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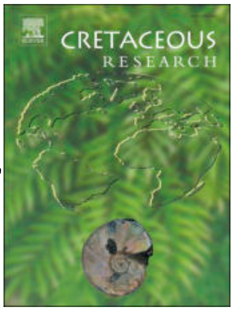


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# A carcharodontosaurid tooth from "Boca de Forno" Ravine of the Itapecuru Formation, Parnaíba Basin, Maranhão, Brazil

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**Abstract**

Carcharodontosauridae forms a clade of medium- to very large-sized (6-14 m long) allosauroid theropods mostly restricted to the Early and mid Cretaceous with an almost global distribution, and characterized by deep and narrow ornamented skulls and strongly compressed ziphodont teeth. In Brazil, the carcharodontosaurid fossil record is limited to shed teeth and isolated postcranial elements from the Aptian-Cenomanian deposits of the eastern part of the country. Here we describe and identify a shed tooth from a little-known outcrop of the Early Cretaceous (Aptian-Albian) Itapecuru Formation of the Maranhão State, northeastern Brazil. Although some teeth have already been reported from the Aptian-Albian deposits of this unit, this specimen represents the first isolated dental material from the Parnaíba Basin that can be confidently assigned to a carcharodontosaurid through cladistic and morphometric techniques, but also based on a systematic study. The results of the herein conducted study suggest that the specimen belongs to a carcharodontosaurine closely related to the Patagonian taxa *Giganotosaurus* and *Mapusaurus*, which are younger in age. Although the specimen is closely related to the abovementioned Patagonian taxa, the faunal composition of the Parnaíba Basin seems to be more similar to that of North Africa. Nevertheless, further collecting efforts are needed in these localities to find skeletal carcharodontosaurid remains and to broaden the comparative base for the identification

of theropod dentition.

*Keywords*: Lower Cretaceous, shed crown, Carcharodontosauria, Allosauroidea, Theropoda, Itapecuru Formation, Parnaíba Basin

## 1. Introduction

Carcharodontosauridae is a clade of medium- to large-bodied theropod dinosaurs (6-14 m long) diagnosed by a long and low skull, fused nasals covered with rugosities, textured rugosities on the lacrimal and postorbital, as well as dorsal vertebrae with tall neural spines (Novas 1997; Holtz et al. 2004; Ortega et al. 2010; Eddy and Clarke 2011; Carrano et al. 2012; Canale et al. 2014, 2022). Their lateral crowns are particularly large (>5 cm), elongated, and labio-lingually compressed and typically show pronounced marginal undulations. The denticulated distal and mesial carina of carcharodontosaurids additionally have chisel-like denticles and elongated interdenticular sulci (Hendrickx and Mateus 2014; Hendrickx et al. 2015, 2019, 2020b). Carcharodontosaurids had a cosmopolitan distribution during the Aptian–Turonian, with various taxa discovered in Africa, Asia, Europe, North and South America (Depéret and Savornin 1925; Stromer 1931; Stovall and Langston 1950; Coria and Salgado 1995; Coria and Currie 2006; Sereno and Brusatte 2008; Brusatte et al. 2010, 2012; Ortega et al. 2010; Cau et al. 2013). The Brazilian carcharodontosaurid record is limited to isolated teeth and poorly preserved postcranial bones such as caudal vertebrae (Medeiros 2001; Ribeiro et al. 2003; Medeiros et al. 2014; Carvalho and Santucci 2018; Pereira et al. 2020). These fossil remains have been mainly found in Lower Cretaceous deposits of northeastern Brazil, and include several isolated teeth from the Cenomanian Alcântara Formation (Góes and Rossetti 2001; Medeiros 2001; Medeiros et al. 2014) and the Aptian-Albian Itapecuru Formation (Medeiros and Schultz 2002; Ribeiro et al.

2003; Corrêa-Martins 2019), as well as two caudal vertebrae from the Albian-Cenomanian Açu Formation, Potiguar Basin (Araripe and Feijo 1994; Pereira et al. 2020). Carcharodontosaurid material from southeastern Brazil is extremely scarce and restricted to a single isolated tooth from the Aptian Quiricó Formation of the Sanfranciscana Basin, Minas Gerais (Carvalho and Santucci 2018). A fragmentary maxilla with an *in situ* tooth as well as some isolated crowns from Maastrichtian beds of the Bauru Basin were also referred to Carcharodontosauridae by Azevedo et al. (2013) and Candeiro et al. (2004, 2006, 2012), respectively. Nevertheless, Delcourt and Grillo (2018) and Delcourt et al. (2020a, 2024) re-evaluated the phylogenetic affinities of these specimens and concluded that they rather belonged to Abelisauridae (Carrano and Sampson 2008; Delcourt 2018).

This paper aims to describe and identify an isolated shed tooth (CPHNAMA VT-1502) from a little-known outcrop of the Aptian–Albian Itapecuru Formation of the Parnaíba Basin, Maranhão State, northern Brazil (Pedrão et al. 1993a, 1993b). This specimen represents the first carcharodontosaurid record from this region to be identified using cladistic and morphometric techniques and expands our knowledge of the theropod record from the Early Cretaceous of Southern America.

*Institutional abbreviations.* **CPHNAMA**, Centro de Pesquisa de História Natural e Arqueologia do Maranhão, São Luís, Maranhão, Brazil; **MN**, Museu Nacional, Rio de Janeiro, Brazil; **UFABC**, Universidade Federal do ABC, São Bernardo do Campo, São Paulo, Brazil; **UFMA**, Universidade Federal do Maranhão, São Luís, Maranhão, Brazil; **UFRJ**, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; **UNICAMP**, Universidade Estadual de Campinas, São Paulo, Brazil.

