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NEW CONTRIBUTIONS TO THE KNOWLEDGE OF ABELISAURIDAE (DINOSAURIA, THEROPODA) FROM THE UPPER CRETACEOUS IBERO-ARMORICAN LANDMASS

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Abstract. Abelisaurids were medium- to large-bodied theropods that inhabited Gondwana and Europe, even becoming the apex predators in the latest Cretaceous ecosystems of many of these areas. European abelisaurids remain elusive, but their remains are becoming increasingly abundant in the Upper Cretaceous Ibero-Armorica. In this work, systematic, morphometric, and cladistic analyses of tooth samples from the Campanian–Maastrichian deposits of three localities (Chera 2, Montrebei and Viso) from the Iberian Peninsula have allowed these elements to be reassigned to abelisaurids. The specimen from Chera 2 is assigned to *Arcovenator* sp. whereas teeth from Montrebei and Viso are classified as Abelisauridae indet. The latter represents the first confirmed abelisaurid remain from the Cretaceous of Portugal. The axial remains identified as belonging to *Rhabdodon* from Laño are here attributed to cf. *Arcovenator*. These findings indicate that abelisaurids were the only apex terrestrial predators and among the most abundant theropods in the Upper Cretaceous of the Ibero-Armorican landmass. The reclassification of mid- to large-sized isolated teeth from Ibero-Armorica as abelisaurids, rather than carcharodontosaurids or closely related forms, suggests that Abelisauridae had already become the dominant apex theropod lineage by the Cenomanian. The abelisauroid fossil record in Ibero-Armorica spans from the Albian to the latest Maastrichtian, indicating a complex and temporally extensive presence. Despite most of the specimens being fragmentary, the available evidence supports the persistence and diversification of abelisaurids across Ibero-Armorica, with multiple lineages arising either from a possible Albian stock or resulting from successive dispersals, followed by insular diversification throughout the Late Cretaceous.

Key words. Dinosaur. Ceratosauria. Abelisaurid. Late Cretaceous. Iberian Peninsula. Paleobiogeography.

Resumen. NUEVOS APORTES AL CONOCIMIENTO DE ABELISAURIDAE (THEROPODA, DINOSAURIA) DEL CRETÁCICO SUPERIOR IBERO-ARMORICANO. Los abelisáuridos fueron terópodos de tamaño medio a grande que habitaron Gondwana y Europa, convirtiéndose incluso en depredadores ápice en los ecosistemas del Cretácico final en muchas de estas regiones. Los restos europeos de abelisáuridos son limitados, pero comienzan a ser más abundantes en el Cretácico Superior ibero-armoricano. En este trabajo, los análisis sistemáticos, morfométricos y cladísticos de dientes campanienses–maastrichtienses de tres localidades (Chera 2, Montrebei y Viso) de Iberia han permitido reasignar estos elementos a Abelisauridae. El espécimen de Chera 2 se asigna a *Arcovenator* sp., mientras que los dientes de Montrebei y Viso se clasifican como Abelisauridae indet. Este último representa el primer resto de abelisáurido del Cretácico de Portugal. Los restos axiales identificados anteriormente como *Rhabdodon* procedentes de Laño se atribuyen a cf. *Arcovenator*. El registro fósil muestra que los abelisáuridos fueron los únicos depredadores terrestres dominantes y los terópodos más abundantes en el Cretácico Superior Ibero-Armóricano. La reclasificación de dientes aislados como pertenecientes a abelisáuridos, en lugar de a carcarodontosáuridos u otros grupos cercanos, sugiere que Abelisauridae ya se había convertido en el depredador ápice hacia el Cenomaniense. El registro de abelisauroideos en Ibero-Armórica abarca desde el Albiense hasta el Maastrichtiense final, indicando una presencia compleja y prolongada en el tiempo de estos terópodos. A pesar de su naturaleza fragmentaria, la evidencia apunta a la persistencia y diversificación de los abelisáuridos en Ibero-Armorica, con múltiples linajes surgidos a partir de un posible stock albiense o de dispersiones sucesivas, experimentando una diversificación durante el Cretácico Tardío europeo.

Palabras clave. Dinosaurio. Ceratosauria. Abelisáurido. Cretácico Tardío. Península Ibérica. Paleobiogeografía.

ABELISAURIDAE comprises medium- to large-bodied (5–9 m in length) ceratosaurian theropods characterized by deep, heavily sculptured skulls with bony protuberances, and short, rounded snouts (Bonaparte, 1991; Wilson *et al.*, 2003; Carrano & Sampson, 2008; Canale *et al.*, 2009; Pol & Rauhut, 2012; Cerroni *et al.*, 2022; Amudeo-Plaza *et al.*, 2023). They are recovered as a sister clade to the smaller-bodied Noasauridae within Abelisauroidea (*e.g.*, Bonaparte, 1991, 1996; Novas, 1991; Novas *et al.*, 2013; Baiano *et al.*, 2021). The oldest abelisaurid remains are from the Jurassic of

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South America and include an isolated abelisaurid tooth from the Late Jurassic of Uruguay (Soto *et al.*, 2022) and a relatively complete skeleton of the putative early-branching abelisaurid *Eoabelisaurus mefi* from the Lower Jurassic of Patagonia (Pol & Rauhut, 2012). Despite being present throughout the Cretaceous of Europe and Gondwana, abelisaurids only became the dominant apex predators after carcharodontosaurids and spinosaurids declined and/or went extinct in the mid–Cretaceous (Hendrickx *et al.*, 2015a and references therein). However, they may have been more abundant than other inland predators (Sales *et al.*, 2016). After the Cenomanian/Turonian transition, abelisaurids started to dominate the western European and Gondwanan landmasses (Candeiro & Martinelli, 2005; Carrano *et al.*, 2012; Novas *et al.*, 2013; Tortosa *et al.*, 2014; Csiki-Sava *et al.*, 2015; Hendrickx *et al.*, 2015a).

The European abelisaurid record has significantly increased over the last decades (*e.g.*, Allain & Pereda-Suberbiola, 2003; Buffetaut, 2005; Ősi *et al.*, 2010; Ősi and Buffetaut, 2011; Tortosa *et al.*, 2014; Csiki-Sava *et al.*, 2015; Pérez-García *et al.*, 2016; Isasmendi *et al.*, 2022, 2024; Malafaia *et al.*, 2025). The oldest definitive European abelisauroid is currently *Genusaurus sisteronis* from the Albian of Provence, southern France. Nevertheless, its phylogenetic position remains unresolved, having been recovered as a noasaurid (*e.g.*, Carrano & Sampson, 2008), an early-branching abelisaurid (*e.g.*, Tortosa *et al.*, 2014; Baiano *et al.*, 2023), or a later-branching abelisaurid more related to Furileusauria (Buffetaut *et al.*, 2024; Buffetaut, 2025). *Caletodraco cottardi* is the second abelisaurid from the mid–Cretaceous of France. It is based on a partial skeleton likely recovered from lower Cenomanian deposits in northwestern France and identified as a furileusaurian brachyrostran (Buffetaut *et al.*, 2024). *Tarascosaurus salluvicus* was the first abelisaurid reported from lower Campanian deposits in southern France (Le Loeuff & Buffetaut, 1991), and despite its fragmentary nature and some authors considering it as a *nomen dubium* (Rauhut, 2003; Allain & Pereda-Suberbiola, 2003), this taxon was recovered amongst Abelisauridae in the phylogenetic analyses performed by Tortosa *et al.* (2014). Other material from the Iberian Peninsula, such as the Laño femora, have been compared with *Tarascosaurus* (Le Loeuff & Buffetaut, 1991), even though there is no conclusive evidence to support this attribution (Isasmendi *et al.*, 2022; Malafaia *et al.*, 2025). The best-known European abelisaurid is *Arcovenator escotae* from the upper Campanian of southern France, which has been recovered within Majungasaurinae (Tortosa *et al.*, 2014). The holotype of *Arcovenator* is composed of a partial skeleton including cranial, axial, and appendicular material. Additional isolated teeth and caudal vertebrae from other horizons and areas of the type locality have also been referred to this taxon. Furthermore, other skeletal elements from the Upper Cretaceous of France and the Iberian Peninsula have been assigned to this taxon (Tortosa *et al.*, 2014; Pérez-García *et al.*, 2016; Isasmendi *et al.*, 2022; Malafaia *et al.*, 2025). First regarded as Ceratosauria indet. by Carrano and Sampson (2008), *Betasuchus bredai*, from Maastrichtian strata of the Netherlands, was finally recovered as an abelisauroid more closely related to *Tarascosaurus* by Tortosa *et al.* (2014) and currently represents the latest record of the clade in Europe (Csiki-Sava *et al.*, 2015). Other than abelisaurids, theropod remains from the uppermost Cretaceous Ibero-Armorican mainly belong to small-sized coelurosaurians (*e.g.*, Antunes & Sigogneau-Russell, 1991, 1992; Allain & Taquet, 2000; Garcia *et al.*, 2000; Laurent *et al.*, 2002; Laurent, 2003; Ortega *et al.*, 2015; Torices *et al.*, 2015; Marmi *et al.*, 2016; Puertólas-Pascual *et al.*, 2018; Isasmendi *et al.*, 2022, 2024; Santos Brilhante *et al.*, 2022; Malafaia *et al.*, 2023) whereas the majority of fossils from large bodied theropods have been either identified as indeterminate theropods (Antunes & Sigogneau-Russell, 1992; Laurent, 2003; Company, 2005; Ortega *et al.*, 2015; Torices *et al.*, 2015; Pérez-García *et al.*, 2016), tetanurans (Carrano *et al.*, 2012), or ornithomimosaurs (Pereda-Suberbiola *et al.*, 2000).

This study aims to review the large-bodied theropod material from several uppermost Cretaceous Iberian sites (Chera 2, Laño, Montebrei and Viso), which comprises isolated teeth and some axial elements, including a previously undescribed caudal vertebra. Aside from the systematic studies, morphometric and cladistic analyses were performed on the revised dental elements, and the presence of Abelisauridae in Ibero-Armorica is evaluated.

Institutional abbreviations. DPM, Departamento de Paleontología de Madrid, Universidad Complutense de Madrid, Madrid, Spain; **IIPG,** Instituto de Investigación en Paleobiología y Geología, General Roca, Argentina; **MA,** Musée d'Angoulême, Angoulême, France; **MACN,** Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; **MAU,** Museo Municipal "Argentino Urquiza", Neuquén, Argentina; **MCNA,** Museo de Ciencias Naturales de Álava/Arabako Natura Zientzien Museoa, Vitoria/Gasteiz, Spain; **MG,** Museu Geológico, Lisbon, Portugal; **MPCA,** Museo Provincial Carlos Ameghino, Cipolletti, Argentina; **MPCN,** Museo Patagónico de Ciencias Naturales, General Roca, Argentina; **MPEF,** Museo Paleontológico Egidio Feruglio, Trelew, Argentina; **MPZ,** Museo de Ciencias Naturales de la Universidad de Zaragoza, Zaragoza, Spain; **UCPC,** Paleontology Collection of the University of Chicago, Chicago, USA; **UPUAM,** Unidad de Paleontología, Universidad Autónoma de Madrid, Madrid, Spain.

Anatomical abbreviations. cdl, centrodiapophyseal lamina; **cv,** cervix; **dc,** distal carina; **dl,** dentine layer; **dt,** denticle; **fch,** facet for chevron; **iet,** irregular enamel-texture; **mc,** mesial carina; **ns,** neural spine; **pc,** pulp cavity; **poz,** postzygapophysis; **tp,** transverse process; **tu,** transverse undulation; **vg,** ventral groove.

GEOGRAPHICAL AND GEOLOGICAL SETTINGS

The skeletal elements here studied were recovered from four Iberian fossil sites, namely, Chera 2, Laño, and Montebrei from Spain, and Viso from Portugal. The Chera 2 site is situated near the locality of Chera in the province of Valencia (Valencian Community), about 60 km west of the city of Valencia, in the eastern part of the Iberian Peninsula. The Laño site is located about 30 km south of the city of Vitoria/Gasteiz, in an abandoned sand quarry (the Laño quarry) between the towns of Laño and Albaina (County of Treviño), in the northern Iberian Peninsula. The Montrebei locality is located around 25 km southwest of the Tremp locality, east of the Congost de Montrebei, in the Alsamora municipality (Lleida, northeastern Iberian Peninsula). Finally, the locality of Viso is situated in the Montemor-o-Velho region (Coimbra), at km 20 of the railway (Sauvage, 1897, 1898), in the western part of the Iberian Peninsula (Fig. 1.1).

Geologically, the Chera 2 site is located in the Chera Basin (southwestern Iberian Range), specifically in the Sierra Perenchiza Formation (*e.g.*, Company, 2005; Company &

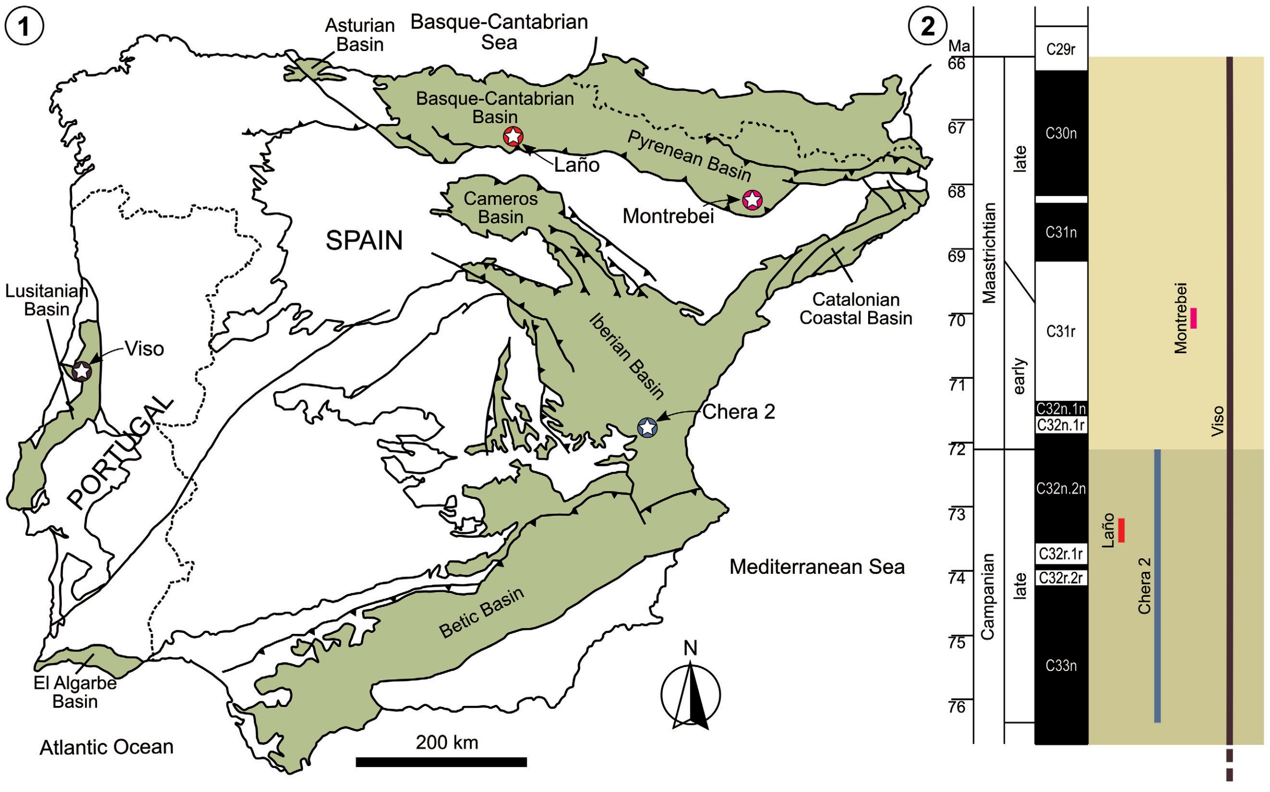

Figure 1. Geologic and chronostratigraphic setting of the uppermost Cretaceous fossil sites where the studied remains were recovered. **1,** map of the Iberian Mesozoic basins showing the locations of the Chera 2, Laño, Montrebei, and Viso fossil sites (modified from Gómez *et al.*, 2019); **2,** chronostratigraphic position of the Chera 2, Laño, Montrebei, and Viso fossil sites.

