyond high taxonomic level, it clearly differs from any of previously known penecontemporary theropod taxa, suggesting a higher theropod faunal diversity during the Early Cretaceous of the Iberian Peninsula than previously though.

4.2 Large-size theropod diversity during the Barremian.

Due to its central position in the Pangea supercontinent during the Early Cretaceous, the Iberian Peninsula played a key role in the paleobiogeographic distribution of non-avian theropods, acting as a crossroad between both Laurasian and Gondwanan faunas. The area of origination of spinosaurids remains controversial, but the clade rapidly dispersed and diversified throughout Western Europe during the early Cretaceous (Berker et al. 2021; Santos-Cubedo et al. 2023). In this regard the Iberian Peninsula emerges as a pivotal point to understand the early radiation of spinosaurids, given that this region includes the earliest representative of the two main clades of spinosaurids (see Malafaia et al. 2020a; 2020c; Smathi et al. 2021; Berker et al. 2021; Mateus and Estraviz-López 2022; Santos-Cubedo et al. 2023).

The report of a dental element (IPS919) tentatively attributed to the genus *Protathlitis* from the upper part of the Arcillas de Morella Formation (late Barremian) outside from the type locality (Anna site; Santos-Cubedo et al. 2023) constitutes an additional evidence of the geographic and time distribution of Iberian baryonychines. It is worth noting that the current Iberian spinosaurid fossil record seems to suggest a decrease of biodiversity throughout the Barremian (for details of the biostratigraphic context see Malafaia et al. 2020c). At least five spinosaurid taxa could coexist during the early Barremian, including *Camarillasaurus*, *Iberospinus*, one intederminate spinosaurine and two indeterminate baryonychines (see Alonso and Canudo 2015). Three taxa could persist in the late Barremian, being well represented in the Morella sub-basin by *Vallibonavenatrix*, *Protathlitis* and at least another indeterminated baryonychines (see Canudo et al. 2008; Alonso and Canudo 2016). And only *Baryonyx* is recorded from the Aptian of the Cameros Basin (see Malafaia et al. 2020c).

On the other hand, carcharodontosaurids could have been originated in the Late Jurassic of southern Africa (Rauhut 2011). The clade rapidly spread along South America, North America, Asia, and Europe. In the Iberian Peninsula, this group of allosauroids were present from the Late Jurassic (Malafaia et al. 2020b) to the end of the Barremian (i.e. Canudo and Ruíz-Omeñaca 2003). However their distribution and diversity along that time is uneven in the Iberian record. While the occurrence of carcharodontosaurids is well documented in the early Barremian and represented by at least two different species, including *Concavenator* (Ortega et al. 2010) and an indeterminate carcharadontosaurid from the Morella sub-basin (Maestrasgo Basin; Gasca et al. 2014), their occurrence in upper Barremian strata has remained controversial for some time due to the scarcity and fragmentary nature of their fossil record. In fact, only a single element has been tentatively attributed to carcharodontosaurids: an isolated tooth (Santafé et al. 1978; 1982; Canudo and Ruíz-Omeñaca 2003) from the upper part of the Arcillas de Morella Formation. Therefore, the vertebral elements described in this study represent the second evidence of carcharodontosaurid allosauroids in the late Barremian of the Iberian Peninsula. Furthermore, the studied elements differ from those of *Concavenator,* and suggest the presence of at least another carcharodontosaurid taxon in the Early Cretaceous of the Iberian Peninsula, as previously postulated by some authors (see Gasca et al. 2014).