*Morphometric abbreviations.* **AL**, apical length; **CBL**, crown base length; **CBR**, crown base ratio; **CBW**, crown base width; **CH**, crown height; **CHR**, crown height ratio; **DC**, distocentral denticle density; **MC**, mesiocentral denticle density; **MCL**, mid-crown length; **MCR**, mid-crown ratio; **MCW**, mid-crown width.

### *1.1. Geographical, stratigraphic and paleoenvironmental settings*

CPHNAMA VT-1502 was collected in December 2016 during an expedition led by the Centro de Pesquisa de História Natural e Arqueologia do Maranhão (CPHNAMA), in partnership with the Universidade Federal do Maranhão (UFMA). The specimen comes from an outcrop known as "Boca de Forno Ravine" (Fig. 1) and located along the Itapecuru River valley, nearby Conceição Village in Coroatá Municipality, Maranhão State, Brazil (coordinates 3°55'39.56''S, 44°09'38.41''W).

Campbell (1949) used a sandy succession under a bridge spanning the Itapecuru River from the municipality of Itapecuru-Mirim, northern Parnaíba Basin to define the Itapecuru Formation. The composite section is formed by predominantly red and light gray fine-grained sandstones interlayered with mudstone, siltstone and shales (Campbell 1949; Lima and Leite 1978). This continental succession extends along the lower course of the Itapecuru River. It is prominently represented near the coast of Maranhão State and extends from the southern part of the municipality of Coroatá to the city of Rosário. The Itapecuru Formation was dated as upper Aptian to Albian (approximately 125.0–100.5 Ma; Pedrão et al. 1993a, 1993b; Vicalvi and Carvalho 2002) and overlies the bituminous shales of the Aptian Codó Formation (Caputo 1984).

The vertebrate paleofauna of the Itapecuru Formation is diverse and currently includes dinosaurs, crocodylomorphs, testudines and fishes (Carvalho 1994; Kischlat and Carvalho 2000; Batista 2009; Carvalho 2002; Dutra and Malabarba 2001; Medeiros and Schultz 2001; Medeiros et al. 2007, 2014). Theropods are mainly represented by isolated theropod teeth referred to carcharodontosaurids and spinosaurids (Medeiros and Schultz 2001; Medeiros et al. 2007, 2014). Two sauropod clades i.e., Titanosauria and Diplodocoidea, are known from this formation. Titanosaurian remains are represented by a right humerus and fragmentary dorsal and caudal vertebrae (Castro et al. 2007) whereas the diplodocoid record consists of the rebbachisaurid *Amazonsaurus maranhensis*, which preserves a few postcranial elements (e.g., dorsal neural spines, posterior caudal vertebra, ilium, pubis; Carvalho et al., 2003), as well as fragmentary neural arch referred to Rebbachisauridae (Castro et al. 2007).

Crocodyliformes are restricted to the notosuchian *Candidodon itapecuruense* represented by two mandibular rami (Carvalho 1994). Postcranial elements referred to the same species, such as presacral vertebrae, humerus, femur, and osteoderms, were also found (Nobre 2004). Testudines from the Itapecuru Formation include *Araripemys barretoi*, wich was originally reported from the Crato and Romualdo formations of the Santana Group, Araripe Basin (Kischlat and Carvalho 2000; Batista 2009).

Fish remains are common and sometimes abundant in the Itapecuru Formation. This is particularly the case of the mawsoniid *Mawsonia gigas,* a coelacanth described from large and well-ornamented angular and parietal bones (Carvalho 2002). Dipnoi fishes such as *Ceratodus africanus* and *Asiatoceratodus tiguidiensis* (Pereira et al. 2013), mainly represented by dental plates in these deposits (Dutra and Malabarba 2001). The invertebrate records from Itapecuru Formation finally include Conchostraca, Ostracoda, and Mollusca such as bivalves and gastropods (Ferreira et al. 1991; Carvalho 1994; Dutra and Malabarba 2001).

## 2. Material and Methods

*2.1.Comparative anatomy and followed terminology*

Specimen CPHANAMA VT-1502 was photographed with a Canon EOS 77D DSLR Camera coupled with an EF-S 60 mm f/2.8 Macro USM Lens in mesial, labial, distal, lingual, apical, and basal views. This shed crown was compared to the teeth of 118 non-avian theropods deposited in the collections of 35 institutions from 13 countries (Argentina, Belgium, Canada, China, France, Germany, Italy, Portugal, Qatar, Switzerland, South Africa, the United Kingdom, and the USA; see the supplementary material of Hendrickx et al., 2020a).

The shed tooth crown was described and illustrated following the anatomical terminology and tooth orientation proposed by Hendrickx et al. (2015). We also followed the descriptive order to the isolated theropod teeth of this study, emphasizing condition, crown, denticles and ornamentations.

*2.2.Morphometric analysis*

Specimen CHPHNAMA VT-1502 was measured using an analog caliper and double-checked on ImageJ 1.53 software (Schneider et al. 2012); measurements followed the variable proposed by Smith et al. (2005) and were obtained as follows: AL, CBL, CBR, CBW, CH, CHR, DC, MC, MCL, MCR, and MCW (Table 1; to access a complete description of measurements, see Hendrickx et al. 2015). These were added to the dataset of Delcourt et al. (2020a), which is a slightly modified version of that of Hendrickx et al. (2020a). The dataset was restricted to South American Cretaceous taxa (i.e., Abelisauridae, Carcharodontosauridae, early-branching Ceratosauria, Compsognathidae, Dromaeosauridae, Neovenatoridae, Noasauridae, Pantyrannosauria, and Spinosauridae) to reduce the potential noise in the analysis.

The modified dataset resulted in a database containing 683 tooth crowns. To better reflect a normally distributed multivariate dataset, all data were log-transformed according to Smith et al. (2005) and Hendrickx et al. (2020a). The statistical analysis was performed using Past v4.02 software (Hammer et al. 2001), followed by discriminant analysis (LDA) conducted to create an ordinated morphospace in which the analyzed clades were maximally separated. Specimen CPHNAMA VT-1502 was labeled as "mysterious species" allowing the LDA analysis to identify which taxon was more similar to it according to the given variables. The LDA was performed solely at clade-level.