Szentesi, 2012) (Fig. 1.1). Even though this lithostratigraphic unit reaches a maximum thickness of 300 m, it is only 50 m thick in the Chera area. It comprises lagoonal micritic and brecciated limestones at the base, which transition upwards into palustrine carbonates with evidence of pedogenic alterations towards the top (Platt, 1989; Alonso *et al.*, 1991; Company, 2005). This formation has been interpreted as a continental, shallow carbonate environment (Vilas *et al.*, 1982) with shallow, low-salinity water bodies at the base (Platt & Wright, 1992) and restricted, ephemeral coastal carbonate lakes and ponds towards the top (Company, 2005). In this context, the Chera 2 site is thought to have formed in an isolated pond that developed in floodplains, where the fossils were transported after high-energy flows (Company, 2005). Peyrot *et al.* (2020) suggested a late Campanian–?early Maastrichtian age for the Chera site based on palynological studies; however, Company *et al.* (2005) proposed a late Campanian age for it (Fig. 1.2).

The Laño site is located in the Northern Castilian Ramp of the Basque-Cantabrian Basin, specifically on the southern margin of the Miranda-Treviño Syncline (Pereda-Suberbiola *et al.*, 2015; Corral *et al.*, 2016) (Fig. 1.1). In the Laño quarry, the Sedano Formation crops out (Berreteaga, 2008; Corral *et al.*, 2016). This formation mainly comprises siliciclastic deposits that can be divided into two units: (1) a lower unit consisting of marine marls and clays, and (2) an upper unit composed of silty quartzarenites with interbedded dolomitized limestone layers (Floquet *et al.*, 1982). The Sedano Formation represents a littoral environment, with a siliciclastic sequence in its upper part formed by deltaic aggradation in the subtidal and intertidal areas, prior to the progradation of the delta plain (Corral *et al.*, 2016; Martín-Chivelet *et al.*, 2019). At the Laño quarry, the Sedano Formation is 22 m thick and comprises two different units: (1) the basal unit, which begins with lag deposits of siliciclastic gravel overlain by different sandstone packs with conglomeratic and erosive bases, and (2) the upper unit, which is mainly composed of almost unconsolidated clayey sandstones. The fossils studied herein come from the L1A and L2 vertebrate-bearing beds. Astibia *et al.* (1990) and Pereda-Suberbiola *et al.* (2000) interpreted the Laño area as a braided river system, where channels, sandbars and pools developed. Corral *et al.* (2016) dated the continental vertebrate site of Laño to the late Campanian (chron C32n, 72–73.5 Ma) based on the combination of lithostratigraphic and magnetostratigraphic analyses (Fig. 1.2).

The fossil locality of Montebrei is located in the South Pyrenean Basin, precisely in the eastern Tremp Syncline (Fondevilla *et al.*, 2016, 2019) (Fig. 1.1). The latter is the largest of the various sub-basins formed by the compartmentalization of the synform syntectonic sub-basins (Fondevilla *et al.*, 2016). The uppermost Cretaceous and Paleocene lithostratigraphic units crop out in the Tremp Syncline, encompassing marine, transitional, and continental deposits. These include the middle Campanian–Maastrichtian Arén Formation and the Maastrichtian–Paleocene Tremp Formation (Mey *et al.*, 1968; Nagtegaal *et al.*, 1983; Mutti & Sgavetti, 1987). The latter overlays and laterally transitions into the Arén Formation (Ardevol *et al.*, 2000; Fondevilla *et al.*, 2016). The Tremp Formation has been informally divided into four units: the 'Grey Garumnian', the 'Lower Red Garumnian', the 'Vallcebre limestones and equivalents', and the 'Upper Red Garumnian' (Rosell *et al.*, 2001; Pérez-Pueyo *et al.*, 2021). The Montrebei fossil locality is situated within the 'Grey Garumnian', specifically in La Posa Formation (Torices Hernández, 2002; Torices *et al.*, 2015; Fondevilla *et al.*, 2019). This unit consists of grey marls and mudstones intercalated with sandstones, limestones, and occasional coal beds, containing mixed marine and freshwater invertebrate faunas. It has been interpreted as representing transitional environments such as lagoons, tidal mudflats, and marshes (Eichenseer, 1988; Rosell *et al.*, 2001; Díez-Canseco *et al.*, 2014; Oms *et al.*, 2016). The 'Grey Garumnian' is dated to the latest Campanian–Maastrichtian (Díez-Canseco *et al.*, 2014; Vicente *et al.*, 2015, 2016; Fondevilla *et al.*, 2016; Puertolas-Pascual *et al.*, 2018) and the Montrebei fossil site dates more precisely to the 'mid' early Maastrichtian (C31r) (Fondevilla *et al.*, 2019) (Fig. 1.2).

The vertebrate-bearing site of Viso is found in the Lusitanian Basin, either in the "Sandstones and Mudstones of Viso" of Barbosa *et al.* (2008) or Viso Formation of Malafaia *et al.* (2024) (Fig. 1.1). In the latter, a sandstone sequence is predominant, but mudstones, which have been dated to the Campanian–Maastrichtian, based on palynological studies, also crop out (Barbosa *et al.*, 2008) (Fig. 1.2).

MATERIAL AND METHODS

Geographic and stratigraphic context of the material

The studied material consists of three isolated teeth from the Chera 2 site (CH 168), Montrebei (DPM-MON-T10 1), and Viso (MG 73), and two vertebrae from the Laño site (MCNA 8366 and 17433). MCNA 8366 comes from the L1A vertebrate-bearing bed, and MCNA 17433 was recovered from the L2 fossiliferous level. The specimens are in three separate institutions, namely, the Universidad Complutense de Madrid of Spain (DPM-MON-T10 1), Museu Geológico of Lisbon, Portugal (MG 73), and the Arabako Natura Zientzien Museoa/Museo de Ciencias Naturales de Álava of Vitoria-Gasteiz, Spain (MCNA 8366 and 17433). The tooth CH 168 was studied based on photographs and a cast.

Historically, DPM-MON-T10 1 was considered as the tooth of an indeterminate theropod by Torices *et al.* (2015), before being assigned to an indeterminate Abelisauridae by Isasmendi *et al.* (2024). It should be noted that this specimen never received a proper description. The tooth MG 73 was first attributed to *Megalosaurus* sp. by Sauvage (1897, 1898) at the end of the 19th century, then to *Megalosaurus* cf. *pannoniensis* by Lapparent and Zbyszewski (1957), and recently to Theropoda indet. by Malafaia *et al.* (2024). The neural arch MCNA 8366 was originally assigned to *Rhabdodon* by Pereda-Suberbiola and Sanz (1999), while the vertebra MCNA 17433 (previously labeled as MCNA 14077) was tentatively identified as Abelisauridae indet. by Isasmendi *et al.* (2021). Finally, the tooth CH 168 was referred to as Theropoda indet. by Company (2005), as ?Neoceratosauria indet. by Company *et al.* (2009) and as cf. *Arcovenator* by Isasmendi *et al.* (2022).

Comparative methodology and terminology for the isolated teeth. Unlike the postcranial remains, which were studied first-hand, the isolated teeth were studied under a stereo microscope (Nikon® SMZ645) and through first-hand observations. Crown-based measurements were taken using a digital caliper (Juning®), while denticle-based measurements were taken either under the stereo microscope or with the Imagej software (v.1.51j8). The study of the isolated teeth follows the anatomical, positional, directional, and morphometric nomenclature proposed by Smith and Dodson (2003), Smith *et al.* (2005), and Hendrickx *et al.* (2015b).

Measurements taken on the isolated teeth. The following measurements were taken on the studied sample based on Currie *et al.* (1990), Smith *et al.* (2005), and Hendrickx *et al.* (2015b, 2020) methodology (see Supplementary Online Information 1): crown base length (**CBL**), crown base width (**CBW**), mid-crown length (**MCL**), mid-crown width (**MCW**), crown height (**CH**), apical length (**AL**), extent of the mesiobasal denticles (**MDE**), length of the mesial serrated carina (**MSL**), distoapical denticle density (**DA**), distobasal denticle density (**DB**), distocentral denticle density (**DC**), mesioapical denticle density (**MA**), mesiobasal denticle density (**MB**), mesiocentral denticle density (**MC**), mesial denticle length (**MDL**), and distal denticle length (**DDL**). In addition, the crown base ratio (**CBR**; as CBW/CBL), crown height ratio (**CHR**; as CH/CBL), mid-crown ratio (**MCR**; as MCW/MCL), mesial angle of the crown (**CMA**), distal angle of crown (**CDA**), average mesial denticle density (**MAVG**; as (MA+MC+MB)/ 3), average distal denticle density (**DAVG**; as (DA+DC+DB)/ 3), and denticle size density index (**DSDI**; as MC/DC) were calculated. The MCA and DCA were calculated using the following equation (Smith, 2007; Serrano-Martínez *et al.*, 2015):

$$CMA = arcos\ \frac{CBL^2+AL^2-CH^2}{2 \times CBL \times AL} \quad \text{and} \quad CDA = arcos\ \frac{CBL^2+CH^2-AL^2}{2 \times CBL \times AL}$$

Linear discriminant analyses (LDA) on the isolated teeth. The classification of the isolated teeth was supported by several linear discriminant analyses performed using PAST v.4.05 (Hammer *et al.*, 2001). When performing the LDAs, variables expressed as ratios (CBR, CHR, and MCR) as well as the crown angles (CDA and CMA) were excluded, as these are not independent but weighted variables (Hendrickx *et al.*, 2015b). Furthermore, to ensure that all variables were metric-based, measurements of denticle length (MLD and DDL) were used instead of denticle densities, in accordance with the approach of Hendrickx *et al.* (2020). Following Malafaia *et al.* (2025), the number of flutes on the labial and lingual surfaces (**LAF** and **LIF**, respectively) was not included in the analyses, as there are non-metric variables. Therefore, a total of 10 variables were used in the performed LDAs, as Malafaia *et al.* (2025). These variables are: CBL, CBW, CH, AL, MCL, MCW, MDE, MSL, MDL, and DDL. To perform the LDAs, the database and a similar methodology proposed by Malafaia *et al.* (2025) were used (see Supplementary Online Information 1). Prior to conducting the morphometric analyses, the data were normalized using a Log (x+1) transformation for all variables to avoid zero values. In addition, as proposed by Young *et al.* (2019) and Hendrickx *et al.* (2020), an arbitrary value of 100 denticles per five millimeters was used for those specimens with non-denticulated carinae. Finally, specimens studied herein were not assigned to any predefined group for the LDAs and were instead treated as belonging to an "unknown taxon".

Firstly, two linear discriminant analysis, one at the taxon level and another at the clade level, were carried out using a database comprising 528 teeth with the data from Hendrickx *et al.* (2020) (Database 1; Supplementary Online Information 1) belonging to 24 Cretaceous taxa (22 genera, and two indeterminate family-level clades), with the aim of minimizing potential noise (see Malafaia *et al.*, 2025; Supplementary Online Information 1). This dataset gathers dental measurements from one non-abelisauroid ceratosaurian (*Genyodectes*), nine abelisaurids (*Abelisaurus*, *Arcovenator*, *Aucasaurus*, *Carnotaurus*, *Chenanisaurus*, '*Indosuchus*', *Majungasaurus*, *Skorpiovenator*, and Abelisauridae indet.), three spinosaurids (*Baryonyx*, *Suchomimus* and Spinosaurinae indet.), one neovenatorid (*Neovenator*), two megaraptorans (*Australovenator* and *Fukuiraptor*), five carcharodontosaurids (*Acrocanthosaurus*, *Carcharodontosaurus*, *Eocarcharia*, *Giganotosaurus*, and *Mapusaurus*), and six tyrannosaurids (*Albertosaurus*, *Alioramus*, *Daspletosaurus*, *Gorgosaurus, Tyrannosaurus* and *Zhuchengtyrannus*).

Afterwards, two additional LDAs were performed, one at the taxon level and another at the clade level, excluding the groups that plotted well-separated from the herein studied teeth (Database 2; Supplementary Online Information 1), as these were considered not closely related. The excluded specimens belonged to all spinosaurids, as well as the tyrannosaurids *Daspletosaurus*, *Tyrannosaurus*, and *Zhuchengtyrannus*, and the carcharodontosaurid *Carcharodontosaurus*.

