

Original Article

Biogeography of theropod dinosaurs during the Late Cretaceous: evidence from central South America

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ABSTRACT

In central South America, theropod remains are relatively scarce in comparison to the southern part of the continent, with shed teeth being the primary fossils found in this region. We examined 179 isolated teeth from the Bauru Basin, Brazil, using linear discriminant analysis (LDA; $N = 178$) and phylogenetic analysis ($N = 174$). The LDA used eight measurements, and the phylogenetic analysis used seven morphotypes. Although the results of the LDA suggest the presence of various South American theropod clades, such as Carcharodontosauridae, Noasauridae, and Spinosauridae, the phylogenetic analysis using a constrained dentition-based matrix classified the morphotypes as Abelisauridae (morphotypes I–IV, VI, and VII) and Therizinosauria (morphotype V). Given the considerable number of homoplastic characters and missing data, the phylogenetic analyses could not precisely determine the taxonomy of morphotypes V, VI, and VII in the unconstrained dataset. Morphological comparisons, nevertheless, strongly suggest that all morphotypes should be classified as abelisaurid theropods. We propose that the palaeogeographical distribution of Abelisauridae in South America was influenced by climatic conditions. These apex carnivores are likely to have adapted well to increased climate changes that led to semi-arid conditions. Our research sheds light on the evolutionary and ecological aspects of theropod dinosaurs in this region, contributing to a better understanding of the ancient ecosystems of central South America.

Keywords: Bauru Basin; Brazil; Gondwana; morphometry; cladistics; tooth crown

INTRODUCTION

Theropod dinosaurs from South America are known from several localities (e.g. [Bittencourt and Langer 2011](#), [Novas et al.](#)

[2015](#), [Canale et al. 2022](#), [Langer et al. 2022](#)), but especially from Patagonia, Argentina, which is considered to have the richest record of dinosaurs from Gondwana ([Novas et al. 2013](#)). The

southern part of the continent is suitable for yielding fossil remains owing to its vast arid areas, sparse vegetation cover, and abundant exposed rocks (Cashmore and Butler 2019). Conversely, despite the vast territory of Brazil, its dense vegetation cover and higher chemical weathering make finding fossils more difficult (Bittencourt and Langer 2011), which might be causing a bias in our understanding of Gondwanan dinosaur diversity and distribution. That is why any information from fossils from this area is particularly relevant.

Several new theropod dinosaurs from Brazil have been described in the last few decades and are helping to fill gaps in the evolution of ceratosaurs (Langer *et al.* 2019, Zaher *et al.* 2020, de Souza *et al.* 2021) and spinosaurs (Kellner and Campos 1996, Sues *et al.* 2002, Sales and Schultz 2017, Schade *et al.* 2023), for example. Other records and species, however, have been described based on very fragmentary materials (Delcourt and Iori 2020, Brum *et al.* 2021, Iori *et al.* 2021), but they are still important because they help to reveal part of the hidden diversity of dinosaurs from central South America.

Central South America has important fossiliferous geological units dating from the Cretaceous (Bittencourt and Langer 2011). One of them is the Upper Cretaceous Bauru Group of the Bauru Basin, which preserves an exceptional diversity of nearly complete and articulated crocodyliforms (Zaher *et al.* 2006, Nascimento and Zaher 2010, Pol *et al.* 2014, Godoy *et al.* 2016, Bandeira *et al.* 2018, Darlim *et al.* 2021, Langer *et al.* 2022, Marchetti *et al.* 2022). Although also diverse, its record of dinosaurs is mostly fragmentary (Bandeira *et al.* 2018, Brum *et al.* 2021, Delcourt and Langer 2022, Langer *et al.* 2022, Navarro *et al.* 2022, Silva Junior *et al.* 2022), with rare exceptions of partly articulated specimens (Kellner and de Azevedo 1999, Kellner *et al.* 2006a, Silva Junior *et al.* 2022). Theropods from the Bauru Group include mostly Abelisauroida (Brum *et al.* 2018, Delcourt and Iori 2020, Iori *et al.* 2021), but there is also evidence of Megaraptora (Méndez *et al.* 2012, Martinelli *et al.* 2013) and Maniraptora (Machado *et al.* 2008, Candeiro *et al.* 2012b, Delcourt and Grillo 2014, Brum *et al.* 2021). Theropod bone material is comparatively rare in the unit and always very fragmentary and disarticulated, but isolated teeth are abundant and diverse (Ghilardi and Fernandes 2011, Tavares *et al.* 2014, Brusatte *et al.* 2017, Delcourt *et al.* 2020a, Langer *et al.* 2022).

The Caiuá Group (Lower Cretaceous) of the Bauru Basin, in contrast, has exceptionally preserved fossils of pterosaurs and dinosaurs (Manzig *et al.* 2014, Kellner *et al.* 2019, Langer *et al.* 2019, de Souza *et al.* 2020, 2021), including specialized forms of theropods (e.g. *Berthasaura leopoldinae* Souza *et al.*, 2021). Its known dinosaur diversity is low when compared with the Bauru Group, with only two species of dinosaurs having been described so far, both abelisauroids (i.e. *Vespersaurus paranaensis* Langer *et al.*, 2019 and *Berthasaura*). However, dinosaur body fossils from this unit have been discovered only recently, and there is still much to be explored and described.

Another important fossiliferous geological unit of central South America, dating to the end of the Cretaceous, is located in the Mato Grosso state. The ‘Cambambe Basin’ (Upper Cretaceous) has yielded several dinosaur remains (Kellner and Campos 2002, Franco-Rosas *et al.* 2004, Bittencourt and Langer 2011, Sales *et al.* 2018, Bandeira *et al.* 2019), but only one formal species has been described from it so far: the abelisaurid *Pycnonemosaurus nevesi*

(Kellner and Campos, 2002 (Kellner and Campos 2002, Delcourt 2017)), based on an incomplete skeleton. The theropod record of the unit additionally includes teeth referred to abelisaurids (Bittencourt and Kellner 2002, Sales *et al.* 2018) and a mid-caudal centrum attributed to a megaraptoran (Sales *et al.* 2018). The depositional context of the ‘Cambambe Basin’ is still a subject of ongoing debate in the geoscientific community (Kuhn and da Paz 2020). Nevertheless, some authors have suggested a chronocorrelation between depositional events from the upper interval of the Adamantina and Presidente Prudente formations and the lowermost interval of Marília Formation of the Bauru Group based on taxonomic identification of some materials (Brusatte *et al.* 2017) (but see ‘The evolution of knowledge on the Cretaceous in Southeast Brazil’ below).

Despite the relatively poor record of theropod skeletal material from the Bauru Group and the ‘Cambambe Basin’, the dental record of both units is abundant and has increased in recent years (e.g. Candeiro *et al.* 2004, 2006, Ghilardi and Fernandes 2011, Tavares *et al.* 2014, Delcourt and Grillo 2018a), easily surpassing the non-dental record, especially in the Bauru Group. The morphology of isolated theropod teeth is relatively variable, especially those from the Bauru Group, which led some authors to classify them into different theropod clades using external morphological characteristics. These isolated theropod teeth have been classified as belonging to Carcharodontosauridae (Candeiro *et al.* 2004, 2006, 2012c, Azevedo *et al.* 2013), Spinosauridae (Candeiro *et al.* 2004), Abelisauridae (Candeiro *et al.* 2004, 2006, Tavares *et al.* 2014, Delcourt and Grillo 2018a, Delcourt *et al.* 2020a), and Dromaeosauridae (Ghilardi and Fernandes 2011, Tavares *et al.* 2014). The record of carcharodontosaurids and spinosaurids has recently been disproved and reinterpreted as belonging to abelisaurids based on phylogenetic analyses (Delcourt and Grillo 2018a, Delcourt *et al.* 2020a) and undetermined theropods (Candeiro *et al.* 2006), respectively. However, most teeth remain unidentified and others need to be reassessed in light of new methods for taxonomic identification of isolated teeth (Hendrickx and Mateus 2014, Hendrickx *et al.* 2015, 2019).

In this paper, we assess or reassess the theropod dental record from the Upper Cretaceous of central South America, focusing on the Bauru Basin. We analyse material collected and housed in different collections, including specimens that were burned in the Museu Nacional (National Museum) fire in 2018. Fortunately, hundreds of high-quality photographs were taken before the accident. The goal of this study is to describe and identify the theropod fauna from the Bauru Basin based on their large dental record, with the aim of understanding their diversity, palaeogeographical distribution, and possible relationship with the palaeoenvironments of central South America at the end of the Cretaceous.

The evolution of knowledge on the Cretaceous in Southeast Brazil

The Bauru Basin has a long history of disagreements in understanding its geological deposits. Although its deposits have been known since the late 19th century (Gonzaga de Campos 1889), the first proposal for stratigraphic organization is attributed to Soares *et al.* (1980), who proposed a simple vertical filling of Mesozoic units belonging to the Paraná Basin. This understanding of the Bauru Basin as being associated with the

geological history of the Paraná Basin was reaffirmed by Milani (1997) within the concept of allosequence. The recognition of Bauru deposits as a separate sedimentary basin comes from the works of Fernandes and Coimbra (1996, 2000), who also proposed a chrono-correlation between the two major sedimentary environments, creating the Bauru and Caiuá groups and an extensive number of formations and members, although subsurface data (core drills) were not included. One of the most striking characteristics of the Bauru Basin, the 'geosols' or palaeosol horizons, was first used by Fulfaro *et al.* (1999a, b) to individualize the aeolian deposits at the base as the Caiuá Basin.

The three-dimensionality of the basin arises with a large volume of drilling data and geophysical profiles provided by Paula e Silva *et al.* (2005), who presented a new operational proposal for subsurface data, encompassing part of the units previously defined by Soares *et al.* (1980) and Fernandes and Coimbra (2000). Faced with the incongruence observed between the proposal made by Fernandes and Coimbra (2000) and its field application, Zaher *et al.* (2006), based on the results presented by Riccomini (1997) and Paula e Silva *et al.* (2005), suggested a new stratigraphic model that resumed the classic nomenclature of Soares *et al.* (1980), incorporating the Araçatuba Formation (*sensu* Suguio 1980) and the Presidente Prudente Formation (*sensu* Fernandes and Coimbra 2000).

Pires-Domingues *et al.* (2007) were amongst the first authors to highlight the importance of choosing an appropriate geological model for palaeontological studies in the Bauru Basin. Until then, 'biogeographical' studies were based on classical stratigraphy (Goldberg and Garcia 2000), taxon grouping (Santucci and Bertini 2001), or taxonomic lists (Candeiro *et al.* 2006), which provided an assessment of the faunal diversity present in the fossil assemblages of the Bauru Basin. However, there was still insufficient information regarding sedimentary environments, active tectonics, contemporaneity of environments, and the interaction of faunas in a spatiotemporal context. These absences were obstacles to a more reliable analysis of the biogeographical events.

The difficulty in achieving a representative stratigraphic model for the geological history of the Bauru Basin lies in the fact that it covers a vast area (379 362 km² continuously, plus occurrences in Mato Grosso, Brazil) with only 270 m of sedimentary column and a significant basal unconformity, leading to uncertainty about the onset of sedimentation. The record of the Bauru Basin might extend even further, with assignments in the Upper Cretaceous of Paraguay and Uruguay (e.g. Veroslavsky *et al.* 2019). This information gap has been filled in recent years, and as a result, our understanding of the biogeography of the Late Cretaceous central South American fauna should be revised.

The genetic model for the formation of the Bauru Basin was revised by Menegazzo *et al.* (2016), who suggested that the accommodation space was driven by the retroarc foreland system that developed in response to Andean orogenic events during the Cenomanian and Palaeogene. Within this model, the Bauru (Brazil), Parecis (Brazil), and Andean [Santa Cruz (Bolivia), Potosi (Bolivia), and Acre (Brazil) localities] basins would have their sedimentation sequences synchronized in time and equivalent in depth of fill.

In parallel, Batezelli and Ladeira (2016) found similarities between the Bauru, Parecis, and San Francisco basins using outcrop correlations, architectural and system tract analysis, thus reinforcing the contemporaneity of regional unconformities between neighbouring basins. Delgado *et al.* (2021) demonstrated that all sequence boundaries in the Bauru Basin are marked by deposition gaps large enough for the formation of soil horizons. This study emphasizes the importance of palaeosol studies from 1999, which were neglected for 20 years.

The lack of continuity of Upper Cretaceous deposits of the Bauru Basin and the lack of a comprehensive approach to the basin (often focused on the states of São Paulo, Minas Gerais, and Paraná) led to regional names for the same depositional cycles. The best example of this is the presence of the Bauru Basin in the state of Mato Grosso. Some authors (e.g. Bandeira *et al.* 2019) treat it as unquestionable, but since the work of Coimbra (1991) it has been suggested that the Cretaceous of Chapada dos Guimarães constitutes its own basin. There is significant discussion in the scientific community, ranging from the nature of the basin to whether it represents a single geological unit or a stacking of multiple formations. Sales *et al.* (2018) present this discussion in detail and opt for the proposal of treating it as the 'Cambembe Unit' within the Bauru Basin (an informal stratigraphic unit). Although there are recent studies that support the proposal of the Cambembe/Poxoréu Basin (e.g. Kuhn and da Paz 2020), they do not address the issues raised by Sales *et al.* (2018).

Finally, when creating geological maps of this region at a scale of 1:250 000 (sheets SD-21-Z-D and SE-21-X-B), the Geological Survey of Brazil (Abreu Filho and de Albuquerque 2016) concluded that there are deposits from the Marília Formation (Bauru Basin) overlying the Bauru Group in Mato Grosso. Figure 1 illustrates the different proposals presented at this point.

Convergent thinking about the Bauru Basin

Accommodation space

The apparent disagreement among authors reflects observations from different sets of evidence and does not involve refutations of the same evidence. The mechanisms of accommodation space in the basin exhibit a mixed configuration of thermomechanical subsidence (Milani 1997) and depocentres formed by structural reactivation (Riccomini 1997). This mixed nature implies non-uniformity and a variable rate of subsidence across the basin domain. Tectonic control operates at the following different scales: (i) at the outcrop scale, evidenced by the formation of fossil assemblages (Pires-Domingues *et al.* 2007) and seismites (Coimbra and Fernandes 1992, Alessandretti *et al.* 2020); (ii) at the local scale, evidenced by tectonism along the borders of the basin, creating source areas for sediments (Menegazzo *et al.* 2016, Dias *et al.* 2018); and (iii) at the regional scale, evidenced by the migration of depocentres over time in response to the geodynamics of the retroarc foreland system (Suguio *et al.* 1977, Milani 1997, Menegazzo *et al.* 2016).

Sediment supply

The evidence of palaeosol horizons in all stratigraphic units (Delgado *et al.* 2021) and the high interdigitation between the same units present in the same outcrops (Fernandes and

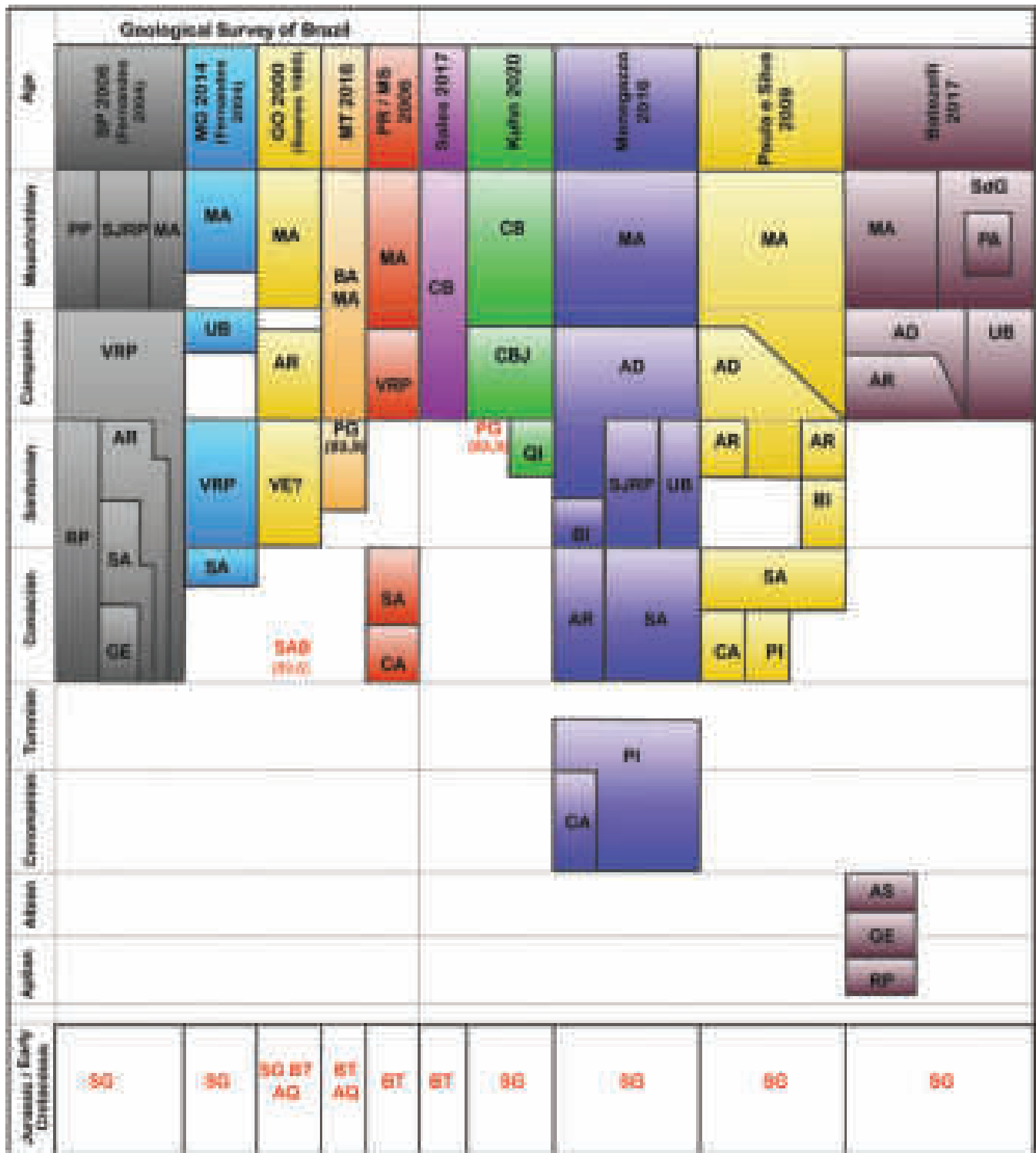


Figure 1. Comparative time chart of generalized stratigraphic tables from different authors. Abbreviations of federal states: GO, Goiás; MG, Minas Gerais; MS, Mato Grosso do Sul; MT, Mato Grosso; SP, São Paulo. Abbreviations of stratigraphic units: AD, Adamantina; AR, Araçatuba; BA, Bauru (Grupo Indiviso); BI, Birigui; CA, Caiuá; CB, Cambambé; CBJ, Cachoeira Bom Jardim; GE, Goio Erê; MA, Marília; PG, Paredão Grande; PI, Pirapozinho; PP, Presidente Prudente; QI, Quilombinho; RP, Rio Paraná; SA, Santo Anastácio; SAB, Santo Antônio da Barra; SdG, Serra da Galga; SJRP, São José do Rio Preto; UB, Uberaba; VE, Verdinho; VRP, Vale do Rio do Peixe. Abbreviations of basement: AQ, Aquidauana; BT, Botucatu; CG, Serra Geral.

Coimbra 2000, Paula e Silva *et al.* 2005, Pires-Domingues *et al.* 2007) show that the high-frequency hiatus, despite its wide range, is not continuous throughout the entire basin.

The Bauru Basin has been considered as the record of the Upper Cretaceous in the classical understanding (Fernandes and Coimbra 2000, Zaher *et al.* 2006). The most recent

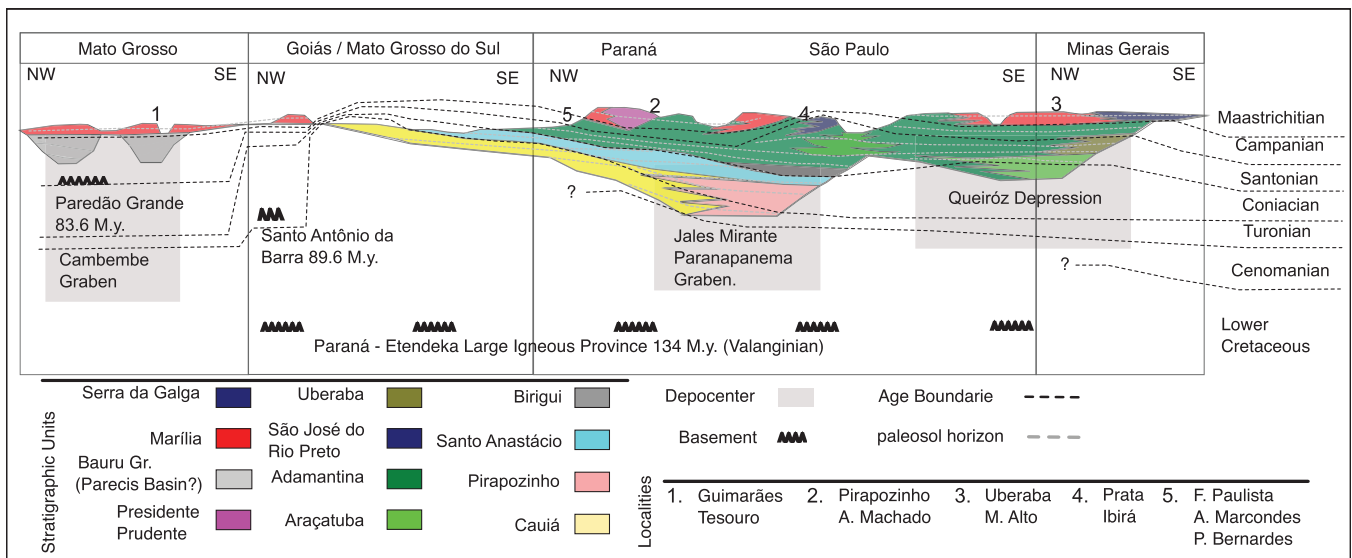


Figure 2. Geological model of the Bauru Basin in Brazil.

stratigraphic proposals, which have gathered a large volume of secondary palaeontological and isotopic data (Menegazzo *et al.* 2016, Batezelli 2017), mostly converge to this understanding. However, the proposal by Batezelli (2017) pushes back the onset of sedimentation to the Lower Cretaceous, and the only work using this proposal until now is a short conference note about the occurrence of a *Caiuajara dobruskii* Manzig *et al.*, 2014 bone bed in the Paraná state (Guimarães *et al.* 2012). Since the full article about this bonebed was published by the same research group (Manzig *et al.* 2014), the species has been attributed to the Upper Cretaceous, aligning with the understanding presented by Menegazzo *et al.* (2016).