*2.3.Cladistic analysis*

Specimen CHPHNAMA VT-1502 was additionally included in the dentition-based datamatrix of Hendrickx et al. (2020a), which comprises 148 dental characters scored in 107 non-avian theropod taxa. The specimen was scored as a lateral tooth (char. 69 to 119). The cladistic analysis was performed using TNT software version 1.5 (Goloboff and Catalano 2016) following the search parameters used by Hendrickx et al. (2020a - TNT command used is "xmult = hits 100 rss fuse 5 ratchet 20", after we run the "bb" command). These commands represent a combination of Wagner trees, TBR, sectorial searches, Ratchet with 20 substitutions, and Tree Fusion with five rounds, whereupon 100 hits of the same minimum tree length were achieved.

## 3. Systematic Paleontology

Dinosauria Owen, 1842

Saurischia Seeley, 1888

Theropoda Marsh, 1881

Allosauroidea Marsh, 1878

Carcharodontosauridae Stromer, 1931

Carcharodontosaurinae Brusatte & Sereno, 2008

Gen. and sp. indet.

*Material.* One isolated tooth (CPHNAMA VT-1502; Fig. 2, Table 1)

## 4. Descriptive anatomy

*Condition.* Specimen CPHANAMA VT-1502 is a shed tooth crown showing signs of wear, breakage, and deformation (Fig. 2). The mesial carina is worn out at mid-crown (Fig. 2A) and even though the distal margin of the crown exhibits breaks, most of the distal carina is well preserved (Fig. 2C). The enamel layer is almost intact on both lingual and labial surfaces. The cervical line is visible along the mesial and labial surfaces of the crown but only partially preserved distally.

*Crown.* Specimen CPHNAMA VT-1502 is a typical blade-shape ziphodont tooth crown with a distal curvature and denticulated carinae. The crown is strongly labiolingually compressed (CBR = 0.38), with a moderate baso-apical elongation (CHR = 1.85) and slightly distally recurved so that the apex does not extend beyond the basodistalmost point of the crown (Fig. 2). The extension of the enamel is symmetrical on both mesial and distal surfaces. In lateral view, the mesial margin is strongly convex. Controversely, the distal margin is sigmoid, with the basal and apical halves being slightly concave and convex, respectively (Fig. 2A, C). The labial side of the crown exhibits a centrally positioned and slightly flattened surface along the basal one-third of the crown. The cross-section of the base crown is lenticular and subsymmetrical (Fig. 2E, F). Both mesial and distal carinae are denticulated all along their length and the basalmost denticles extend well-beneath the cervix (Fig. 2A, C). No concave surface is present adjacent to the carinae. The mesial carina is straight and slightly lingually displaced in medial view (Fig. 2A). Conversely, the distal carina is slightly bowed, almost sigmoid, and centrally positioned on the distal surface of the crown in distal view (Fig. 2C).

*Denticles.* Both carinae bear denticles with parabolic and symmetrically to asymmetrically convex external margins. Mesial and distal denticles extend apically close to the apex and basally below the cervical line (Fig. 2A, B, C, D). No biconvex denticles have been observed on the carinae. Apical denticles on the mesial carina project perpendicular from the mesial margin of the crown, whereas distal denticles from the distal carina are apically inclined at mid-crown (Fig. 2B, D). Mesial denticles at two-thirds of the crown and more apically (MC-MA) have a subquadrangular shape (i.e., they are as long mediodistally as apicobasally). Distoapical denticles (DA) on the distal carina have the same subquadrangular shape. Conversely, both mid-crown distal denticles (DC) and distobasal denticle (DB) have a horizontal subrectangular shape (i.e., they are longer mediodistally than apicobasally). Mesiobasal denticles (MB) on the mesial carina have the same subrectangular shape. Denticles have a similar morphology along the carinae, but their size increases apically (Fig. 2A, B, C, D). However, the distal denticles slightly decrease in size close to the apex. Mesial and distal denticles share the same width at mid-crown (i.e., DSDI~1).

The interdenticular spaces (idsp) between mid-crown distal denticles are broad and occupy more than one-third of the denticle width. Obliquely oriented interdenticular sulci (= *blood grooves sensu* Currie et al. 1990) extending basally can be observed between mesial and distal denticles (Fig. 2B, C). The sulci between mesial denticles are short, poorly developed, and restricted to the crown apex. Conversely, those between distal denticles are long, well-developed (i.e., longer than the proximodistal height of the denticles) and visible on the basal and central portions of the distal carina.

*Ornamentations and other attributes.* The crown apex is well-preserved and slightly rounded, with a subtle sign of enamel wear (Fig. 2B, C, D). A few transverse undulations are present on both labial and lingual surfaces where they are tenuous and barely visible under light. No other enamel ornamentation are present on the tooth. The enamel surface texture is braided, with a baso-apically oriented pattern that is not clearly visible with light.

## 5. Results

### *5.1.Discriminant analysis*

Specimen CPHNAMA VT-1502 is identified as a lateral crown based on its particularly low crown base ratio (CBR; *sensu* Smith et al. 2005) as mesial teeth are always more labiolingually thicker, with typically a CBR higher than 0.6 (Hendrickx et al. 2015). This specimen was retrieved as a non-abelisauroid ceratosaurian by the LDA analysis. The specimen is, however, plotted in the intersection of the convex hulls of Abelisauridae and Carcharodontosauridae (Fig. 3). The length measurements (MCW, MCL, AL, CH, CBL, CBW) were the main variables that distinguished the clades along Axis 1, whereas denticle densities (DC, MC) separated groups along Axis 2. About 74.52% of the 683 crowns included in this analysis were correctly identified, compared to 73.94% in the Jackknife reclassification. The rate of classification was variable between the groups for non-jackknife classification: 100% for non-abelisauroid ceratosaurians, early-branching coelurosaurians and compsognathids; 86.84% for neovenatorids; 89.65% for spinosaurids; 85.71% for pantyrannosaurians; 77.08% for abelisaurids; 84.94% for carcharodontosaurids; 68.03% for dromaeosaurids; and 41.6% for noasaurids.