5 Conclusions

The study of historical theropod remains from the Arcillas de Morella formation has provided new information about the composition of the middle to large-size theropod communities during the Late Barremina in the Easter Iberian Peninsula. The description of the second record of the basal baryonychine *Protathlitis* coupled with the presence of a carcharodontosaurid different from *Concavenator*, herein represented by two caudal elements, constitute new evidence of the coexistence of spinosaurides and carcharodontosaurids till the late Barremian in the Iberian Peninsula. Such association of middle to large-bodied theropods is, in fact, well known from South America, Africa, and Asia, but mainly in later periods (e.g. Aptian and Albian) and in association with other theropod clades like megaraptorines, abelisauroids or tyrannosauroids. In fact, the current theropod assemblage from Spain seems to lack the presence of basal tyrannosauroids, a clade present in other regions from Eastern Europe like

England (*Eotyrannus*) and Portugal (*Aviatyrannis*). Perhaps, the high diversity of both spinosaurids and carcharodontosaurids from Spain could leave no ecological niche available for the presence of a third group of predatory dinosaurs. We hope that further findings could elucidate this and other ecological questions.

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FIGURES AND TABLES

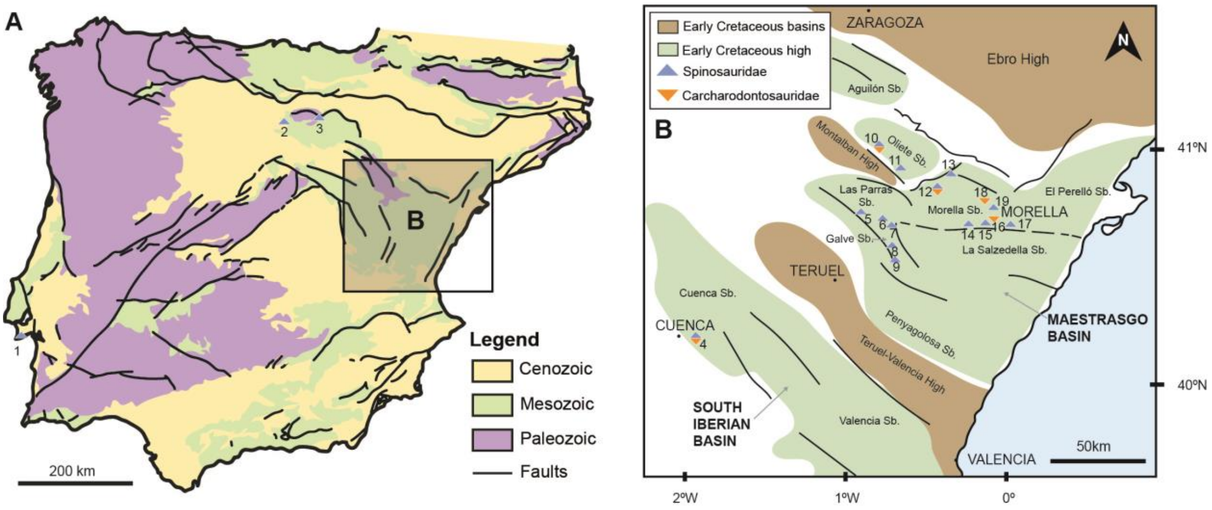

Figure 1. Geographic distribution of current spinosaurid (up-pointing blue triangles) and carcharodontosaurid (down-pointing orange triangles) theropod remains in the Lower Cretaceous of the Iberian Peninsula. **A**. Distribution of the Iberian Mesozoic basins (modified from Pereira et al., 2015); **B**. Distribution of the Early Cretaceous sub-basins of eastern Iberia and the location of the spinosaurid and carcharodontosaurid fossil record (map modified from Capote et al., 2002) Legend for the fossil localities: 1, Cabo Espichel (Setubal); 2, Salas de los Infantes (Burgos) 3, Igea (La Rioja); 4, Las Hoyas (Cuenca); 5, Galve; 6, Camarillas; 7, Miravet de la Sierra; 8, Allepús; 9, Gudar; 10, Josa; 11, Estercuel; 12, Ladruñan; 13, Vallipón (Teruel); 9, Morella and 10, Val- libona (Castellón); 14, Anna; 15, Mas de la Parreta; 16, Tejería Bertran; 17, Vallibona; 18; Mas de Romeu; 19; Morella (Castellón). Data source: Malafaia et al. (2020c); Gasulla et al. (2009); Sanguino et al. (2020), Santos-Cubedo et al. (2023).