Stratigraphic units

A significant part of the classical stratigraphic division of the Bauru Basin (Soares *et al.* 1980) is still validated by subsequent authors, beginning with the Caiuí and Santo Anastácio formations. The Caiuí Formation comprises palaeodunes and other palaeodesert facies, whereas the Santo Anastácio Formation represents sand sheets facies overlain by palaeosol horizons. Surface outcrops of these formations are observed in the states of Mato Grosso do Sul and Paraná. The Pirapozinho Formation (*sensu* Paula e Silva *et al.* 2005, 2009) is a subsurface unit consisting of lacustrine or floodplain sediments interbedded laterally with the Caiuí desert. The Pirapozinho Formation is limited to the Jales Mirante Parapanema Graben (Pires-Domingues *et al.* 2007) and represents a humid valley of the Caiuí desert. The Santo Anastácio Formation overlies both these formations.

Following a well-defined unconformity at the top of the Santo Anastácio Formation, another subsurface unit, the Birigui Formation, represents a fluvial braided system restricted to the central part of the basin (Paula e Silva *et al.* 2009). The Araçatuba and Adamantina formations extend to the easternmost part of the basin, primarily within the state of São Paulo. The Araçatuba Formation represents a palaeoswamp environment, and the Adamantina Formation represents a fluvial braided system (Soares *et al.* 1980, Suguio 1980, Paula e Silva *et al.* 2005, 2009, Zaher *et al.* 2006 and others). The westward and central

migration of the Araçatuba Formation throughout time suggests horizontal changes in the local base level (Batezelli 2017). The Uberaba and São José do Rio Preto formations (Fernandes and Coimbra 2000) are units with more restricted occurrence. Both formations are characterized by the presence of conglomerates, poorly mature grains, and sandstone amalgamation. These characteristics can be interpreted as borders or proximal environments of the depositional system within the basin. The Marília Formation (*sensu* Soares *et al.* 1980), Presidente Prudente Formation (Fernandes and Coimbra 2000), and Serra da Galga Formation (Soares *et al.* 2020) represent the last units of the Cretaceous. The proximal fluvial and alluvial fans of the Marília Formation are widely distributed along the basin borders, characterized by a discordant base and well-contrasted facies with overlain beds. These features make the Marília Formation a point of consensus among all authors. A synthesis of this knowledge is illustrated in Figure 2.

MATERIALS AND METHODS

Morphological and morphometric abbreviations

AL, apical length; CBL, crown base length; CBR, crown base ratio; CBW, crown base width; ce, cervix; CH, crown height; CHR, crown height ratio; co, crown; DC, distocentral denticle density; dca, distal carina; DSDI, denticle size density index; ids, interdenticular sulcus; MC, mesiocentral denticle density; mca, mesial carina; MCL, mid-crown length; MCW, mid-crown width; ro, root.

Institutional abbreviations

CPP, Centro de Pesquisas Paleontológicas 'Llewellyn Ivor Price', Peirópolis, Brazil; LPP, Laboratório de Paleocologia e Paleocnologia, São Carlos, Brazil; MCT, Museu de Ciências da Terra, Rio de Janeiro, Brazil; MN, Museu Nacional/UFRJ, Rio de Janeiro, Brazil; MPMA, Museu de Paleontologia 'Prof. Antonio Celso de Arruda Campos', Monte Alto, Brazil; UFRJ, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil.

Material

The sampled material included in this study comes from nine sites located in different regions along the Bauru Basin (Fig. 3). The sites are attributed to the Marília Formation (Mato Grosso and Minas Gerais states), the Adamantina Formation (Minas Gerais and São Paulo states), and the Presidente Prudente Formation (São Paulo state). Table 1 shows the main attributes of these sites.

Although the sites have other fossil occurrences (e.g. Kellner *et al.* 2006, Bittencourt and Langer 2011, Delcourt 2017, Sales *et al.* 2018, Langer *et al.* 2022, Navarro *et al.* 2022), the concentrations of teeth are always found in well-defined bonebeds with layers of geometry and isolated horizons within the site. All sedimentary facies are associated with well-known environments that contribute to the time averaging of the fossil record.

The materials are housed in different palaeontological collections in Brazil (CPP, LPP, MCT, MN, MPMA, and UFRJ).

The linear measurements of 178 crowns were taken and added to a modified dataset from the studies by Hendrickx *et al.* (2020) and Delcourt and Grillo (2018a). This modified dataset also includes the linear measurements of 10 crowns from the study of Tavares *et al.* (2014), resulting in a large database of 1515 dental elements.

The anatomical, positional, directional, and morphometric nomenclatures for the teeth follow the recommendations of Smith and Dodson (2003) and Hendrickx *et al.* (2015) (Fig. 4).

All the Bauru Basin crowns were photographed using a Canon EOS Rebel T3i camera and a Canon EF-S 60 mm f/2.8

Macro USM lens in labial, lingual, apical, and basal views. Several detailed photographs were also taken in different non-morphological views.

The crowns that were housed in the Museu Nacional are still lost after the fire (O.N.G., personal observation; Lopes 2018). Nevertheless, all the material used in this research was photographed, and the photographs are available from the corresponding authors (R.D. and O.N.G.) and from the curators of Vertebrate Palaeontology at Museu Nacional (Sergio A. K. Azevedo and Luciana B. Carvalho) upon request.

Morphotypes

The teeth were categorized into different morphotypes to explore their taxonomic significance according to several features shared among them. The features used to separate the morphotypes followed previous detailed description of theropod teeth (Hendrickx and Mateus 2014, Hendrickx *et al.* 2019, 2020). To obtain the most complete picture of the theropod fauna of central South America during the Late Cretaceous, we reassessed the taxonomic affinities of the teeth published by Delcourt *et al.* (2020a) and Tavares *et al.* (2014) using the same method for the new unpublished teeth. Our final dataset contains 174 tooth crowns separated into seven morphotypes.

Phylogenetic analyses

To test the relationships of the Bauru Basin teeth, we performed a phylogenetic analysis using the dentition-based data matrix published by Hendrickx *et al.* (2020) and Meso *et al.* (2021a), which is

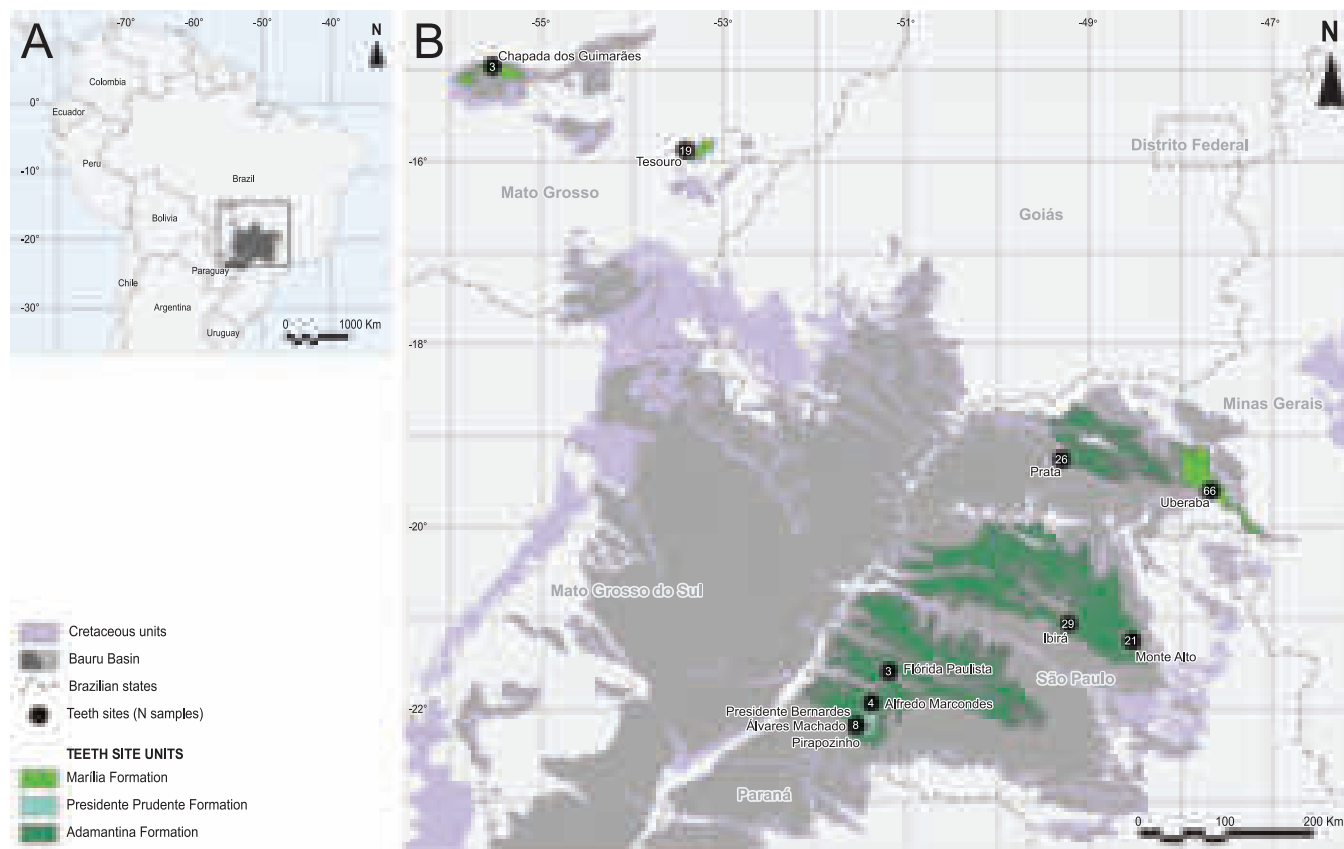


Figure 3. Location of teeth fossil sites. A, South American context. B, Bauru Basin and map of teeth outcrops by geological unit.

Table 1. Stratigraphic attributes of the sampled sites.

Localities	Formation	Age	Sedimentary facies
Chapada dos Guimarães	Marília	Maastrichtian	Proximal alluvial (calciferosus sandstones)
Tesouro	Marília	Maastrichtian	Amalgamated palaeosols
Flórida Paulista	Adamantina	Campanian/Maastrichtian	Channel-fill
Alfredo Mardondes	Adamantina	Campanian/Maastrichtian	Amalgamated palaeosol
Presidente Bernardes	Adamantina	Campanian/Maastrichtian	Amalgamated palaeosol
Pirapozinho	Presidente Prudente	Maastrichtian	Channel-fill
Álvares Machado	Presidente Prudente	Maastrichtian	Channel-fill
Prata	Adamantina	Campanian	Proximal alluvial (sandstones)
Ibirá	Adamantina	Campanian	Amalgamated palaeosol
Uberaba	Marília	Maastrichtian	Proximal alluvial (calciferosus sandstones)
Monte Alto	Marília	Maastrichtian	Amalgamated palaeosol

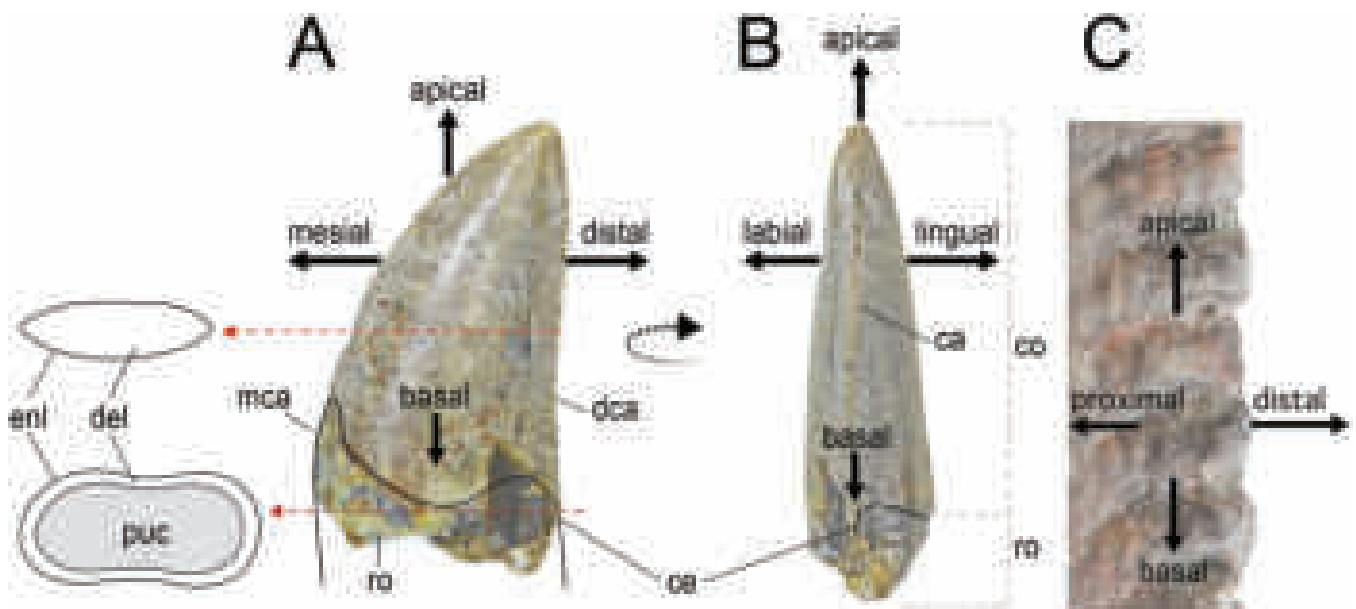


Figure 4. Schematic representation of a lateral theropod tooth, showing: labial view with mid-height and basal cross-sections (A), distal view (B) of LPP-PV 1102 (mirrored); and mesial denticles on the crown (C) of MCT.R. 859 (mirrored). Abbreviations: ca, carina; ce, cervix; co, crown; dca, distal carina; del, dentine layer; enl, enamel layer; mca, mesial carina; puc, pulp cavity; ro, root.

a modified version of the original matrix of [Hendrickx and Mateus \(2014\)](#). This modified data matrix encompasses 146 discrete dentition-based characters based on dentition information scored originally in 101 genus-level terminals and phylogenetically bracketed between *Herrerasaurus ischigualastensis* Reig, 1963 and *Archaeopteryx lithographica* Meyer, 1861 ([Hendrickx et al. 2020](#)).

The phylogenetic analyses were conducted following the parameters proposed by [Hendrickx et al. \(2020\)](#), in which the search of each analysis used a blend of the tree-search algorithms Wagner tree, TBR branch swapping, sectorial searches, Ratchet with perturbation phase stopped after 20 substitutions, and Tree Fusing with five rounds, until 100 hits of the same minimum tree length were achieved. The best trees found were subjected to a final round of TBR branch swapping, keeping up to 10 000 trees, using the TNT command 'xmult = hits 100 rss fuse 5 ratchet 20' followed by the 'bb' command. Any recovered most parsimonious trees had zero-length branches

collapsed. The consensus and retention indices were calculated using the 'Stats' script.

We enforced the constraints as in the studies by [Hendrickx et al. \(2020\)](#), [Delcourt et al. \(2020a\)](#), and [Meso et al. \(2021a\)](#) in the dentition-based dataset, and collapsed the trees after the search. All analyses were performed in TNT v.1.6 ([Goloboff and Morales 2023](#)). The constrain command was used to build a phylogram based on the backbone tree topology from the results of [Müller et al. \(2018\)](#) for non-neotheropod saurischians, [Ezcurra \(2017\)](#) for non-averostran neotheropods, [Rauhut and Carrano \(2016\)](#) for Ceratosauria, [Carrano et al. \(2012\)](#) and [Rauhut et al. \(2012, 2016\)](#) for non-coelurosaurian tetanurans, [Delcourt and Grillo \(2018b\)](#) for Tyrannosauoidea, and [Cau et al. \(2017\)](#) for neocoelurosaurs.

Differing from the method used by [Delcourt et al. \(2020a\)](#), in which each tooth crown was analysed individually, we followed [Meso et al. \(2021a\)](#) in scoring each dental

morphotype separately such that each of them was treated as a floating terminal. Morphotypes VI and VII were evaluated individually, then combined to assess their features as a single morphotype.

Morphometric analyses

The morphometric analysis was performed using the modified dataset available in the [Supporting Information](#). The data were log-transformed before analyses to better reflect a normally distributed multivariate dataset (Smith *et al.* 2005). The analyses were conducted using the statistical software PAST v.4.11 (Hammer *et al.* 2001). We took six different measurements using digital callipers (AL, CBL, CBW, CH, MCL, and MCW), and the denticles densities (DC and MC) were measured using Adobe Photoshop image edition software.

The first step of our morphometric analysis was to identify the morphospace for each tooth from the Bauru Group. For this first examination, we performed a linear discriminant analysis (LDA) following Delcourt and Grillo (2018a) and Delcourt *et al.* (2020a), in which taxa that were not recovered from South American Cretaceous rocks were excluded to reduce potential noise, which reduced the dataset from 1515 to 860 tooth crowns. Therefore, all theropods from the dataset were excluded, except for basal Coelurosauria, Ceratosauridae, Abelisauridae, Noasauridae, Spinosauridae, Neovenatoridae, Carcharodontosauridae, Compsognathidae, basal Pantyrannosauria, and Dromaeosauridae; the presence of these taxa in South American Cretaceous beds is supported by several reports (Naish *et al.* 2004, Rauhut 2004, Novas *et al.* 2013, Sales and Schultz 2017, Delcourt and Grillo 2018b, Langer *et al.* 2022). The modified dataset has 860 dental crowns, including the data from Tavares *et al.* (2014), Delcourt and Grillo (2018a), Hendrickx *et al.* (2020), and the 178 Brazilians specimens here added.

The LDA was conducted to create a morphospace in which the analysed clades (i.e. abelisaurid, noasaurid, spinosaurid, etc.) were separated maximally from each other. The teeth examined were labelled as ‘mystery specimens’ with ‘?’; allowing the algorithm to classify them according to which group they would be more similar to in the discriminant space (Hammer *et al.* 2001).

RESULTS

Systematic palaeontology

Dinosauria

Saurischia

Theropoda

Ceratosauria

Abelisauroidea

Abelisauridae

Gen. et sp. indet.

Morphotype I

The first morphotype encompasses typical abelisaurid lateral teeth characterized by their weakly distally curved crown, with a straight to slightly convex distal profile. The mesial and distal

denticulated carinae are always centrally positioned on their surfaces in mesial and distal views, respectively, and extend to the cervix or slightly below the cervical line. The distal carina is straight or weakly sigmoid, while the mesial carina is straight (never twisted). The crown is strongly to normally labiolingually compressed (CBR ranging from .4 to .6), and subsymmetrical in basal/apical view, with the lingual and labial profiles showing the same convexity, conferring a symmetrical lenticular cross-sectional outline in basal view. DSDI is typically close to one, and MC and DC have a denticle density between 9 and 15 denticles per 5 mm. Distal denticles are typically asymmetrically convex to distally hooked, and mesial denticles are asymmetrically convex and rarely hooked. There are often poorly to strongly developed interdental sulci between distal denticles and less frequently between mesial denticles. The enamel surface texture is irregular. Many teeth show poorly to well visible and sometimes numerous and closely spaced transverse undulations on the crown surface and more rarely pronounced marginal undulations next to the distal carina. There are variations in the crown elongations, with some crowns being particularly elongated (CHR close to 2.5), but typically normally elongated (CHR ~1.5–2.0).

Identification: Teeth from morphotype I are confidently referred as pertaining to the lateral dentition of young, subadult, and adult abelisaurids.

Specimens from Uberaba, Minas Gerais state, Marília Formation: CPP 002, CPP 021, CPP 121, CPP 123, CPP 124, CPP 127, CPP 129b, CPP 131, CPP 132, CPP 134, CPP 135, CPP 136, CPP 144, CPP 150, CPP 152, CPP 158, CPP 161, CPP 197, CPP 200, CPP 207, CPP 208, CPP 216, CPP 241, CPP 242, CPP 372, CPP 375-2, CPP 446, CPP 449, CPP 452-1, CPP 463, CPP 474, CPP 475, CPP 476, CPP 477, MCT.R. 893, MCT.R. 895 (Fig. 5), MCT.R. 897, MCT.R. 899, MCT.R. 900a, MCT.R. 900b, MCT.R. 900c, MCT.R. 908, MCT.R. 913a, MCT.R. 913b, MCT.R. 913c, MCT.R. 1961, MCT.R. 1962, MCT.R. 1964, MN 4509-V, and MN 4996-V.

