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The first record of Abelisauridae (Theropoda: Ceratosauria) from Uruguay (Late Jurassic, Tacuarembó Formation)

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ABSTRACT

An incomplete albeit well preserved tooth from the Late Jurassic Tacuarembó Formation (Uruguay) shows a character combination only found in abelisaurid theropods, i.e. irregular enamel, hooked distal denticles, interdenticular sulci, lanceolate cross-sectional shape, and straight distal border. Its referral to Abelisauridae was tested via a phylogenetic analysis, with the Uruguayan taxon deeply nested within the clade. This is the first record of abelisaurids in Uruguay and one of the few Jurassic records of the group worldwide. Abelisaurids occur together with ceratosaurids and megalosaurines in the Tacuarembó Formation, revealing a rich Late Jurassic theropod assemblage.

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Gondwana; Tooth; South America; theropod; abelisaurid

Introduction

The Jurassic record of South American theropods is scarce when compared with that of Cretaceous age (e.g. Bittencourt and Langer 2011; Novas et al. 2013), with only few taxa named so far. This includes, from the La Quinta Formation, Venezuela, the stem averostran *Tachiraptor admirabilis* (Langer et al., 2014), from the Cañadón Asfalto Formation, Argentina, the abelisaurid *Eoabelisaurus mefi* (Pol & Rauhut, 2012), the piatnitzkysaurids *Piatnitzkysaurus floresi* (Bonaparte, 1986) and *Condorraptor curru-mili* (Rauhut, 2005), the allosauroid *Asfaltovenator vialidadi* (Rauhut & Pol, 2019), the aberrant *Chilesaurus diegosuarezi* (not considered a theropod by Baron and Barrett 2017), from the Toqui Formation, Chile (Novas et al. 2015), and the tetanuran *Pandoravenator fernandezorum*, from the Cañadón Calcáreo Formation, Argentina (Rauhut and Pol 2017). The osteological record is complemented by fragmentary remains of a possible abelisaurid from the latter unit (Rauhut and Pol 2021), a possible carcharodontosaurian from the Sergi Formation (Bandeira et al. 2021), and a neotheropod from the Aliança Formation, Brazil (Oliveira et al. 2022).

Hence, the theropod record of the Tacuarembó Formation, although represented only by isolated teeth and tracks (Perea et al. 2003; Soto and Perea 2008; Mesa and Perea 2015), is relevant. Rigorous descriptions, supported by multivariate and cladistics analyses, recently allowed the recognition of Ceratosauridae and Megalosaurinae teeth in that geological unit (Soto et al. 2020a, 2020b). In this contribution, we apply the same methodology to assign a tooth fragment to Abelisauridae, which represents a third theropod taxon for the Jurassic of Uruguay, and discuss the implications of the finding.

Anatomical abbreviations

dc, distal carina. hdt, hooked denticle tip. idc, interdenticular chamber. ids, interdenticular sulcus. idsl, interdenticular slit. mc, mesial carina. tu, transverse undulation.

Measurements and ratios

Measurements and ratios (see Table 1) follow Smith et al. (2005) and Hendrickx et al. (2015). AL, apical length. CH, crown height. CBL, crown base length. CBW, crown base width. CBR, crown base ratio. DA, distoapical denticle count. DB, distobasal denticle count. DC, distocentral denticle count. DSDI, denticle size difference index. MA, mesioapical denticle count. MB, mesiobasal denticle count. MC, mesiocentral denticle count. MCL, mid-crown length. MCW, mid-crown width. MCR, mid-crown ratio.

Institutional abbreviations

FC-DPV, Facultad de Ciencias, Montevideo, Uruguay.

Geological setting

Cropping out in northern Uruguay (Figure 1), the Tacuarembó Formation was defined by Bossi (1966). Its main lithologies are subarkosic, fine to very fine grained sandstones, with predominantly pale colours (whitish, yellowish, greenish), with subordinate thin pelitic layers and intraconglomerates. All these lithologies were deposited in a fluvio-aeolian environment, under an arid to semi-arid climate. Indeed, five facies associations have been recently described for the unit, including distal braided fluvial channels, ephemeral channels, sheetflood, aeolian dunes, and aeolian sand-sheets. The fluvial facies disappear towards the overlying Rivera Formation (previously considered as the upper member of the unit), deposited in hyperarid climates (Ferrando et al. 1987). The Tacuarembó Formation is considered of Kimmeridgian-Tithonian age (see Soto et al. 2021), whereas the Rivera Formation is Hauterivian in age, due to its close relation with the Arapey Formation basalts (see Féraud et al., 1999). No fossils have so far been found in the Rivera Formation, but the Tacuarembó Formation shows an increasing diversity of vertebrates, with the record of hybodontid sharks, ginglymodians, mawsoniid

Table 1. Measurements of FC-DPV 3531. A few of them cannot be measured due to incompleteness of the material, and are indicated with