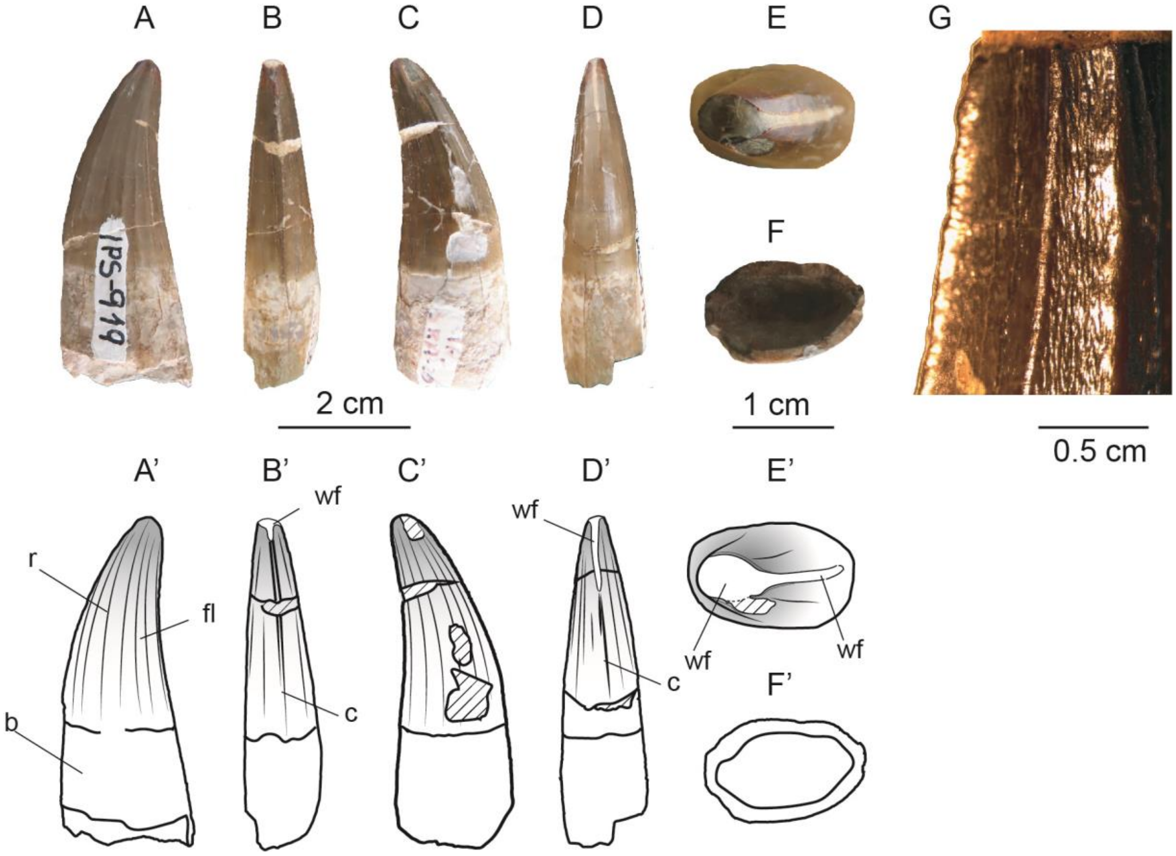

Figure 2. Isolated tooth attributed to cf. *Protathlitis* sp. (IPS919) from the upper Barremian Arcillas de Morella Formation in lingual (**A**), distal (**B**), labial (**C**), mesial (**D**), apical (**E**), and basal (**F**) view; and detail of the distal denticles and crenulation of the tooth enamel (**G**).

