



## PALEONTOLOGY

# A lost tooth in the jungle: revisiting the sole dinosaurian record from northern Brazil

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**Abstract:** The record of Mesozoic reptiles in the Northern region of Brazil is extremely limited, with the only definite occurrence consisting of two ziphodont teeth recovered from an oil well core in the municipality of Nova Olinda do Norte, Amazonas state, from strata of the Alter do Chão Formation (Cenomanian) of the Amazonas Basin. In this study, we aim to reevaluate MCT.R.514 using the most recent methodologies available for the identification of isolated theropod teeth. The cladistic analyses recovered MCT.R.514 as a possible metriacanthosaurid or non carcharodontosaurid allosauroid while the LDAs showed affinities between the specimen and Abelisauridae, Piatniktzysauridae, and Tyrannosauridae. MCT.R.514 was assigned as an abelisaurid due to its overall morphology that lacked metriacanthosaurid synapomorphies (i.e. spiraling mesial carina, strongly labially displaced distal carina, and well-marked mesiolingual longitudinal groove), while maintaining homoplastic features between both groups (i.e. irregular enamel texture, a lingually biconcave cross section, and a straight distal margin). This, together with a mostly Laurasian distribution of Metriacanthosauridae favors the assignment of MCT.R.514 as an abelisaurid as the most parsimonious hypothesis in this occasion. The identification of the specimen as an abelisaurid further expands the still scarce “Mid” Cretaceous record of this clade in Brazil.

**Key words:** Alter do Chão Formation, cladistic analysis, theropod tooth, quantitative analysis.

## INTRODUCTION

The fossil record of Mesozoic reptiles in the Brazilian Legal Amazon (BLA) is not particularly abundant, being composed mostly by remains from the Itapecuru Formation, São Luís Grajaú Basin, in the Northeastern state of Maranhão (Ferreira et al. 1992, Carvalho et al. 2003, Ribeiro et al. 2003, 2023, Castro et al. 2007, França et al. 2022). The remainder of the BLA, that spread throughout most of the Brazilian North, has a much sparser fossil record for Mesozoic reptiles, with the only definitive occurrence in the region consisting of two ziphodont teeth (Price 1960).

Those teeth were recovered from an oil well core (1-NO-1-AM) in the municipality

of Nova Olinda do Norte, Amazonas state, in the Cretaceous strata of the Alter do Chão Formation, Amazonas Basin (Price 1960). While one of these teeth is presently unaccounted for, the other is now part of the Collection of Fossil Reptiles of the Museum of Earth Sciences (Museu de Ciências da Terra; MCT) as specimen MCT.R.514. This tooth was studied by the Brazilian paleontologist Llewellyn Ivor Price (1905-1980), who regarded it as an indeterminate carnosaur theropod (Price 1960).

Even though it represents the sole dinosaur record for the Brazilian North, Price’s original description of the fossil attracted little attention, being only briefly discussed in stratigraphic

studies of the Amazonas Basin (e.g., Daemon 1975, Caputo 2011) and reviews about the Brazilian dinosaur record (e.g. Bittencourt & Langer 2011, Ribeiro et al. 2023).

This lack of interest can be partially explained by the fact that isolated theropod teeth were for a long time regarded as mostly non diagnostic, mainly due to their highly homoplastic morphology, which difficult a more precise identification of those specimens (Smith et al. 2005, Hendrickx et al. 2019). However, the proposal of new methodologies for the identification of isolated theropod teeth (e.g., Smith et al. 2005, Hendrickx and Mateus 2014, Hendrickx et al 2020a) allowed a more accurate assignment of those elements. In this study we aim to reevaluate MCT.R.514 using the most recent methodologies available for the identification of isolated theropod teeth, in order to obtain a new and more robust assignment for the specimen.

### Measurement abbreviations

AL, apical length; CA, crown angle; CBL, crown base length; CBR, crown base ratio; CH, crown height; CHR, crown height ratio; CBW, crown base width; DA, distoapical denticle density; DB, distobasal denticle density; DC, distocentral denticle density; DDL, distal denticle length;

DSDI, denticle size density index; LAF, labial flutes; LIF, lingual flutes; MA, mesioapical denticle density; MB, mesio basal denticle density; MC, mesiocentral denticle density; MCL, mid-crown length; MCR, mid-crown ratio; MCW, mid-crown width; MDL, mesial denticle length.