AL	-
CH	-
CBL	14.63 mm
CBW	7.24 mm
CBR	0.49
CHR	-
MCL	13.35 mm
MCW	5.14 mm
MCR	0.39
MA	-
MC	14.5 in 5 mm
MB	21 in 5 mm
DA	-
DC	15 in 5 mm
DB	17.5 in 5 mm
DSDI	0.96

coelacanth, arganodontid lungfishes, testudines, pholidosaurid crocodyliforms, ctenochasmatid pterosaurs, and ceratosaurid and megalosaurid theropods (Perea et al. 2001; 2003; Soto and Perea 2008; 2010; Perea et al. 2009; Fortier et al. 2011; Soto et al. 2012a; 2012b; Perea et al. 2014, p. 2018; Soto et al. 2020a; 2020b, 2021; Toriño et al. 2021).

The tooth fragment described herein (FC-DPV 3531) comes from the Bidegain Quarry (Figure 1), the most important fossil site of the Tacuarembó Formation that, among other remains, yielded ginglymodian scales and bones, coelacanth bones, dipnoan tooth plates, pterosaur teeth and bones, and crocodyliform and theropod teeth. The fossils come from a 1.5 m-thick layer of massive silty sandstones, believed to represent a fast depositional event due to the presence of nearly articulated coelacanth remains, delicate structures such as bones attached to dipnoan toothplates, and a large theropod tooth preserved perpendicular to the bed boundaries (Soto et al. 2020a; Toriño et al. 2021).

Methodology

The theropod tooth was examined and photographed under a Nikon SMZ 800 binocular lens. It was also gold-coated (lingual face only) and analysed with a JEOL JSM-5900 LV scanning electron microscope (SEM) at Facultad de Ciencias (Uruguay). Measurements were made with a Mitutoyo electronic caliper (Table 1). Given that a few key variables could not be measured (CH, AL), multivariate analyses such as those performed in recent papers (e.g. Young et al. 2019; Delcourt et al. 2020; Hendrix et al. 2020; Soto et al. 2020a, 2020b; Meso et al. 2021) were not employed. However, bivariate analyses were made for abelisaurid theropods, based on data from Meso et al. (2021), using the software PAST (Hammer et al. 2001).

We added the new partial tooth to the data matrix of Meso et al. (2021), resulting on a set of 108 OTUs and 146 characters related to the anatomy of teeth and tooth-bearing bones, 48 of which were scored for FC-DPV 3531. The phylogenetic analyses were performed using the TNT software (Goloboff et al. 2008a, b) with and without the defined constraints as defined by Meso et al. (2021; see SOM). We conducted traditional search, perturbing Wagner trees with 100 replications, using tree bisection reconnection as swapping algorithm, and keeping 10 trees per replication. The script WSTATS was ran to obtain consistency and retention indices. Bremer support values were calculated

saving suboptimal trees up to 10 steps longer than the multinomial processing tree, absolute supports, and saving 10,000 trees.

Systematic palaeontology

Dinosauria (Owen 1842)

Saurischia (Seeley 1887)

Theropoda (Marsh 1881)

Ceratosauria (Marsh 1884)

Abelisauroidea (Bonaparte 1991)

Abelosauridae Bonaparte and Novas 1985

Abelosauridae gen. et sp. indet

Material – FC-DPV 3531, an incomplete lateral tooth (Figures 2–3).

Locality and Horizon – Bidegain Quarry, Tacuarembó city, Tacuarembó Department, northeastern Uruguay. Tacuarembó Formation (Late Jurassic).

Description – The crown is incomplete, missing the apical portion and the basal-most portion of the cervix, but is otherwise very well preserved, including mesial denticles, which are rarely seen in theropod teeth from the Tacuarembó Formation. It is strongly labiolingually compressed (i.e. ziphodont, CBR of 0.49 and MCR = 0.39; Figure 2D) with two serrated carinae. The distal carina is rather straight whereas the mesial is strongly apico-basally convex in labial/lingual views. The mesial and distal carinae extend to the cervix, although the former ends slightly above the level of the latter. Both carinae are positioned centrally and the distal carina seems to be slightly bowed towards the lingual face (Figure 2B). The crown lacks concave surfaces bordering both carinae. The labial and lingual surfaces are mesiodistally convex and there is no signal of a basal depression. In cross section, the crown shows a symmetrical, lanceolate outline at the base that becomes lanceolate towards the middle of the crown (Figure 2D).