Specimens from Ibirá, São Paulo state, Adamantina Formation: LPP-PV 1103, LPP-PV 1105, LPP-PV 1108, LPP-PV 1112 (Fig. 6), LPP-PV 1113, LPP-PV 1116, LPP-PV 1117, LPP-PV 1119, LPP-PV 1120, LPP-PV 1122, LPP-PV 1124, and LPP-PV 1127.

Specimens from Álvares Machado, São Paulo state, Presidente Prudente Formation: MN 4502-V/A, MN 4502-V/C, and MN 4505-V.

Specimen from Pirapozinho, São Paulo state, Presidente Prudente Formation: MN 5033-V.

Specimens from Prata, Minas Gerais state, Adamantina Formation: MN 6255-V, MN 6256-V, MN 6261-V (Fig. 7), MN 6265-V, MN 6267-V, MN 6271-V, MN 6278-V, MN 6283-V, MN 6285-V, MN 6286-V, MN 6293-V, MN 629?-V/A, and MN 629?-V/B?.

Specimens from Tesouro, Mato Grosso state, Marília Formation: MN 6821-V, MN 6823-V, MN 6825-V, MN 6835-V, MN 6841-V, MN 7328-V, MN 7330-V, MN 7333-V, and MN 7638-V.

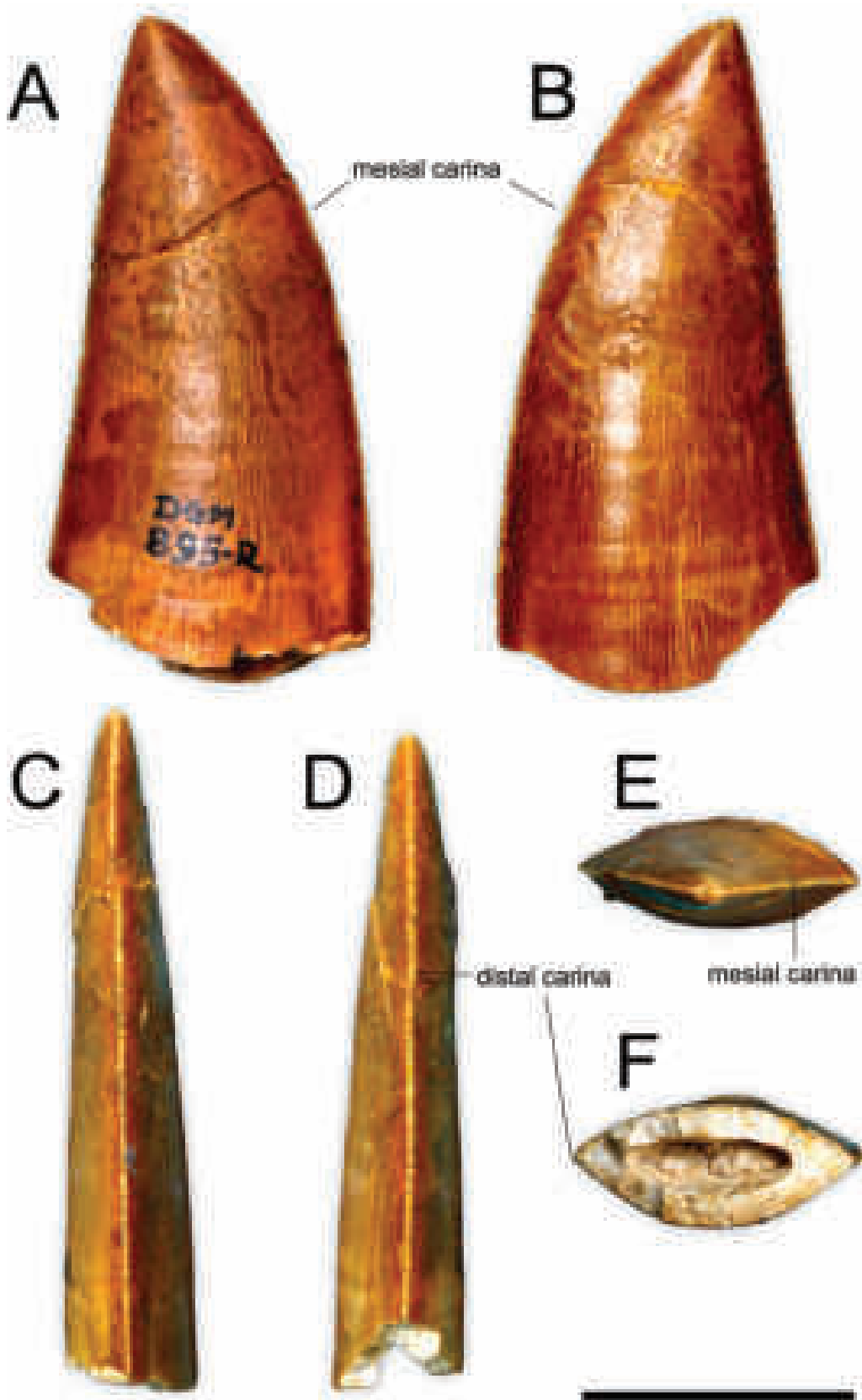


Figure 5. Abelisaurid theropod lateral tooth of morphotype I (MCT.R. 895) from Peirópolis, Minas Gerais state, Marília Formation, in lingual (A), labial (B), mesial (C), distal (D), apical (E), and basal (F) views. Scale bar: 20 mm.

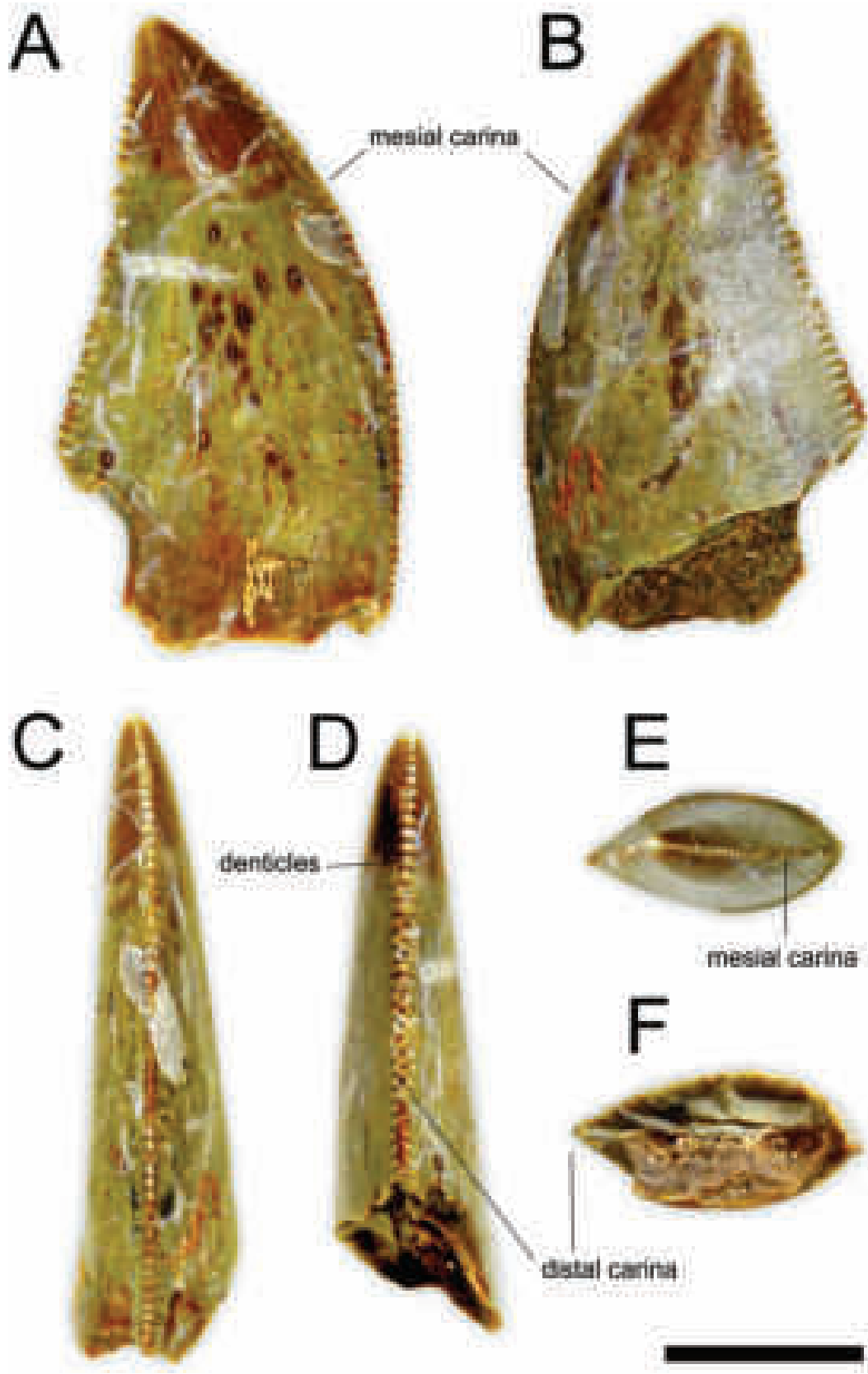


Figure 6. Abelosaurid theropod left lateral tooth of morphotype I (LPP-PV 1112) from Ibirá, São Paulo State, Adamantina Formation, in lingual (A), labial (B), mesial (C), distal (D), apical (E), and basal (F) views. Scale bar: 5 mm.

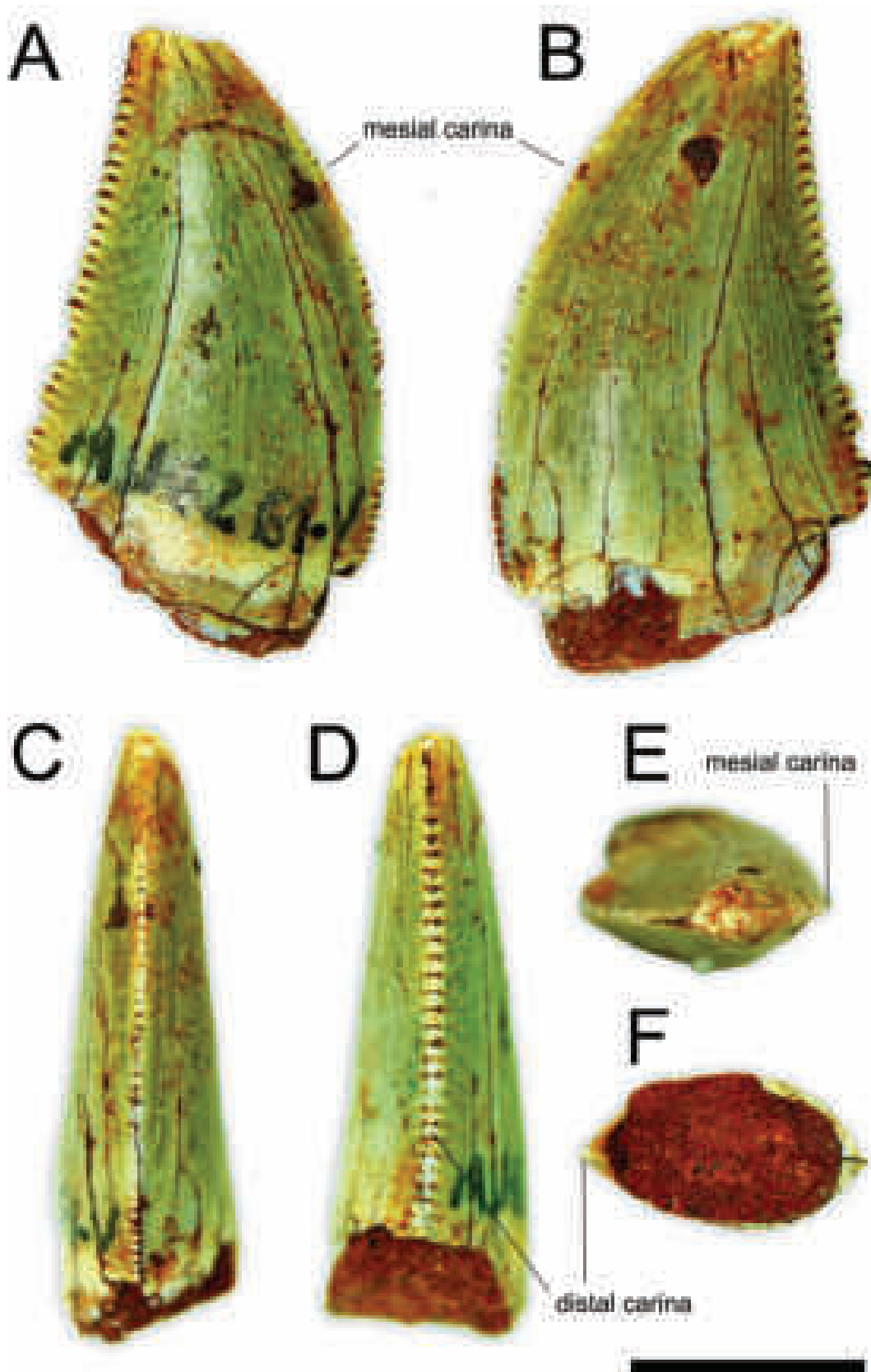


Figure 7. Abelisaurid theropod lateral tooth of morphotype I (MN 6261-V) from Prata, Minas Gerais state, Adamantina Formation, in lingual (A), labial (B), mesial (C), distal (D), apical (E), and basal (F) views. Scale bar: 5 mm.

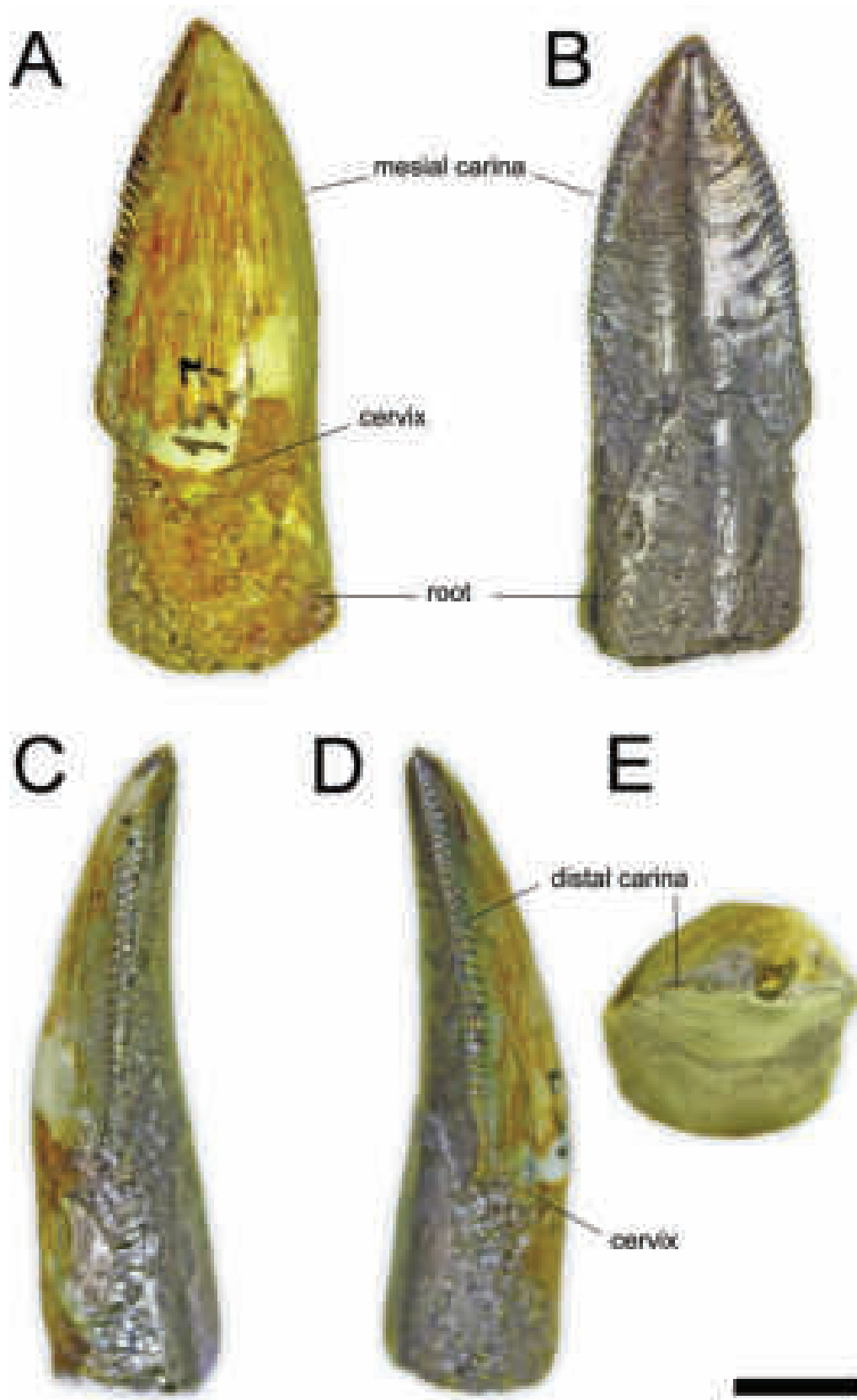


Figure 8. Abelisaurid theropod right mesial tooth of morphotype II (CPP 157) from Periópolis, Minas Gerais state, Marília Formation, in labial (A), lingual (B), mesial (C), distal (D), apical (E), and basal (F) views. Scale bar: 5 mm.

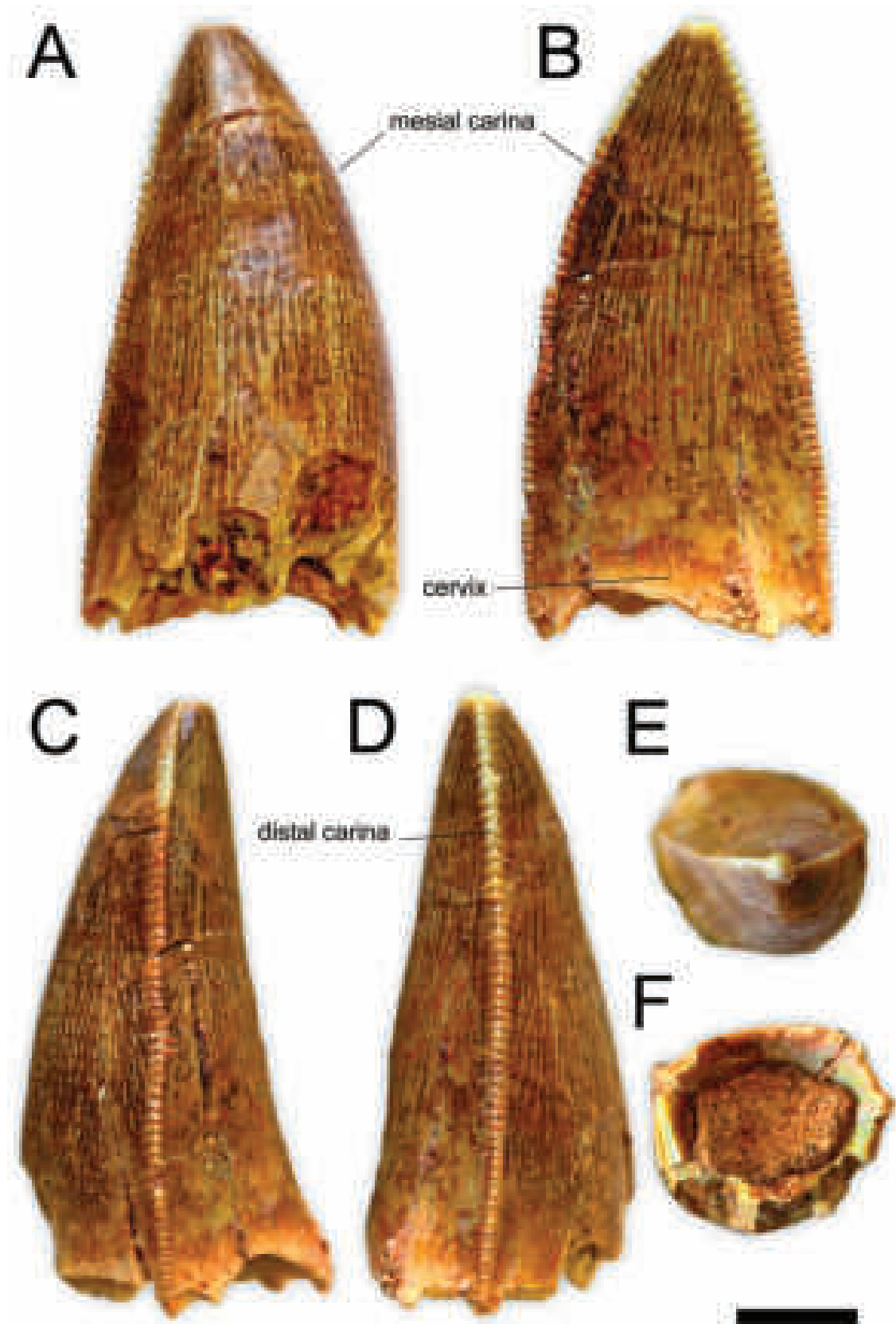


Figure 9. Abelisaurid theropod mesial tooth of morphotype II (MCT.R. 1963) from Periópolis, Minas Gerais state, Marília Formation, in labial (A), lingual (B), mesial (C), distal (D), apical (E), and basal (F) views. Scale bar: 5 mm.