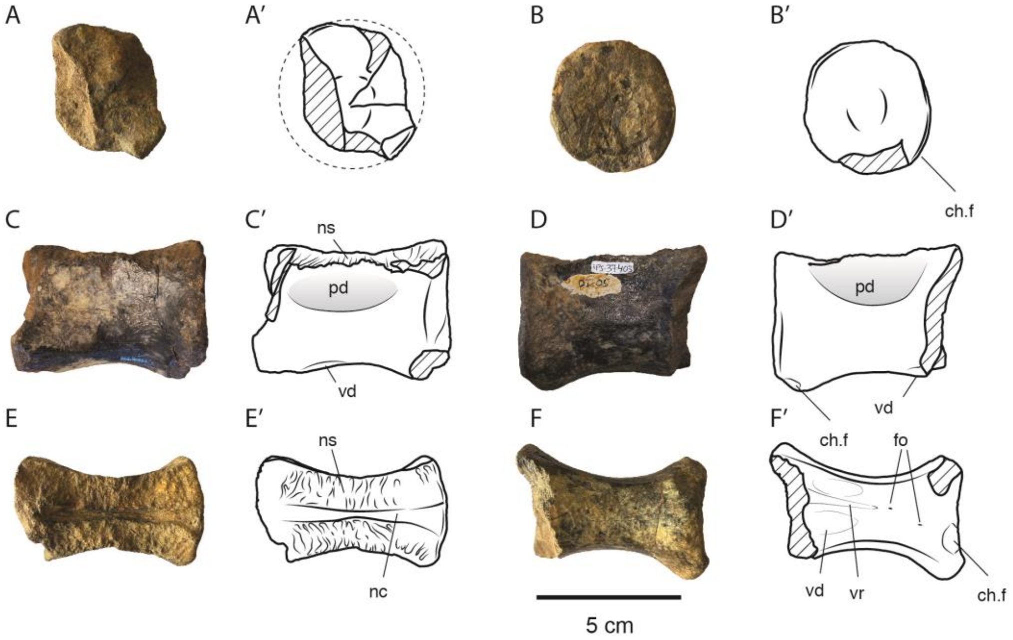

Figure 3. Carcharodontosauria indet. Anterior caudal centrum (IPS137683) in (**A**) anterior, (**B**) posterior (**C**), left lateral, (**D**) right lateral, (**E**) dorsal, and (**F**) ventral view. Abbreviations: ch.f, articular facet for chevrons; fo, foramina; nc, neural canal; pd, pleurocoel depression; vd, ventral depression; vr, ventral ridge.