There are roughly three denticles per mm at the mid-crown and the mesial and distal denticles are almost the same size (MC = 14.5, DC = 15, DSDI = 0.96; Figure 2F-H), although distal denticles are twice as long (mesiodistally) than the mesial ones. The distal denticles are sub-rectangular, perpendicular to the distal edge and apically hooked along the carina (specially visible in labial view; Figures 2A, G, H and 3A). Denticle proportions do not change towards the base but denticle size decreases slightly in the preserved portion of the carina (DB = 17.5; its basalmost portion is missing). The long axis of the denticles seems to be apically curved rather than straight (Figure 2G), which we interpret to be correlated to the hooked condition. The interdenticular spaces are narrow to moderate, although with wide interdental chambers and deep interdenticular slits (Figures 2G and 3A). Short and slightly basally pointing interdenticular sulci are developed among denticles bases along the distal carina (specially visible in lingual view; Figures 2B,H and 3D), even among basal denticles, although they are shorter. The mesial denticles change in size along the carina, becoming small (4 and even 5 per mm; MB = 21) at the base (Figure 2F). Differently from the distal denticles, the mesial ones are sub-quadrangular, asymmetrical and chisel-shaped instead of hooked (Figures 2F and 3B). The interdenticular spaces are narrower and interdenticular sulci are developed only near the tip of the preserved portion of the tooth (Figure 2C).

The crown has three faint transverse undulations on the lingual surface that are well-separated and irregularly spaced (Figure 3C). The enamel surface texture is irregular and not oriented

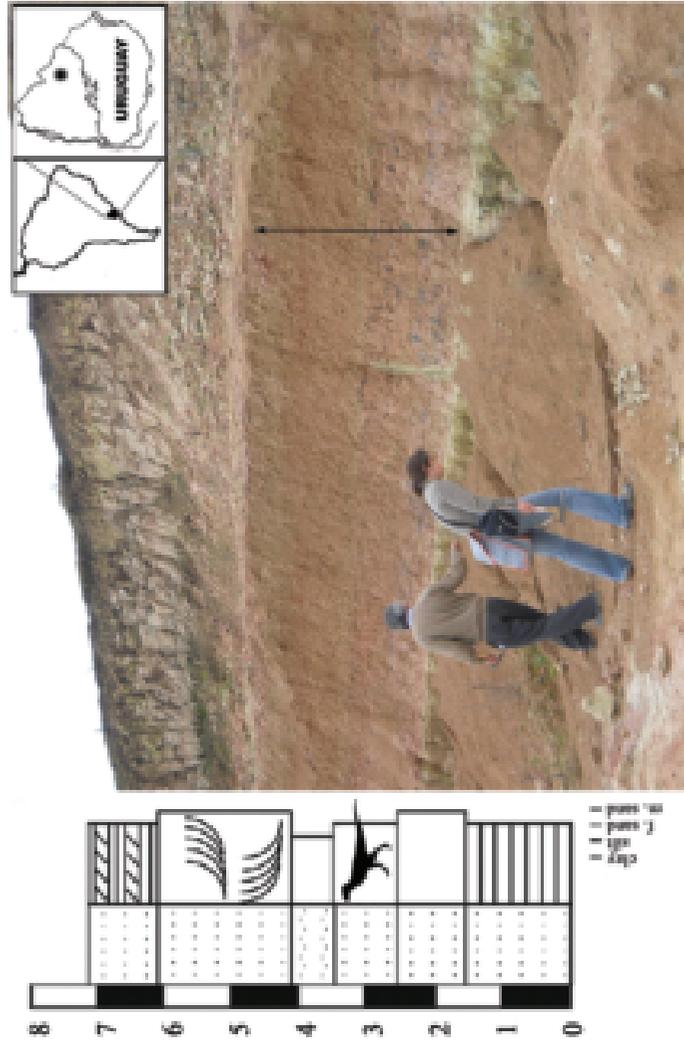


Figure 1. Sedimentological log of the Bidegain Quarry (indicating the fossil bearing horizon) and general view of the outcrop. Inset shows location of Uruguay within South America.