### *5.2.Cladistic analysis*

The cladistic analysis yielded a single most parsimonious tree (MPT) (dentition and crown-based characters) in which CPHNAMA VT-1502 was recovered as a carcharodontosaurine allosauroid (consistency index = 0.195; retention index = 0.435; length = 1,362) and the sister taxon of the clade gathering the South American forms *Mapusaurus* and *Giganotosaurus* (Fig. 4). The dental synapomorphies (Fig. 5) constraining the South American carcharodontosaurine clade are: absence of biconvex apical denticles (i.e., biconvex external margin of denticle) on the mesial carina in lateral teeth (char. 98:0); apical denticles oriented perpendicularly from the mesial carina in lateral teeth (char. 99:0); presence of interdenticular sulci between mid-crown denticles on the distal carina of lateral teeth (char. 109:2).

## 6. Discussion

### *6.1.Systematic affinities of CPHNAMA VT-1502*

Despite the abundance of theropod shed teeth in many fossil sites, the identification of isolated teeth remains challenging, leading to the misidentification of many specimens (e.g., Candeiro 2004, 2006, 2012; reassessed by Delcourt et al. 2020a, 2024). Discriminant and cladistic analyses have been useful methods to explore the phylogenetic identification of isolated teeth (Hendrickx et al. 2019; Berrocal-Casero et al. 2023). Although the discriminant analysis classified CPHNAMA VT-1502 as a non-abelisauroid ceratosaurian, this specimen is recovered in the convex hull of both Abelisauridae and Carcharodontosauridae theropods, whereas the results of the cladistic analysis retrieved this specimen within Carcharodontosaurinae. Abelisauridae are particularly common in the Cretaceous of Brazil, with three species described: *Pycnonemosaurus*, *Thanos*, and *Spectrovenator* (Kellner and Campos 2002; Delcourt 2017; Delcourt and Iori 2018; Zaher et al. 2020). Although abelisaurid and carcharodontosaurid lateral teeth share many dental features, these include: a mesial carina extending to the cervix, poorly recurved crowns with a straight to slightly concave distal profile, well-developed interdenticular sulci between distal denticles, and an asymmetrically convex external margin of the denticles (Hendrickx et al. 2019). Specimen CPHNAMA VT-1502 does not exhibit several dental characters typically seen in abelisaurid lateral teeth. These characters include the irregular enamel surface texture, hooked distal denticles, and symmetrically convex labial and lingual profiles of the crown. Instead, the enamel-texture of CPHNAMA VT-1502 is braided, the distal denticles are strongly mesio-distally elongated and separated by wide interdenticular spaces, the distal carina is slightly sigmoid in distal view, and the apicodistal profile of the crown is weakly convex in lateral view. This combination of dental features is typical of carcharodontosaurid theropods (Hendrickx et al. 2019). Results of the cladistic analysis further support the carcharodontosaurine affinities of CPHNAMA VT-1502, which is recovered in the same clade as the Patagonian taxa *Mapusaurus* and *Carcharodontosaurus*. Comparative anatomy combined with the results of the morphometric and cladistic analyses all support an assignment of CPHNAMA VT-1502 to Carcharodontosaurinae so that this specimen is confidently identified as belonging to this clade. This study is, therefore, the first to confirm the presence of carcharodontosaurine carcharodontosaurids in the Parnaíba Basin of Brazil using computational techniques.

### *6.2.Remarks on the Paleogeographic history of Carcharodontosauridae*

Carcharodontosauridae is traditionally defined as all taxa that share a more recent common ancestor with *Carcharodontosaurus saharicus* than with *Allosaurus fragilis* or *Sinraptor dongi* (Weishampel et al. 2004, Novas et al. 2013). Coined by Stromer

(1931), the clade Carcharodontosauridae has a wide paleogeographic distribution during the Cretaceous (Candeiro et al 2018; Meso et al. 2021) and represent an important radiation of allosauroid theropods, spanning from the Late Jurassic to the mid-Cretaceous (Brusatte and Sereno 2008; Rauhut 2011; Malafaia et al. 2020; Canale et al. 2022). Carcharodontosaurids were present in Gondwana (Africa and South America – e.g., *Carcharodontosaurus*, *Giganotosaurus, Meraxes*) and in Laurasia (Asia, Europe and North America - e.g., *Acrocanthosaurus*, *Concavenator*, *Kelmayisaurus*, *Shaochilong*) (Stovall and Langston 1950; Ortega et al. 2010; Coria et al 2020; Canale et al. 2022).

Carcharodontosaurid taxa appear to be particularly common from the Barremian (127-121 Ma) to the Turonian (94-90 Ma) (Medeiros et al. 2014; Carvalho and Santucci 2018; Pereira et al. 2020; Meso et al 2021). Carcharodontosaurids from Brazil are mostly represented by isolated teeth (Medeiros and Schultz 2001, 2002; Medeiros et al 2014) and other fragmentary postcranial elements, such as two caudal vertebrae (Pereira et al. 2020). The Brazilian carcharodontosaurid remains were assigned to Carcharodontosauridae indet. and no Brazilian species has been proposed so far.