Finally, a fifth LDA was performed with the third database (Database 3; Supplementary Online Information 1) compiled by Malafaia *et al.* (2025), which includes Ibero-Armorican abelisaurids or specimens classified among Abelisauridae. These consist of the indeterminate abelisaurids from the Western Tremp Syncline (South Pyrenean Basin) (Isasmendi *et al.*, 2024), the abelisaurid teeth closely related to *Arcovenator* from Poyos (Malafaia *et al.*, 2025), the specimens referred to cf. *Arcovenator* from Armuña (Pérez-García *et al.*, 2016), and the *Arcovenator* specimens from Jas Neuf Sud and Laño (Tortosa *et al.*, 2014; Hendrickx *et al.*, 2020; Isasmendi *et al.*, 2022). In this analysis, the isolated teeth of an indeterminate tetanuran from Iharkút (Ősi *et al.*, 2010) were excluded from the dataset.

Cladistic analysis. A cladistic analysis was performed based on the dentition-based matrix (146 morphological dental characters) of Hendrickx *et al.* (2020), into which we scored the isolated teeth MG 73, CH 168, and DPM-MON-T10 1 (see Supplementary Online Information 2). The positive constraints defined by Hendrickx *et al.* (2020) were applied in these analyses to recover a topology consistent with the most recent phylogenetic hypotheses. Additionally, to test the phylogenetic affinities of the studied specimens within the Abelisauridae clade, we constrained their placement and evaluated the additional steps required to achieve that position. The phylogenetic analysis was carried out using TNT 1.6 (Goloboff & Morales, 2023). The studied specimens were scored using Mesquite 3.7 (Maddison & Maddison, 2011) and subsequently imported into TNT. The search strategy follows the protocol used by Hendrickx *et al.* (2020), beginning with a combination of the tree-search algorithms, including Wagner trees, TBR branch swapping, sectorial searches, Ratchet (with the perturbation phase stopped after 20 substitutions), and Tree Fusing (5 rounds), until 100 hits of the same minimum tree length were achieved. The best trees recovered were subjected to a final round of TBR branch swapping. Zero-length branches in any of the recovered most parsimonious trees were collapsed. Consistency (**CI**) and retention (**RI**) indexes were obtained using the STATS.RUN command.

SYSTEMATIC PALEONTOLOGY

THEROPODA Marsh, 1881
CERATOSAURIA Marsh, 1884
ABELISAURIDAE Bonaparte & Novas, 1985

Abelisauridae indet.

Figure 2

Morphotype 1

Referred material. DPM-MON-T10 1, one isolated mesial tooth (Fig. 2.1–2.7).

Geographic occurrence. Montrebei (Lleida, Spain).

Stratigraphic occurrence. 'Grey Garumnian' strata of the Tremp Formation; La Posa Formation; 'mid' early Maastrichtian (C31r) (Torices Hernández, 2002; Torices *et al.*, 2015; Fondevilla *et al.*, 2019).

Description. DPM-MON-T10 1 consists of a crown that lacks its basal portion and the apex (Fig. 2.2–2.5). It is here interpreted as a mesial tooth, based on its symmetrical 'D'-shaped cross-section, relatively thick crown, and asymmetrical labial and lingual surfaces (Hendrickx *et al.*, 2015b, 2020). No denticles are complete, but the bases of the mesial denticles and some distal denticle bases are preserved (Fig. 2.1). The enamel is also largely missing, but a patch is preserved on the mesioapical part of the labial surface (Fig. 2.6). The crown is ziphodont, not very compressed labiolingually, and quite distally curved, with its apicalmost part extending beyond the basodistalmost point of the crown (Fig. 2.2–2.5). The mesial margin of the crown is strongly convex, and the distal margin is concave in lateral view (Fig. 2.5). In distal view, the labial surface is convex, and the lingual one is mostly straight, making the crown slightly lingually tilted (Fig. 2.4). The lingual and labial

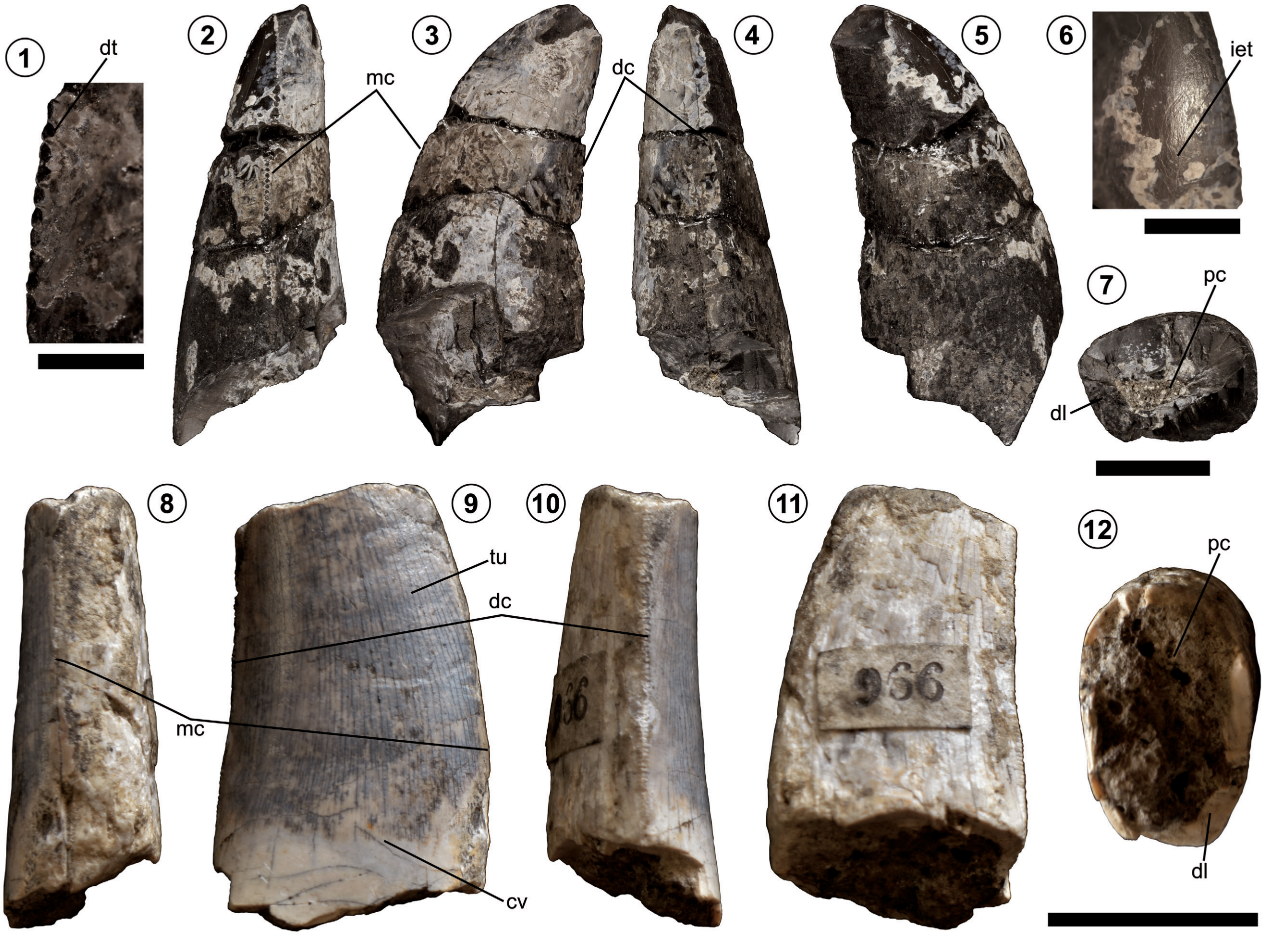

Figure 2. Abelisauridae indet. teeth from Montrebei and Viso. Morphotype 1 (**DPM-MON-T10** 1); **1,** close up of mesial denticles and crown in **2,** mesial; **3,** lingual; **4,** distal; and **5,** labial views; **6,** close up of enamel texture; and **7,** basal cross section in basal view. Morphotype 2 (**MG** 73) tooth in **8,** mesial; **9,** lingual; **10,** distal; **11,** labial; and **12,** basal views (modified from Malafaia *et al.*, 2024). Abbreviations: **cv,** cervix; **dt,** denticle; **mc,** mesial carina; **dc,** distal carina; **dl,** dentine layer; **iet,** irregular enamel texture; **pc**, pulp cavity; **tu,** transverse undulation. Scale bar equals 1 cm, except for denticles (**1;** 2,5 mm) and texture (**6;** 5 mm).

surface are convex, but the lingual surface becomes flatter close to the distal carina. The basalmost cross-section of the preserved crown is nearly subsymmetrical 'D'-shaped, whereas the mid cross-section is lanceolate (Fig. 2.7).

Both mesial and distal carinae are present and denticulated, but because the basal part of the crown is not preserved, their entire extension cannot be assessed. The mesial carina is mesiolingually oriented and straight; it is centered apically but slightly displaces lingually toward the base (Fig. 2.2). On the other hand, the distal carina is straight and strongly labially deflected (Fig. 2.4). The mesial dentile density is 10 denticles per five millimeters apically and at mid crown and there is no random variation of denticle-size.

The preserved enamel surface is slightly polished and exhibits micro-scratches. The enamel-texture is subtle, non-oriented, and irregular (Fig. 2.6).

Morphotype 2

Referred material. MG 73, one isolated lateral tooth (Fig. 2.8–2.12).

Geographic occurrence. Viso locality, region of Montemor-o-Velho, Coimbra, Portugal (Sauvage, 1897, 1998; Malafaia *et al.*, 2024).

Stratigraphic occurrence. Viso Formation (also known as Sandstones and Mudstones of Viso); Campanian–Maastrichtian (Barbosa *et al.*, 2008; Malafaia *et al.*, 2024).

Description. MG 73 consists of a lateral tooth crown that lacks the apex and a fragment of the root (Fig. 2.8–2.12). It is interpreted as a lateral tooth based on its symmetrical cross-section outline and low CBR value (see Hendrickx *et al.*, 2015b, 2019, 2020). The enamel layer is eroded on its lingual surface (Fig. 2.11), and the mesial carina is almost entirely abraded (Fig. 2.8). The distal carina is also poorly preserved, but the bases of the denticles are visible along the carina, and the basal denticles are relatively well preserved (Fig. 2.10–2.11).

This crown is relatively elongate, ziphodont, and strongly labiolingually flattened (Fig. 2.8–2.12), with a CBR of 0.58 (CBL=12 mm and CBW=7 mm). The crown is distally curved, but it is not possible to determine whether the apex would have extended beyond its basodistalmost point (Fig. 2.11). In lateral view, the mesial margin is convex, while the distal margin is slightly concave, becoming straighter toward the base (Fig. 2.11). In distal view, the lingual surface is slightly concave, and the labial surface is convex, suggesting that the apex was slightly tilted lingually (Fig. 2.10). There is no concave surface adjacent to the carinae, but the lingual surface becomes flat near the distal carina (Fig. 2.9). The basal cross-section of the crown is lanceolate (Malafaia *et al.*, 2024) and the cross-section of the root is oval (Fig. 2.12). No basal constriction is present between crown and root.

The distal carina reaches the cervix, and the distal denticles are present along the entire preserved length (Fig. 2.10). Denticles also appear to be present on the mesial carina, but only their bases are visible at mid-crown (Fig. 2.8). The full extent of the mesial carina cannot be determined (Malafaia *et al.*, 2024). The distal carina is centrally located and slightly bowed, whereas the mesial carina is more lingually positioned and straight (Fig. 2.8 and 2.10). There is no random variation in denticle size along the distal carina, and the denticles decrease in size towards the base. Only the distal denticle densities could be measured. The DC value is 20 denticles per five millimeters, and the DB is 22.5 denticles per five millimeters. The basal denticles are sub-quadrangular with slightly convex external margins and are separated by narrow interdenticular spaces. The denticles are poorly preserved at mid-crown, with only the bases of some visible. These are also separated by narrow interdenticular spaces and seem slightly longer apicobasally than mesiodistally. However, because the external end is not preserved, this morphology cannot be confirmed. Interdenticular sulci are not visible adjacent to either the distal or mesial carinae. Some subtle transverse undulations are present on the enamel of the lingual surface of the crown (Fig. 2.9). The enamel texture is subtle, non-oriented, and irregular (Malafaia *et al.*, 2024).

Arcovenator Tortosa, Buffetaut, Vialle, Dutour,
Turini, & Cheylan, 2014
cf. ***Arcovenator*** sp.
Figures 3

Referred material. MCNA 8366, an anterior dorsal vertebra; MCNA 17433, an anterior to middle caudal vertebra.

Geographic occurrence. Laño site, Treviño County, Spain.

Stratigraphic occurrence. Sedano Formation; upper Campanian (C32n) (Corral *et al.*, 2016).

Description

Axial skeleton

Dorsal vertebra (Fig. 3.1–3.4). MCNA 8366 comprises the neural arch of an anterior dorsal vertebra (probably a D1 or D2, based on O'Connor, 2007). This neural arch is covered by an iron patina and lacks both prezygapophyses (Fig. 3.1–3.4). The neural spine and the left transverse process are badly damaged, with only their bases preserved. The right transverse process is laterally projected and horizontal but slightly inclined anteriorly, forming an angle of less than 20° relative to the horizontal plane (Fig. 3.1–3.4). It measures 46 mm in length and is developed in the anterior half

Figure 3. cf. ***Arcovenator*** axial elements from Laño. Anterior dorsal vertebra (**MCNA** 8366) in **1**, posterior; **2**, lateral; **3**, anterior; and **4**; dorsal views. Caudal vertebra (**MCNA** 17433) in **5**, ventral; **6**, anterior; **7**, lateral; and **8**, posterior views. Abbreviations: **cdl**, centrodiapophyseal lamina; **fch**, facet for chevron; **ns**, neural spine; **poz**, postzygapophysis; **tp**, transverse process; **vg**, ventral groove. Scale bar equals 5 cm.

of the vertebra. In dorsal view, the right transverse process expands anteroposteriorly towards the diapophysis, making it fan-shaped in this view (Fig. 3.4). The posterior edge of the transverse process is straight, and its anterior margin is convex. In lateral view, the diapophysis is D-shaped and faces ventrolaterally (Fig. 3.2). The base of the neural spine is mediolaterally narrow anteriorly and broadens posteriorly. It extends posteriorly beyond the bases of the prezygapophyses, almost reaching the posterior margin of the postzygapophyses (Fig. 3.4). The postzygapophyses face ventrolaterally, are subcircular in outline, and appear to overhang the centrum (Fig. 3.1 and 3.2). The presence or absence of a hyposphyene-hypantrum articulation cannot be determined (Fig. 3.1).