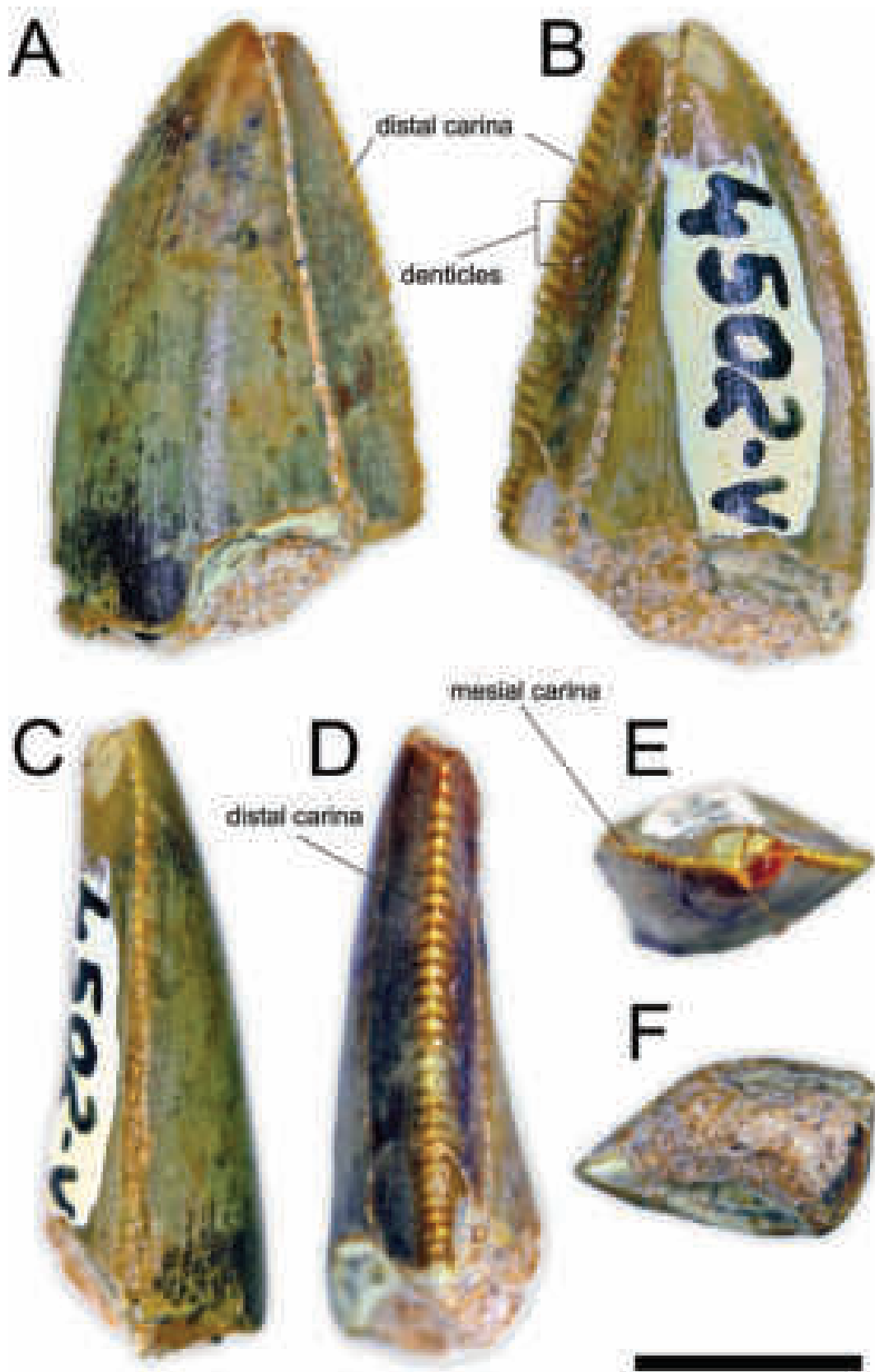


Figure 10. Abelisaurid theropod left mesial tooth of morphotype II (MN 4502-V/B) from Álvares Machado, São Paulo state, Adamantina Formation, in labial (A), lingual (B), mesial (C), distal (D), apical (E), and basal (F) views. Scale bar: 5 mm.

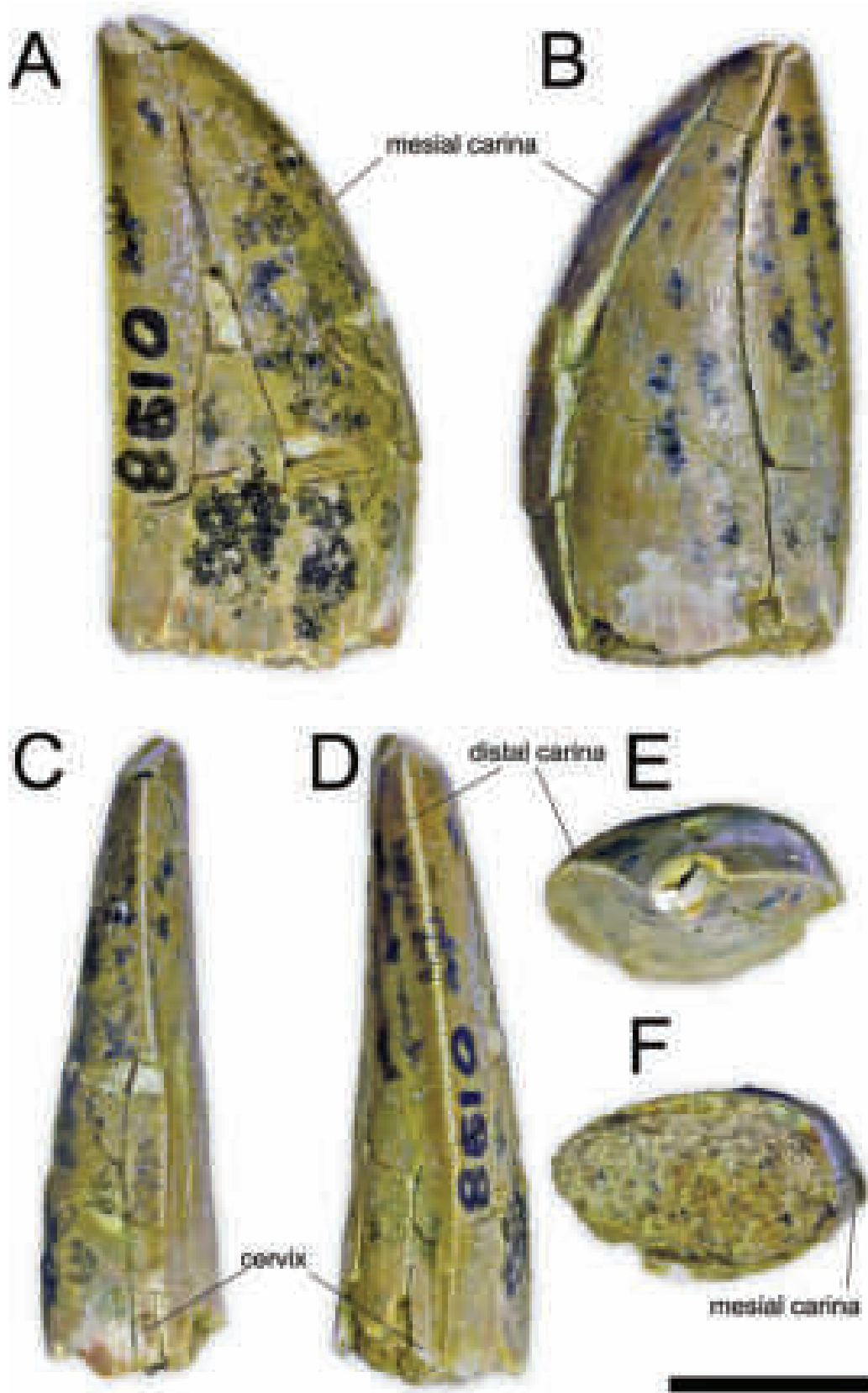


Figure 11. Abelisaurid theropod right transitional tooth of morphotype III (CPP 198) from Peirópolis, Minas Gerais state, Marília Formation, in labial (A), lingual (B), mesial (C), distal (D), apical (E), and basal (F) views. Scale bar: 10 mm.

Specimens from Monte Alto, São Paulo state, Marília Formation: MPMA 1, MPMA 2, MPMA 3, MPMA-12-00D13-97, MPMA-12-00D14-97, MPMA-12-00D1-97, MPMA-12-00D2-97, MPMA-12-00D4-97, MPMA-12-00D5-97, and MPMA-12-00D7-97.

Specimen from Flórida Paulista, São Paulo state, Adamantina Formation: UFRJ-DG 371-Rd.

Figure 22. Allosauroid-*Specimens from Alfredo Marcondes, São Paulo state, Adamantina Formation:* UFRJ-DG 377-Rd, UFRJ-DG 379-Rd, and UFRJ-DG 409-Rd.

Morphotype II

The second morphotype is composed of symmetrical to asymmetrical crowns with the characteristic morphology of abelisaurid mesial teeth. These teeth have a lingually curved crown with slightly to strongly convex mesial and distal profiles and are weakly to moderately compressed (CBR ranging from .6 to .9). The mesial and distal carinae are straight and often centrally positioned on their surfaces in mesial and distal views, respectively. More rarely, the mesial carina is strongly deflected lingually on the crown. There are concave surfaces adjacent to both mesial and distal carinae or restricted to the distal carina on the lingual surface, conferring a salinon to J-shaped cross-sectional outline in basal view. Both mesial and distal carinae always extend to the root. The DSDI is close to one, with mesial and distal denticles usually being asymmetrically convex or distally hooked. The enamel surface texture is irregular. Interdenticular sulci are typically present between the distal and sometimes mesial denticles. Transverse and marginal undulations can be present, typically lingually and more rarely labially. The tooth can be slightly constricted between the crown and root.

Identification: These teeth are confidently referred to the mesial dentition of young, subadult to adult abelisaurids.

Specimens from Uberaba, Minas Gerais state, Marília Formation: CPP 156, CPP 157 (Fig. 8), CPP 447, MCT.R. 1963 (Fig. 9), and MCT.R. 1965.

Specimens from Ibirá, São Paulo state, Adamantina Formation: LPP-PV 1111, LPP-PV 1114, and LPP-PV 1151.

Specimen from Álvares Machado, São Paulo state, Presidente Prudente Formation: MN 4502-V/B (Fig. 10).

Specimen from Chapada dos Guimarães, Mato Grosso state, Marília Formation: MN 4566-V.

Specimen from Pirapozinho, São Paulo state, Presidente Prudente Formation: MN 5032-V.

Specimens from Prata, Minas Gerais state, Adamantina Formation: MN 6258-V and MN 6269-V.

Specimens from Tesouro, Mato Grosso state, Marília Formation: MN 6822-V and MN 6839-V.

Specimens from Monte Alto, São Paulo state, Marília Formation: MPMA 6 and MPMA 8.

Morphotype III

This morphotype includes a series of teeth intermediate in morphology between morphotypes I and II and representing abelisaurid transitional teeth. Similar to the lateral teeth in terms of crown ornamentations and denticle size and morphology, they differ in that the crown is slightly thicker (CBR ranging from .55 to .7), sometimes lingually curved, and more asymmetrical. They have concave surfaces next to the mesial and/or distal carinae on the lingual surface, conferring a transitional cross-sectional outline between the clear parlinon and the lenticular outline (e.g. salinon-shaped outline). The mesial carina can be straight or slightly twisted lingually.

Identification: The isolated dental material grouped in morphotype III is most likely to represent transitional crowns situated between the more mesial and lateral teeth of young, subadult to adult abelisaurids.

Specimens from Uberaba, Minas Gerais state, Marília Formation: CPP 020, CPP 198 (Fig. 11), CPP 199, CPP 205, CPP 376, and MCT.R. 1959.

Specimens from Ibirá, São Paulo state, Adamantina Formation: LPP-PV 1107, LPP-PV 1125, LPP-PV 1110, LPP-PV 1131, and LPP-PV 1132.

Specimen from Chapada dos Guimarães, Mato Grosso state, Marília Formation: MN 4567-V.

Specimen from Presidente Bernardes, São Paulo state, Adamantina Formation: MN 4990-V/A.

Specimens from Prata, Minas Gerais state, Adamantina Formation: MN 6264-V/A (Fig. 12), MN 6264-V/B, MN 6268-V, MN 6272-V, MN 6273-V, MN 6279-V, and MN 6280-V.

Specimens from Tesouro, Mato Grosso state, Marília Formation: MN 6816-V, MN 6824-V (Fig. 13), MN 6836-V, and MN 7231-V.

Specimens from Monte Alto, São Paulo state, Marília Formation: MPMA 4, MPMA 5, MPMA 7, MPMA-12-00D3-97, MPMA-12-00D8-97, MPMA-12-00D10-97, MPMA-12-00D11-97, MPMA-12-00D12-97, and MPMA-12-00D6-97.

Specimen from Alfredo Marcondes, São Paulo state, Adamantina Formation: UFRJ-DG 376-Rd.

Morphotype IV

The morphology of the teeth referred to this morphotype is somewhat reminiscent to that seen in the lateral teeth of Noasauridae. They are similar to typical abelisaurid lateral teeth, but differ in that they are much smaller (<2 cm) and typically short (CHR < 1.5). They have a small number of comparatively large denticles on both mesial and distal carinae, which are often asymmetrically convex to apically hooked. The DSDI is always close to one. The teeth have a lanceolate cross-sectional outline, a straight to weakly concave distal profile, and centrally positioned mesial and distal carinae that always extend to the root. The enamel surface texture is irregular, and there are no crown ornamentations, such as transverse or marginal undulations. The mesial and distal denticles are typically asymmetrically to distally hooked.

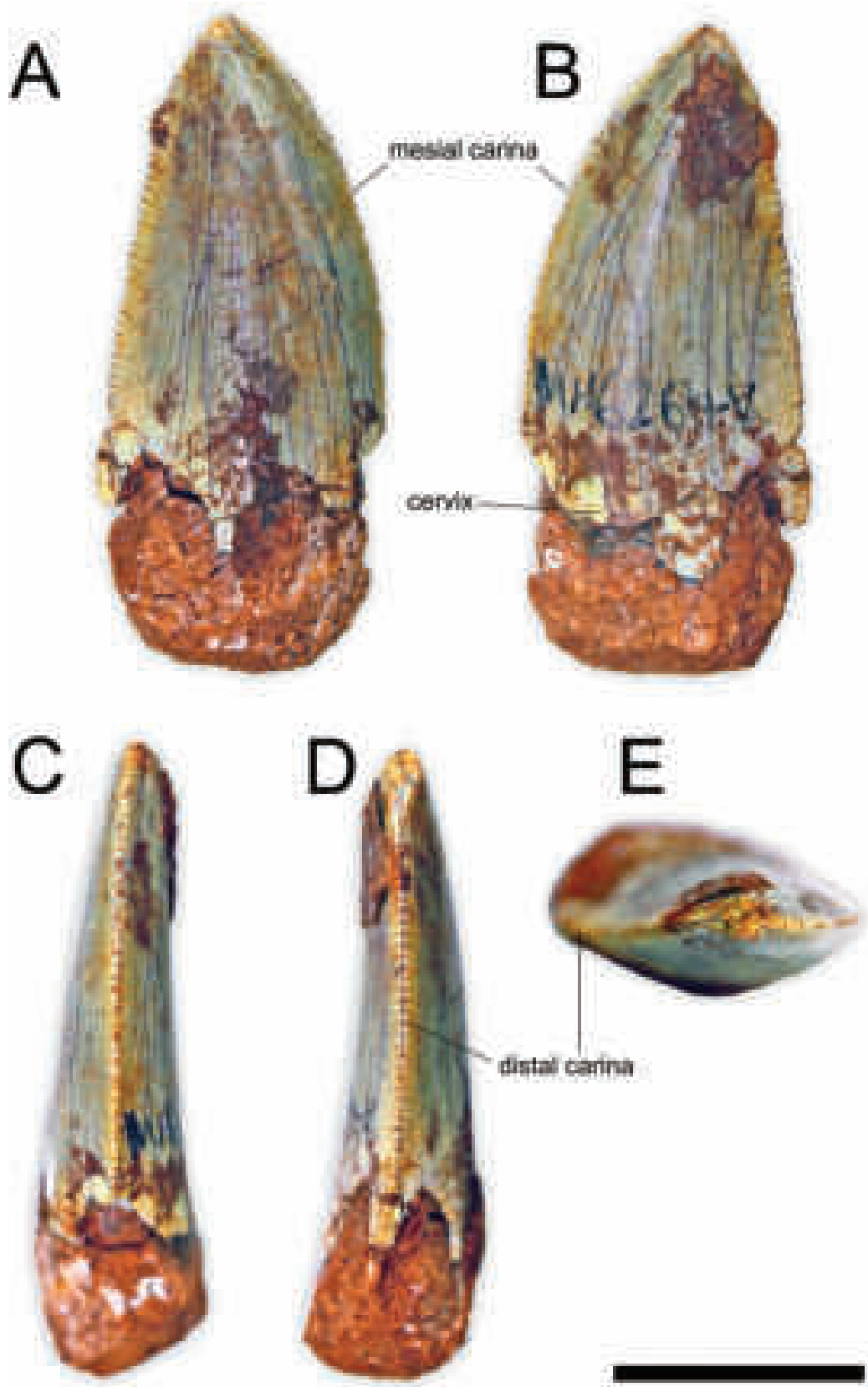


Figure 12. Abelisaurid theropod right transitional tooth of morphotype III (MN 6264-V/A) from Prata, Minas Gerais state, Adamantina Formation, in labial (A), lingual (B), mesial (C), distal (D), apical (E), and basal (F) views. Scale bar: 10 mm.

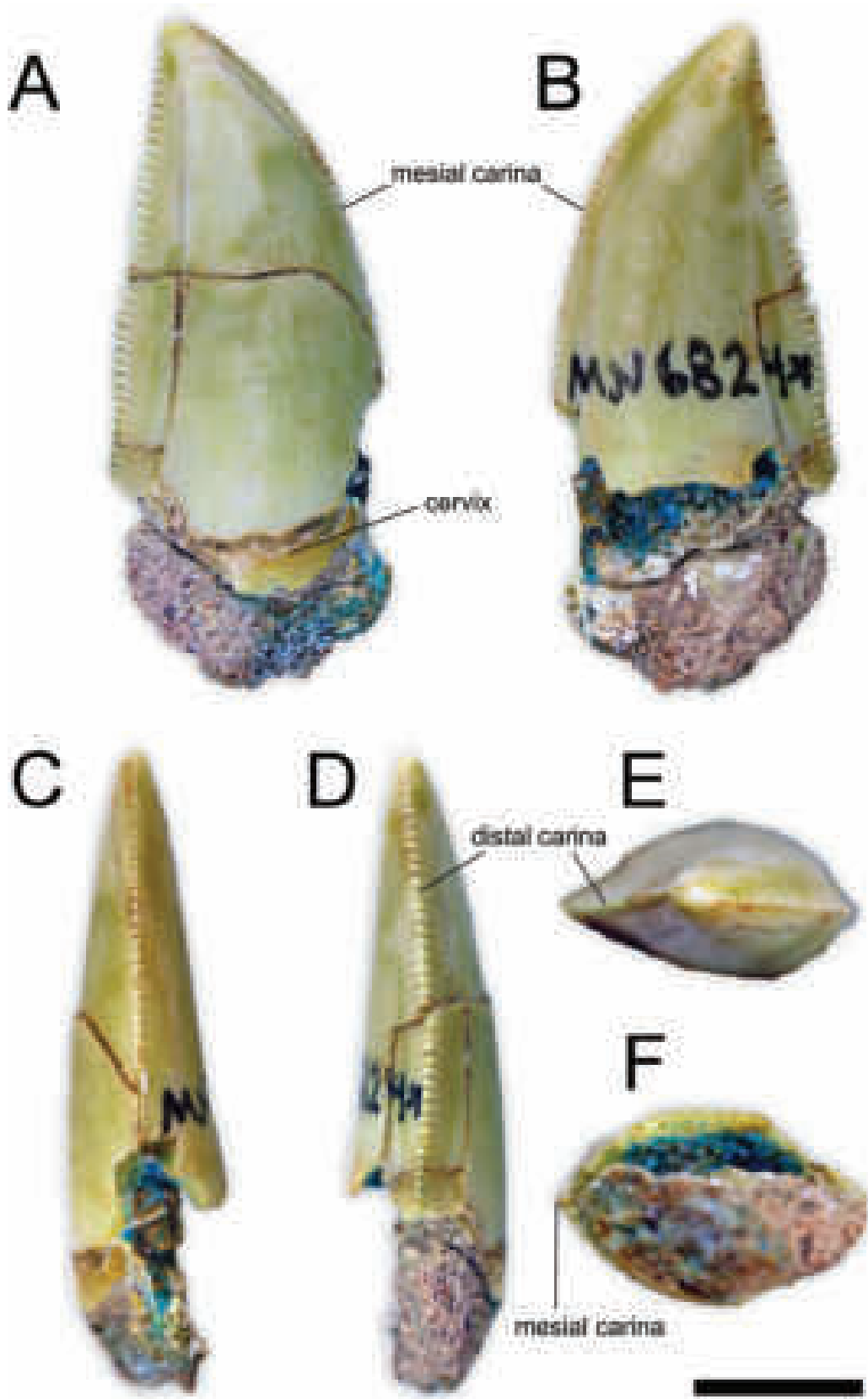


Figure 13. Abelisaurid theropod right transitional tooth of morphotype III (MN 6824-V) from Tesouro, Mato Grosso state, Marília Formation, in labial (A), lingual (B), mesial (C), distal (D), apical (E), and basal (F) views. Scale bar: 5 mm.