Despite the scarce record of carcharodontosaurid remains in Brazil, the presence of isolated crowns suggests that the faunal composition in the Quiricó, Itapecuru, and Alcântara formations appears to be as complex as seen in North Africa (Ibrahim et al. 2020), Patagonia (Novas et al. 2013), and the Iberian Peninsula (Alonso et al. 2018; Isasmendi et al. 2020), where these theropods shared their environments with other large-bodied predatory dinosaurs. Three reasons could explain the absence of non-dental remains in Brazil: 1) tooth replacement rates and higher dentary resistance to weathering, which may explain that these are almost the only remains that have been recovered; 2) the preservation of skeletal remains is biased by climatic conditions, as seen in the Bauru Basin, Upper Cretaceous of Brazil (Delcourt et al. 2024); and 3) habitat preferences: abelisaurids and carcharodontosaurids occupied more inland habitats while spinosaurids lived in more coastal environments than inland territories (Sales et al. 2016). In any case, more collecting effort must be undertaken in these localities to find skeletal carcharodontosaurid remains.

## 7. Conclusion

Results of the cladistic and morphometric analyses identified CPHNAMA VT-1502 as a lateral shed crown of a carcharodontosaurine carcharodontosaurid. This assignment is consistent with the paleogeographic and stratigraphic distribution of this clade in South America during the Cretaceous. This study is the first to confirm the presence of carcharodontosaurids in the Parnaíba and São Luís basins using computational techniques as the sole use of comparative anatomy can often lead to misidentifications.

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**Declaration of interest statement**

The authors declare no conflict of interests.

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**Figure Captions**

Figure 1. Geographic and stratigraphic distribution of CPHNAMA VT-1502 from the Lower Cretaceous Parnaíba Basin. The star marks the outcrop's location (coordinates 3°55’39.56’’S, 44°09’38.41’’W). Modified from França et al. (2021).

Figure 2. CPHNAMA VT-1502, a shed tooth crown referred to Carcharodontosaurinae indet. in (A) mesial, (B) labial, (C) distal, (D) lingual, (E) apical and (F) basal views. Abbreviations: dca, distal carina; ids, interdenticular sulcus; mca, mesial carina. Scale bar = 1 cm.

Figure 3. Graphical results of the discriminant analysis at clade level (79.93% of the crowns were correctly identified) of 682 teeth belonging to 45 taxa and ten groups of

non-avian theropods: Abelisauridae (yellow), early-branching Coelurosauria (violet), Carcharodontosauridae (magenta), Compsognathidae (light green), Dromaeosauridae (blue), Neovenatoridae (red), non-abelisaurid Ceratosauria (orange), Noasauridae (brown), Pantyrannosauria (purple), and Spinosauridae (dark green). Specimen CHPHNAMA VT-1502 (black dot) plots within the morphospaces of the Abelisauridae and Carcharodontosauridae. Theropod silhouettes from phylopic.org (artist: Dromaeosauridae by Emily Willoughby; Scott Hartman for the other silhouettes).

98

Figure 4. Most parsimonious tree from a cladistic analysis performed on a dentition-based datamatrix of 148 characters scored in 107 non-avian theropod taxa (L=1,362; CI =0.195; RI=0.435). Black silhouettes taken from phylopic.org (artist: Scott Hartman). I. s.: *Incertae sedis*.

Figure 5. Dentition-based synapomorphies in Carcharodontosauridae. The dental synapomorphies 98, 99 and 109 constrain the clade Carcharodontosaurinae. Black silhouette taken from phylopic.org (artist: Scott Hartman).

Table 1. Crown-based measurements taken on CPHNAMA VT-1502.

Color legend: green, measurements in millimeters; yellow, crown-based ratios; rose, number of denticles per five millimeters.

**APPENDIX**

Coding of CPHNAMA VT-1502 in Hendrickx et al.'s (2020) dentition based datamatrix. See Supplementary Data for the dentition-based character list.

CPHNAMA VT-1502

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**APPENDIX**

Coding of CPHNAMA VT-1502 in Hendrickx et al.'s (2020a) dentition based datamatrix.

See Supplementary Data for the dentition-based character list.