Caudal vertebrae (Fig. 3.5–3.8). MCNA 17433 consists of the centrum and the base of the neural arch of an anterior to middle caudal vertebra (posterior to C5 due to its straighter anterior and posterior margins, based on Méndez, 2014), which are slightly mediolaterally compressed due to deformation (Fig. 3.5–3.8). The centrum and neural arch are almost fully fused, with the suture line being almost indiscernible (Fig. 3.7). The centrum is amphicoelous, spool-shaped, and slightly elongated (Fig. 3.5–3.8). MCNA 17433 measures 79 mm in anteroposterior length. Its anterior articular surface is 57 mm in height and 46 mm in width, while the posterior articular surface is 64 mm in height and 46 mm in width. Both the anterior and posterior articular surfaces are elliptical (Fig. 3.6 and 3.8). In lateral view, the anterior and posterior surfaces are straight, and the ventral margin is concave (Fig. 3.7). The centrum is medially compressed and exhibits relatively shallow pleurocentral depressions. However, the base of the neural arch is wider than the mid-centrum. The ventral surface of the centrum features an anteroposterior longitudinal groove, which is laterally delimited by a ridge on each side (Fig. 3.5). In the same view, the posterior end of the centrum exhibits quite prominent facets for articulation with the haemal arches, making the posterior end of the centrum more ventrally projected (Fig. 3.5).

The preserved portion of the neural arch includes the bases of the transverse processes (Fig. 3.5 and 3.7), which are centrally located and ventrally positioned in the neural arch. These processes are relatively thin and sheet-like and the preserved parts taper laterally. The ventral surface of the left transverse process exhibits a possible broad but not very protruding centrodiapophyseal lamina (Fig. 3.5 and 3.7).

***Arcovenator* sp.**

Figure 4

Referred material. CH 168, one isolated lateral tooth.

Geographic occurrence. Chera, Valencia, Spain.

Stratigraphic occurrence. Sierra Perenchiza Formation; upper Campanian (Company, 2005; Company *et al.*, 2005).

Description. CH 168 preserves the crown and part of the root. It is interpreted as a lateral tooth based on its symmetrical cross-section outline and low CBR value (see Hendrickx *et al.*, 2015b, 2019, 2020). The base of the crown is distally damaged, and fractures are present throughout the crown (Fig. 4). Parts of the carinae are also missing. An apically located elliptical wear facet is present on the labial surface (Fig. 4.5). The crown is ziphodont, labiolingually compressed, and distally curved. The apex extends slightly beyond the basodistalmost point of the crown (Fig. 4). In lateral view, the mesial margin is convex, while the distal margin is concave apically, becoming straighter toward the base (Fig. 4.3 and 4.5). In distal view, the lingual surface is straight basally and convex apically whereas the labial margin is convex basally and becomes straighter apically (Fig. 4.4). Both labial and lingual surfaces are convex, with no concave surfaces adjacent to any carinae. The lingual margin becomes more planar near the base of the distal carina. The basal cross-section of the crown is oval to lanceolate (Fig. 4.6), and the mid cross-section is lenticular. The cross-section of the root is more oval, with no basal constriction between the root and the crown.

The CBL measures 15.47 mm, whereas the CBW measures 9.88 mm, resulting in a CBR of 0.64. The CH is 30.02 mm, being the CHR of 1.94. The AL measures 33.52 mm.

Both mesial and distal carinae are denticulated (Fig. 4.1 and 4.8). The mesial carina is straight, centered apically, and mesiolingually displaced toward the base of the crown. The mesial carina does not reach the cervix but extends from the apex to approximately two-thirds of the crown (Fig. 4.2). The distal carina reaches the cervix, and it is sigmoidal in distal view and labially deflected (Fig. 4.4).

The denticles are largest at mid-crown on the mesial carina and gradually decrease in size basally (Fig. 4.2, 4.3,

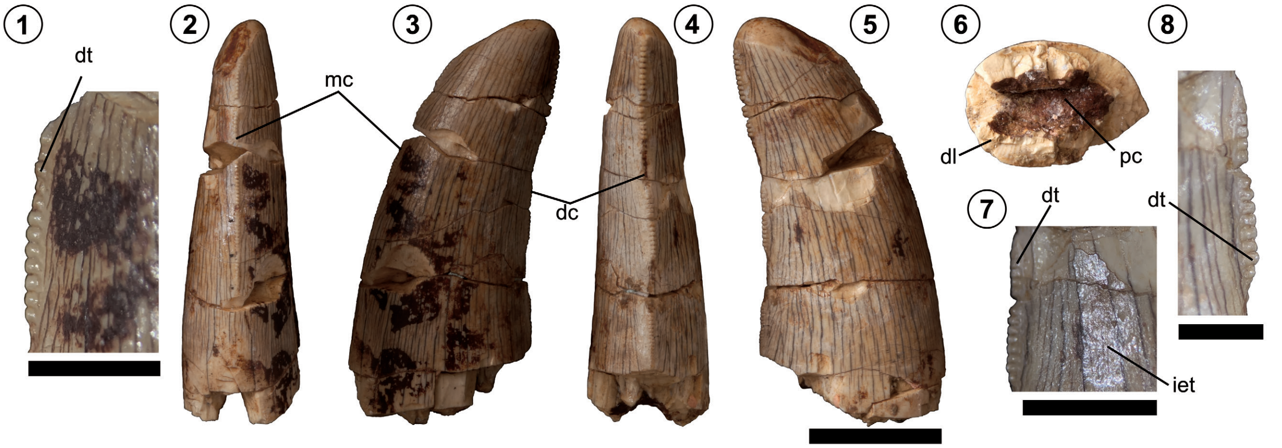

Figure 4. ***Arcovenator*** sp. tooth from Chera 2 (**CH** 168). **1**, mesial denticles; crown in **2**, mesial; **3**, lingual; **4**, distal; **5**, labial; and **6**, basal views. 7, close up of enamel texture; and **8**, distal denticles. Abbreviations: **dt**, denticle; **mc**, mesial carina; **dc**, distal carina; **dl**, dentine layer; **iet**, irregular enamel texture; **pc**, pulp cavity. Scale bar equals 1 cm, except for denticles and texture (1, 7 and 8) (5 mm).

and 4.5). The wear facet prevents determining whether there was a denticle-size discrepancy apically. Nevertheless, the distal denticles are larger apically (Fig. 4.3–4.5). There is no random variation in denticle size along the carinae. The denticles are almost equal in size or slightly larger on the mesial carina, with a DSDI value of 1. The mesial denticle density is 15 denticles per five millimeters, whereas the distal denticle density is 12 denticles per five millimeters apically, 15 denticles per five millimeters at mid-crown, and 17 denticles per five millimeters at the base. The outline of the denticles is symmetrically to slightly asymmetrically convex and perpendicular to the carinae (Fig. 4.1 and 4.8). The mesial denticles are mainly subquadrangular but become slightly apicobasally subrectangular apically (Fig. 4.1). The distal denticles, on the other hand, are mesiodistally subrectangular at mid-crown and basally, but almost subrectangular apically (Fig. 4.8). Subtle interdenticular sulci are present on both carinae. These are short, straight, and basally inclined.

A few transverse undulations are present on the crown, but they are particularly subtle. Subtle marginal undulations are similarly present on the labial surface of the crown, close to the distal carina. The enamel texture is non-oriented and irregular (Fig. 4.7).

RESULTS

Morphometric analyses

The discriminant analyses exhibit similar variance in their axes (Figs. 5 and 6). Axis 1 accounts for 42.45–55.62% of the total variance, while Axis 2 explains 20.54–30.06%. The reclassification rates obtained in the LDAs are relatively high, ranging from 63.42 to 75.85%, and are significantly higher using the clade-level databases (see Supplementary Online Information 1).

The classification of the specimens studied herein within Theropoda varies depending on the database and the linear discriminant analysis (Tab. 1). In LDA 1 (clade level, database 1), the tooth from Viso (MG 73) is classified as Abelisauridae (Jackknifed), the tooth from Chera 2 (CH 168) as a non-abelisauroid ceratosaurian (Jackknifed), and the Montrebei tooth (DPM-MON-T10 1) as Carcharodontosauridae (classification and Jackknifed). In LDA 2 (taxon level, database 1), MG 73 is classified as *Carnotaurus* (classification and Jackknifed), CH 168 as *Gorgosaurus* (Jackknifed), and DPM-MON-T10 1 as *Acrocanthosaurus* (classification and Jackknifed). In LDA 3 (clade level, database 2), MG 73 is classified as a megaraptoran (Jackknifed), CH 168 as a tyrannosaurid (classification and Jackknifed), and DPM-MON-T10 1 as a megaraptoran (Jackknifed). In LDA 4 (taxon level, database 2), MG 73 is again classified as *Carnotaurus* (classification and Jackknifed), CH 168 as *Gorgosaurus* (Jackknifed), and DPM-MON-T10 1 as *Aucasaurus* (classification and Jackknifed). Finally, the discriminant analysis performed using the Ibero-Armorican abelisaurid dental record (database 3) classifies MG 73 as *Arcovenator* (Jas Neuf Sud) (classification and Jackknifed), CH

168 as the indeterminate abelisaurid teeth from Poyos, which are closely related to *Arcovenator* (Jackknifed), and DPM-MON-T10 1 as Abelisauridae indet. 1 from the Western Tremp Syncline (Jackknifed) (Tab. 1).

Cladistic analyses

The cladistic analysis performed on the data matrix, including MG 73 and using a constrained tree topology, recovered a single most parsimonious tree (CI = 0.200;

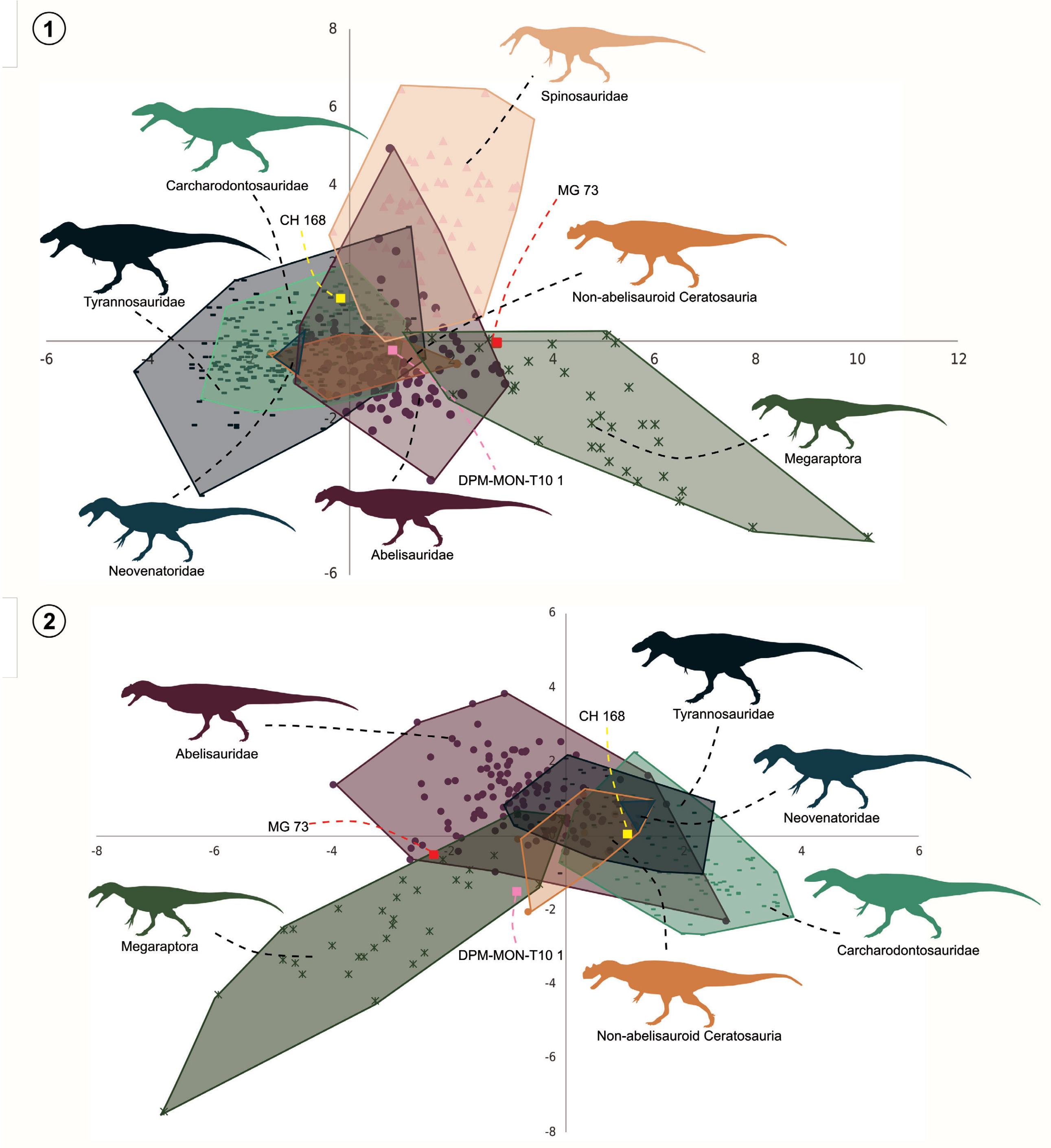

Figure 5. Graphical results of the LDAs (LDA 1 and 3) carried out at the clade-level. **1**, LDA performed using database 1 at clade-level. Axis 1 accounts for 47.67 % of the variance (Eigenvalue = 2.6735), and Axis 2 accounts for 24.67 % of the variation (Eigenvalue = 1.3703). **2**, LDA performed using database 2 at the clade-level. Axis 1 accounts for 55.62 % of the variance (Eigenvalue = 2.6056), and Axis 2 for 30.06 % of the variation (Eigenvalue = 1.4081). Silhouettes courtesy of Scott Hartman.