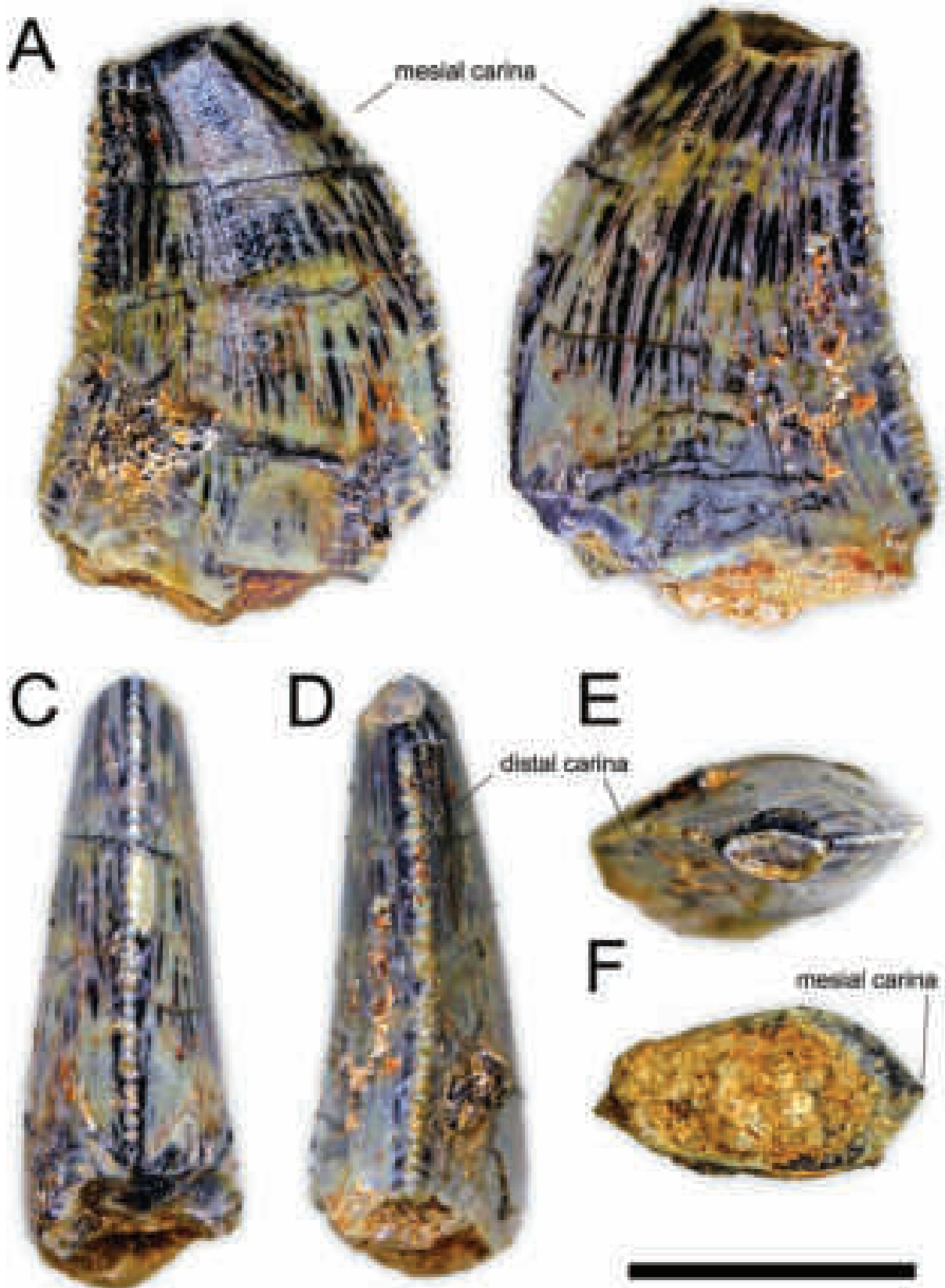


Figure 14. Noosaurid-like right lateral tooth of morphotype IV (LPP-PV 1123) from Ibirá, São Paulo state, Adamantina Formation, in labial (A), lingual (B), mesial (C), distal (D), apical (E), and basal (F) views. Scale bar: 5 mm.

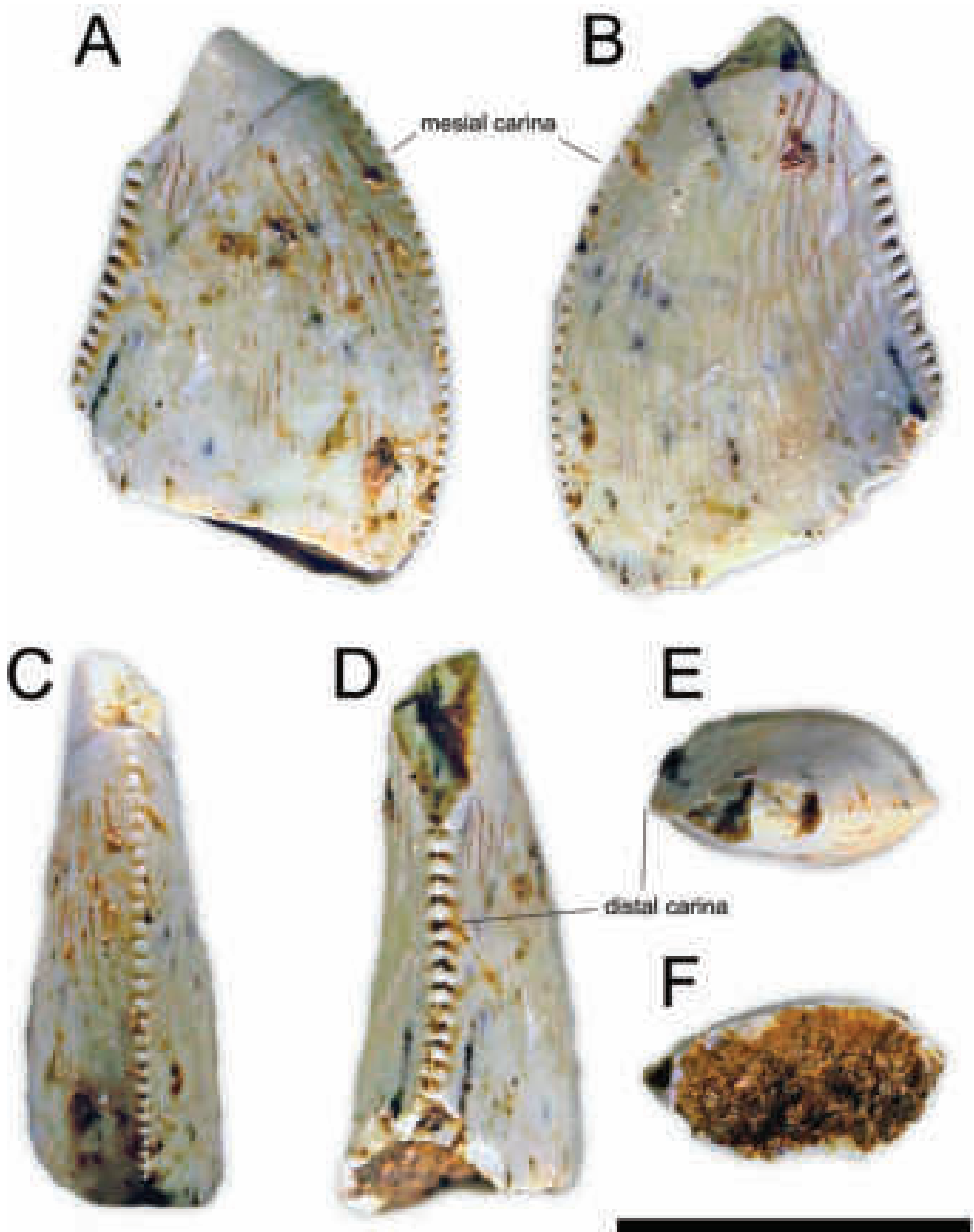


Figure 15. Noosaurid-like right lateral tooth of morphotype IV (LPP-PV 1146) from Ibirá, São Paulo state, Adamantina Formation, in labial (A), lingual (B), mesial (C), distal (D), apical (E), and basal (F) views. Scale bar: 5 mm.

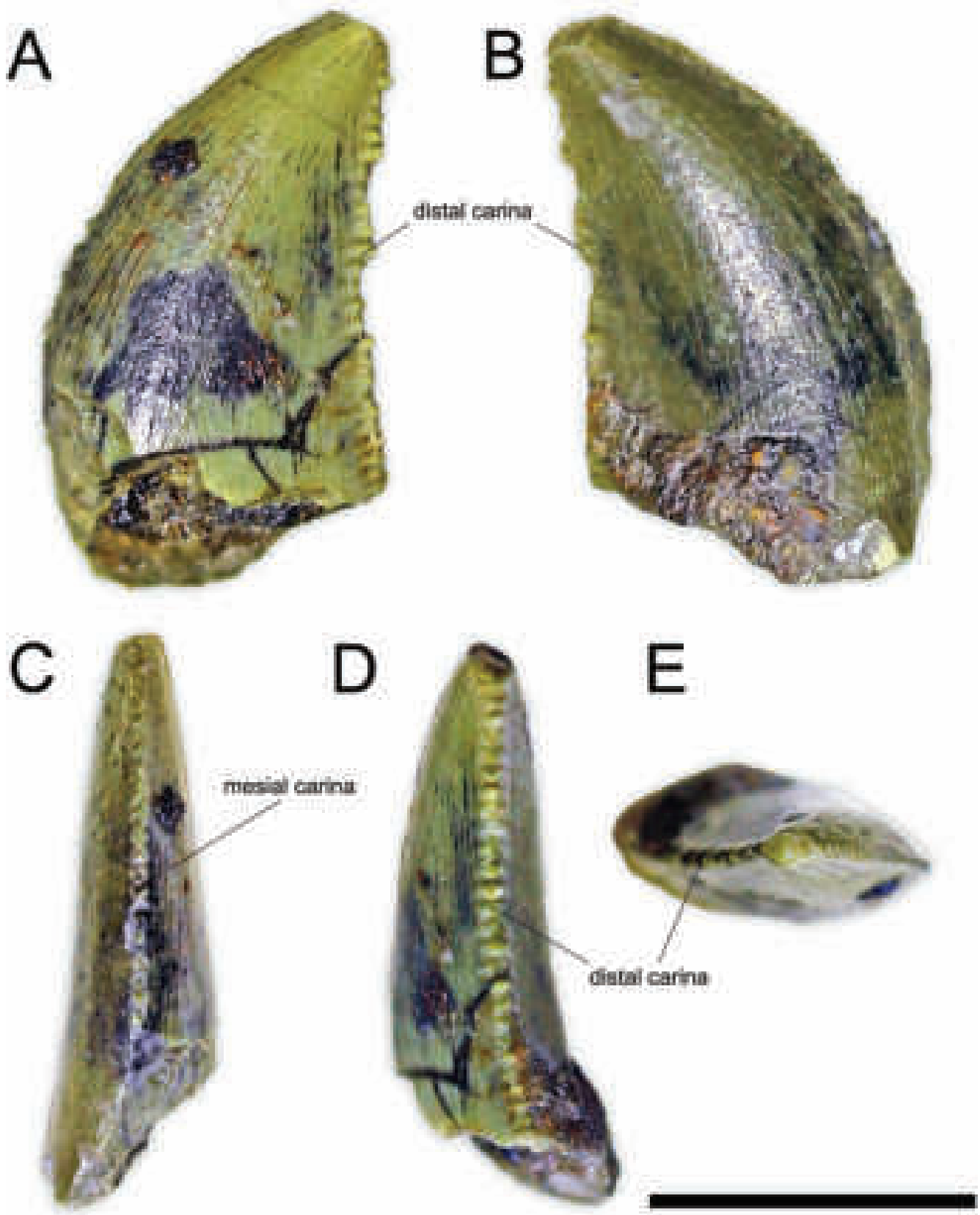


Figure 16. Noosaurid-like left lateral tooth of morphotype IV (UFRJ-DG 374-Rd) from Flórida Paulista, São Paulo state, Adamantina Formation, in labial (A), lingual (B), mesial (C), distal (D), apical (E), and basal (F) views. Scale bar: 5 mm.

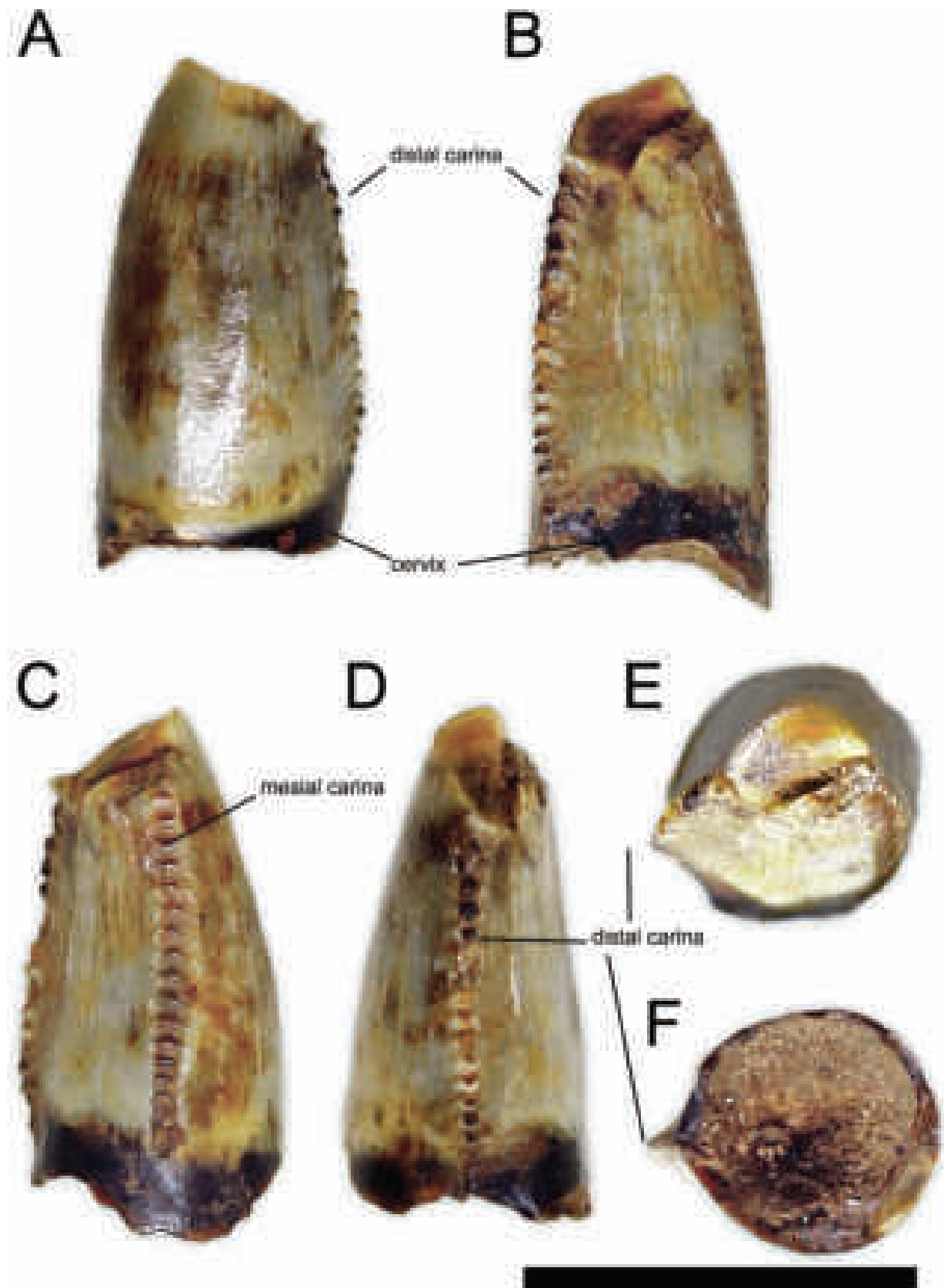


Figure 17. Noasaurid-like left mesial tooth of morphotype V (LPP-PV 1150) from Ibirá, São Paulo state, Adamantina Formation, in labial (A), lingual (B), mesial (C), distal (D), apical (E), and basal (F) views. Scale bar: 5 mm.

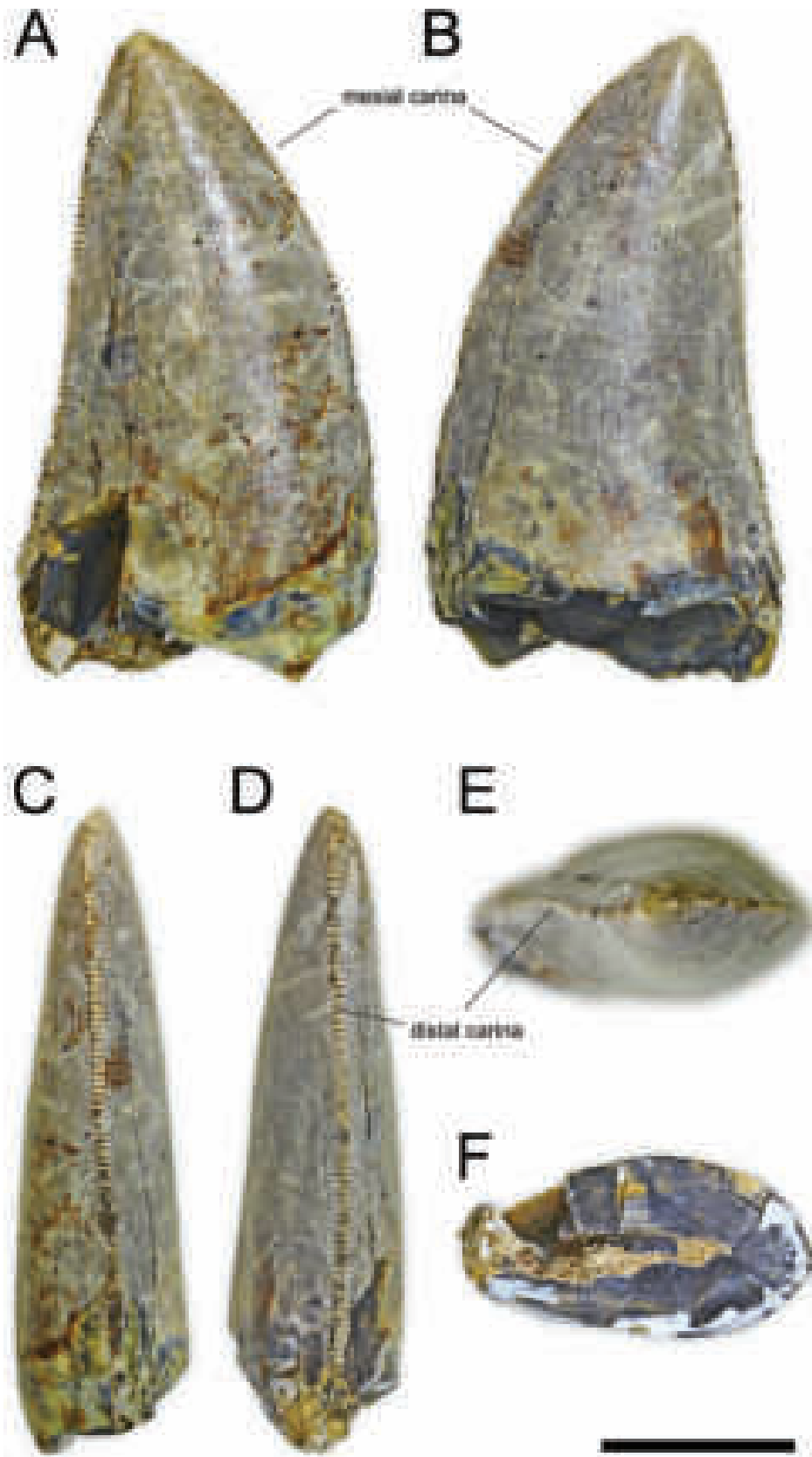


Figure 18. Allosauroid-like right lateral tooth of morphotype VI (LPP-PV 1102) from Ibirá, São Paulo state, Adamantina Formation, in labial (A), lingual (B), mesial (C), distal (D), apical (E), and basal (F) views. Scale bar: 10 mm.