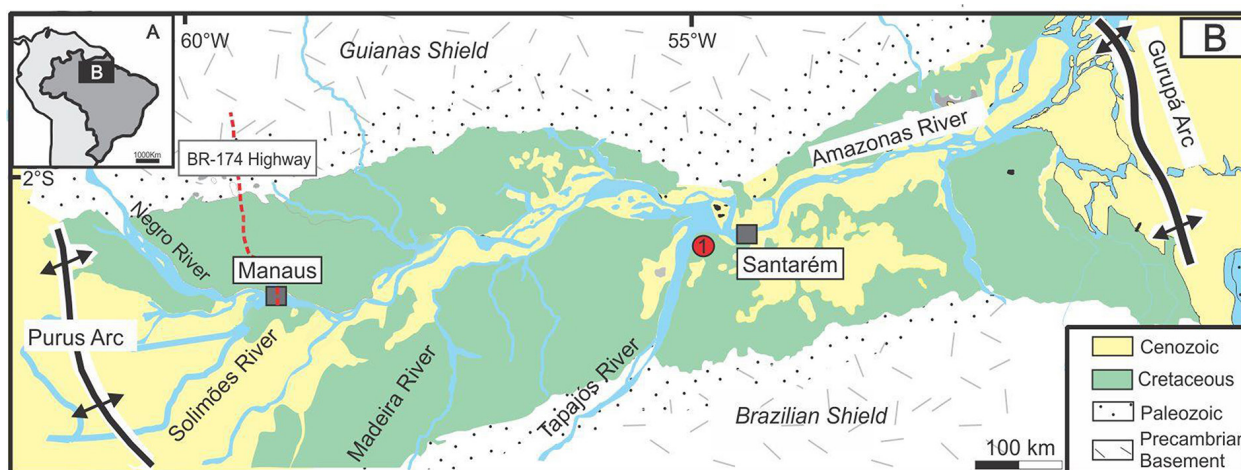
### Institutional abbreviations

CPRM, Companhia de Pesquisa de Recursos Minerais; MCT, Museu de Ciências da Terra.

### GEOLOGICAL SETTING

The Amazon Basin (Figure 1) is an intracratonic basin with an approximate extension of 515,000 km<sup>2</sup>, covering the Brazilian states of Pará, Amazonas and Amapá (Cunha et al. 2007). This unit is delimited to the North by the Guiana Shield; to the south by the Central Brazil Shield; to the East, the Gurupá Arch and the Purus Arch to the West (Wanderley Filho et al. 2005, Cunha et al. 2007).

One of the most important geological units in the Amazon Basin is the Alter do Chão Formation, which is composed of sandstones and pelites interbedded with conglomerates (Cunha et al. 2007). This formation was first proposed by Kistler (1954) to identify a post-Paleozoic



**Figure 1.** Geological map of the Amazon Basin with the position of the Alter do Chão region highlighted (point 01). Cities of Santarém and Manaus as gray squares. Modified from Mendes (2015).

sedimentary succession of the Amazon Basin. This succession is composed of reddish sandstones, mudstones, conglomerates and intraformational breccias and the depositional environment would be attributed to fluvial and lacustrine/deltaic systems (Daemon 1975). The fossil record is scarce, being best represented by trace fossils (Caputo & Rodrigues 1972, Nogueira et al. 1999, Souza & Nogueira 2009).

Over time, numerous sedimentological and faciological studies have been carried out, showing that the main lithofacies of the Alter Formation are: massive conglomerates (e.g. Mendes et al. 2012, Palma 2014); sandstones with channeled cross-stratification (e.g. Franzinelli & Igreja 2011); sandstones with tabular cross-stratification (e.g. Mendes et al. 2012); Massive sandstones (e.g., Rossetti & Netto 2006) and bioturbated pelites (Rossetti & Netto 2006, Mendes 2015).