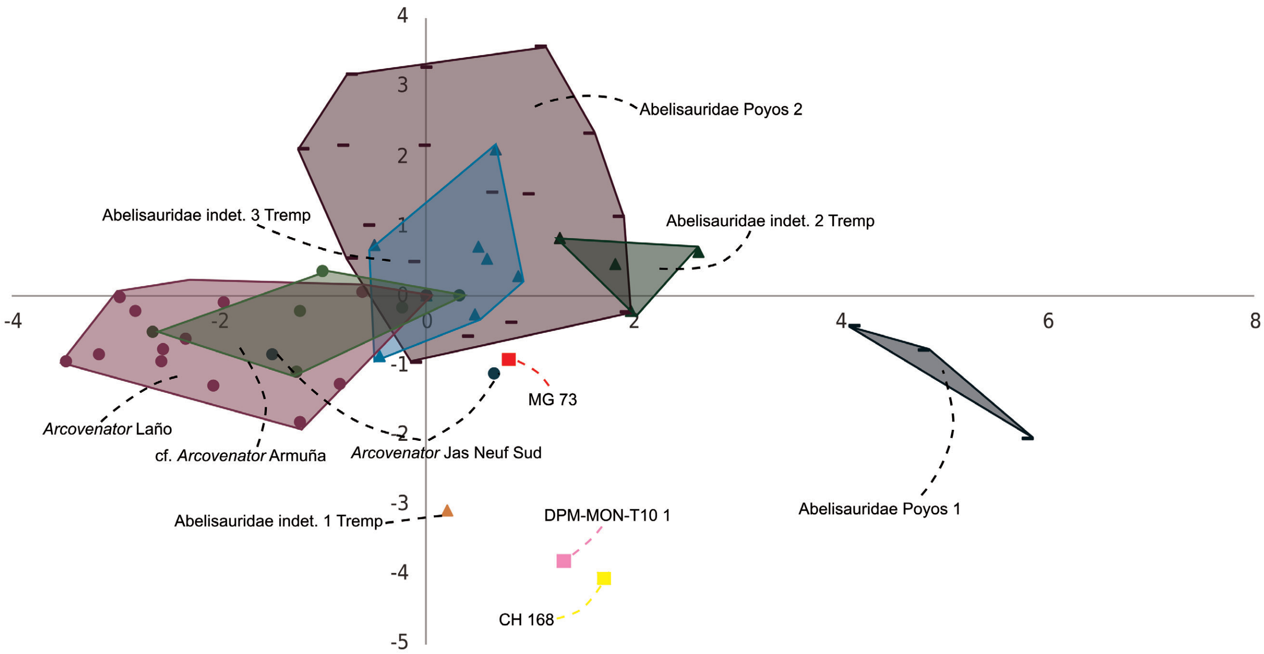

Figure 6. Graphical results of the LDA performed with the Ibero-Armorican abelisaurid teeth (database 3). Axis 1 accounts for 49.29 % of the variance (Eigenvalue = 2.8359), and Axis 2 for 26.72 % of the variation (Eigenvalue = 1.5371).

TABLE 1. Results of the discriminant analyses performed with databases 1, 2, and 3. Databases in Supplementary Online Information 1.

	LDA 1 (clade)		LDA 2 (taxa)		LDA 3 (clade)		LDA 4 (taxa)		LDA 5 (Ibero-Armorica)	
	Classification	Jackknifed	Classification	Jackknifed	Classification	Jackknifed	Classification	Jackknifed	Classification	Jackknifed
MG 73		Abelisauridae	*Carnotaurus*	*Carnotaurus*		Megaraptora	*Carnotaurus*	*Carnotaurus*	*Arcovenator* Jas Neuf Sud	*Arcovenator* Jas Neuf Sud
CH 168		Non-abelisauroid Ceratosauria		*Gorgosaurus*	Tyrannosauridae	Tyrannosauridae		*Gorgosaurus*		Abelisauridae indet. closely related to *Arcovenator* Poyos. Morphotype 1
DPM-MON-T10 1	Carcharodontosauridae	Carcharodontosauriae	*Acrocanthosaurus*	*Acrocanthosaurus*		Megaraptora	*Aucasaurus*	*Aucasaurus*		Abelisauridae indet. 1 Western Tremp Syncline

RI = 0.457; L = 1304). MG 73 is grouped with noasaurids within a well-resolved Abelisauroidea clade (Fig. 7.1). The specimen from Viso shares with other abelisauroids the spacing between mid-crown denticles on the distal carina, which is less than one-third of the denticle width (state 0; character 107), and the presence of a smooth or irregular (non-oriented) enamel-texture (state 0; character 121). The only synapomorphy found for Noasauridae that can be verified in MG 73 is the average number of mid-crown denticles per five millimeters on the distal carina (character 89), which ranges between 16 and 29 (state 1), whereas in abelisaurids it is usually lower, between 9 and 15 (state 2). Within Noasauridae, the specimen from Viso is positioned as the sister taxon to *Masiakasaurus*, based on the presence of tenuous transverse undulations on the crown (state 1; character 113). Forcing the specimen from Viso into the

Abelisauridae clade recovered three most parsimonious trees, with the consensus tree (CI = 0.199; RI = 0.451) being four steps longer (L =1311) than that obtained when treating the specimens as a floating taxon. Interestingly, constraining MG 73 within the group comprising *Arcovenator*, *Majungasaurus*, and *Indosuchus* yielded a single most parsimonious tree (CI = 0.200; RI = 0.453) and did not require additional steps (L = 1307) relative to the analysis with the specimens as floating taxon. However, no synapomorphies were recovered for this group in the analysis.

The analysis performed for specimens CH 168 recovered five most parsimonious trees (CI = 0.200; RI = 0.453; L = 1307) and the consensus tree (CI = 0.199; RI = 0.452; L = 1309) places this specimen within Coelurosauria, allied with the tyrannosauroids *Gorgosaurus*, *Raptorex*, *Alioramus*, *Tyrannosaurus*, and *Daspletosaurus* (Fig. 7.2). The analysis found the following tyrannosauroid synapomorphies present in the Chera 2 specimen: (i) crown height between 1 and 6 cm (state 1; character 69); (ii) the denticles on the mesial carina at two-thirds height of the crown have a subquadrangular shape (state 1; character 95); and (iii) mesial and distal denticles of similar size (0.8 < DSDI < 1.2) (state 0; character 105). However, all these features are also shared with most abelisaurids (Hendrickx *et al.* 2020). Forcing the specimen from Chera into the Abelisauridae clade recovered three most parsimonious trees (CI = 0.199; RI = 0.451; L = 1310), with the consensus tree (CI = 0.199; RI = 0.449) being five steps longer (L = 1314) than that obtained when treating the specimens as a floating taxon. This analysis recovered the following abelisaurid synapomorphies present in CH 168: (i) subquadrangular shape of denticles at two-thirds height of the crown on mesial carina in lateral view (state 1; character 95) and (ii) horizontal subrectangular shape of mid-crown denticle on distal carina in lateral view (state 1; character 96).

Finally, the analysis performed for DPM-MONT-T10 1 recovered seven most parsimonious trees (CI = 0.200; RI =

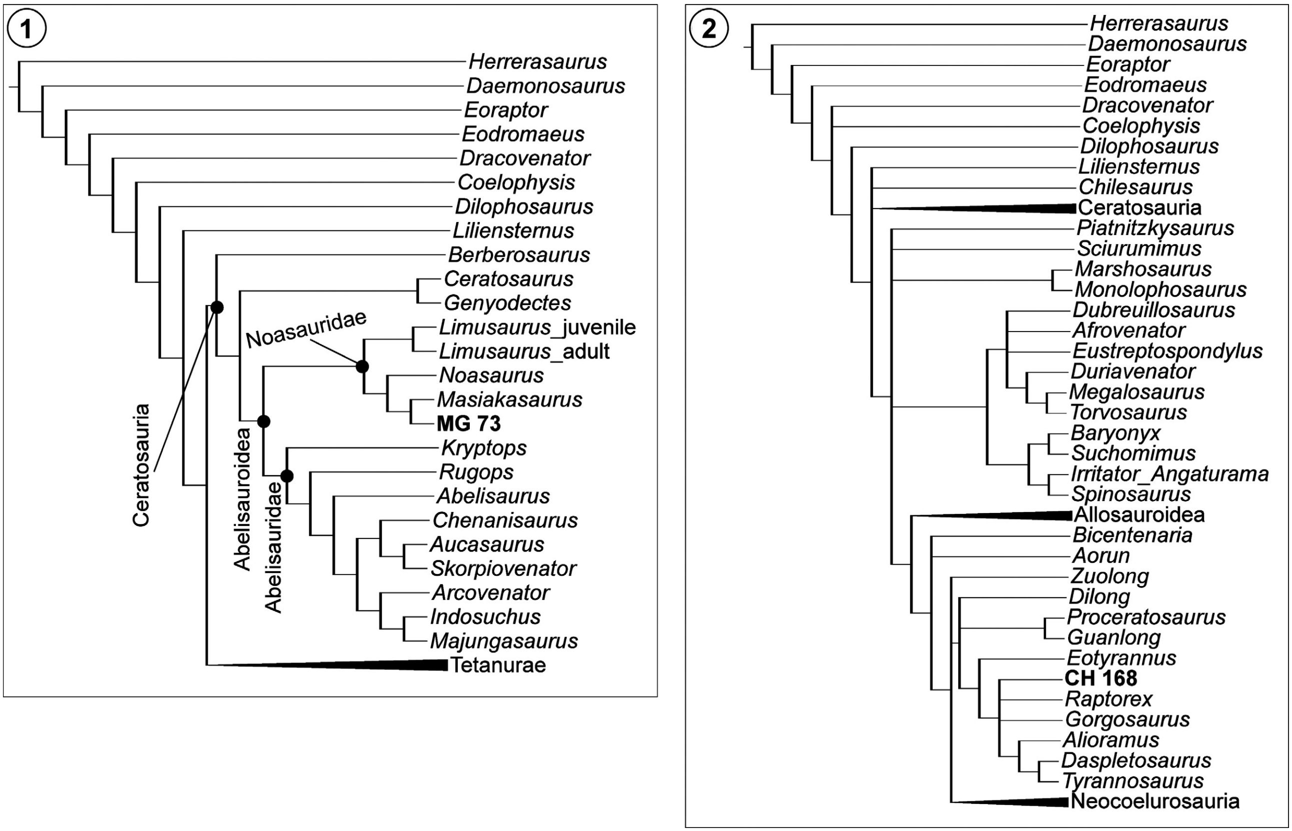

Figure 7. Results of the phylogenetic analyses performed for specimens **MG** 73 and **CH** 168 based on the dentition-based data matrix (constrained search) of Hendrickx *et al.* (2020). **1**, simplified single MPT (CI = 0.203; RI = 0.542) obtained from the phylogenetic analysis, showing the position of specimen **MG** 73 from Viso (highlighted in bold). **2**, simplified consensus tree (CI = 0.199; RI = 0,452) obtained from five MPTs recovered in the phylogenetic analysis, showing the position of specimen **CH** 168 from Chera 2 (highlighted in bold).

0.454; L = 1305; consensus tree CI = 0.180; RI = 0.376; L = 1454). The strict consensus tree shows a poor resolution, with most taxa placed in a large polytomy (Fig. 8). Only a few clades, such as Megalosauroidea, Abelisauridae, Allosauroidea, and some coelurosaurian groups, are better resolved. The most parsimonious trees from this analysis placed the specimen from Montrebei within the Paraves clade, sometimes allied with troodontids and other times with avialan taxa. Forcing the specimen into the Abelisauridae clade recovered a single most parsimonious tree (CI = 0.199; RI = 0.452) and required four additional steps (L = 1309) relative to the most parsimonious trees obtained when treating the specimens as a floating taxon. On the other hand, constraining its position within a group comprising *Arcovenator*, *Majungasaurus*, and *Indosuchus* also yielded a single most parsimonious tree (CI = 0.199; RI = 0.451) and required only one further step (L = 1310) compared to the previous analysis.

DISCUSSION

Comparisons and identification of the isolated teeth

Almost every morphometric analysis supports the attribution of the MG 73 specimen to Abelisauridae, as this tooth consistently grouped within Abelisauridae, *Arcovenator*, or *Carnotaurus* in the LDAs (Tab. 1). The classification of CH 168 and DPM-MON-T10 1 is more ambiguous, as neither was grouped within Abelisauridae in any of the first three LDAs performed. Indeed, the CH 168 specimen was classified as a tyrannosaurid, a non-abelisauroid ceratosaurian, or *Gorgosaurus*, while DPM-MON-T10 was grouped within Carcharodontosauridae, Megaraptora, or *Acrocanthosaurus*. Nevertheless, DPM-MON-T10 was also grouped with Abelisauridae indet. morphotype 1 from the Western Tremp Syncline or *Aucasaurus*. Therefore, the morphometric analyses also strongly suggest abelisaurid affinities for this specimen. Regarding the cladistic analyses, the results do not support direct attribution of the teeth to Abelisauridae. The Viso specimen was recovered within Abelisauroidea, but more closely related to Noasauridae. Nevertheless, forcing the specimen into Abelisauridae, in a group comprising *Arcovenator*, *Majungasaurus*, and *Indosuchus*, does not require any additional steps, suggesting that this hypothesis is as parsimonious as the position recovered in the

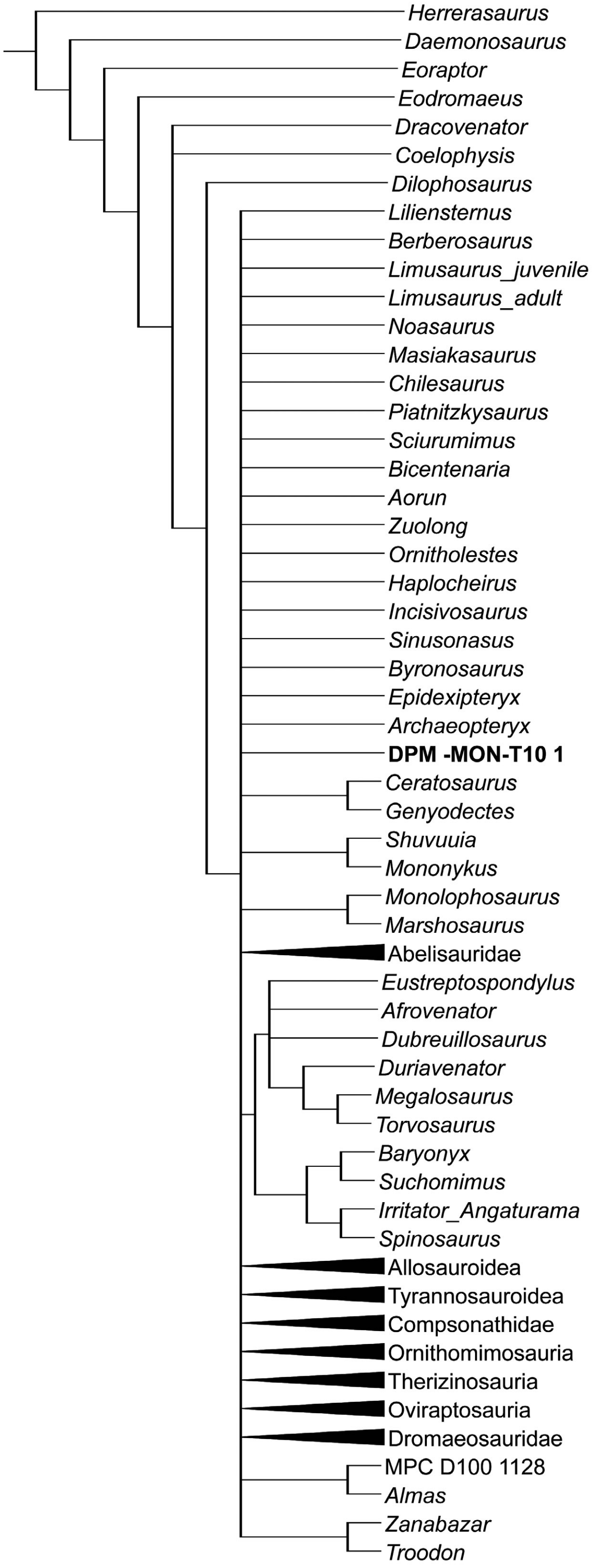

Figure 8. Simplified strict consensus tree (CI = 0.1809; RI = 0.376) obtained from seven MPTs recovered in the phylogenetic analysis based on the dentition-based data matrix (constrained search) of Hendrickx *et al.* (2020), showing the position of **DPM-MONT-T1** 1 from Montrebei (highlighted in bold).

unconstrained analysis. The Chera 2 specimen was allied with Tyrannosauroidea. However, all features found as synapomorphies for this clade are also shared with most abelisaurids. Forcing the specimen into Abelisauridae requires five additional steps compared to the length of the consensus tree recovered on the unconstrained analysis and one extra step to place it within the group comprising *Arcovenator*, *Majungasaurus*, and *Indosuchus*. The analysis performed for the Montrebei specimen yielded very poor resolution, with most taxa placed in a large polytomy. The most parsimonious trees placed the specimen within the Paraves clade and forcing its position into Abelisauridae required four additional steps. The lack of European abelisaurid dental and mandibular elements, along with the limited representation of European tooth data in the matrix, may account for the poor resolution of the cladistic analyses.