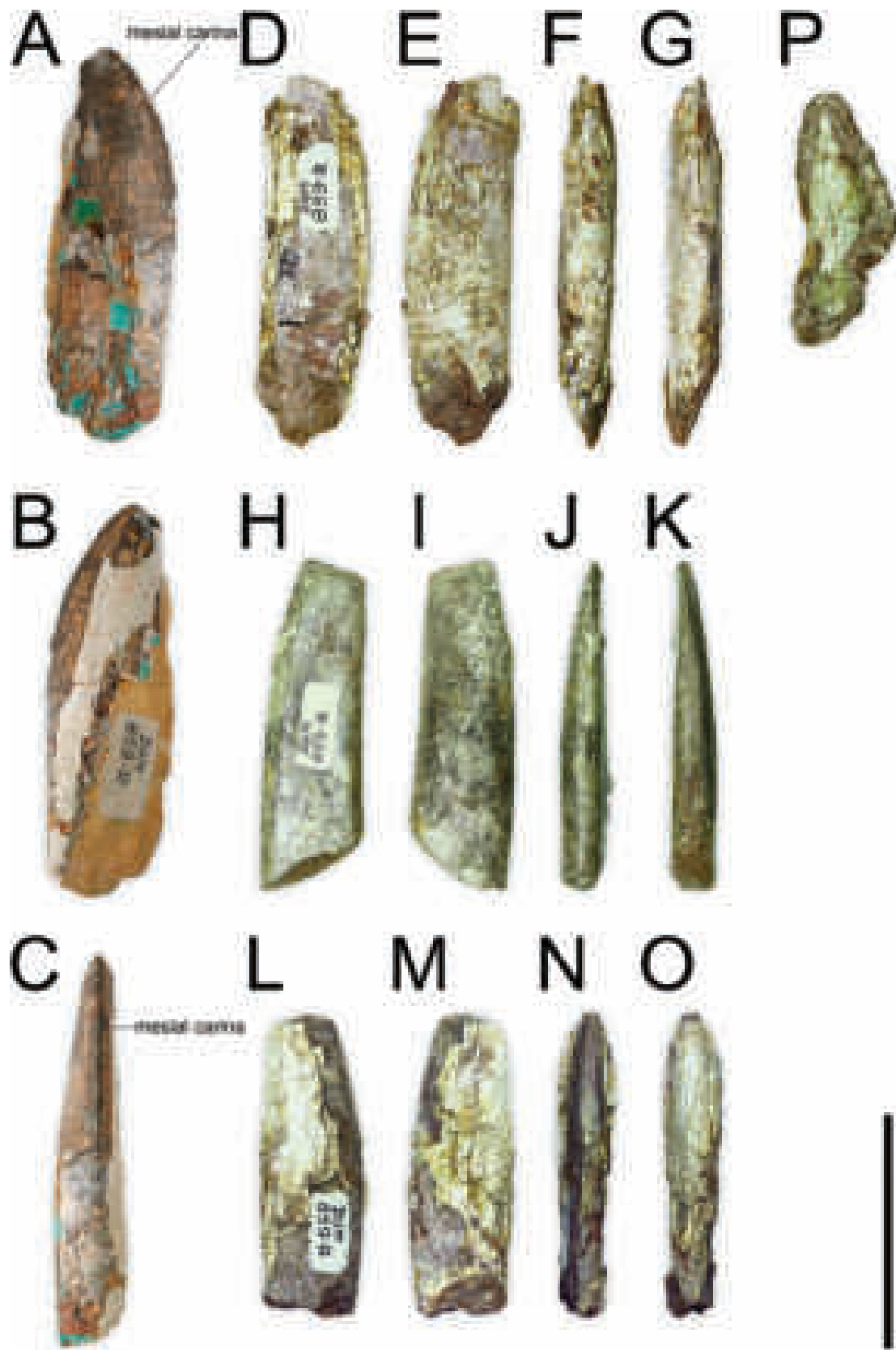


Figure 19. Allosauroid-like lateral teeth of morphotype VI (MCTR. 859) from Chapada dos Guimarães, Mato Grosso state, Marília Formation: MCTR. 859a in labial (A), lingual (B), and mesial (C) views; MCTR. 859b in labial (?; D), lingual (?; E), mesial (F), and distal (G) views; MCTR. 859c in labial (H), lingual (I), mesial (J), and distal (K) views; MCTR. 859d in labial (?; L), lingual (?; M), mesial (N), and distal (O) views; and MCTR. 859e in labial (?; P) view. Scale bar: 50 mm.

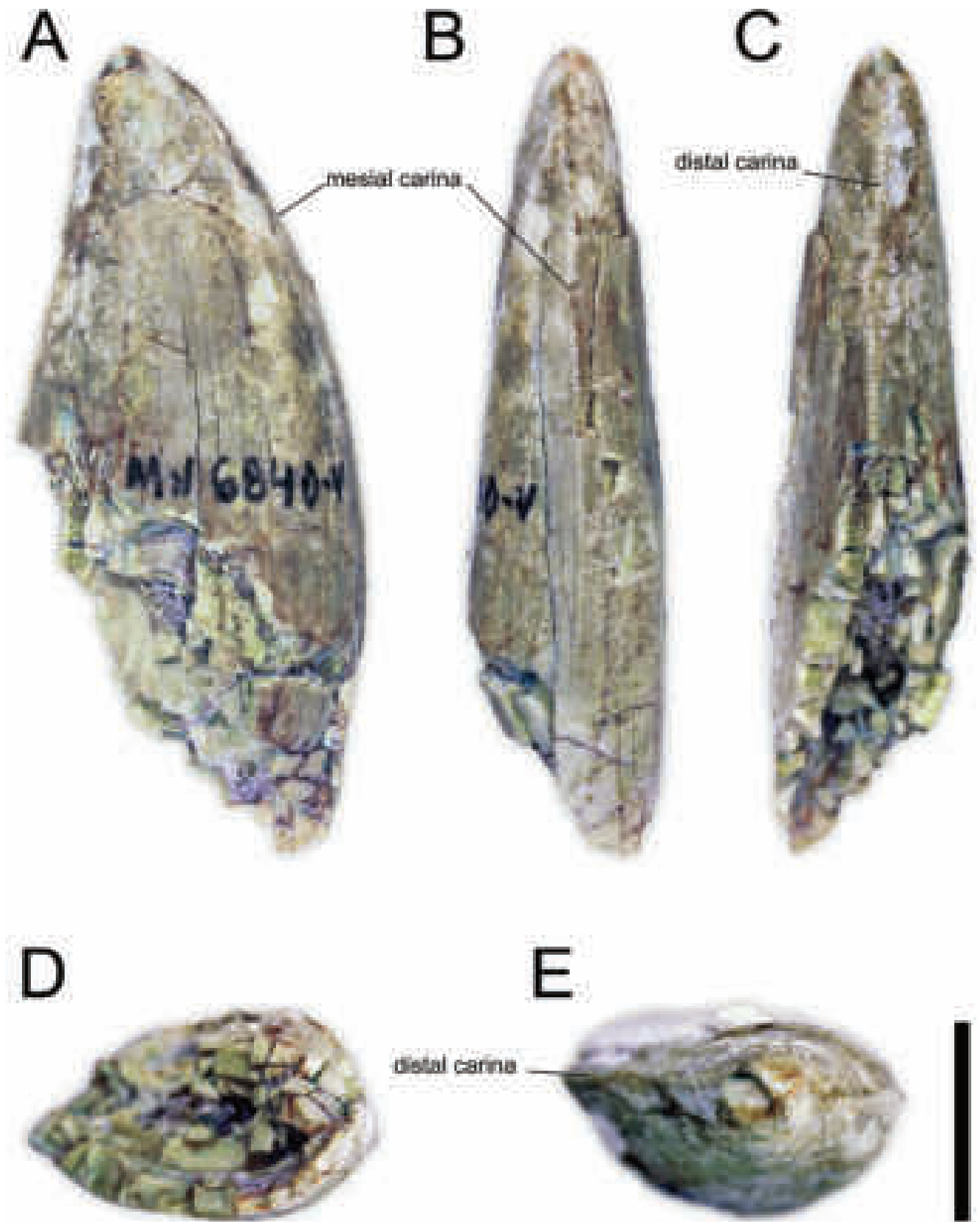


Figure 20. Allosauroid-like right lateral tooth of morphotype VI (MN 6840-V) from Tesouro, Mato Grosso state, Marília Formation, in labial (A), lingual (B), mesial (C), distal (D), apical (E), and basal (F) views. Scale bar: 10 mm.

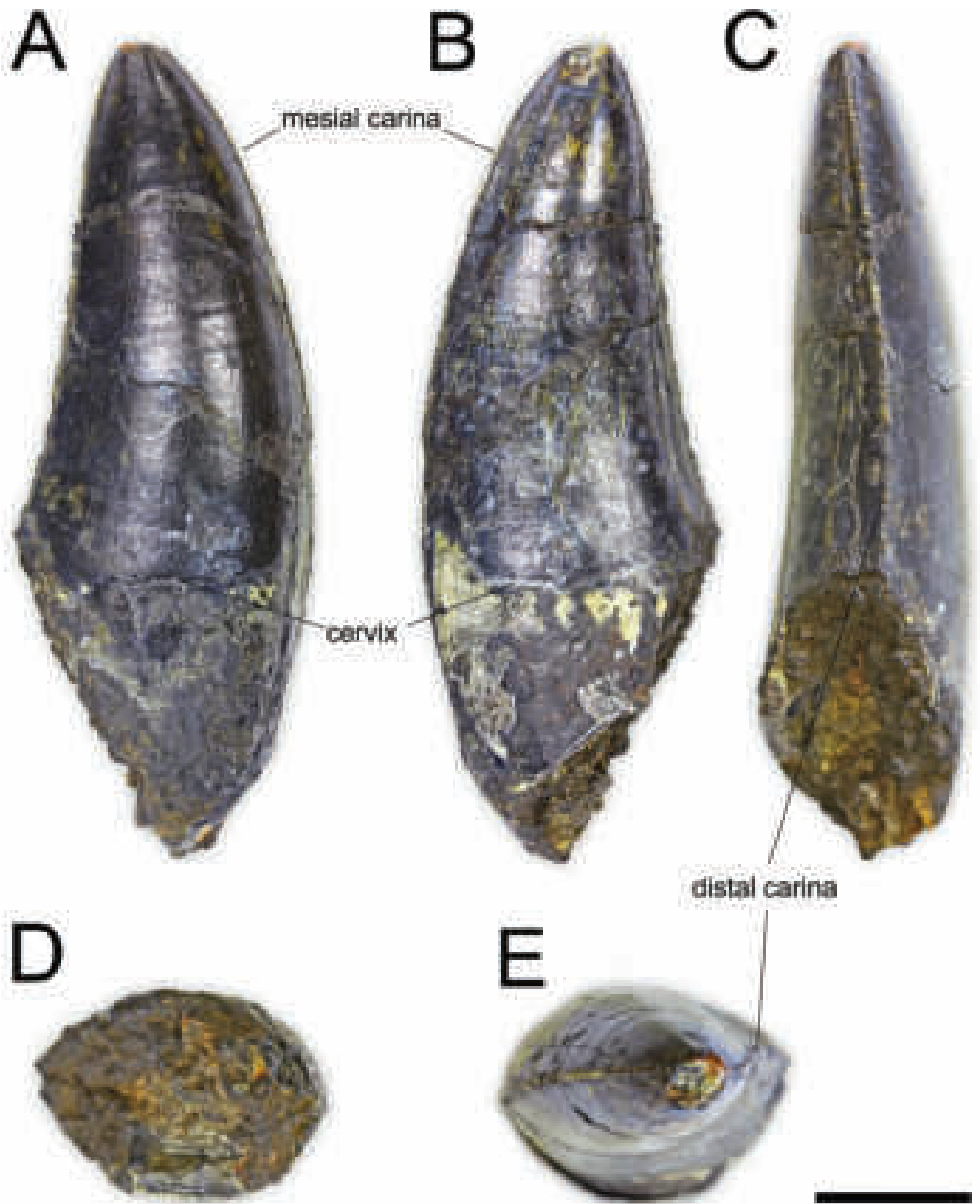


Figure 21. Allosauroid-like right mesial tooth of morphotype VII (LPP-PV 1100) from Ibirá, São Paulo state, Adamantina Formation, in labial (A), lingual (B), mesial (C), distal (D), apical (E), and basal (F) views. Scale bar: 10 mm.

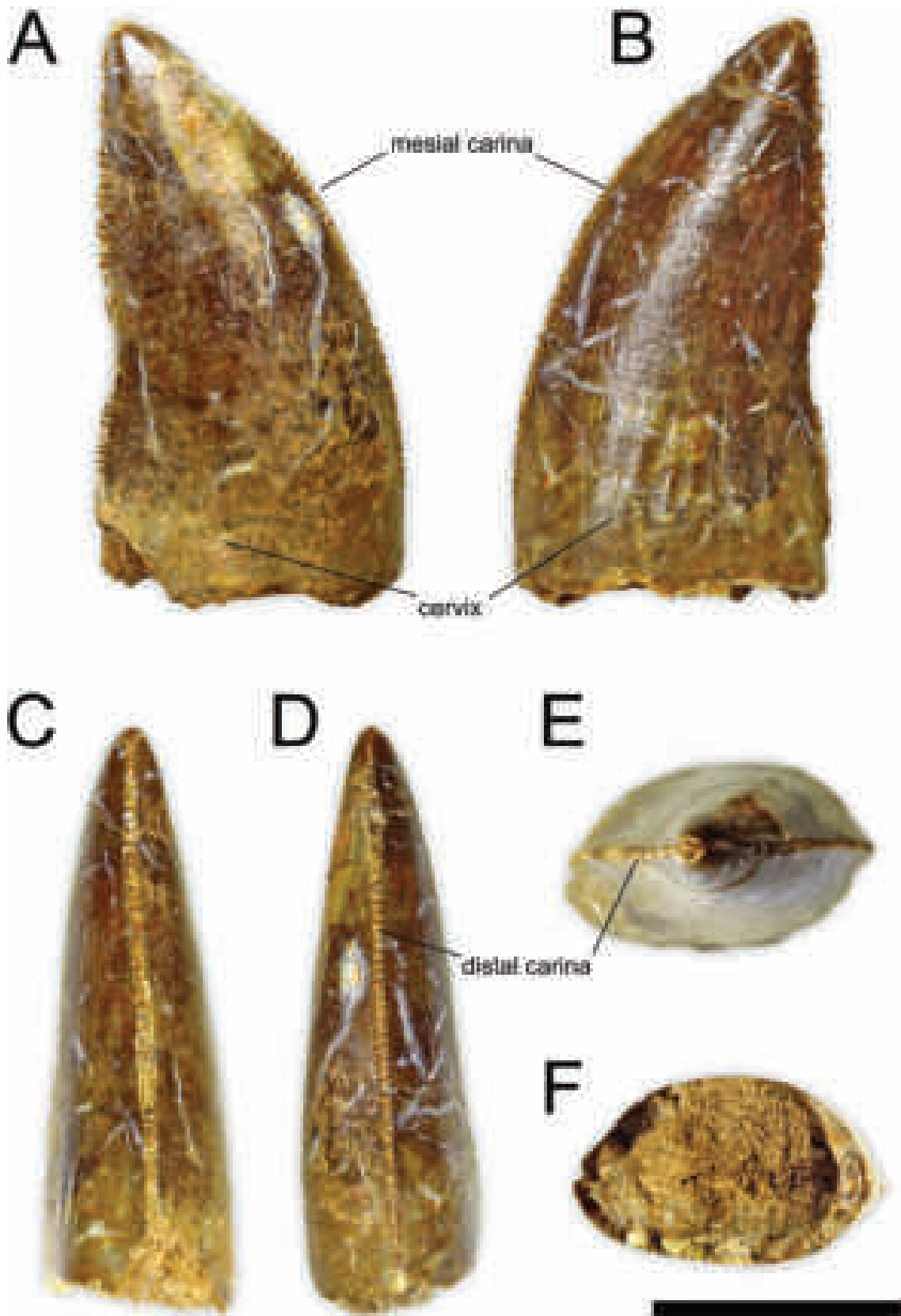


Figure 22. Allosauroid-like mesial tooth of morphotype VII (LPP-PV 1104) from Ibirá, São Paulo state, Adamantina Formation, in labial (A), lingual (B), mesial (C), distal (D), apical (E), and basal (F) views. Scale bar: 10 mm.

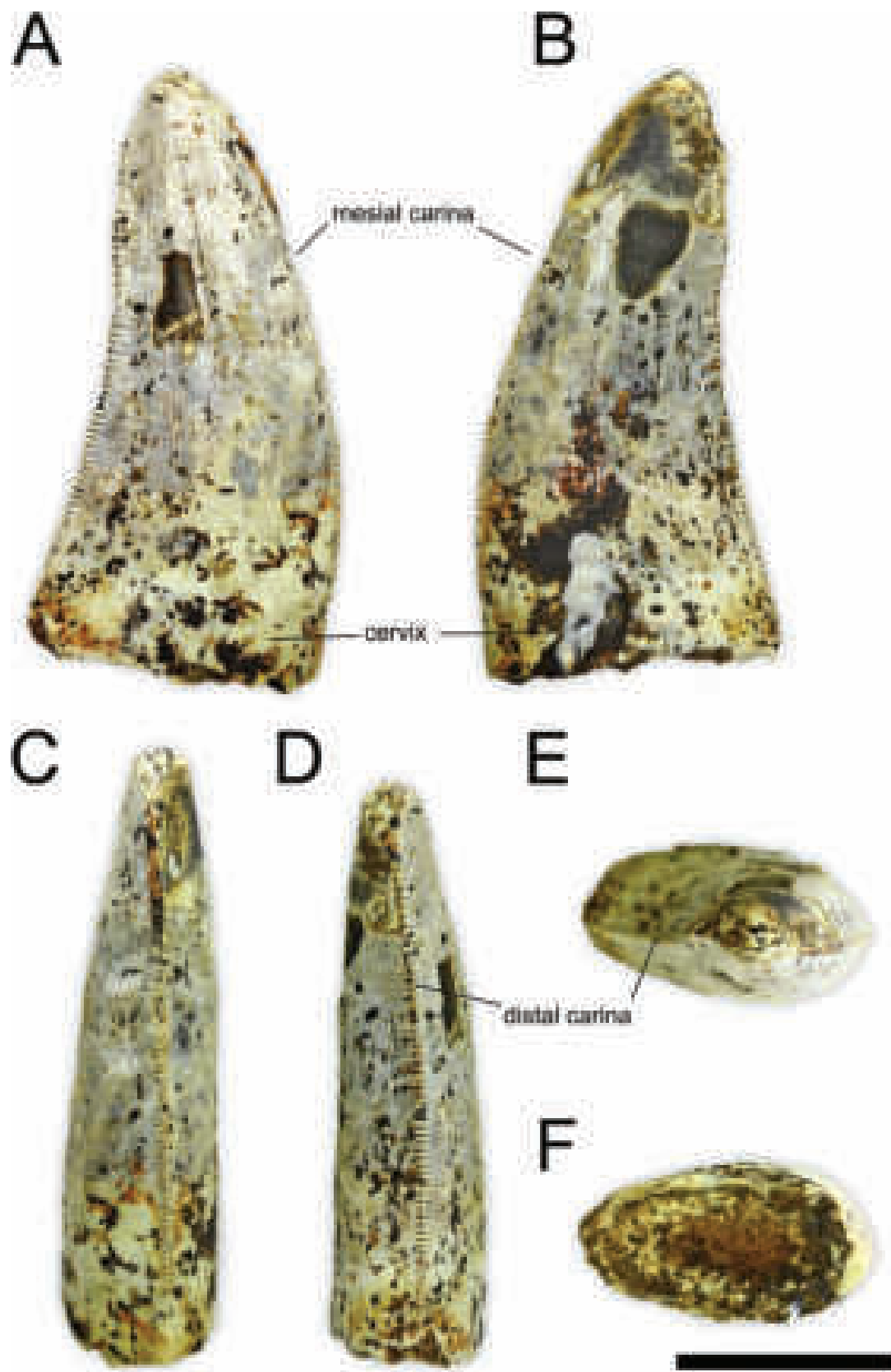


Figure 23. Allosauroid-like left mesial tooth of morphotype VII (LPP-PV 1106) from Ibirá, São Paulo state, Adamantina Formation, in labial (A), lingual (B), mesial (C), distal (D), apical (E), and basal (F) views. Scale bar: 10 mm.

Identification: Specimens from morphotype IV probably represent lateral teeth from juvenile to very young abelisaurids and not noasaurids, because they differ from the latter by having crowns with a DSDI close to one.

Specimens from Uberaba, Minas Gerais state, Marília Formation: CPP 129a, CPP 129c, CPP 375-1, and CPP 452-2.

Specimens from Ibirá, São Paulo state, Adamantina Formation: LPP-PV 1109, LPP-PV 1123 (Fig. 14), LPP-PV 1146 (Fig. 15), and LPP-PV 1149.

Specimens from Prata, Minas Gerais state, Adamantina Formation: MN 6274-V, MN 6287-V, and MN 6295-V.

Specimen from Flórida Paulista, São Paulo state, Adamantina Formation: UFRJ-DG 374-Rd (Fig. 16).

Morphotype V

Teeth grouped in this morphotype resemble those from the mesial dentition of noasaurid theropods. They are similar to typical abelisaurid mesial teeth, but differ from them in their very small size (<1 cm), strongly lingually deflected mesial carina, which faces lingually (the mesial denticles point lingually), a single concave surface adjacent to the distal carina on the lingual surface, and a cross-sectional outline between a salinon and a D-shaped outline.

Identification: A tooth of this morphotype is identified as belonging to the mesialmost dentition of a juvenile abelisaurid. It differs from noasaurid mesial teeth in having a DSDI close to one and the absence of a constriction between the crown and root, flutes on the lingual surfaces, and poorly developed mesial denticles or an unserrated mesial carina, making the referral to this clade unlikely.