CPHNAMA VT-1502

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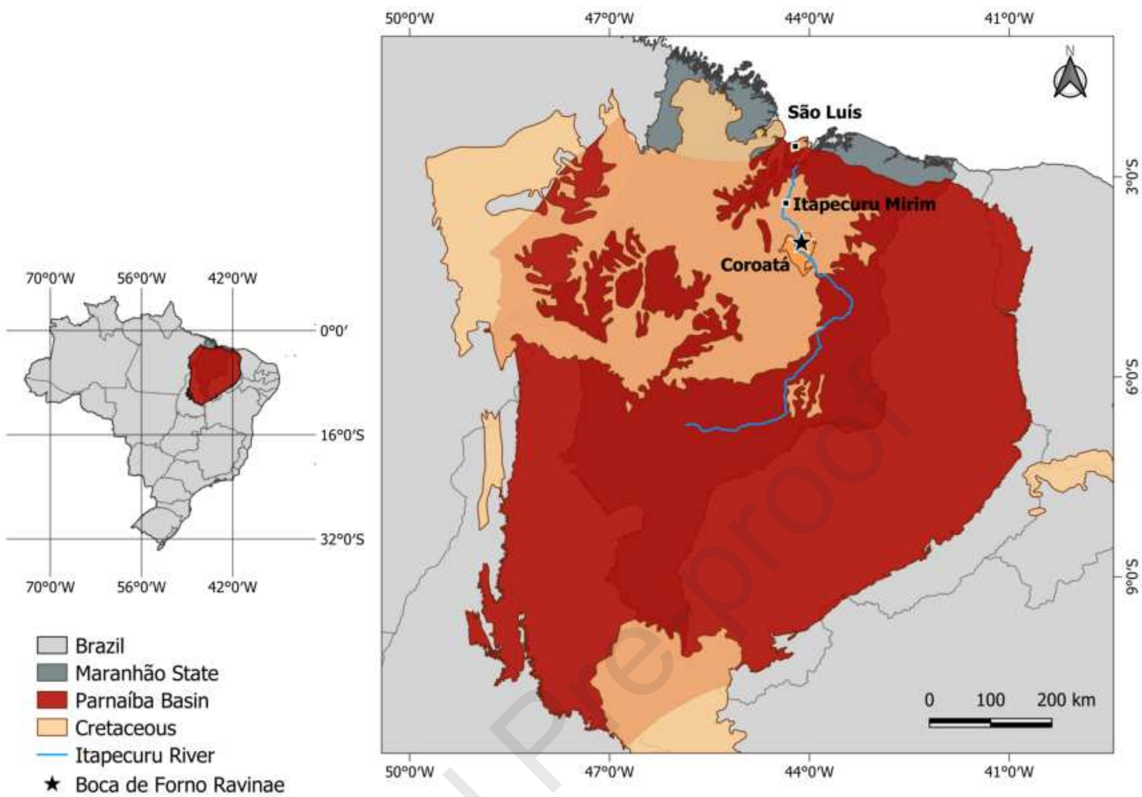
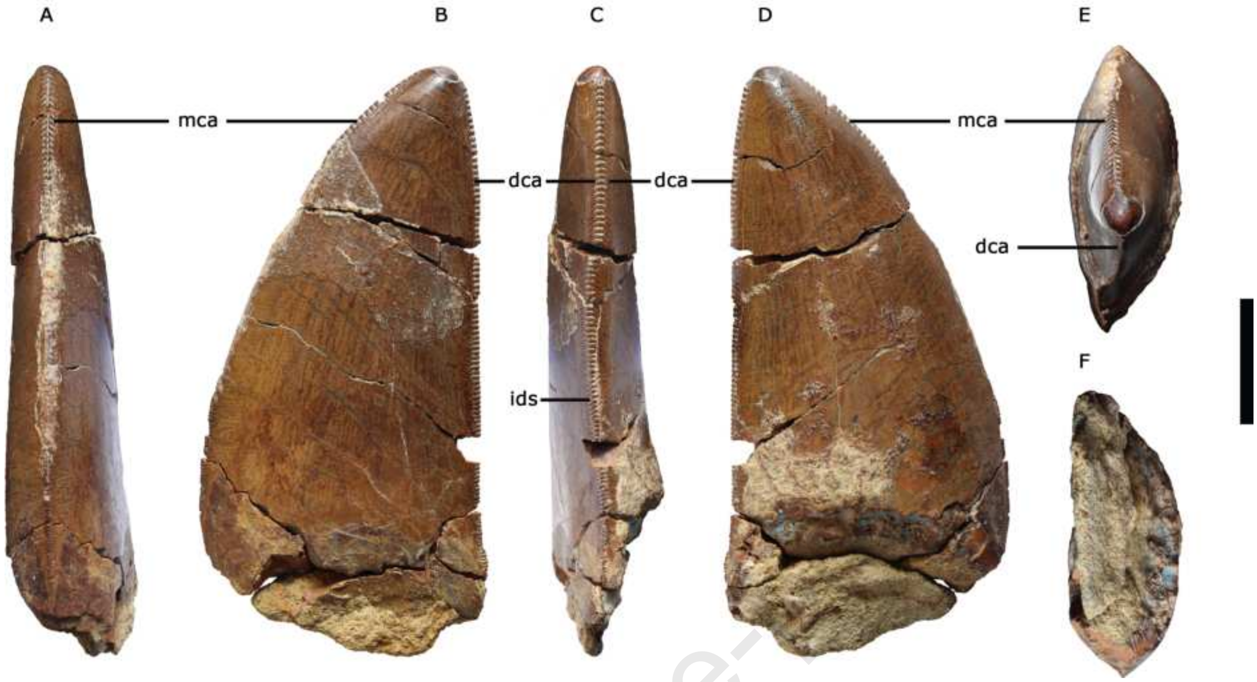
| CBL | CBW | CH | AL | CBR | CHR | MCL | MCW | MCR | MC | DC |
|---|---|---|---|---|---|---|---|---|---|---|
| 22.8 | 8.78 | 42.8 | 42.7 | 0.39 | 1.88 | 18.7 | 7.29 | 0.39 | 10 | 11 |



50°0'W
47°0'W
44°0'W
41°0'W
São Luís
Itapecuru Mirim
Coroatá
3°0'S
6°0'S
9°0'S
0 100 200 km
70°0'W
56°0'W
42°0'W
0°0'
16°0'S
32°0'S
Brazil
Maranhão State
Parnaíba Basin
Cretaceous
Itapecuru River
Boca de Forno Ravinae