Abelisauridae indet.

Morphotype 1. The isolated tooth DPM-MON-T10 1 from Montrebei shares with Abelisauridae a ziphodont crown with a 'D'-shaped cross-section and the irregular, non-oriented enamel-texture (Hendrickx *et al.*, 2019, 2020). Therefore, this tooth can be confidently assigned to Abelisauridae, which is also supported by the results of some morphometric analyses, despite the cladistic analysis not yielding sufficient resolution to test this attribution. Furthermore, the distal position of the apex and the profile of the distal margin are similar to the condition found in the distal teeth of the mesial dentition in abelisaurids, with the crown being more distally recurved (Hendrickx *et al.*, 2020).

Despite most abelisaurid taxa exhibiting a salinon-to J-shaped basal cross-section, specimen DPM-MON-T10 1 has a 'D'-shaped cross-section, as observed in *Rahiolisaurus* and MPCN-PV 69 (Novas *et al.*, 2010; Gianechini *et al.*, 2015; Hendrickx *et al.*, 2020). The Montrebei tooth is particularly thick, a condition similarly present in the mesialmost teeth of several abelisaurid taxa such as *Chenanisaurus*, *Majungasaurus*, and *Rahiolisaurus* (Hendrickx *et al.*, 2020) but differing from the more labiolingually compressed mesial teeth of other abelisaurids such as the premaxillary teeth of *Majungasaurus* (see Hendrickx *et al.*, 2020). Although the crown lacks its cervical portion, it seems to have been weakly elongated, as in all known members of Abelisauridae (Hendrickx *et al.*, 2020).

The mesiolingually oriented mesial carina of the Montrebei specimen resembles that of the first premaxillary tooth of abelisaurids, as well as some teeth possibly belonging to *Abelisaurus* (MPCA 1, 5 and 267; see Hendrickx *et al.*, 2020), mesial abelisaurid crowns from the Western Tremp Syncline (Abelisauridae indet. 1) and Poyos (Abelisauridae indet. morphotype 1), along with the lateral teeth of *Arcovenator* and closely related specimens from Poyos (Hendrickx and Mateus, 2014; Tortosa *et al.*, 2014; Hendrickx *et al.*, 2020; Isasmendi *et al.*, 2022, 2024; Malafaia *et al.*, 2025). The strongly lingually deflected distal carina of DPM-MON-T10 is a feature shared with the mesial abelisaurid crown from the Western Tremp Syncline, the isolated mesial crown IIPG-09, and the lateral crowns of *Arcovenator* (Hendrickx *et al.*, 2020; Meso *et al.*, 2021; Isasmendi *et al.*, 2022, 2024). Two distinctive features of the Montrebei crown are the position of the apex, which apparently extended beyond its basodistalmost point, and its concave distal profile. These features resemble the condition seen in '*Indosuchus*' and differ from the mesial dentition of *Chenanisaurus*, *Majungasaurus*, *Skorpiovenator*, the mesial teeth closely related to *Arcovenator* from Poyos, and mesial teeth from the Allen Formation in Patagonia (Smith, 2007; Hendrickx *et al.*, 2020; Meso *et al.*, 2021; Malafaia *et al.*, 2025). However, the distal maxillary teeth of '*Indosuchus*' do not exhibit a distal profile as concave as that of the Montrebei specimen (see Hendrickx *et al.*, 2020, fig. 6f). Therefore, in light of these considerations, DPM-MON-T10 1 is here assigned to Abelisauridae indet.

Morphotype 2. The isolated tooth MG 73 from Viso shares a combination of features with other members of Abelisauridae, namely a ziphodont crown, a straight or gently convex distal profile, a lanceolate basal cross-section, denticulated mesial and distal carinae (with the distal carina reaching the cervix), presence of large number of small denticles in the distal carina (c. 20 denticles per five millimeters), sub-quadrangular distal denticles, narrow interdenticular space, and an irregular, non-oriented enamel texture (see Hendrickx *et al.*, 2020). Furthermore, the cladistic and morphometric analyses carried out herein further support its referral to Abelisauridae or, at least to Abelisauroidea.

An irregular enamel surface texture and the presence of transverse undulations are two dental features typically observed in Abelisauridae dentition (*e.g.*, Canale *et al.*, 2009; Longrich *et al.*, 2017; Hendrickx *et al.*, 2019, 2020; Meso *et al.*, 2021; Isasmendi *et al.*, 2022, 2024). Transverse undulations are also present in other Iberian abelisaurid teeth such as the three abelisaurid morphotypes from the latest Maastrichtian of the Western Tremp Syncline (South Pyrenean Basin) (Isasmendi *et al.*, 2024) and the teeth of *Arcovenator* from the upper Campanian of Armuña (UPUAM 14044) and Laño (Isasmendi *et al.*, 2022). Unlike MPZ 2004/8, MPZ 2017/804, and MPZ 2022/86 from the Maastrichtian of Western Tremp Syncline but similar to the lateral teeth of most Abelisauridae (Hendrickx *et al.*, 2020), concave surfaces adjacent to the carinae are absent in MG 73.

MG 73 shares a moderately compressed crown (CBR of 0.58) with *Abelisaurus*, *Arcovenator*, *Aucasaurus*, and *Majungasaurus* (Hendrickx *et al.*, 2020), as well as the Abelisauridae indet. morphotypes 1 and 3 from the Western Tremp Syncline (Isasmendi *et al.*, 2024) and many teeth from Poyos (Malafaia *et al.*, 2025).

Typically, the mesial and distal carinae in lateral abelisaurid crowns are centrally located on their respective mesial and distal margins (Hendrickx *et al.*, 2020). However, in the MG 73 specimen, the mesial carina is lingually positioned and straight, resembling the condition present in the teeth referred to *Arcovenator* or a closely related taxon from Jas Neuf Sud, Laño, and Poyos (Tortosa *et al.*, 2014; Hendrickx *et al.*, 2020; Isasmendi *et al.*, 2022; Malafaia *et al.*, 2025). The distal carina of MG 73 is centrally located, as in most abelisaurids (Hendrickx *et al.*, 2020), differing from the strongly deflected distal carinae of *Arcovenator* from Jas Neuf Sud, the largest teeth from Laño, and most of the Abelisauridae indet. lateral morphotypes from the Western Tremp Syncline (Tortosa *et al.*, 2014; Hendrickx *et al.*, 2020; Isasmendi *et al.*, 2022, 2024).

The distocentral denticle density of MG 73 is 20 denticles per five millimeters, which is slightly higher than the range typically found in most Abelisauridae taxa that have 9 to 15 denticles per five millimeters (Hendrickx *et al.*, 2020). The sub-quadrangular basal distal denticles of MG 73 are similar in shape to those located at mid-crown in *Abelisaurus*, *Kryptops*, *Rugops*, some *Aucasaurus*, and most *Majungasaurus*, differing from the denticle shape present in *Arcovenator*, some teeth of *Aucasaurus*, and a few crowns of *Majungasaurus* (Hendrickx *et al.*, 2020). Although many abelisaurids exhibit interdenticular sulci, MG 73 lacks them, similar to the condition present in the crowns of *Aucasaurus*, *Arcovenator*, *Rugops*, and UCPC 10, which either lack these sulci or have them restricted to the base of the distal denticles (Smith, 2007; Hendrickx *et al.*, 2020). Therefore, despite MG 73 exhibiting many abelisaurid traits, some features are distinct from any previously described member of Abelisauridae, and hence, this crown is regarded as Abelisauridae indet.

***Arcovenator* sp.**

The isolated tooth CH 168 from Chera 2 has traits present in abelisaurid teeth, including an irregular and non-oriented enamel texture, CHR and CBR values, denticle shape, denticle density, and the DSDI value (see Hendrickx *et al.*, 2020). Furthermore, one of the LDA classifies this specimen as *Arcovenator*. Nevertheless, the cladistic analyses do not clarify the phylogenetic affinities of the Chera 2 specimen. This tooth lacks some typical dental features found in most members of Abelisauridae (see Hendrickx *et al.*, 2020), such as a straight or gently convex distal profile, a mesial carina extending to the cervix, or the characteristic arrangement of the carinae. The CBR is moderate for a lateral tooth, a feature shared with *Aucasaurus*, *Carnotaurus*, *Majungasaurus*, some teeth assigned to *Arcovenator* sp. from Laño, and some teeth from Poyos (Hendrickx *et al.*, 2020; Isasmendi *et al.*, 2022; Malafaia *et al.*, 2025). Its CHR value is also moderate (1.94), similar to those of *Arcovenator*, *Chenanisaurus*, and some lateral teeth of *Majungasaurus*, among others (Hendrickx *et al.*, 2020). Comparable CHR values are also found in teeth assigned to *Arcovenator* sp. from Laño and in lateral teeth belonging to an abelisaurid closely related to *Arcovenator* from Poyos (Isasmendi *et al.*, 2022; Malafaia *et al.*, 2025). Furthermore, among abelisaurid teeth, only those referred to *Arcovenator* from Armuña, Jas Neuf Sud, and Laño, as well as those closely related to *Arcovenator* from Poyos, exhibit an apex that extends beyond the basodistalmost point of the crown (Tortosa *et al.*, 2014; Hendrickx *et al.*, 2020; Isasmendi *et al.*, 2022; Malafaia *et al.*, 2025; this study).

The lateral crowns of abelisaurid theropods typically have mesial and distal carinae that extend along the midline of the crown from the apex to the root (Hendrickx *et al.*, 2020), unlike the CH 168 tooth from Chera 2. Indeed, in this specimen, the mesial carina is straight, displaces mesiolingually toward the base, and extends from the apex to approximately two-thirds of the crown. On the other hand, the distal carina reaches the cervix but is sigmoidal and labially deflected. This condition more closely resembles that present in teeth referred to *Arcovenator* from the Jas Neuf Sud locality (Tortosa *et al.*, 2014; Hendrickx *et al.*, 2020), the largest teeth assigned to *Arcovenator* from Laño (Isasmendi *et al.*, 2022), and the morphotype 2 abelisaurid teeth from Poyos (Malafaia *et al.*, 2025).

Regarding the denticles, the DSDI value of the Chera 2 tooth is 1, similar to the teeth referred to *Arcovenator* from Jas Neuf Sud and Laño, as well as some specimens closely related to this taxon from Poyos, but differing from some *Arcovenator* teeth, in which the DSDI exceeds 1.2 (Hendrickx *et al.*, 2020; Isasmendi *et al.*, 2022; Malafaia *et al.*, 2025). The mesiocentral denticle density of CH 168 (MC of 15 denticles per five millimeters) is similar to the MC values of *Abelisaurus* and *Arcovenator*, while the distocentral denticle density of the specimen studied here (DC of 15 denticles per five millimeters) more closely resembles those of *Arcovenator* or *Aucasaurus*, whereas *Abelisaurus* teeth have lower DC values (Tortosa *et al.*, 2014; Hendrickx *et al.*, 2020).

The outline of the denticles in CH 168 is symmetrically to slightly asymmetrically convex as in *Arcovenator* teeth from Jas Neuf Sud and Laño, the teeth from Poyos, *Skorpiovenator*, and some abelisaurid teeth from the Cenomanian of northern Africa (Richet *et al.*, 2013; Hendrickx *et al.*, 2020; Isasmendi *et al.*, 2022; Malafaia *et al.*, 2025). The CH 168 tooth further resembles the teeth of *Arcovenator* in exhibiting subquadrangular or apicobasally subrectangular mesial denticles and mesiodistally subrectangular distal denticles (Hendrickx *et al.*, 2020; Isasmendi *et al.*, 2022; Malafaia *et al.*, 2025). Therefore, based on the results of the morphometric analyses and the morphological similarities of the CH 168 tooth with other *Arcovenator* teeth, this specimen is assigned to *Arcovenator* sp.

Postcranial remains

Despite their fragmentary nature, the Laño specimens exhibit several morphological features that support their attribution to Abelisauroidea. The presence in MCNA 17433 of a centrodiapophyseal lamina on the transverse processes of the anterior and middle caudal vertebrae allows it to be confidently referred to this clade (Méndez, 2014; Tortosa *et al.*, 2014), and Abelisauridae according to Baiano *et al.* (2023). In addition, the neural arch is also broader than the mid-centrum, which is a feature shared with *Masiakasaurus* and several abelisaurids (Baiano *et al.*, 2023). In addition, the elliptical shape of the articular surfaces of the caudal vertebra, the presence of a ventral longitudinal groove on the centrum, and the lateral orientation of the transverse process of the anterior dorsal and the anterior to middle caudal vertebra, and the fan-shaped morphology of the transverse processes of the anterior dorsal vertebra, allow these specimens to be referred to Majungasaurinae. Furthermore, since the presence of *Arcovenator* has previously been documented in Laño (Isasmendi *et al.*, 2022), these remains are assigned to cf. *Arcovenator* sp., pending the discovery of additional diagnostic material.