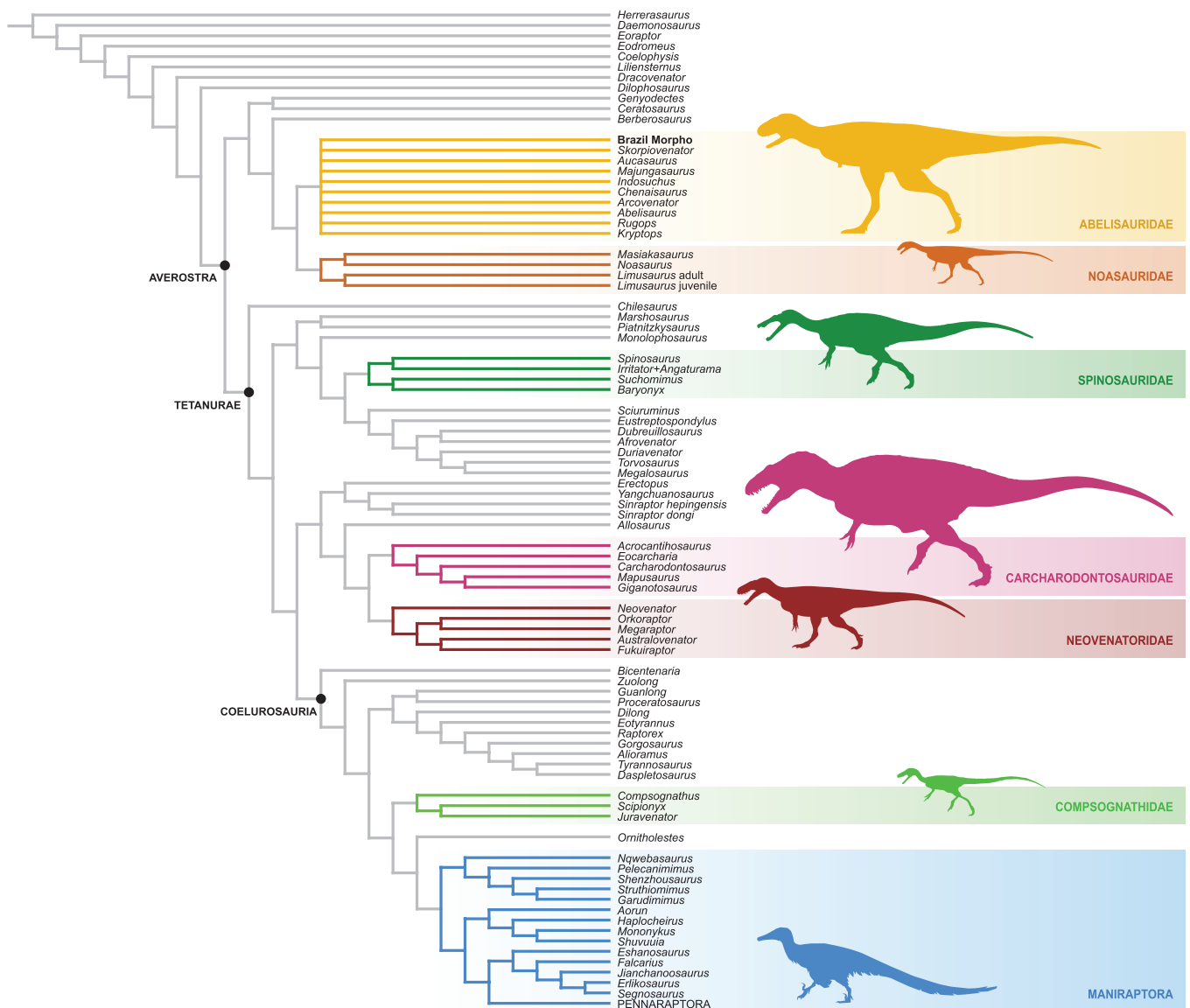


Figure 24. General topology recovered by our results (see main text) showing the phylogenetic relationships among the Brazilian morphotypes and different theropod groups. The morphotypes analysed in the present work are referred to as ‘Brazil Morpho’. The three consensus trees with Bremer support are figured in the [Supporting Information \(Figs S1–S3\)](#). The theropod silhouettes were all downloaded from phylopic.org (artist: Scott Hartman).

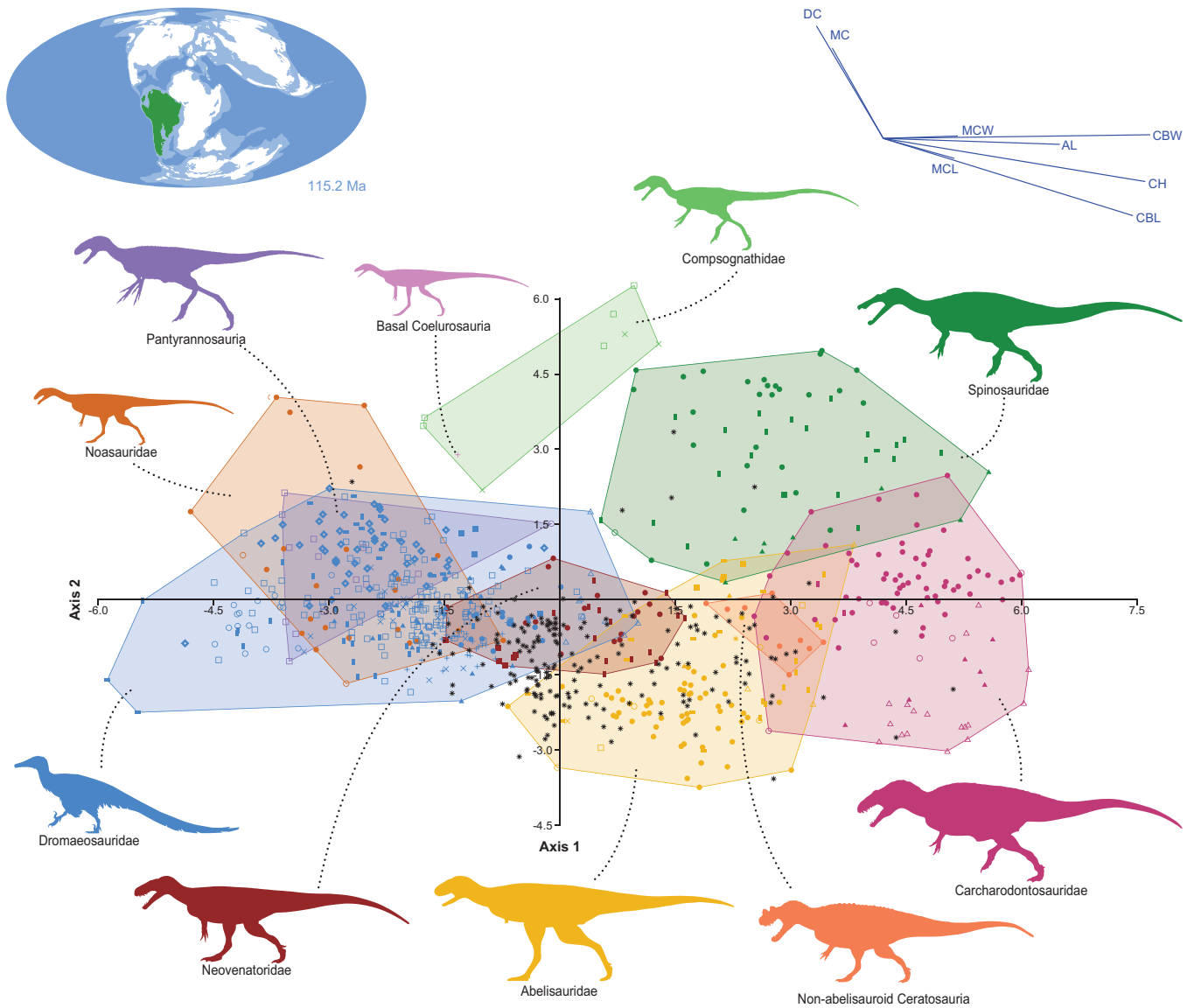


Figure 25. Graphical results of the linear discriminant analysis of 860 dental crowns belonging to 10 different groups of theropods from the Cretaceous period in South America. The eigenvalue of axis 1 is 6.6508, which accounts for 71.46% of the total variation, and the eigenvalue of axis 2 is 1.4966, which accounts for 16.08% of the total variation. The palaeogeographical map was modified from [Scotese \(2014\)](#). All theropod silhouettes were downloaded from phylopic.org (artist: Scott Hartman and Tasman Dixon (for the Dromaeosauridae)).

Specimen from Ibirá, São Paulo state, Adamantina Formation: LPP-PV 1150 (Fig. 17).

Morphotype VI

A few isolated theropod teeth could be described as resembling those of the lateral dentition of an allosauroid. They are, once again, relatively similar to abelisaurid lateral teeth of morphotype I but differ from the latter in being asymmetrical in basal/apical view, with the distal carina being slightly deflected labially, while the mesial carina is straight to weakly twisted lingually. The crown is also slightly thicker (but also in abelisaurids), and the mesial and distal denticles are symmetrically convex. The distal margin can show a convex apical profile in lateral view, as is typical of carcharodontosaurids (in LPPV-PV 1102).

Identification: We refer these allosauroid-like teeth tentatively to abelisaurids, whose lateral dentition would be convergent to that of carcharodontosaurids.

Specimen from Ibirá, São Paulo state, Adamantina Formation: LPP-PV 1102 (Fig. 18).

Specimen from Chapada dos Guimarães, Mato Grosso state, Marília Formation: MCT.R. 859 (Fig. 19).

Specimen from Tesouro, Mato Grosso state, Marília Formation: MN 6840-V (Fig. 20).

Morphotype VII

These are allosauroid-like mesial teeth, similar to morphotype VI but differing in being more elongated (CHR > 1.6) and/or thicker (CBR > .55). The mesial carina is either straight and centrally positioned on the mesial surface or slightly twisted lingually. They differ from the abelisaurid mesial teeth in the absence of concavity adjacent to the carinae on the crown, the symmetrical appearance of the tooth (i.e. lanceolate cross-sectional outline at

Table 2. Numerical results from linear discriminant analysis for each dental element from the Bauru Basin.

Taxa	Number of crowns	Percentage
Abelisauridae	54	30.51
Carcharodontosauridae	4	2.23
Dromaeosauridae	3	1.67
Neovenatoridae	87	49.15
Noasauridae	4	2.23
Non-abelisauroid Ceratosauria	20	11.17
Non-tyrannosaurid Pantyrannosauria	2	1.12
Spinosauridae	3	1.67
Total	177	100.00

Table 3. Reclassification of the isolated crowns obtained from our linear discriminant analysis. The MPMA specimens were originally described by [Tavares et al. \(2014\)](#); MCT.R. 859a was described by [Bittencourt and Kellner \(2002\)](#), and UFRJ-DG409-R was classified by [Delcourt and Grillo \(2018a\)](#).

Specimen	Original classification	New classification
UFRJ-DG409-R	Abelisauridae	Non-abelisauroid Ceratosauria
MPMA12-00D1-97	Abelisauridae	Non-abelisauroid Ceratosauria
MPMA-12-00D3-97	Abelisauridae	Neovenatoridae
MPMA-12-00D4-97	Abelisauridae	Neovenatoridae
MPMA-12-00D5-97	Abelisauridae	Neovenatoridae
MPMA-12-00D7-97	Abelisauridae	Abelisauridae
MPMA-12-0D10-97	Abelisauridae	Noasauridae
MPMA-12-0D11-97	Abelisauridae	Neovenatoridae
MPMA-12-0D12-97	Abelisauridae	Neovenatoridae
MPMA-12-0D13-97	Dromaeosauridae	Neovenatoridae
MPMA-12-0D14-97	Dromaeosauridae	Neovenatoridae
MCT.R. 859a	Abelisauridae	Spinosauridae

the base of the crown), and the slightly to strongly concave distal profile.

Identification: Probably abelisaurid mesial or transitional teeth from a taxon with vaguely convergent similarity to carcharodontosaurid teeth.

Specimens from Ibirá, São Paulo state, Adamantina Formation: LPP-PV 1100 ([Fig. 21](#)), LPP-PV 1101, LPP-PV 1104 ([Fig. 22](#)), and LPP-PV 1106 ([Fig. 23](#)).

Specimen from Flórida Paulista, São Paulo state, Adamantina Formation: UFRJ-DG 372-Rd.

Phylogenetic analyses

The phylogenetic analysis performed on the dentition-based matrix using the constrained tree topologies recovered 128 most parsimonious trees with 1321 steps (consistency index = .197,

retention index = .461). The constrained consensus trees recovered the consensual topologies amongst theropods, and Ceratosauria was placed in a polytomy with the morphotypes I, II, III, IV, VI, VII, and VI + VII. Morphotype V was recovered as Therizinosauria ([Supporting Information, Fig. S1](#)). The phylogenetic analysis performed on the dentition-based matrix using the unconstrained tree topologies recovered 10 000 most parsimonious trees with 1079 steps (consistency index = .242, retention index = .585). Unconstrained consensus trees recovered morphotypes I, II, III, IV, VI, VII, and VI + VII within a polytomy with abelisaurids, *Neovenator*, *Erectopus*, *Piatnitzkysaurus*, Carcharodontosaurinae, and the clade *Allosaurus* + Metriacanthosauridae. Morphotype V was found within a polytomy with troodontid, ornithomimosaur, therizinosaur, and alvarezsaurid taxa ([Supporting Information, Fig. S2](#)).

The cladistic analysis performed on the crown-based matrix recovered 10 000 most parsimonious trees with 657 steps (consistency index = .240, retention index = .630). The consensus tree resulted in several polytomies with few usual clades. The morphotypes I–IV were recovered within abelisaurids, morphotype V was recovered as a therizinosaurian, and morphotypes VI, VII, and VI + VII were recovered as Carcharodontosaurinae ([Supporting Information, Fig. S3](#)).

The results of each analysis are provided in the [Supporting Information \(Supplementary Figs, S1–S3\)](#). [Figure 24](#) summarizes the general topology found in the phylogenetic analyses and the morphological comparisons among the morphotypes from the Bauru Basin.

Discriminant analyses

In the LDA, the biplot shows that the CBW, CH, and CBL make the strongest contributions in the direction of axis 2. In the same direction, but with lesser contributions, are the measurements MCL, MCW, and AL. The denticle density (MC and DC) makes more contribution in the direction of positive axis 1 and negative axis 2 ([Fig. 25](#)).

The analysis found that 74.23% of all teeth were correctly identified, and 72.47% were correctly identified in the jackknife reclassification. For the non-jackknife classification, the rate of correct identification varied for different groups: 100% for non-abelisauroid Ceratosauria, basal Coelurosauria, and Compsognathidae; 50% for Noasauridae; 76.29% for Abelisauridae; 81.03% for Spinosauridae; 89.47% for Neovenatoridae; 84.95% for Carcharodontosauridae; 85.71% for non-tyrannosaurid Pantyrannosauria; and 67.74% for Dromaeosauridae.

Of the 177 analysed crowns (excluding UFRJ-DG409-R), the majority were recovered as Neovenatoridae (87), followed by Abelisauridae (54), non-abelisauroid ceratosaurian (20), Carcharodontosauridae (4) and Noasauridae (4), Spinosauridae (3) and Dromaeosauridae (3), and non-tyrannosaurid Pantyrannosauria (2). The clades Compsognathidae and basal Coelurosauria were not recovered for the analysed crowns ([Table 2](#)).

Some of the results obtained were discordant with classifications presented in previous works. For example, some specimens analysed by [Tavares et al. \(2014\)](#) and [Delcourt and Grillo \(2018a\)](#) were found to be discordant with the original publication. [Table 3](#) displays the differences found.

DISCUSSION

Remarks on the results of the discriminant and phylogenetic analyses

As expected, we found some discrepancies in the results of the analyses conducted. The morphometric analysis (i.e. LDA) recovered unusual taxonomic groups for the Late Cretaceous of the Bauru Basin. Carcharodontosaurids and spinosaurids are considered extinct in all Cretaceous beds after the Turonian (Novas *et al.* 2005b, Carrano *et al.* 2012, Delcourt *et al.* 2020a, Meso *et al.* 2021b). Additionally, there are no records of non-tyrannosaurid pantyrannosaurians in the Southern Hemisphere after the Albian (Benson *et al.* 2010, 2012, Delcourt and Grillo 2018b). Although the taxonomic results obtained by the LDA could suggest that some theropod groups might have survived throughout the latest Cretaceous, this type of analysis might not be sufficient for assessing isolated materials, as already noted by Hendrickx *et al.* (2020) and Delcourt *et al.* (2020a).

Hendrickx *et al.* (2020) suggested that a broad phylogenetic range and wide distribution of teeth along the tooth row could lead to imprecise taxonomic results. In agreement with these authors, Delcourt *et al.* (2020a) evaluated several isolated teeth and found that LDA might not be the most effective method to use on its own for taxonomic purposes. This is because when there are too many missing data (i.e. incomplete measurements) in the dataset, the remaining measurements might not be able to separate taxonomic groups accurately in LDA. When data are missing, certain variables may have more or less influence in classifying isolated crowns, and some groups may be identified incorrectly based on a limited number of measurements. The analysis attempts to categorize each 'mysterious crown' by using the variables provided and fitting them into the predetermined groups (Delcourt *et al.* 2020a).

It is important to note that the influence of certain measurements on taxonomic groups can vary. Delcourt *et al.* (2020a) found that CBL, CBW, and CH have a greater influence on abelisaurid teeth than MCL and MCW. As a result, if an abelisaurid tooth is missing some of these variables, it might fall into a different morphospace than that of abelisaurid. The absence of key variables in some teeth can compromise the accuracy of taxonomic recovery. The influence of certain measurements can also explain the overlap of morphospaces, particularly among groups that have teeth with very similar measurements. For example, among the Cretaceous Southern American theropods, the spinosaurids, carcharodontosaurids, and abelisaurids can have teeth with large base widths (Delcourt *et al.* 2020a; this study). In this case, the morphospaces might overlap according to the width of their teeth. Therefore, when using morphometric analyses for taxonomic purposes, caution must be exercised, especially when evaluating multiple groups (Hendrickx *et al.* 2020).

A similar issue was observed in the phylogenetic analysis. Although this is one of the best methods for assessing isolated teeth taxonomically (Hendrickx *et al.* 2019, Delcourt *et al.* 2020a; see also Wills *et al.* 2021, 2023), missing data in the character matrix can bias the phylogenetic analysis and deserves closer examination of certain specimens. Owing to the presence of several homoplastic features in theropod teeth, resulting from the morphological convergence of distantly related clades

(Hendrickx *et al.* 2019), teeth with few scored characters might be recovered incorrectly in the topology. It is also important to consider that missing data for morphotypes can result in a weak resolved tree, as shown in the Supporting Information (Fig. S2). This occurs because the scored characters for each morphotype are distributed among different theropod groups, particularly those of morphotypes VI and VII, which resembled both allosauroids and abelisaurids (see descriptions).

The specimen LPP-PV 1150 from Ibirá (morphotype V) of the Adamantina Formation is a mesial tooth morphologically resembling those of noasaurids. However, it shares several features with abelisaurids, including the absence of constriction between the base of the crown and the root, absence of flutes on the lingual surfaces, poorly developed or fully absent mesial denticles, and a DSDI close to one. Despite this, all phylogenetic analyses have recovered this specimen as a therizinosaurian, a clade not yet found in Mesozoic deposits of the Southern Hemisphere geological beds (Yao *et al.* 2019). However, this specimen lacks features shared with therizinosaurians, such as the denticulated carina never reaching the cervix and large apical denticles (see Hendrickx *et al.* 2019). The placement of LPP-PV 1150 close to this taxon is attributable to features shared with several averostran theropods. If future discoveries eventually indicate the presence of therizinosaurians in Gondwana, this must be based on stronger evidence than an isolated tooth crown.

The study of theropod teeth has increased substantially in recent years, with pivotal works that help to identify isolated elements (Smith *et al.* 2005, Smith 2007, Hendrickx and Mateus 2014, Hendrickx *et al.* 2015, 2019, D'Emic *et al.* 2019), and many others using those methods to investigate the theropod fauna through dental records (e.g. Delcourt and Grillo 2018a, Young *et al.* 2019, Delcourt *et al.* 2020a, Soto *et al.* 2020a, b, Soto *et al.* 2023, Meso *et al.* 2021a, b). However, despite the scientific advances, care must be taken to avoid misinterpreting data. Theropod teeth are often homoplastic (Hendrickx *et al.* 2019), and morphospaces overlap when several taxonomic groups are assessed and measurements are missing (Delcourt *et al.* 2020a, Hendrickx *et al.* 2020). Therefore, we suggest that as much data as possible should be available to infer the taxonomic status of isolated teeth. To be more precise in the identification, the morphometric and phylogenetic results must be interpreted in light of the following factors: (i) morphological features compared with more complete specimens; (ii) the age of the geological unit; and (iii) the global distribution of the given taxa so far.

The abundance of abelisaurid teeth

All morphotypes were identified as abelisaurids through phylogenetic analyses and morphological comparisons. Even the teeth that Tavares *et al.* (2014) referred as dromaeosaurid using squared Mahalanobis distance, discriminant analyses, and canonical variate analyses (MPMA-12-00D13-97 and MPMA-12-00D14-97), and here representing morphotype I, were recovered as an abelisaurid in the phylogenetic analysis. Morphotypes IV and V, which have similarities with noasaurid teeth, were recovered as abelisaurid and therizinosaurian, respectively, in the phylogenetic analysis. Morphotype IV is regarded as abelisaurid instead of noasaurid owing to the similar size between the mesial and lateral denticles in lateral teeth

(character 105). In noasaurids, the distal denticles are larger than the mesial (Hendrickx *et al.* 2019). Owing to the small size of the teeth grouped in morphotype IV, they could have belonged to particularly young and/or juvenile abelisaurids. However, the presence of a small-bodied and mature abelisaurid in the Bauru Group (Presidente Prudente Formation; Delcourt and Langer 2022) could also justify the presence of such small teeth. It is worth noting that the specimens CPP 129a and CPP 375-1, classified as morphotype IV, were recovered as abelisaurids by Delcourt *et al.* (2020a). The morphological traits of morphotype V (LPP-PV 1150) are detailed in the previous section.