The age of the Alter do Chão Formation continues to be debated. A Cretaceous age was suggested in one of the first dating attempts by Price (1960) based on the occurrence of the material studied here. Later, Daemon (1975) suggested an Albian-Cenomanian/Turonian age through palynological studies.

This dating was later corroborated with stratigraphic and palynological studies obtaining Aptian ages for the lower layer of the unit and Cenomanian age for the upper sequence (Dino et al. 1999). In the same work, the authors recognized two sequences related to two depositional environments for the formation: i) a meandering fluvial system that evolves into an anastomosed system, with aeolian reworking for the lower sequence and ii) recognitions of fluvial-deltaic lacustrine progradational cycles for the upper sequence (Dino et al. 1999).

Daemon & Contreiras (1971), carrying out palynological analyses inferred a Late Cretaceous date for the Alter do Chão Formation, ranging

from the beginning of the Cenomanian to the Maastrichtian. Caputo (2011) differs from most works and infer a Cenozoic age for the Alter do Chão Formation. The author argues that the Alter do Chão Formation would cover another Mesozoic unit informally named "Jazida da Fazendinha Formation". All work to date using palynological and seismic analyzes would have been wrongly used for the formation (Caputo 2011).

In the present work, we consider that the material comes from the Alter do Chão Formation of Cretaceous age until further studies detailing the stratigraphic limits confirming the division reported by Caputo (2011) and formally description of the new formation in accordance with the international code.

## MATERIALS AND METHODS

The specimen described here consists of a single isolated tooth crown (MCT.R.514), retrieved from an oil-well core (1-NO-1-AM) drilled in the municipality of Nova Olinda, Amazonas State, Brazil. MCT.R.514 is housed at the Fossil Reptile Collection of the MCT, which is linked to the CPRM (Companhia de Pesquisa de Recursos Minerais, part of the Brazilian Geological Survey).

The specimen has a partially complete crown, with well-preserved denticles, a nearly complete apex, while part of its crown base being missing. We identified MCT.R.514 based on a combination of morphological features (see Hendrickx et al. 2019), cladistic (Hendrickx et al. 2020a) and morphometric analyses (e.g., Brusatte & Clark 2015, Csiki-Sava et al. 2016, Young et al. 2019, Hendrickx et al. 2020a). Our preliminary morphological description of the teeth follows the nomenclature proposed by Hendrickx et al. (2015). The morphometric analysis for the theropod tooth was based on measurements first proposed by Smith et al. (2005), using the

methodology detailed by Young et al. (2019) and Hendrickx et al. (2020a).

The tooth was photographed with an AxioCam 208 color digital camera attached to a Zeiss Stemi 2000-C stereoscopic binocular microscope, using the ZEN lite 3.2 software. Measurements were digitally taken with the software ImageJ.

### Cladistic analysis

In order to state de phylogenetic affinities of MCT.R.514, we performed a cladistic analysis on the data matrix published by Hendrickx et al. (2020a) that focuses on the dentition of non-avian theropods. This matrix includes 146 dental characters scored across 105 theropod genera. MCT.R.514 was then scored as a single operational taxonomic unit (OTU).

We followed the methodology detailed by Young et al. (2019) and Hendrickx et al. (2020a) and conducted the cladistic analysis with TNT 1.1 (Goloboff et al. 2008) using a backbone tree topology and the positive constraint command, setting MCT.R.514 as a floating terminal (Supplementary Material - Table SI). The topological tree was built based on the results of the phylogenetic analyses of Müller et al. (2018) for non-neotheropod saurischians, Ezcurra (2017) for non-averostran neotheropods, Rauhut & Carrano (2016) and Wang et al. (2017) for Ceratosauria, Carrano et al. (2012) and Rauhut et al. (2012, 2016) for non-coelurosaurian tetanurans, Brusatte and Carr (2016) for Tyrannosauroida, and Cau et al. (2017) for neocoelurosaurs.