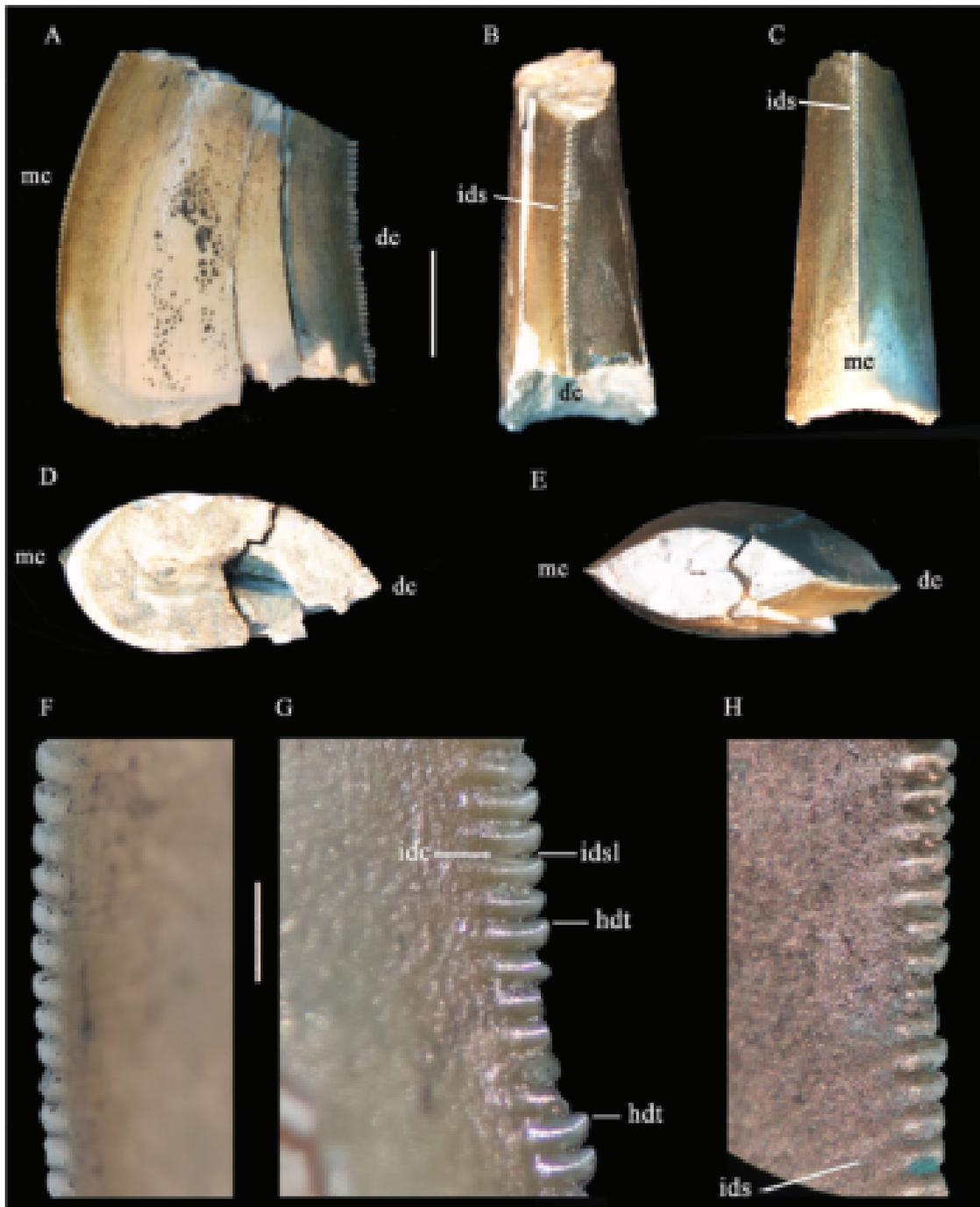


Figure 2. FC-DPV 3531, tooth fragment. A, labial view. B, distal view. C, mesial view. D, basal view. E, apical view. F, detail of mesial denticles in labial view. G, detail of distal denticles in labial view. H, detail of distal denticles in lingual view (reversed). Scale bar equals 5 mm (A-E) and 1 mm (F-G).

(Figures 2G and 3C,D). There are no signals of flutes, longitudinal grooves, ridges, nor marginal undulations.

Remarks – FC-DPV 3531 shows typical features of abelisaurid lateral teeth (Smith 2007; Hendrickx and Mateus 2014; Hendrickx et al. 2019, 2020). Although some characters are shared with other theropod taxa, such as the basal extension of the mesial carina (e.g. Spinosauridae, Pantyrannosauria, Eudromaeosauria), hooked denticles (e.g. *Masiakasaurus knopfleri*, *P. floresi*, Therizinosauroidea, Eudromaeosauria, Troodontidae), and irregular enamel texture (e.g. Metriacanthosauridae, Tyrannosaurinae, Noosauridae except for *Mas. knopfleri*, certain *P. floresi* and *Allosaurus fragilis* teeth), the combination of these features and the straight distal profile of

the crown are diagnostic for abelisaurid teeth (Hendrickx et al. 2019, 2020).

Despite being incomplete, the size and curvature of the preserved portion suggest that the entire FC-DPV 3531 tooth was about 25 mm long. Due to its labiolingual compression, we suggest that FC-DPV 3531 is a lateral tooth crown. Compared to the well-known dentition of *Majungasaurus crenatissimus*, FC-DPV 3531 is probably not a mesial lateral teeth. A CBR of 0.49 is close to the lowermost range seen in several abelisaurids, such as *Maj. crenatissimus*, *Indosuchus raptorius*, *Aucasaurus garridoi*, *Arcovenator escotae*, and *Abelisaurus comahuensis* (Hendrickx et al., 2020) (Figure 4A).