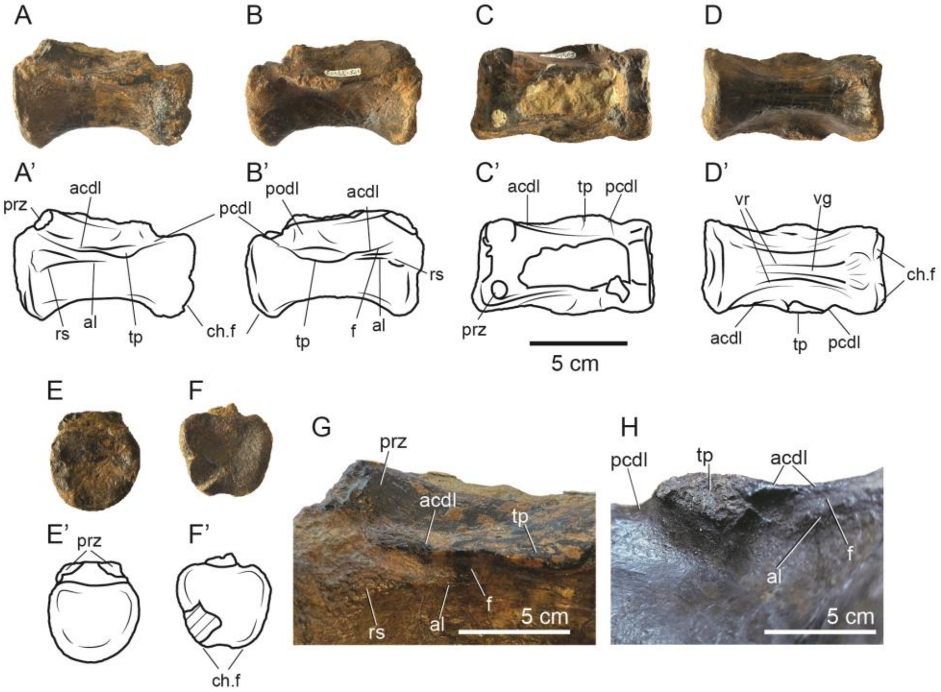

Figure 4. Carcharodontosauria indet. Posterior caudal centrum (IPS137684) in (**A**) left and (**B**) right lateral view, and (**C**) dorsal, (**D**) ventral, (**E**) anterior, and (**F**) posterior views. Detail of the peculiar vertebral lamination on both (**G**) left and (**H**) right lateral surfaces. Abbreviations: acdl, anterocentrodiapophiseal lamina; al, accessory lamina; "atp", accessory transversal process (*sensu* Harris, 1998); ch.f, articular facet for chevrons; f, fossa; pcdel, posterocentrodiapophiseal lamina; podl, postzygapophiseal-diapophiseal lamina; prz, prezygapophisis; rs, rouge surface; tp, transversal process; vg, ventral groove; vr, ventral ridge.

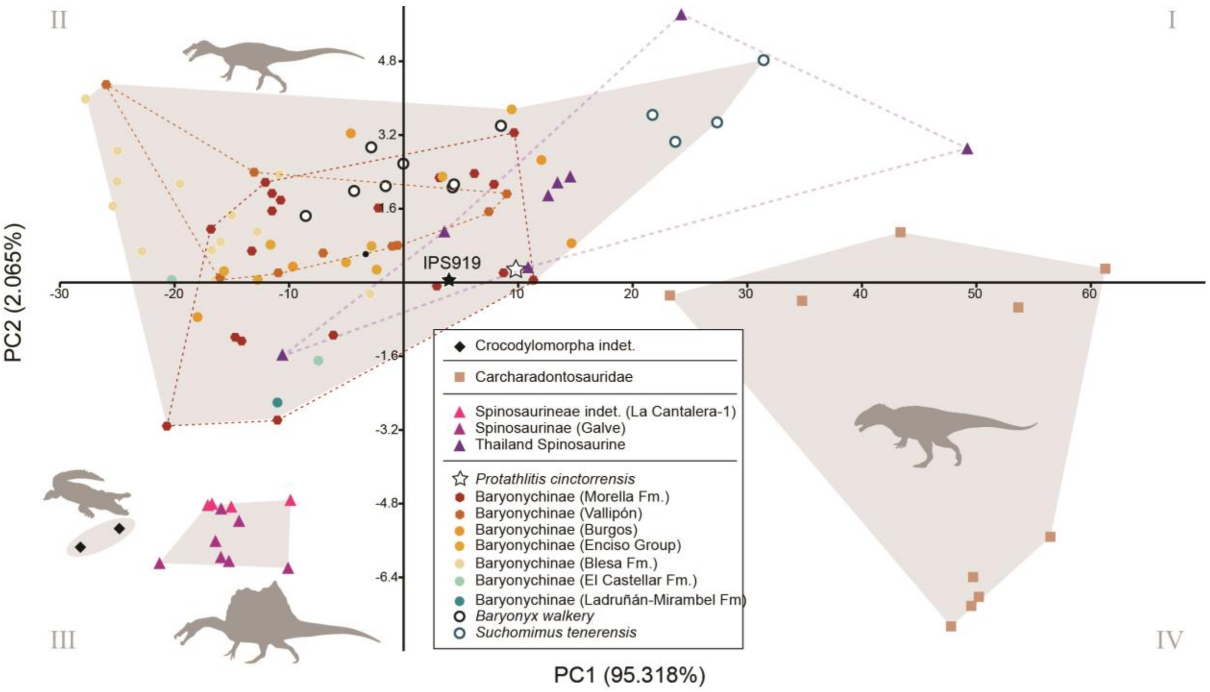

Figure 5. Principal component analyses plot of most of non-avian large-size theropods from the Early Cretaceous of Iberian Peninsula. IPS919 is indicated with a black star mark. Data available in the Supplementary Information S1. Dinosaur and crocodile silhouettes were modified from http://phylopic.org.