A combination of the tree-search algorithms Wagner trees, TBR branch swapping, sectorial searches, Ratchet (perturbation phase stopped after 20 substitutions) and Tree Fusing (5 rounds), until 100 hits of the same minimum tree length were reached, were used as the search strategy. The trees were subjected to a

final round of TBR branch swapping (the TNT command used was “xmult = hits 100 rss fuse 5 ratchet 20” followed by “bb”). We also performed two additional cladistic analyses, one using the dentition-based dataset without constraints, the second on a data matrix restricted to crown-based characters (Young et al. 2019, Hendrickx et al. 2020a). Due to particularities on the tooth morphology, MCT.R.514 was scored both as a mesial and a lateral tooth in different analyses.

### Morphometric analyses

Fourteen linear measurements were taken from specimen MCT.R.514 (AL, CA, CBL, CBW, CH, DDL, DC, MC, MCL, MDL, MCW, MSL, LAF, LIF; *sensu* Hendrickx et al. 2015) with the free software ImageJ so that it could partake in a battery of morphometric analyses. Some measurements (CBL, CBW, CH, AL and CA) and ratios (CBR, CHR) were affected due to the damaged crown base, those being marked with an asterisk (\*) in order to display their incompleteness.

In order to assign specimen MCT.R.514 to a known theropod group we included it to four different datasets, the first three that used the twelve variables proposed by Hendrickx et al. (2020a) (AL, CA, CBL, CBW, CH, DDL, MCL, MDL, MCW, MSL, LAF, LIF; Tables SII and SIII) while the last one employed the eight variables proposed by Delcourt et al. (2020, 2024) (AL, CBL, CBW, CH, DC, MC, MCL, MCW; Table SIV).

The first and most complete dataset had measurements taken from 1367 teeth belonging to 80 non-avian theropod taxa and two avian taxa, all separated in 20 different family level groupings first proposed by Brum et al. (2021). We removed the two indeterminate dromaeosaurid teeth originally published by Tavares et al. (2014) from this dataset in order to diminish the number of specimens not identified to taxon level. The second dataset, proposed by Hendrickx et al. (2020a), was

composed solely by specimens with a CH (crown height) higher than 20 mm. The third dataset was based on the one proposed first by Delcourt et al. (2020), being composed solely by South American taxa present during the Cretaceous period. The fourth and last dataset was also composed solely by Cretaceous South American taxa, differing itself from the latter by the usage of the eight variables employed by Delcourt et al. (2020, 2024; Table SIV). As proposed by the Young et al. (2019) protocol, all measurements were log transformed in order to normalize the quantitative variables (Tables SIII and SIV).

The exploratory multivariate analyses performed in this study were based on the protocols of Young et al. (2019), Hendrickx et al. (2020a) and Delcourt et al. (2020), in which seven linear discriminant analysis (LDA). We choose to not carry out the clustering analyses proposed by those protocols, as there is no proper method of testing its efficiency through reclassification rates (RR) or other similar methods. The LDAs were conducted on the three datasets using the classifier function of the open-source software PAST v4.07b (Hammer et al. 2001), in order to assign it either in family and in taxon level.

The sole exception to this protocol was the LDA performed on the South American dataset with Delcourt et al. (2020, 2024) variables, in which only clade level searches were employed.