The horizontally projected transverse processes seen in MCNA 8366 are also present in the anterior dorsals of *Majungasaurus* and *Sinraptor* (Currie and Zhao, 1993; O'Connor, 2007) and differ from those of *Allosaurus* and *Sigilmassasaurus* (Madsen, 1976; Evers *et al.*, 2015), in which the transverse processes are more ventrally projected. Furthermore, the fan-shaped transverse processes, which are laterally projected in MCNA 8366, are also seen in the anteriormost dorsal of *Majungasaurus* and *Sigilmassasaurus* (O'Connor, 2007; Evers *et al.*, 2015). The morphology of the transverse process in the specimen from Laño, with an anterior convex and posterior straight edge that makes the diapophysis project face laterally, is similar to that of *Majungasaurus* (UA 8678; O'Connor, 2007, fig. 3), although in this taxon the anterior convex edge is less pronounced. The posterior straight edge of the transverse processes of MCNA 8366 differs from the concave edges and posterolaterally facing diapophysis exhibited by the anteriormost dorsals of, for instance, *Carnotaurus* (MACN-CH 894), *Eoabelisaurus* (MPEF PV 3990), *Viavenator* (MAU-Pv-LI-530; Filipi *et al.*, 2018, fig. 7D) and the indeterminate brachyrostran (MAU-Pv-LI-665; Méndez *et al.*, 2022, fig 6D). This indicates that this condition could be a majungasaurine synapomorphy. Nevertheless, this hypothesis needs to be phylogenetically tested.

The ventral surface of the MCNA 17433 caudal vertebra exhibits a ventral longitudinal groove, a feature also present in *Allosaurus*, *Arcovenator*, *Aucasaurus*, *Ceratosaurus*, *Majungasaurus*, and *Viavenator*, as well as in many spinosaurids and megalosaurids (*e.g.*, Madsen, 1976; Madsen and Welles, 2000; O'Connor, 2007; Benson, 2010; Méndez, 2014; Tortosa *et al.*, 2014; Filippi *et al.*, 2018; Malafaia *et al.*, 2020). This contrasts with some abelisaurids, such as *Ekrixinatosaurus* and *Rajasaurus*, which exhibit a keeled ventral surface (Méndez, 2014). The presence of a centrodiapophyseal lamina on the ventral surface of the preserved transverse processes is a feature shared with Abelisauridae (*e.g.*, *Arcovenator*, *Aucasaurus*, *Carnotaurus*, *Ekrixinatosaurus*, *Kurupi,* and *Majungasaurus*) and *Masiakasaurus*, but not with *Allosaurus* or *Ceratosaurus* (Carrano *et al.*, 2002; Coria *et al.*, 2002; Calvo *et al.*, 2004; O'Connor, 2007; Méndez, 2014; Tortosa *et al.*, 2014; Iori *et al.*, 2021; Baiano *et al.*, 2023). Nevertheless, despite deformation, the bases of the transverse processes in MCNA 17433 do not appear to be strongly dorsally directed. This differs from many abelisaurids such as *Aucasaurus*, *Carnotaurus*, *Ekrixinatosaurus,* and *Skorpiovenator*, and is more similar to the condition observed in *Allosaurus*, *Arcovenator*, *Ceratosaurus*, *Majungasaurus*, and *Rahiolisaurus* (Madsen, 1976; Madsen and Welles, 2000; O'Connor, 2007; Méndez, 2014; Baiano *et al.*, 2023). The anterior and posterior articular facets of the MCNA 17433 caudal vertebra are close to elliptical in outline (note that although the centrum appears strongly mediolaterally compressed, this is likely a taphonomic artifact). This shape is more similar to that observed in *Arcovenator*, *Majungasaurus*, *Rajasaurus*, and *Sinraptor*, and differs from the more subcircular surfaces of, for instance, *Allosaurus*, *Aucasaurus*, *Carnotaurus*, *Ekrixinatosaurus*, *Ichthyovenator*, *Kurupi*, *Tyrannosaurus* or *Viavenator* (Currie and Zhao, 1993; Brochu, 2003; Wilson *et al.*, 2003; O'Connor, 2007; Allain *et al.*, 2012; Méndez, 2014; Tortosa *et al.*, 2014; Filippi *et al.*, 2018; Iori *et al.*, 2021; Baiano *et al.*, 2023).

New contributions to the knowledge of European abelisaurids

In the Late Cretaceous European archipelago, skeletal remains of mid- to large-bodied theropods have been recovered in Central and Western Europe (*e.g.*, Ősi *et al.*, 2010; Ősi and Buffetaut, 2011; Tortosa *et al.*, 2014; Isasmendi *et al.*, 2022; Buffetaut *et al.*, 2024). Among these remains, indeterminate tetanurans and abelisaurids have been identified. In the central European region, specifically at the Santonian site of Iharkút in Hungary and the Campanian site of Styria in Austria, teeth assigned to early-branching indeterminate tetanurans have been recovered (Ősi *et al.*, 2010, 2012). Additionally, the Iharkút site has yielded further theropod remains referred to Abelisauridae (Ősi *et al.*, 2010; Ősi and Buffetaut, 2011), indicating that two mid- to large-sized theropod clades coexisted in Central Europe during the Santonian. However, the scarce theropod remains in this area make it challenging, at this moment, to provide a more accurate interpretation of the phylogenetic relationships of this fauna. Western Europe, on the other hand, appears to lack mid- to large-bodied early-branching tetanurans, with Abelisauridae representing the main apex predator (*e.g.*, Csiki-Sava *et al.*, 2015; Isasmendi *et al.*, 2022; Buffetaut *et al.*, 2024; Malafaia *et al.*, 2025).

Abelisaurid theropods have historically been interpreted as biogeographical indicators of Gondwanan affinities within Late Cretaceous European dinosaur assemblages (Buffetaut *et al.*, 1988; Le Loeuff and Buffetaut, 1991; Csiki-Sava *et al.*, 2015). Current evidence supports the persistence of multiple abelisauroid lineages within the European archipelago up to the latest Cretaceous (Carrano and Sampson, 2008; Tortosa *et al.*, 2014; Buffetaut *et al.*, 2024; Buffetaut, 2025). Based on the French fossil record, Tortosa *et al.* (2014) proposed that small-bodied abelisaurids likely originated from an Albian lineage of early-branching abelisaurids represented by *Genusaurus sisteronis* from Provence, which subsequently diversified into distinct lineages. It should be noted that this taxon has, however, been variably interpreted as a noasaurid (*e.g.*, Carrano and Sampson, 2008), an early-branching abelisaurid (*e.g.*, Tortosa *et al.*, 2014; Baiano *et al.*, 2023), or an abelisaurid more closely related to Furileusauria (Buffetaut *et al.*, 2024; Buffetaut, 2025).

The Cenomanian fossil record of Ibero-Armorica is scarce and currently consists of the considerably incomplete *Caletodraco cottardi* from the early Cenomanian glauconitic Chalk of Normandy (Buffetaut *et al.*, 2024) (Fig. 9, loc. 1). This taxon, which is known from ilia, some axial elements and a possible tooth, was interpreted as a furileusaurian brachyrostran, potentially reflecting a more intricate evolutionary history of European abelisaurids, with the presence of different abelisaurid lineages in Ibero-Armorica (Buffetaut, 2024; Buffetaut *et al.*, 2024; Malafaia *et al.*, 2025). Other Cenomanian abelisaurid remains from France and Spain include isolated teeth from Algora (Segovia, Spain), "La Buzinie" (Charentes, France), and Limanes (Asturias, Spain). The isolated theropod teeth from Algora (Utrillas Formation) (Fig. 9, loc. 4) were initially referred to Carcharodontosauridae indet. (Torices *et al.*, 2012) before being reassigned to cf. Abelisauridae by Pérez-García *et al.* (2020). Additionally, a medium- to large-sized caudal vertebra (ALG 192) from the same site was attributed to Theropoda indet. (Pérez-García *et al.*, 2020). Two other isolated teeth (MA BZN 1 and 2) from the "La Buzinie" locality (Fig. 9, loc. 2) were similarly assigned to Carcharodontosauridae by Vullo *et al.* (2007) before being reassigned to cf. Abelisauridae indet. by Malafaia *et al.* (2025), based on their crown ornamentation and denticle densities. Another isolated tooth from the Cenomanian La Manjoya Formation in the Limanes municipality (Fig. 9, loc. 3) was also identified as Theropoda indet. closely related to Carcharodontosauridae (Ruiz-Omeñaca *et al.*, 2009). Malafaia *et al.* (2025) agreed on the morphometric affinities suggested by Pérez-García *et al.* (2020) for the teeth from Algora, Charentes, and Limanes. The Limanes tooth belongs to a mid-sized theropod. The apex of the crown does not seem to have extended beyond its basodistalmost point (Ruiz-Omeñaca *et al.*, 2009, fig. 2a, b), both mesial and distal margins are convex in lateral view (Ruiz-Omeñaca *et al.*, 2009), the distal denticles are asymmetrically convex and apically inclined, and the enamel exhibits an irregular texture, all features present in Abelisauridae but absent in Carcharodontosauridae (Hendrickx *et al.*, 2019, 2020). The mesial carina is mesiolingually oriented (Ruiz-Omeñaca *et al.*, 2009, fig. 2c), being straight and centered apically but displaced lingually to the base, as in the first premaxillary tooth of Abelisauridae, some teeth that may belong to *Abelisaurus* (MPCA 1, 5, and 267; see Hendrickx *et al.*, 2020), Abelisauridae indet. morphotype 1 tooth from the Western Tremp Syncline and Poyos, as well as in the lateral teeth of *Arcovenator* and closely related specimens from Poyos (Hendrickx and Mateus, 2014; Tortosa *et al.*, 2014; Hendrickx *et al.*, 2020; Isasmendi *et al.*, 2022, 2024; Malafaia *et al.*, 2025). Ruiz-Omeñaca *et al.* (2009) indicate a mesial denticle density of 2 denticles/mm and a distal denticle density of 2.22 denticle/mm (giving a DSDI value of 0.9). However, these measurements were taken from different positions along the crown, which compromises their comparability. The inferred MA is 14 denticles per five mm, and the DA is 12.5 denticles per five mm. Furthermore, an accurate DSDI value cannot be calculated because the distal carina is not preserved at mid-crown. Therefore, based on the combination of features shared with Abelisauridae, this tooth is here regarded as Abelisauridae indet. These findings suggest that carcharodontosaurians were already extinct in Ibero-Armorica by the Cenomanian and that abelisaurids had become the apex theropods in those ecosystems.

No abelisaurid or large-sized theropod remains that may belong to Abelisauridae have been recovered to date from the Turonian, Coniacian, or Santonian of the Ibero-Armorican landmass. In the Campanian–Maatrichtian Viso locality (Beira Litoral, Portugal) (Fig. 9, loc. 5), several theropod remains were reported and figured by Antunes and Sigogneau-Russell (1992) and Galton (1996). Among the Viso theropod material, tooth VI 1 (Antunes and Sigogneau-Russell, 1992; pl. I, fig. 5) was initially referred to as Theropoda indet. However, due to its considerable size, it may be attributable to Abelisauridae, as the herein studied tooth from Viso (MG 73). The MG 73 specimen had previously been identified as *Megalosaurus* sp. (Sauvage, 1897,1898), *Megalosaurus* cf. *pannoniensis* (Lapparent and Zbyszewski, 1957), and Theropoda indet. (Malafaia *et al.*, 2024). Nonetheless, the morphological characteristics exhibited by this specimen warrant its reassignment to Abelisauridae indet., representing the first unequivocal abelisaurid remains from the Cretaceous of Portugal.

Theropod remains are relatively rare in lower Campanian deposits of Ibero-Armorica. At the Lambeau du Beausset locality in Var (France) (Fig. 9, loc. 6), the abelisaurid *Tarascosaurus* was erected based on fragmentary material (Le Loeuff and Buffetaut, 1991). This taxon has since been regarded as *nomen dubium* (Rauhut, 2003; Allain and Pereda-Suberbiola, 2003) or referred to Abelisauroidea *incertae sedis* (Carrano and Sampson, 2008). Nevertheless, it was recovered as an early-branching member of Abelisauridae in the phylogenetic analyses performed by Tortosa *et al.* (2014). Additional material from the Iberian Peninsula, specifically femora from the Laño site (Fig. 9, loc.