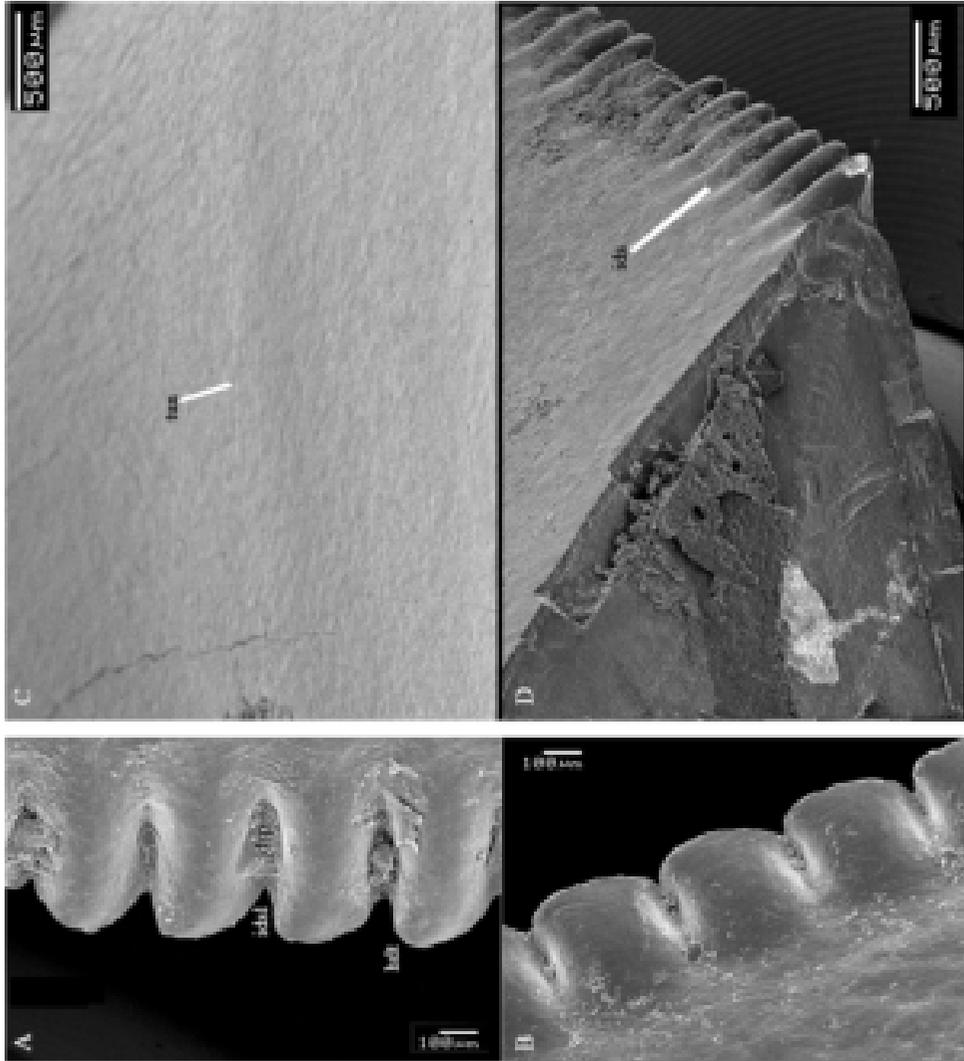


Figure 3. SEM images of FC-DPV 3531. A, distal denticles. B, mesial denticles. C, detail of enamel texture and transverse undulations. D, detail of distal carina in linguoapical view.