A
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mca
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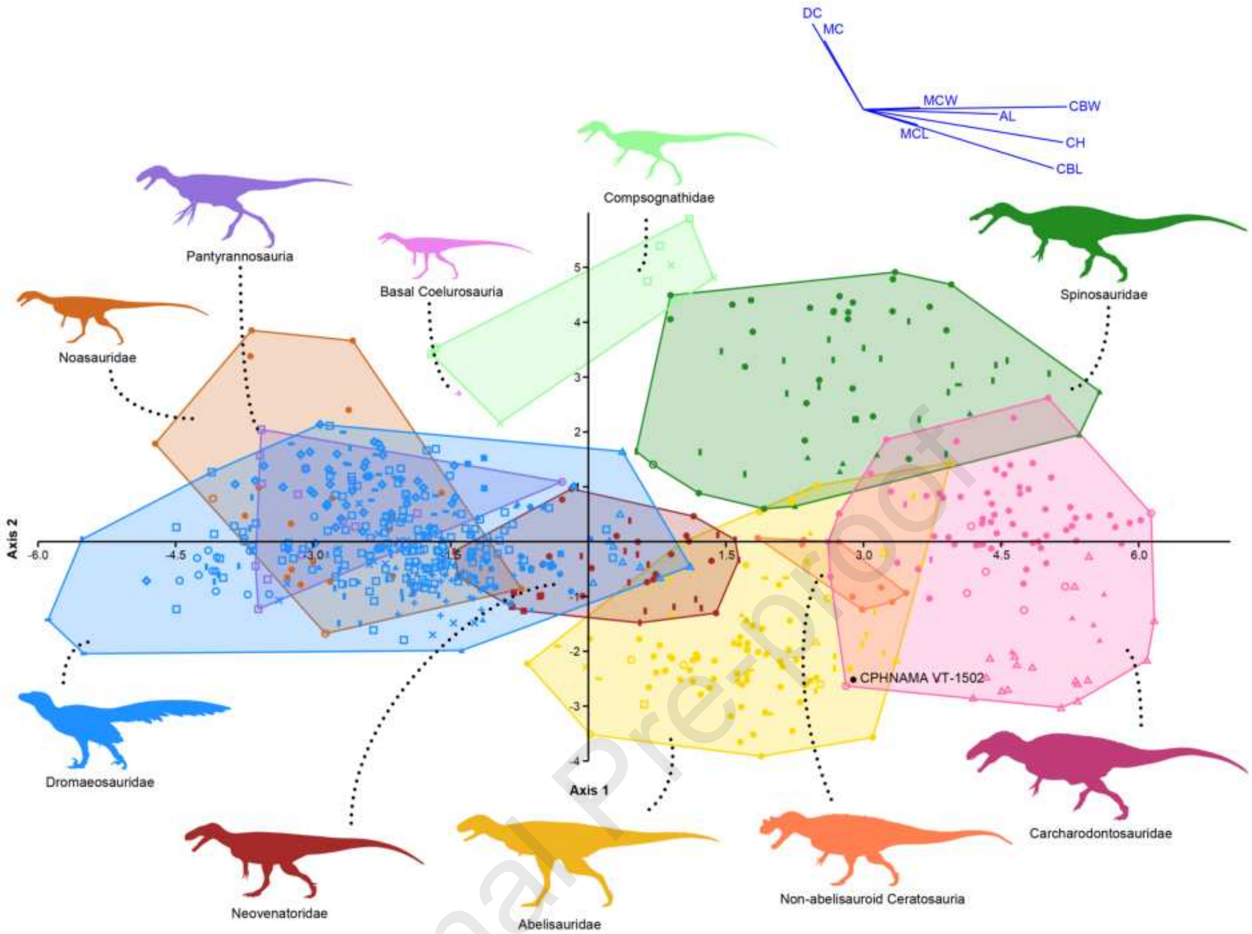
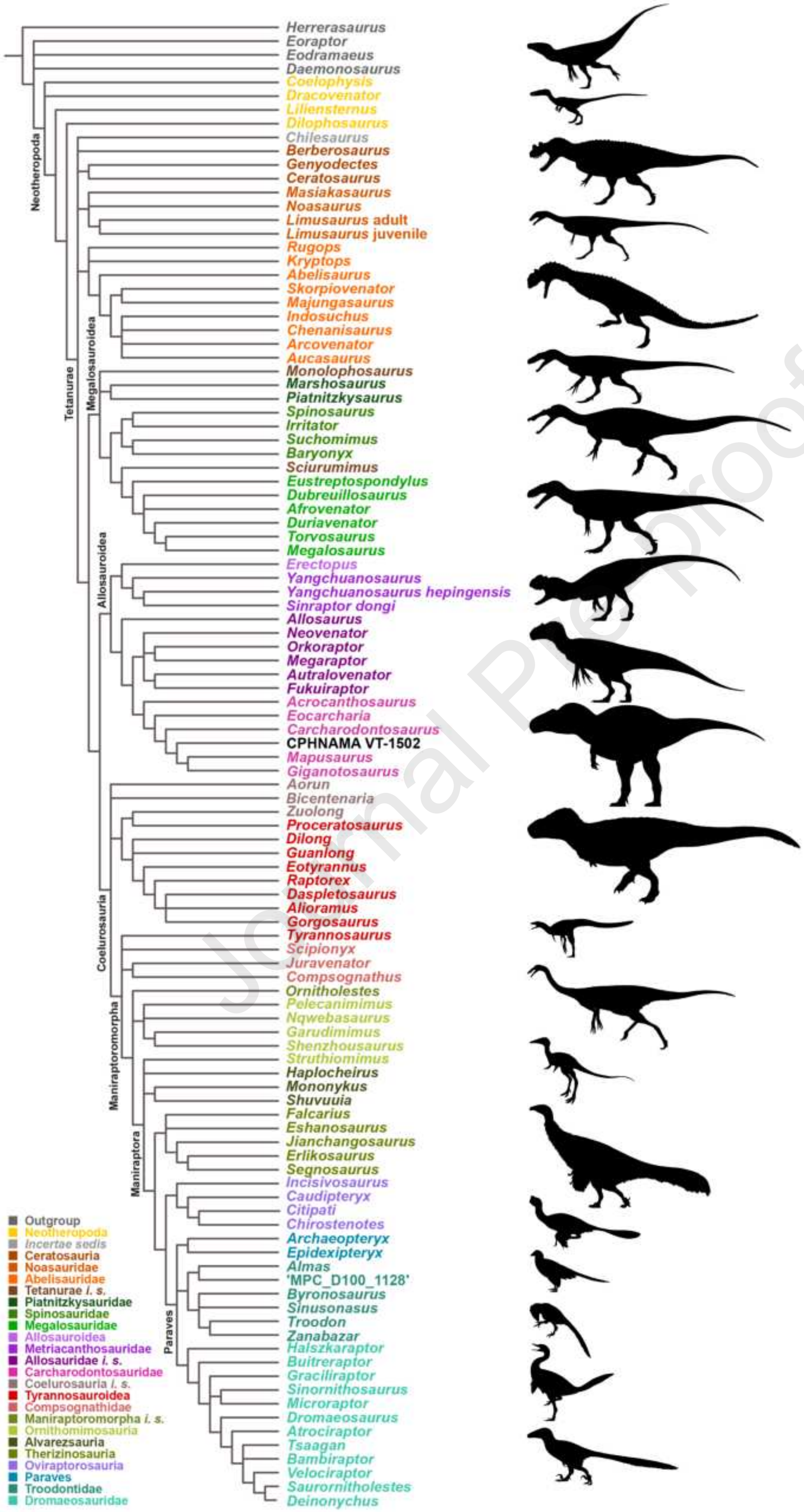
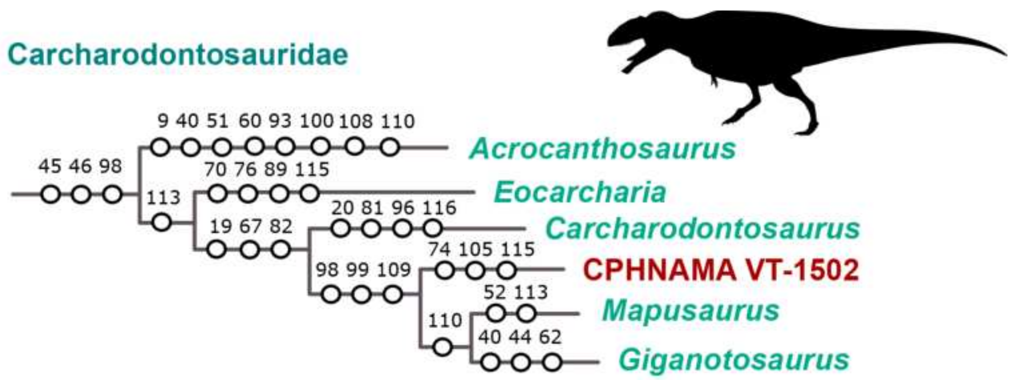