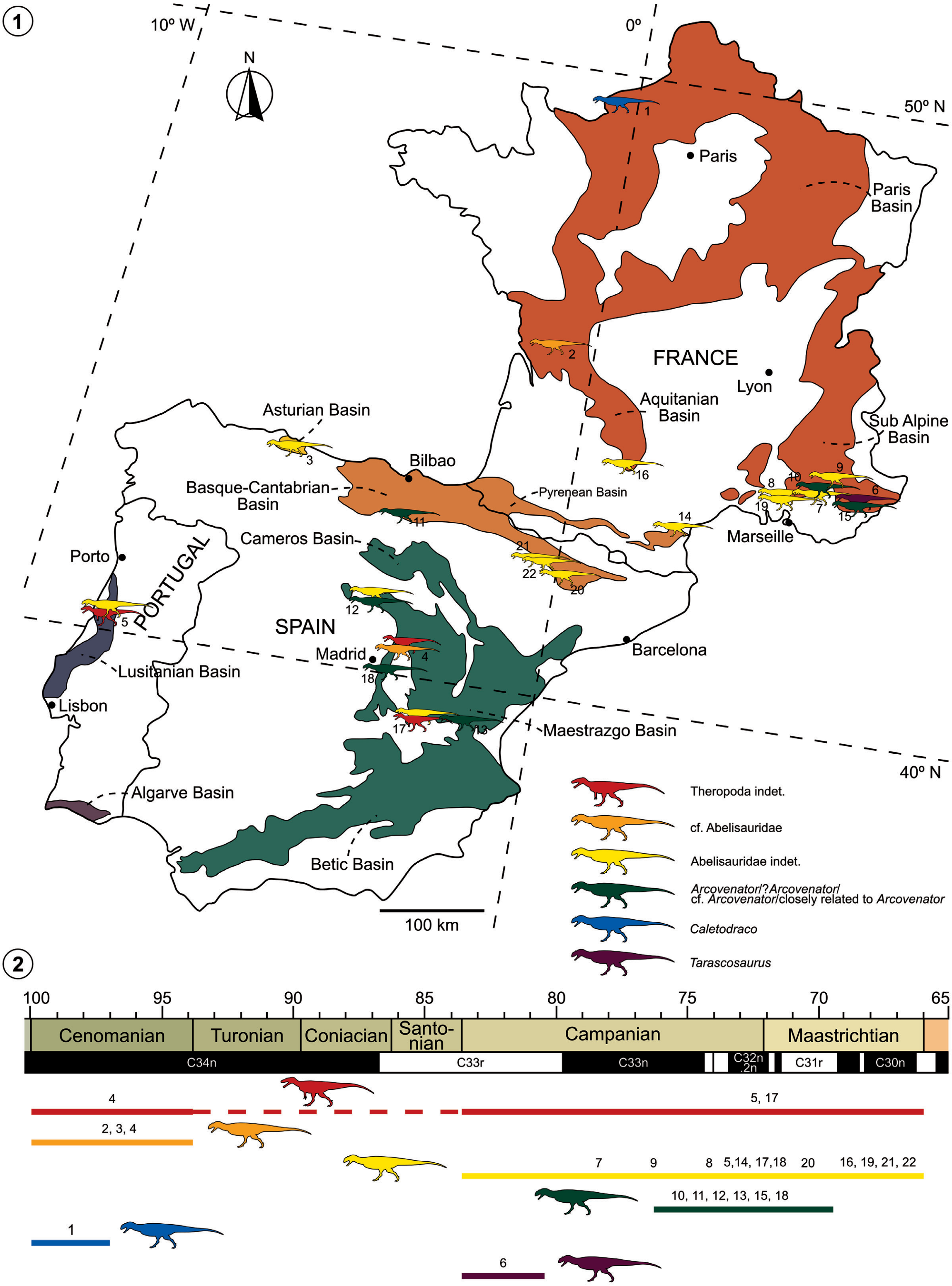

Figure 9. Paleogeographic and temporal distribution of the currently known Ibero-Armorican abelisaurids and large-sized theropod remains that likely belong to Abelisauridae. **1**, map of the Ibero-Armorican Mesozoic basins (modified from Buffetaut *et al.*, 2024; Malafaia *et al.*, 2025) showing the location where Late Cretaceous Ibero-Armorican abelisaurid or large-sized theropod remains have been recovered. **2**, chronological distribution of the Late Cretaceous abelisaurids or large-sized theropods that may be identified as Abelisauridae (modified from Tortosa *et al.*, 2014). Abelisaurid- or large-size theropod-bearing sites or areas: 1, Saint-Jouin-Bruneval; 2, "La Buzinie"; 3, Limanes; 4, Algora; 5, Viso; 6, Lambeau du Beausset; 7, Trets-La Boucharde; 8, Velaux-La Bastide Neuve; 9, Fox-Amphoux; 10, Pourrières-Jas Neuf Sud; 11, Laño; 12, Armuña; 13, Chera 2; 14, Cruzy; 15, Pourcieux-Les Tuillières; 16, Cassagnau 1; 17, Lo Hueco; 18, Poyos; 19, Vitrolles-La Plaine; 20, Montrebei; 21, Blasi; 22, 172-i/04/e.

11), has been compared to *Tarascosaurus* (Le Loeuff and Buffetaut, 1991; Le Loeuff, 1992), but no definitive evidence currently supports this attribution (Isasmendi *et al.*, 2021, 2022; Malafaia *et al.*, 2025).

The middle and upper Campanian abelisaurid record in France and Spain is comparatively richer. In Provence, indeterminate abelisaurid remains have been reported from the Trets-La Boucharde site (Fig. 9, loc. 7), Velaux-Bastide Neuve (Fig. 9, loc. 8), and the Fox-Amphoux area (Fig. 9, loc. 9) (Tortosa *et al.*, 2014). The Trets-La Boucharde specimen from the "Begudian fluvio-lacustrine sandstones" was previously described as an abelisauroid (Allain and Pereda-Suberbiola, 2003), and it is currently regarded as an indeterminate abelisaurid by various authors (Carrano and Sampson, 2008; Tortosa *et al.*, 2014). The abelisaurid remains reported by Tortosa *et al.* (2014) from Velaux-Bastide Neuve ("Begudian sandstones"; Garcia *et al.*, 2010; Cincotta *et al.*, 2015) and the Fox-Amphoux area (middle–late Campanian to early Maastrichtian? "Grès à reptiles") comprise a set of isolated teeth that are yet to be published. *Arcovenator escotae* was erected based on a set of cranial, axial, and appendicular elements recovered from the upper Campanian Pourrières-Jas Neuf Sud locality (Fig. 9, loc. 10) of the lower "Argiles rutilantes" Formation (Tortosa *et al.*, 2014). This is the most complete European abelisaurid currently known and has been classified as a majungasaurine (Tortosa *et al.*, 2014). In addition to the holotype and several referred specimens reported by Tortosa *et al.* (2014), other skeletal elements from Upper Cretaceous deposits of France and the Iberian Peninsula have also been assigned to *Arcovenator* or closely related forms (Tortosa *et al.*, 2014; Pérez-García *et al.*, 2016; Isasmendi *et al.*, 2022; Malafaia *et al.*, 2025). This is the case of the late Campanian to early Maastrichtian Pourcieux specimen from the Les Tuillières site ("Rognacian" coarse sandstone) (Fig. 9, loc. 15) in Provence. This specimen was first regarded as Abelisauridae (Buffetaut *et al.*, 1998, Rauhut, 2003), and Abelisauridae indet. or Carcharodontosauridae (Carrano & Sampson, 2008), before Tortosa *et al.* (2014) referred it to ?*Arcovenator* sp. The coeval "Grès à reptiles" red beds of Cruzy in Languedoc (Fig. 9, loc. 14) has yielded several teeth as well as cranial and postcranial fragmentary remains, which may be attributable to medium- to large-sized abelisaurids (Buffetaut *et al.*, 1999; Buffetaut, 2005; Ősi and Buffetaut, 2011; Tortosa *et al.*, 2014), possibly related to *Arcovenator* (Tortosa *et al.*, 2014). In the Iberian Peninsula, isolated teeth from Laño (County of Treviño), Armuña (Segovia), Chera 2 (Valencia), and Poyos (Guadalajara) were assigned to *Arcovenator* or closely related forms (Pérez-García *et al.*, 2016; Isasmendi *et al.*, 2022; Malafaia *et al.*, 2025; this work). The largest set of isolated teeth assigned to *Arcovenator* sp. comes from the upper Campanian Sedano Formation of Laño (Fig. 9, loc. 11) (Isasmendi *et al.*, 2022), which has also yielded additional postcranial theropod remains. It must be noted that a dorsal neural arch previously assigned to *Rhabdodon* (Pereda-Suberbiola and Sanz, 1999) and the caudal vertebra herein described can be referred to cf. *Arcovenator*. The coeval Vegas de Matute Formation of Armuña (Fig. 9, loc. 12) and Sierra Perenchiza Formation of Chera 2 (Fig. 9, loc. 13) have also yielded several isolated teeth referred to cf. *Arcovenator* and *Arcovenator* sp., respectively (Pérez-García *et al.*, 2016; Company *et al.*, 2005; this work). It is worth noting that the isolated tooth was the subject of varying taxonomic interpretations, having been referred to Theropoda indet. (Company, 2005), ?Neoceratosauria indet. (Company *et al.*, 2009), and cf. *Arcovenator* (Isasmendi *et al.*, 2022). Additionally, the pedal ungual phalanges recovered from the Armuña site were initially assigned to Theropoda indet. (Pérez-García *et al.*, 2016) and later reinterpreted as Abelisauridae indet. (Isasmendi *et al.*, 2024). Two dental morphotypes from the late Campanian–early Maastrichtian Poyos site (Villalba de la Sierra Formation; Gil *et al.*, 2004; Ortega and Pérez-García, 2009) (Fig. 9, loc. 18) were described and referred to an abelisaurid closely related to *Arcovenator* by Malafaia *et al.* (2025). This site has additionally yielded non-dental theropod remains initially referred to Abelisauroidea indet. (Ortega *et al.*, 2019; Pérez-García *et al.*, 2019) and later to Abelisauridae indet. (Malafaia *et al.*, 2025), pending further detailed studies. Some theropod remains from the Lo Hueco site (Fig. 9, loc. 17) were regarded as Theropoda indet. whereas others were referred to Abelisauridae indet. (Ortega *et al.*, 2015, 2022).

The abelisaurid fossil record from the Maastrichtian is comparatively less abundant than that from the Campanian (Isasmendi *et al.*, 2024). The early Maastrichtian Montrebei site (La Posa Formation; 'Grey Garumnian' of the Tremp

Group; Fondevilla *et al.*, 2019) of the Tremp Syncline (Fig. 9, loc. 20) in Lleida (Iberian Peninsula) yielded an isolated tooth initially assigned to Theropoda indet. (Torices *et al.*, 2015), but its subsequent restudy has permitted its referral to Abelisauridae indet. In the western section of the Tremp Syncline, abelisaurid teeth were also reported from the late Maastrichtian Blasi 1, 2B and 3 (Fig. 9, loc. 21) and the latest Maastrichtian 172-i/04/e (Fig. 9, loc. 22) sites, located at the top of the Arén Sandstone and the lower part of the Tremp Group ("Grey Garumnian") (Canudo *et al.*, 2016; Puértolas-Pascual *et al.*, 2018; Isasmendi *et al.*, 2024). Several teeth from the Blasi sites, along with the specimen from 172-i/04/e, were previously referred to Theropoda indet. by Torices *et al.* (2015) and Puértolas-Pascual *et al.* (2018) and later assigned to three different Abelisauridae indet. morphotypes by Isasmendi *et al.* (2024). At the Cassagnau 1 locality (Fig. 9, loc. 16), situated within the late Maastrichtian Auzas Marls Formation in Haute-Garonne, an isolated tooth, originally referred to Theropoda indet. by Laurent (2003), was later reinterpreted as belonging to Abelisauridae by Csiki-Sava *et al.* (2015). In addition to isolated teeth, the Maastrichtian French deposits have yielded several indeterminate abelisaurid postcranial remains. These are the limb bones (femur and tibia) initially assigned to Neoceratosauria by Valentin *et al.* (2012), recovered at the Vitrolles-La Plaine site (Fig. 9, loc. 19) from the "Rognacian clays and mottled marls" deposits in Bouches-du-Rhône. This site has been dated as possibly late Maastrichtian (Valentin *et al.*, 2012) or also as late Campanian–early Maastrichtian (Fondevilla *et al.*, 2019).

Taken together, the abelisaurid fossil record across Ibero-Armorica reveals a complex and temporally extensive presence of this clade, spanning from the Albian to the latest Maastrichtian, with a roughly 10-million-year gap during the Turonian–Santonian without any abelisaurid fossil record. Despite their relatively fragmentary nature, these remains, ranging from isolated teeth to partial skeletons, provide compelling evidence for the persistence and diversification of abelisaurids within the European archipelago throughout the Late Cretaceous. The distribution of taxa such as *Genusaurus*, *Caletodraco*, *Arcovenator*, and additional indeterminate forms suggests multiple evolutionary lineages, potentially some of them stemming from an Albian stock and others likely representing subsequent dispersal events, undergoing insular diversification through the Late Cretaceous. Moreover, the taxonomic revisions of previously misassigned material emphasize the need for ongoing reevaluation of fragmentary theropod remains. Such efforts are crucial to refine our understanding of abelisaurid paleobiogeography and systematics in Europe.

CONCLUSIONS

The systematic, morphometric, and cladistic studies carried out with the tooth sample from late Campanian Chera 2 (Valencia), early Maastrichtian Montrebei (Lleida), and Campanian–Maastrichtian Viso (Beira Litoral) localities from the Iberian Peninsula have allowed us to reassign these elements to abelisaurids. Although incomplete, the Montrebei (DPM-MON-T10 1) and Viso (MG 73) specimens differ from the dentition of the already erected members of Abelisauridae. On the other hand, the crown shape, disposition of the carinae, and denticle shape exhibited by CH 168 tooth from Chera 2 are similar to those found in *Arcovenator* teeth. Hence, the Montrebei and Viso teeth are now considered to belong to Abelisauridae indet., while the Chera 2 specimen is attributed to *Arcovenator* sp. In addition, the postcranial remains (axial elements) recovered from the Laño site (County of Treviño) are here regarded as an abelisaurid, mainly based on the presence of a centrodiapophyseal lamina on the preserved transverse process in the caudal vertebra (MCNA 17433). In addition, the shape and orientation of the transverse processes of the dorsal and caudal vertebrae suggest majungasaurine affinities. Therefore, these features, together with the presence of *Arcovenator* teeth in the site, allow us to assign these elements to cf. *Arcovenator*. The revision of the Laño postcranial remains has allowed to refute earlier interpretations that assigned the anterior dorsal neural arch (MCNA 8366) to *Rhabdodon*. Furthermore, the Viso isolated tooth, now assigned to Abelisauridae indet., is the first unequivocal abelisaurid remains from Portugal.

The fossil record indicates that abelisaurids were among the most prevalent theropod groups in the Late Cretaceous faunas across the Ibero-Armorican landmasses. Indeed, the reclassification of mid- to large-sized isolated teeth from Ibero-Armorica as belonging to abelisaurids, rather than to carcharodontosaurids or closely related forms, indicates that carcharodontosaurians were likely extinct in Ibero-Armorica by the Cenomanian, and that abelisaurids had already taken over as the dominant large theropods in those ecosystems.

The abelisaurid fossil record from Ibero-Armorica reveals a complex and temporally extensive presence of this clade, spanning from the Albian to the latest Maastrichtian, with a significant gap of approximately 10 million years during the Turonian–Santonian, in which no abelisaurid fossils have been found yet. Despite the generally fragmentary nature of these remains, ranging from isolated teeth to partial skeletons, they provide strong evidence for the persistence and diversification of abelisaurids across the European archipelago. The distribution of taxa such as the noasaurid or possibly furileusaurian *Genusaurus*, the putative furileusaurian *Caletodraco*, the majungasaurine *Arcovenator*, and other indeterminate forms suggests the presence of multiple evolutionary lineages, some potentially originating from an Albian stock, while others might have resulted from several dispersal events, undergoing insular diversification throughout the Late Cretaceous. Additionally, the taxonomic revisions of previously misclassified material underscore the need to continuously reevaluate fragmentary theropod remains, thereby refining our understanding of abelisaurid paleobiogeography and systematics in Europe.

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