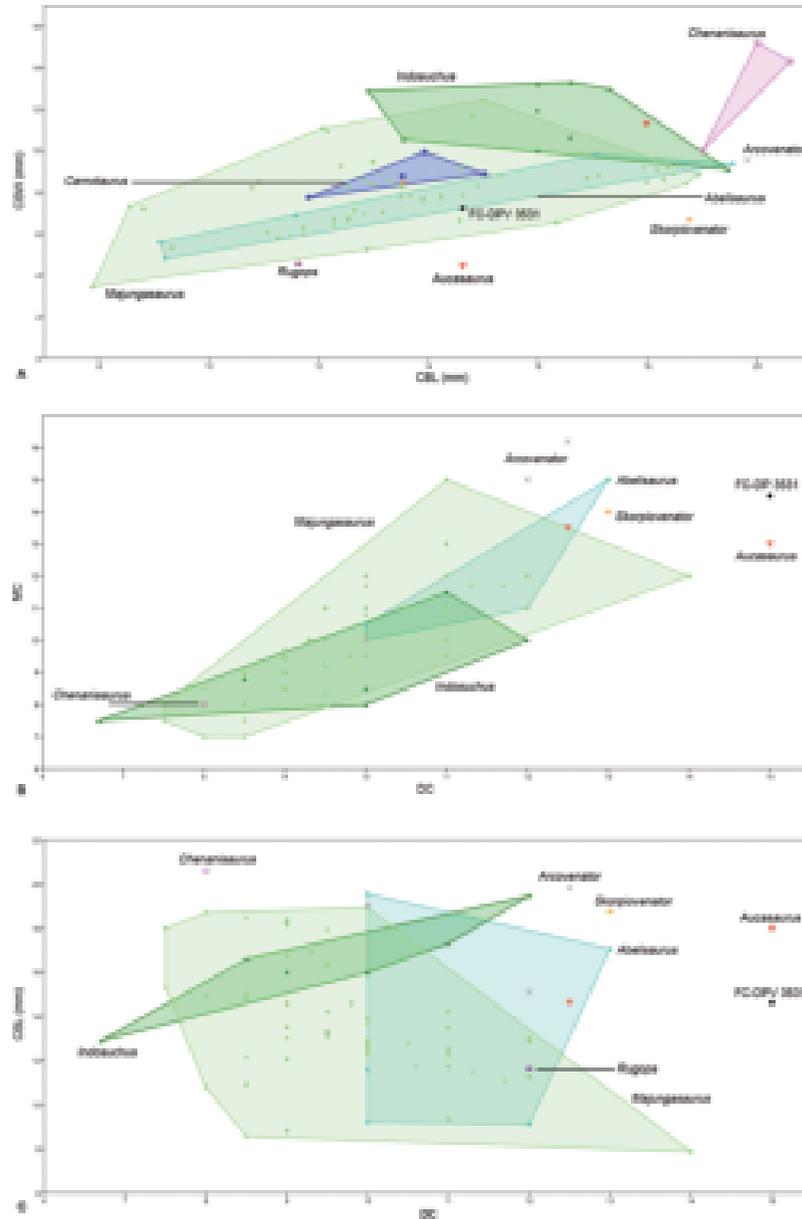


Figure 4. Bivariate analyses. A, CBW vs CBL. B, MC vs DC. C, CBL vs CBL.

Denticle density in the Uruguayan material is one of the highest so far recorded among abelisaurids. An MC of 14.5 is close to the upper range seen in *Abe. comahuensis*, *Auc. garridoi*, and *Skorpiovenator bustingorryi*, and to the lower range seen in *Arc. escotae* and *Auc. garridoi* (Hendrickx et al., 2020) (Figure 4B). A DSDI close to one is the condition seen in most abelisaurids, with only *Arc. escotae*, *Spectrovenator ragei* and isolated *Maj. crenatissimus* teeth showing a DSDI greater than 1.2 (Hendrickx et al. 2020; Zaher et al. 2020).

In bivariate analyses of abelisaurid teeth (CBW vs CBL, MC vs DC, CBL vs DC; Figure 4), FC-DPV 3531 plot very close to *Auc. garridoi*. Interestingly, FC-DPV 3531 also morphologically resembles this Argentinian species in having perpendicular, hooked, and subrectangular distal denticles in some teeth (Hendrickx et al. 2020).

Phylogenetic analysis

The first phylogenetic analyses (unconstrained) retrieved 3000 MPTs with 1067 steps (CI = 0.244, RI = 0.582). Several non-traditional groups were recovered in this analysis as expected (Meso et al. 2021) due to high levels of homoplasy in dental characters (Hendrickx et al. 2019). Nevertheless, some small clades were recovered such as Carcharodontosaurinae, Spinosauridae and Abelisauridae, although with odd arrangements. Despite the large number of MPTs, Abelisauridae is recovered as a clade in the strict consensus tree (Figure 5A; except for the aberrant *Arcovenator*), demonstrating that the dentition of the family is apomorphic among theropods. FC-DPV 3531 was recovered forming with *Indosuchus* the sister clade to all remaining abelisaurids.

The second phylogenetic analyses was run with constrains enforced, retrieving three MPTs of 1,309 steps (CI = 0.198, RI = 0.456). FC-DPV 3531 was found deeply nested within

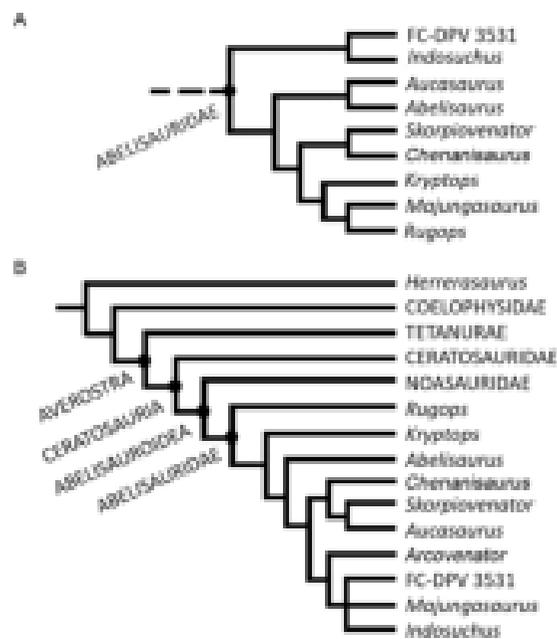


Figure 5. Simplified phylogenetic trees showing the strict consensus trees. A, unconstrained analysis (consensus of 3000 MPTs). B, constrained analysis (consensus of 3 MPTs). For complete trees, see SOM.