DC
MC
MCW
AL
CBW
MCL
CH
CBL
Compsognathidae
Pantyrannosauria
Basal Coelurosauria
Noasauridae
Spinosauridae
Axis 2
Axis 1
-6.0
-4.5
-3.0
-1.5
1.5
3.0
4.5
6.0
5
4
3
2
1
-1
-2
-3
-4
CPHNAMA VT-1502
Dromaeosauridae
Neovenatoridae
Abelisauridae
Non-abelisauroid Ceratosauria
Carcharodontosauridae


Herrerasaurus
Eoraptor
Eodramaeus
Daemonosaurus
Coelophysis
Dracovenator
Liliensternus
Dilophosaurus
Chilesaurus
Berberosaurus
Genyodectes
Ceratosaurus
Masiakasaurus
Noasaurus
Limusaurus adult
Limusaurus juvenile
Rugops
Kryptops
Abelisaurus
Skorpiovenator
Majungasaurus
Indosuchus
Chenanisaurus
Arcovenator
Aucasaurus
Monolophosaurus
Marshosaurus
Piatnitzkysaurus
Spinosaurus
Irritator
Suchomimus
Baryonyx
Sciurumimus
Eustreptospondylus
Dubreuillosaurus
Afrovenator
Duriavenator
Torvosaurus
Megalosaurus
Erectopus
Yangchuanosaurus
Yangchuanosaurus hepingensis
Sinraptor dongi
Allosaurus
Neovenator
Orkoraptor
Megaraptor
Autralovenator
Fukuiraptor
Acrocanthosaurus
Eocarcharia
Carcharodontosaurus
CPHNAMA VT-1502
Mapusaurus
Giganotosaurus
Aorun
Bicentenaria
Zuolong
Proceratosaurus
Dilong
Guanlong
Eotyrannus
Raptorex
Daspletosaurus
Alioramus
Gorgosaurus
Tyrannosaurus
Scipionyx
Juravenator
Compsognathus
Ornitholestes
Pelecanimimus
Nqwebasaurus
Garudimimus
Shenzhousaurus
Struthiomimus
Haplocheirus
Mononykus
Shuvuuia
Falcarius
Eshanosaurus
Jianchangosaurus
Erlikosaurus
Segnosaurus
Incisivosaurus
Caudipteryx
Citipati
Chirostenotes
Archaeopteryx
Epidexipteryx
Almas
'MPC_D100_1128'
Byronosaurus
Sinusonasus
Troodon
Zanabazar
Halszkaraptor
Buitreraptor
Graciliraptor
Sinornithosaurus
Microraptor
Dromaeosaurus
Atrociraptor
Tsaagan
Bambiraptor
Velociraptor
Saurornitholestes
Deinonychus
Neotheropoda
Tetanurae
Megalosauroidea
Allosauroidea
Coelurosauria
Maniraptoromorpha
Maniraptora
Paraves
Outgroup
Neotheropoda
Incertae sedis
Ceratosauria
Noasauridae
Abelisauridae
Tetanurae i. s.
Piatnitzkysauridae
Spinosauridae
Megalosauridae
Allosauroidea
Metriacanthosauridae
Allosauridae i. s.
Carcharodontosauridae
Coelurosauria i. s.
Tyrannosauroidea
Compsognathidae
Maniraptoromorpha i. s.
Ornithomimosauria
Alvarezsauria
Therizinosauria
Oviraptorosauria
Paraves
Troodontidae
Dromaeosauridae


Carcharodontosauridae
9 40 51 60 93 100 108 110
Acrocanthosaurus
45 46 98
70 76 89 115
Eocarcharia
113
20 81 96 116
19 67 82
Carcharodontosaurus
74 105 115
98 99 109
CPHNAMA VT-1502
52 113
Mapusaurus
110
40 44 62
Giganotosaurus

**Declaration of interests**

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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