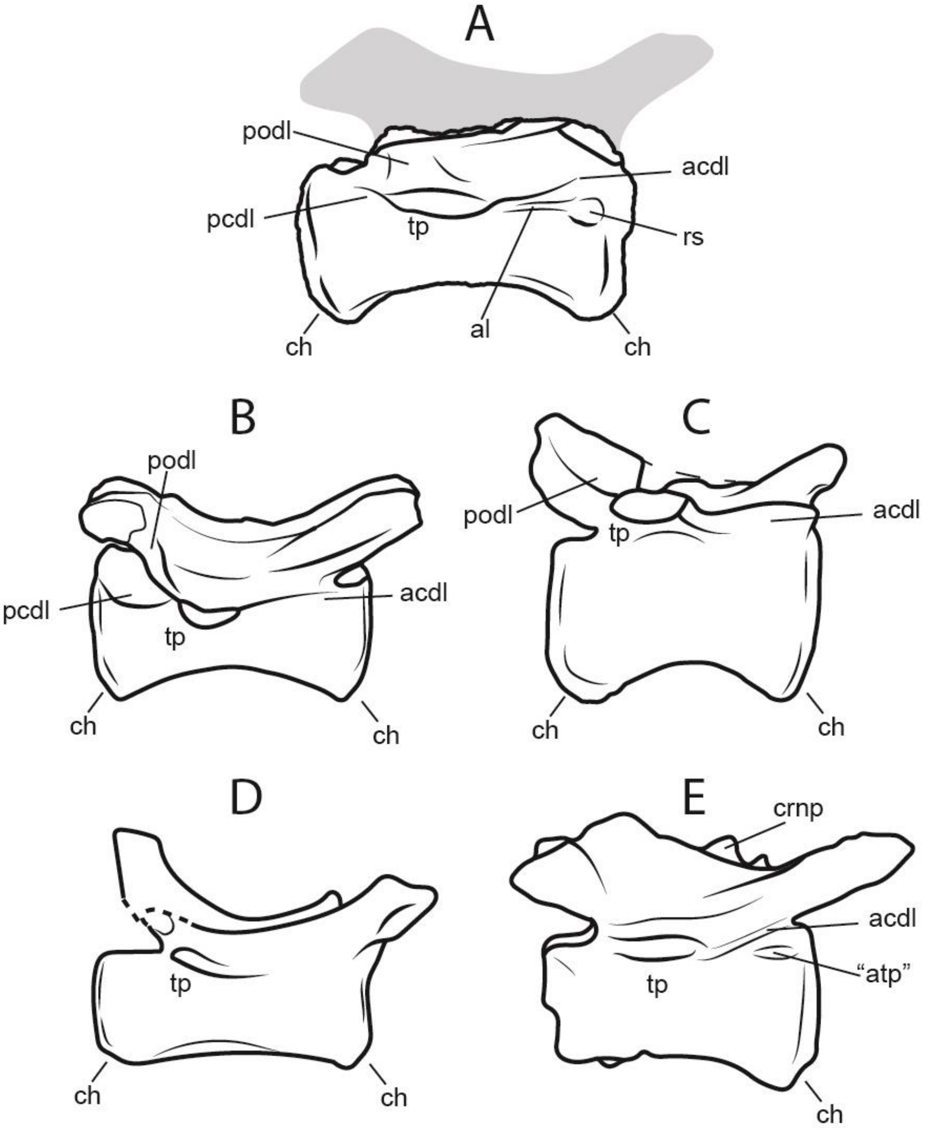

Figure 6. Anatomic comparison of distal caudal vertebra features between selected carcharodontosaurids. A, Carcharodontosauridae indet. (IPS137684, distal caudal, present study); B, *Lusovenator santosi* (SHN.036/59, distal caudal; reversed modified from Malafaia et al. 2017, 2019); C, *Veterupristisaurus milneri* (MB R 1938, distal caudal; reversed, modified from Rauhut, 2011); D, *Concavenator corcovado* (MCCM-LH 6666; 26^{th} caudal; modified from Cuesta et al., 2019); E, *Acrocanthosaurus atokensis* (SUM 74646 K2, 29^{th} caudal; modified from Harris, 1998). Schemes not at scale. Abbreviations: acdl, anterocentrodiapophiseal lamina; al, accessory lamina; "atp", accessory transversal process (*sensu* Harris, 1998); ch, articular facet for chevrons; pcdel, posterocentrodiapophiseal lamina; podl, poszygapophiseal-diapophiseal lamina; rs, rouge surface; tp, transversal process.

Table 1. Measures of the toot element IPS919.

Parameter	Value
Apico-basal length (AL)	353.6 mm
Crown base wide (CBW)	6.6 mm
Crown high (CH)	33.6 mm
Crown angle (CA)	65.3º
Distal mid-point length (DC)	10.9 mm
Mesial apical length (MA)	11.4 mm
Mesial base length (MB)	11.0 mm
Crown base length (CBL)	17.6 mm
Crown base ratio (CBr)	66.0
Crown high ratio (CHr)	14.5
Distal apical length (DA)	10.0 mm
Distal basal length (DB)	10.3 mm
Mesial mid-point length (MC)	11.4 mm