Abelisauridae, in a polytomy with *Majungasaurus* and *Indosuchus* (Figure 5B). Characters related to lateral teeth supporting the monophyly of Abelisauridae are hooked (character 91.2) and apically inclined (character 99.1) denticles on the distal carina. The clade formed by the *Majungasaurus*, *Indosuchus* and Uruguayan abelisaurid is supported by three synapomorphies: asymmetrical denticles on the mesial carina (character 90.1), short interdenticular sulci in mid-crown denticles of the distal carina (character 108.1) and in the basalmost denticles of the distal carina (character 109.1). That clade, plus *Aucasaurus*, *Skorpiovenator*, *Chenanisaurus* and *Arcovenator* shares the presence of denticles on the distal carina that are longer mesiodistally than apicobasally (character 95.1). That clade, plus *Abelisaurus* shares the presence of subquadrangular denticles on the mesial carina (character 94.1). Differing from most abelisaurids, the Uruguayan abelisaurid shows perpendicular distal denticles (character 99.0, only shared with some *Aucasaurus*, *Skorpiovenator* and *Chenanisaurus* teeth), and presence of tenuous enamel transverse undulations (character 112.1), only shared with *Abelisaurus* (transverse undulations are instead conspicuous in *Majungasaurus* and *Aucasaurus*).

Forcing FC-DPV 3531 in other phylogenetic positions within clades which share the presence of irregular enamel and/or hooked denticles requires 2 (sister taxon to *Allosaurus*), 5 (Noosauridae), 6 (sister taxon to *Piatnitzkysaurus*), 3–6 (Metriacanthosauridae) and 9 additional steps (sister taxon to *Saurornitholestes* or *Atrociraptor*).

The phylogenetic analysis recovered the Uruguayan material in a clade of Late Cretaceous abelisaurids from India-Madagascar, whereas bivariate analysis and some shared traits suggest affinities with Late Cretaceous abelisaurids from Argentina, hypotheses that imply long ghost lineages. Yet, teeth are structures with high levels of homoplasy (Hendrickx et al. 2019) and the distribution of dental characters among early abelisaurids, such as *Spectrovenator ragei* and Jurassic forms, except in the Malagasy case (Maganuco et al. 2005), is still poorly known. Hence, we take the phylogenetic results above to confirm the abelisaurid affinity of the Uruguayan tooth, but more material is needed in order to better constrain its

placement within the group and possible affinity to specific taxa. Indeed, some characters of FC-DPV 3531 seem to have appeared early in the history of abelisaurids, such as the irregular enamel – also present in noosaurids, but not in ceratosaurids, so likely synapomorphic for Abelisauroidae – and hooked denticles. Forcing FC-DPV 3531 into clades which share irregular enamel and/or hooked denticles requires two (sister taxon to *Allosaurus*), five (Noosauridae), six (sister taxon to *Piatnitzkysaurus*), three to six (Metriacanthosauridae), and nine (sister taxon to *Saurornitholestes* or *Atrociraptor*) additional steps, corroborating our abelisaurid taxonomic determination. The distribution of other characters, such as apically inclined denticles, is more conflictive. This condition may have either arisen several times within Abelisauridae or independently reversed to the plesiomorphic condition (perpendicular denticles).

Discussion

FC-DPV 3531 lacks the large size, low number of denticles on the carina, braided enamel surface, well-visible transverse undulations, and long interdenticular sulci seen in the megalosaurine and ceratosaurid teeth from the Tacuarembó Formation (Soto et al. 2020a, b). Moreover, distal denticles in both taxa are not as mediolaterally long and never hooked. Although ceratosaurid lateral teeth are yet to be identified in the Tacuarembó Formation, these further differ from FC-DPV 3531 for their flat labial surfaces, labially displaced distal carina, and concave areas adjacent to the carinae (see Hendrickx et al. 2019).

The Uruguayan abelisaurid fits chronologically between the Early Jurassic *Eoabelisaurus mefi*, from Argentina (Pol and Rauhut 2012) and the Early Cretaceous *Spectrovenator ragei*, from Brazil (Zaher et al. 2020). (It should be noted that certain authors have cast doubts on the abelisaurid or even abelisauroid nature of *E. mefi*; e.g. Novas et al. 2013; Delcourt et al., 2017; Wang et al. 2017) Similarly, possible abelisaurids have been described on the basis of fragmentary remains from Late Jurassic beds (Figure 6) of Argentina (Cañadón Calcáreo Formation; Rauhut & Pol, 2021) and



Figure 6. Selected fragmentary Jurassic abelisaurids. A-I, rostral teeth from the Middle Jurassic of Madagascar. A, labial view. B, mesial view. C, lingual view. D, distal view. E, close-up of distal denticles. G, basal cross-section. H, mid-crown section. I, close-up of distal denticles of a second tooth of the same morphotype. J-K, postcranial remains from the Late Jurassic of Tanzania. J, right femur in lateral view. K, left tibia in lateral view. L, cervical vertebra from the Late Jurassic of *Argentina* in anterior view. Taken from Maganuco et al. (2005), Rauhut (2011) and Rauhut and Pol (2021). Scale bars equal 5 mm (A-D), 10 cm (J, K) and 2 cm (L).