Specimens MN 4502-V/C, LPP-PV 1117, 1119, 1120, and 1122 are here interpreted as eroded lateral crowns owing to the absence of enamel and some dentine layers. They were referred to morphotype I owing to the strong labiolingual compression and straight distal margin. Despite Ghilardi and Fernandes (2011) suggesting possible affinity with unenlagiines because of the absence of denticles in both carinae in the last three crowns, this absence could be a taphonomic artefact. We suggest that additional analyses, such as histological sampling, should be carried out on these specimens to confirm our interpretation. The MPMA 5 crown is interpreted as an eroded morphotype III owing to its thickness and similarities with other teeth of the same morphotype (e.g. Fig. 12). These specimens probably suffered a high degree of abrasion and lost their enamel and some dentine layers during the biostratigraphic phase. It is worth noting that the time-averaging before the fossil diagenesis of some fossils collected in the Bauru Group was estimated to be of the order of hundreds to thousands of years (Araújo-Júnior and Marinho 2013).

The morphotypes VI and VII were also interpreted as abelisaurids. The combination of morphotypes VI and VII into a single morphotype did not affect the topologies of the phylogenetic analyses (Supporting Information, Figs S1–S3). Morphotypes VI and VII show some superficial similarities to allosauroid teeth (see description above), but lack unambiguous synapomorphies (Hendrickx *et al.* 2019). The lateral tooth LPPV-PV 1102 is the most peculiar, being similar to carcharodontosaurid teeth in the presence of a distal margin with a convex apical profile and a concave basal half in lateral view (character 72:3). However, the concave surface is less conspicuous than that of *Mapusaurus roseae* Coria and Currie, 2006 (Coria and Currie 2006) and *Eocarcharia dinops* Sereno and Brusatte 2008, resembling those of *Carcharodontosaurus saharicus* Depéret and Savornin, 1925 and *Carcharodontosaurus iguidensis* Brusatte and Sereno, 2007. Despite this, typical features of carcharodontosaurids, such as biconvex mesial denticles and braided enamel texture (Hendrickx *et al.* 2019), are not present in LPPV-PV 1102 or other teeth grouped in these morphotypes.

Some comments should also be made on the orientation of distal denticles in lateral teeth. The lateral dentition of Abelisauridae is diagnosed by the presence of crowns with apically inclined and hooked distal denticles (characters 92, state 2, and 100, state 1; Hendrickx *et al.* 2019). These features are well distributed among known abelisaurids, such as *Rugops primus* Sereno, Wilson and Conrad, 2004 and *Majungasaurus crenatissimus* (Depéret, 1896) Lavocat, 1955 (Hendrickx *et al.* 2019). *Aucasaurus garridoi* Coria, Chiappe and Dingus, 2002

and *Abelisaurus comahuensis* Bonaparte and Novas, 1985 have two states for character 92 through the dental row: lateral teeth having distal denticles asymmetrically convex and hooked. However, *Skorpiovenator bustingorryi* Canale *et al.*, 2009 has lateral teeth with symmetrically convex distal denticles (character 92, state 0) and mid-crown denticles perpendicular and apically inclined from the distal margin (character 100, states 0 and 1) (Hendrickx *et al.* 2019). Therefore, the shape and orientation of denticles are variable in abelisaurids and should not be considered as diagnostic features alone.

It is worth noting that the lateral tooth MCT.R. 859a (morphotype VI; Fig. 19A–C), previously described as belonging to *Pycnonemosaurus* (Bittencourt and Kellner 2002, Kellner and Campos 2002), was later considered to be disassociated from the holotype, because no cranial elements were found and the teeth were isolated (Delcourt 2017). Owing to its size, it should be referred to a large abelisaurid, such as *Pycnonemosaurus* (Grillo and Delcourt 2017). In the present work, we use the most complete specimen (Fig. 19A–C) in our analyses. However, there are other fragmentary dental remains, missing the enamel and dentine layers (Fig. 19D–O) (Bittencourt and Kellner 2002), which are too incomplete to be identified with confidence. Although our analyses reinforce the abelisaurid affinities of the most complete specimen, they could not classify it to a more inclusive taxon, and this specimen is, consequently, referred to an indeterminate abelisaurid.

The large number of dental elements recovered as abelisaurids elucidates a lot about the theropod diversity of the Late Cretaceous in central South America. So far, only four unambiguous species of theropods have been described from the Upper Cretaceous of the Bauru Basin: the abelisaurids *Thanos simonattoi* Delcourt and Iori, 2020 from the Adamantina Formation (Delcourt and Iori 2020), *Pycnonemosaurus* (Kellner and Campos 2002, Delcourt 2017), *Kurupi itaata* Iori *et al.*, 2021 (Iori *et al.* 2021), and the unenlagiine *Ypupiara lopai* Brum *et al.*, 2021 (Brum *et al.* 2021) from the Marília Formation. The age of the noasaurids *Vespersaurus* (Langer *et al.* 2019, de Souza *et al.* 2020) and *Berthasaura* (de Souza *et al.* 2021) from the Caiuá Group is considered to be younger than the record of theropods from the Bauru Group (Menegazzo *et al.* 2016, Batezelli 2017, Langer *et al.* 2022).

The large record of abelisaurid dental material over other theropods might be explained by two factors. The first is that abelisaurids were the main theropod group in terms of diversity in Brazil during the Late Cretaceous. The variety of dental crown morphotypes seems to corroborate this idea, and the reduced number of other taxonomic groups in the osteological record of the basin also supports this hypothesis (Novas *et al.* 2008, Tavares *et al.* 2014, Brum *et al.* 2016, Brusatte *et al.* 2017, Delcourt and Grillo 2018a, Delcourt *et al.* 2020b, Langer *et al.* 2022). This is also true considering that this group includes the main predators in the Southern Hemisphere during the Late Cretaceous (Carrano and Sampson 2008, Delcourt 2018).

When assessing the allometric evolution and body length of abelisauroids, Grillo and Delcourt (2017) observed that during the Cretaceous, the diversity of abelisaurids increased in terms of both size and taxonomic diversity throughout geological time. The reduced number of other taxonomic groups, in addition to the osteological record in the Bauru Basin, support the

hypothesis that abelisaurids were the dominant theropod group in the Upper Cretaceous of central South America. Although our data seem to suggest an increase in the number of abelisaurid teeth from older layers (Adamantina Formation, Campanian) to more recent ones (Marília and Presidente Prudente Formations, Maastrichtian), implying an augmentation in the abundance of this taxon, several critical facets of controlled excavation remain unaddressed. These include the deposit geometry (teeth per square metre), the lateral extent of deposits, and the number of sites across temporal horizons.

The second reason for the abundance of abelisaurid shed teeth lies in the fact that abelisaurids might have had a higher tooth replacement rate than other theropods (D'Emic *et al.* 2019), causing a bias in the record. Evidence shows that *Majungasaurus* had a higher tooth replacement rate than any other group of theropods, similar to those of sauropod and ornithischian dinosaurs. This is probably attributable to its osteophagous behaviour, as recorded in Maevarano Formation fossils (Rogers *et al.* 2003, D'Emic *et al.* 2019). Theropod bite marks are well known in sauropod bones from the Adamantina Formation (e.g. Kellner *et al.* 2006a, Machado *et al.* 2013), although an identification for the bite maker was not proposed in most of them. A recent work described bite traces on a sauropod rib from the Bauru Group in more detail and identified the bite maker as a probable abelisaurid owing to the distance between teeth and other anatomical details (Reis *et al.* 2022). It is likely that abelisaurids from the Bauru Basin would have a similar behaviour and tooth replacement rate to those seen in *Majungasaurus* (Rogers *et al.* 2003, D'Emic *et al.* 2019). As mentioned earlier, this could justify the large number of abelisaurid teeth found in central South America.

The palaeoenvironment of central South America

The fauna from the Late Cretaceous of what is now the Bauru Basin was highly diverse and included non-avian dinosaurs (e.g. Bandeira *et al.* 2016, Delcourt and Iori 2020, Brum *et al.* 2021, Iori *et al.* 2021, Navarro *et al.* 2022), crocodyliforms (e.g. Nascimento and Zaher 2010, Godoy *et al.* 2016, Darlim *et al.* 2021, Marchetti *et al.* 2022), mammals (Castro *et al.* 2018), birds (Candeiro *et al.* 2012a), turtles (e.g. Romano *et al.* 2013), and squamates (Nava and Martinelli 2011). Non-avian theropod dinosaurs are represented by abelisaurids, noasaurids, megaraptorids, and maniraptorans (Novas *et al.* 2005a, Candeiro *et al.* 2012b, Méndez *et al.* 2012, Delcourt and Grillo 2014, Brum *et al.* 2018, 2021, Delcourt and Iori 2020, Iori *et al.* 2021), a faunal association consistent with that of the Patagonian record during the latest Cretaceous (Novas *et al.* 2013) and also considering the distribution of these groups in South America. However, the large record of abelisaurids over other theropod clades in central South America is discordant with the basins from the same age in the rest of the continent (see Novas *et al.* 2013, Brusatte *et al.* 2017), suggesting that the Bauru Basin might have experienced different selective pressures owing to environmental divergences.

According to several authors, during the Cretaceous the Bauru Basin was located in semi-arid to arid palaeoclimatic zones (Weska 2006, Carvalho *et al.* 2010, Fernandes and Magalhães Ribeiro 2015, Basilici *et al.* 2016, Batezelli 2017, Delgado *et al.* 2021), which is likely to have influenced the distribution of

many clades. This is the case for Gondwanan crocodyliforms (Carvalho *et al.* 2010), in which notosuchians and sphagesaurids have been suggested to be endemic in South America by some authors (Pol *et al.* 2014). The better preservation of crocodyliforms over theropods has led to the hypothesis that they were more abundant in the Bauru Group, especially in the Adamantina Formation, and occupied the ecological niche of predators that is typically filled by small- to medium-bodied theropods in other localities (Riff and Kellner 2011). The hypothesis of competition between these groups (Gasparini *et al.* 1993, Candeiro *et al.* 2006, Martinelli and Pais 2008, Riff and Kellner 2011) is based on the large number of species and on the better preservation of crocodyliforms rather than theropods (e.g. Delcourt and Grillo 2014, Darlim *et al.* 2021). However, Bandeira *et al.* (2018) suggested that the abundance of crocodyliforms and the paucity of theropods results from taphonomic bias. According to these authors, crocodyliforms would prefer to live in more humid places, whereas theropods and sauropods would choose to live in drier lands. In other words, they did not share the same micro-environment. Therefore, the preservation of theropods (and other taxonomic groups) would have been compromised by the depositional context rather than being outnumbered by crocodyliforms (Bandeira *et al.* 2018).

Burrowing behaviour has also been suggested for crocodyliforms from the Bauru Group (Marinho and Carvalho 2009, Martinelli *et al.* 2019), which would also contribute to their preservation. However, taphonomic signatures suggest that the crocodyliforms from the Bauru Basin suffered mummification before final burial (Araújo-Júnior and Marinho 2013, Bandeira *et al.* 2018). A burrow from the Bauru Group is regarded as being produced by a notosuchian crocodyliform, but it was not dug near a water body (Martinelli *et al.* 2019).

A slightly different hypothesis about the faunal distribution was proposed by Martine (2013), who argued that the Bauru Group fauna changed with seasonality. During the dry period, part of the fauna would migrate in search for wetter areas, including large sauropods, enantiornithines, and larger theropods. Crocodyliforms, such as notosuchians, sphagesaurids, and possible peirosaurids, would be residents owing to their adaptation to live in drier conditions (Carvalho *et al.* 2010, Martine 2013, Martinelli *et al.* 2019). With the monsoonal regimes and the flooding of rivers, the fauna of dinosaurs and other reptiles would have returned and remained until the next dry season. In this hypothesis, preservation of theropods and of other taxa (except for crocodyliforms) is biased because animals simply decayed too rapidly during the biostratigraphic phase before the fossil diagenesis.

The Bauru Basin has well-distributed palaeosols throughout all its sequences. Different authors, such as Delgado *et al.* (2021), Paula e Silva *et al.* (2009), and Dias *et al.* (2018, 2021), have shown all the defining features of condensed sections (*sensu* Kidwell 1993, Föllmi 2016) applicable to continental environments. Concentrations of teeth and other fossils are generally associated with palaeosols (non-stratified sediments with escape trace fossils and/or root moulds) or omission surfaces in all fossil sites. These pieces of evidence indicate cycles of climate change, involving active interplay between the living biota (in areas where soils and erosive surfaces are dynamic) and climatic events, with sediments capturing the changes in biota (Rogers *et al.* 2007a).

The dominance of theropod teeth can be explained by their polyphyodonty throughout their life cycle (D'Emic *et al.* 2019). However, the concentration of these remains in palaeosols implies a strong stratigraphic and taphonomic bias. Since classic studies from the 1980s, mainly by Hanson *et al.* (1980), Bown and Kraus (1981), and Behrensmeier and Kidwell (1985), it has been revealed that biostratigraphic phenomena, even weak ones, were capable of increasing the relative abundance of teeth in fossil deposits. The density and mechanical resistance of teeth are positive selection variables.

Cleveland *et al.* (2007) used the premise that successive palaeosols with an absence of A and B horizons (i.e. surface soil and subsoil horizons, respectively) owing to erosion do not necessarily imply the existence of complete cycles of aggradation (variation in base level). Successions of palaeosols with an eroded top can occur owing to ephemeral movements of subsidence of the base level owing to eustatic accommodation of the basin. Scarponi *et al.* (2013) demonstrated quantitatively that sections of maximum stratigraphic condensation, which are periods of falling stage systems tract, can increase temporal mixing by up to 10 times when compared with other sections of deposition in a marine environment.

Recently, Soares *et al.* (2020) analysed the architecture of the Bauru Basin, mainly in the Bauru Group (eastern side of the basin), from the point of view of palaeosol formation. The Bauru Group is interpreted as a continental alluvial fan marked by discordances controlled by palaeosols. The evidence from this study reinforces two important aspects: (i) the alternation between semi-arid environments, forming sedimentary deposits, and a mild and humid environment of depositional hiatus where soils develop (range of temperatures 20–35°C and palaeoprecipitation 365–1095 mm/year, extracted from Soares *et al.*, 2020); and (ii) the nature of soils allows inference of the depositional hiatuses that occurred heterogeneously in the landscape, with shorter depositional hiatuses (of the order of hundreds of years) in proximal parts of active channels and longer ones (of the order of 4000 years) in distal portions of the flood area.

We agree with the palaeoecological interpretation of Martine (2013) and the taphonomic model proposed by Bandeira *et al.* (2018). The diversity of theropod dental materials reflects the palaeoecology of predatory dinosaurs in the model proposed by Martine (2013). Following the proposal for distribution of the fauna from the Bauru Basin (Martine 2013), we suggest that theropods with no or few adaptations for living in an arid environment (e.g. unenlagiinae and megaraptorans) were the first groups to leave the arid zone (Delgado *et al.* 2021), mostly probably following the large sauropod dinosaurs. Abelisaurids were better adapted for living in stressed environments than other theropods (Rogers *et al.* 2007b, Delcourt 2018), feeding on carcasses (Rogers *et al.* 2003, 2007b), and remained in the arid plains of central South America for longer periods of time. Therefore, they were the last dinosaurs to leave the semi-arid/arid areas during the dry season, taking the last available resources, such as small prey and carcasses, in a similar way to that of the Maevarano Formation, in which remains of *Majungasaurus* were unearthed (Rogers *et al.* 2007b). This hypothesis would explain the abundance of abelisaurid osteological and dental remains compared with those of other theropod clades in the Bauru Basin.

Furthermore, our data align with the findings of Bandeira *et al.* (2018), who asserted that the preservation of theropods was influenced more by taphonomic factors than by competition with baurusuchids (Gasparini *et al.* 1993, Candeiro *et al.* 2006, Martinelli and Pais 2008, Riff and Kellner 2011). Although the osteological preservation of crocodyliforms in the Adamantina Formation surpasses that of theropods (Bandeira *et al.* 2018, Langer *et al.* 2022), the abundance of theropod teeth (Langer *et al.* 2022; this study) suggests a significant presence of small- to mid-sized theropods in this unit, possibly coexisting with crocodyliforms. Determining whether direct competition occurred between these two archosaur groups of archosaurs is challenging. Nevertheless, it is noteworthy that crocodyliform diversity declined markedly towards the end of the Cretaceous. The only species from the Marília Formation is *Titanochampsia iorii* Fachini *et al.*, 2002 (Fachini *et al.* 2022), and there is no record of baurusuchids in Maastrichtian beds so far (Bandeira *et al.* 2019, Langer *et al.* 2022). The increasing number of theropod teeth in the Marília and Presidente Prudente formations implies that they became diverse and abundant, as discussed earlier and in agreement with the findings of Grillo and Delcourt (2017).

Our data suggest a new approach to interpreting palaeontological evidence of the Bauru Basin, exemplified here by the Adamantina, Presidente Prudente, and Marília formations. Central South America had an ecological dynamic and distribution of theropods differing from that of the southernmost part of the continent (Novas *et al.* 2013). Although the same groups are found throughout South America, the frequency and abundance of some clades in the central region are dramatically distinct from others in the south. We reinforce the hypothesis that the distribution of theropods is driven by climatic conditions, especially at the end of the Cretaceous, with abelisaurids being significantly more abundant in the central part of the continent (Delcourt and Langer 2022; this research), whereas other taxa, such as megaraptorans, were more abundant in the southern regions (Novas *et al.* 2019, Lamanna *et al.* 2020). Although it has been proposed that unenlagiines composed the theropod fauna alongside abelisaurids in northerly palaeolatitudes (Lamanna *et al.* 2020), the fewer records of this group in central South America (Candeiro *et al.* 2012b, Brum *et al.* 2021) and the absence of definite unenlagiine teeth in our sample suggest that these dromaeosaurids preferred to live in a milder climate than in arid/semi-arid environments (Carvalho *et al.* 2010, Delgado *et al.* 2021).

Finally, it is important to highlight some geological and taphonomic aspects of isolated teeth from this portion of central South America. Firstly, the Bauru Basin has more environmental affinities, in terms of basin evolution, with other backarc and retroarc basins of the Andean Orogenic System, which reduces the possibility of a direct correlation with the Neuquén Basin. Secondly, the teeth here described do not have roots (except for CPP 157, morphotype II; Fig. 8) and are therefore interpreted as shed teeth, meaning that they were lost during life (peri-mortem process) by replacement or nibbling. Thirdly, although the age of the Bauru Basin is still disputed, radioisotopic data suggest that the depositional context of the Bauru Group ranges from late Coniacian to late Maastrichtian (Castro *et al.* 2018, see also Langer *et al.* 2022). Some authors proposed a larger time range for the Bauru Group, with the oldest deposition starting during the

Cenomanian and ending during the late Maastrichtian (Pinheiro *et al.* 2018); however, the virtual absence of carcharodontosaurid teeth in deposits of the Bauru Basin (Delcourt *et al.* 2020a; this research) reinforces the idea that the depositional events of the basin (except for Caiuá Group) started after the Turonian, when several species, including carcharodontosaurids, became extinct (Novas *et al.* 2005b, 2013, Meso *et al.* 2021b, Canale *et al.* 2022). Even so, it is important to note that teeth collected from younger units (e.g. Marília Formation, Maastrichtian) could be older owing to time-averaging expected for some outcrops. Araújo-Júnior and Marinho (2013) suggest that taphonomic events at an outcrop in Jales municipality, São Paulo state (Adamantina Formation), occurred over a period ranging from 10^0 to 10^4 years, allowing for temporal mixing among crocodyliform and dinosaur remains from this locality. Thus, it is plausible that several teeth from some outcrops could, in fact, be older. More taphonomic studies should be conducted at the locations where the teeth were collected to estimate the time averaging of preservation for dinosaur teeth and for the remains of other taxa.

CONCLUSION

We analysed 179 isolated theropod shed teeth from the Bauru Basin of central South America, using discriminant (178) and phylogenetic (174) analyses. The dental material was separated into seven morphotypes based on their general morphology. The discriminant analysis was inconclusive owing to the incompleteness of most teeth, which resulted in missing variables and biased results, favouring some taxonomic groups over others. The phylogenetic analyses were performed using seven morphotypes scored in a dental data matrix. We found slight differences among the morphotypes, with morphotypes I, II, III, IV, VI, and VII being recovered within Abelisauridae, whereas morphotype V was recovered as Therizinosauria. However, morphotype V (a single tooth) lacks the unambiguous feature of therizinosaurs and is referred to an abelisaurid based on the absence of constriction between the base of the crown and the root, flutes on the lingual surfaces, poorly developed or fully absent mesial denticles, and a DSDI close to one.

The rich record of abelisaurid teeth is most likely to reflect their abundance over other taxa, suggesting that they were the dominant theropods in this part of central South America. At the top of the falling stage systems tract, there is a distinctive sequence boundary marked by palaeosols indicating a mild to humid climate. In this zone, two-dimensional fossil accumulations, primarily composed of teeth remains, are prevalent. The subsequent layers of semi-arid deposits complete a scenario of climate change with a record of the resilient fraction of a biota from mild to humid climates. We also argue that the distribution of abelisaurids was driven by climatic conditions because they were well adapted to semi-arid conditions and diversified in size and number of species in conducive environments, such as those observed in central South America.

SUPPLEMENTARY DATA

Supplementary data is available at *Zoological Journal of the Linnean Society* online.

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DATA AVAILABILITY

The raw data is available in the Supplementary Materials or upon request from the corresponding authors.

CONFLICT OF INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have influenced this research.

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