Table 2. Measures (in mm) of studied vertebrae. Abbreviations: ACH, anterior condyle high; ACW, anterior condyle width; MH, middle high; MW, middle width; PCH, posterior cotyle high; PCW, posterior cotyle width; TL, total length.

Specimen	TL	ACH	ACW	PCH	PCW	MH	MW
IPS137683	64.14	49.37	44.65	46.82	-	40.86	26.77
IPS137684	69.3	39.21	39.44	66.65	39.82	23.12	20.00

Table 3. Tooth characters in *Torvosaurus tanneri* (as outgroup) and spinosaurid dinosaurs. Data from Mateus et al. (2011), Mateus and Estraviz-López (2021), and Santos-Cubedo et al (2023).

	Torvosaurus tanneri	*Irritator challengeri*	*Spinosaurus aegyptiacus*	*Suchomimus tenerensis*	*Baryonyx walkeri*	*“Suchosaurus girardi”*	*Iberospinus natarioi*	*Protathlitis cinctorrensis*	IPS919
Tooth crown suboval to subcircular in cross-section	no	yes	yes	yes	yes	yes	yes	yes	yes
Presence of flutes	no	yes	yes	yes	yes	yes	yes	yes	yes
Carinae bearing 6 or more denticles per mm	no	N/A	N/A	yes	yes	yes	yes	yes	yes
Exceptionally long and slender tooth roots	no	yes	yes	yes	yes	yes	yes	NA	N/A
Enamel surface of the crown	smooth	smooth	smooth	sculptured	sculptured	sculptured	sculptured	sculptured	sculptured
Base of the crown enamel surface	smooth	smooth	smooth	smooth or sculptured	sculptured	sculptured	sculptured	smooth to sculptured	sculptured
Irregular denticle size	no	N/A	N/A	yes	yes	yes	yes	yes	yes
Number of flutes	N/A	7	5	0-10	6-8	12	9	9-12	11-14
Well-pronounced carinae	yes	yes	yes	no	no	no	no	no	no
Curvature of the crown	yes	no	no	yes	yes	yes	yes	yes	yes
Denticles in mesial (m) and distal (d) sides		N/A	N/A	m & d	m & d	d	m & d	d	d