Tanzania (Tendaguru Formation; Rauhut 2011). Strikingly, among the abundant teeth material from the latter unit, no typical abelisaurid teeth were identified (Malafaia et al. 2022).

Although Middle Jurassic abelisauroids have been reassigned to coelurosaurids or even indeterminate theropods (Rauhut 2012), abelisaurid-like teeth are known from the Middle Jurassic of Madagascar (Isalo IIIb Subunit; Maganuco et al. 2005) (Figure 6A-I) and Portugal (Hendrickx and Mateus 2014). Indeed, Morphotype 1 of Maganuco et al. (2005) includes rostral teeth with salinon cross-sectional shape, hooked and apically inclined denticles, and short interdenticular sulci, a character combination only found in abelisaurid theropods (Hendrickx et al. 2019, 2020). Maganuco et al. (2005) explicitly noted the close resemblance of Morphotype 1 with *Maj. crenatissimus* rostral teeth.

The purported abelisaurid teeth from Portugal reported by Hendrickx and Mateus (2014) show features atypical for abelisaurids, such as a lingually twisted mesial carina at the base of the crown and a conspicuous longitudinal groove; one of them even lacks hooked denticles. Hence, more material is needed in order to confirm the abelisaurid affinities of the Portuguese teeth. Indeed, one of them has been regarded as a possible metriacanthosaurid (Hendrickx et al. 2020).

The new Uruguayan abelisaurid is a valuable addition to the meagre Jurassic record of the group, which shows a strong Gondwanan signal (Figure 7). The Tacuarembó Formation seems to have a mix of taxa traditionally considered restricted to Laurasia (*Ceratosaurus*-like ceratosaurids and *Torvosaurus*-like megalosaurines; Soto et al. 2020a, 2020b) and now more typical Gondwanan theropod taxa

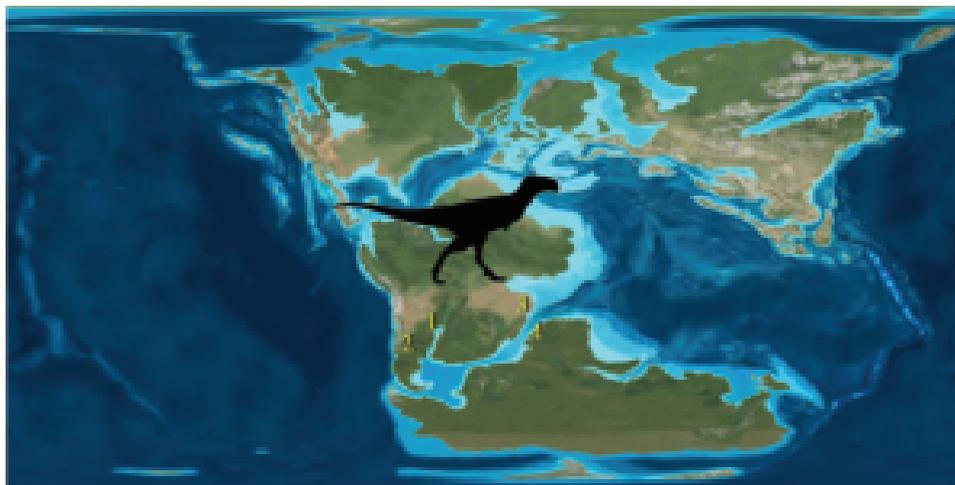


Figure 7. Jurassic occurrence of abelisaurid theropods. 1, Late Jurassic Tacuarembó Formation, Uruguay. 2, Early Jurassic Cañadón Asfalto (*Eoabelisaurus mefi*) and Late Jurassic Cañadón Calcáreo formations, Argentina (Pol and Rauhut 2012; Rauhut and Pol 2021). 3, Late Jurassic Middle and Upper Saurian Beds, Tendaguru Formation, Tanzania (Rauhut 2011). 4, Middle Jurassic Isalo IIIb Subunit, Madagascar (Maganuco et al. 2005). Silhouette after *Spectrovenator* (Zaher et al., 2020).

(Abelisauridae). Taking into account the available evidence, abelisaurids seem to be a rare component of the Tacuarembó Formation assemblage. This is not unexpected, as the group seems to have experienced a major radiation only by the Cretaceous, whereas ceratosaurids, and especially megalosaurids, were more common in the Jurassic.

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