Systematic Paleontology

Theropoda Marsh, 1881

Ceratosauria Marsh, 1886

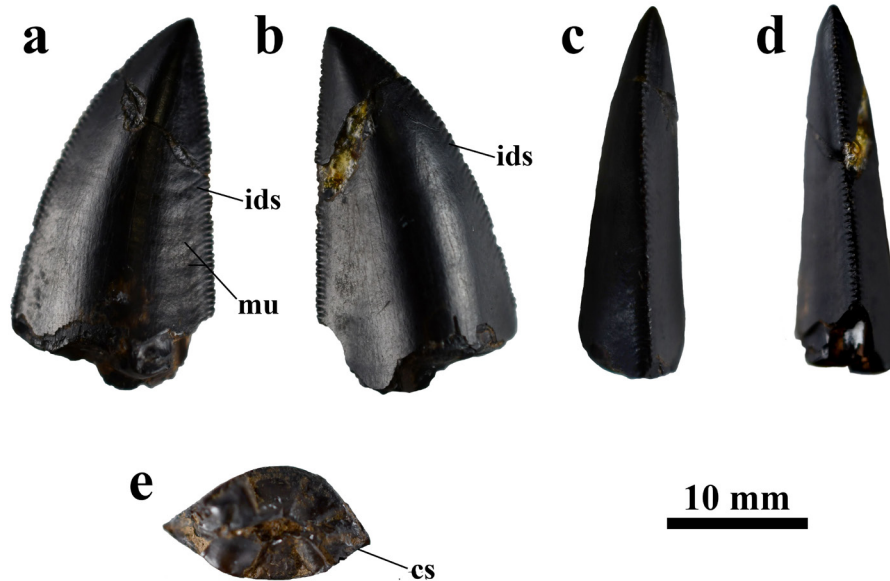
Abelisauridae Bonaparte & Novas, 1985

Abelisauridae indet.

### Description

MCT.R.514 (Figure 2) is a well preserved isolated theropod tooth. The crown is mostly complete, with its basalmost portion being completely damaged, mainly in its distal margin. Both the labial and lingual margins of the crown are also damaged, but to a lesser degree. The apical portion of the tooth has been originally detached from the rest of the crown, later being reattached during the preparation process. This left a large fracture mark in the apical portion of its labial surface and a smaller mark in the same region of the lingual surface.

It is a large theropod crown ( $CH^* = 26,18$  mm; Table I), with a moderately elongated crown ( $CHR^* = 1,79$ ; Table I) and a moderately



**Figure 2.** The Nova Olinda tooth (MCT.R.514) in its labial (a), lingual (b), mesial (c), distal (d) and basal (e) views. Abbreviations: cs, concave surface; ids, interdenticular sulci; mu, marginal undulations.

narrow crown base (CBR\* = 0,52; Table I). The labial profile of MCT.R.514 is slightly convex in mesial and distal views, while the lingual profile is weakly concave, suggesting that the crown may have belonged to either a lateral position in the dental arch or a distalmost mesial position. There is a weak lingual concavity adjacent to the mesial carina and another, even more discrete concavity adjacent to the distal carina. The presence of such mesiolingual and distolingual depressions gives to the crown a lanceolate to parlinon shaped cross section (*sensu* Hendrickx et al 2015; Figure 3e). This sort of concavity is normally not seen in lateral teeth, making a mesial position more likely. There is no preserved root and, therefore, no cervix can be observed.

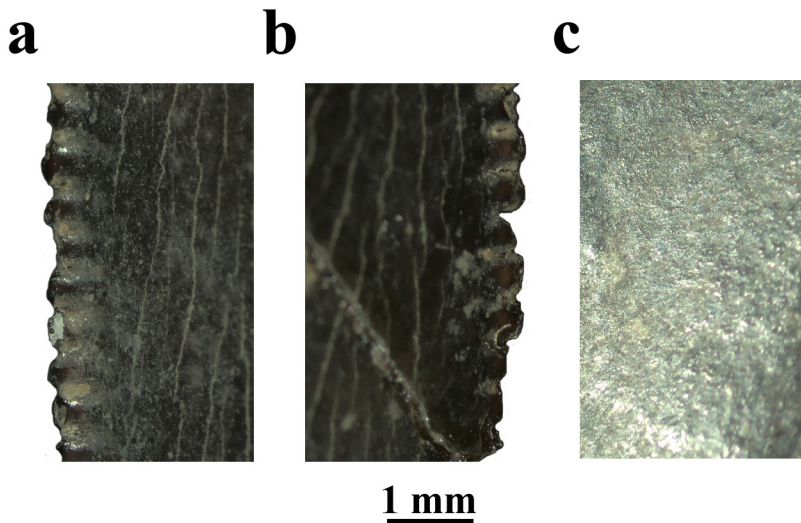
Both carinae are present and fully denticulated in this ziphodont tooth. The mesial carina is strongly convex in labiolingual view

while the distal carina is almost straight. There is a brief apical displacement of the mesial carina towards the labial surface, with the basalmost portion of the same carina being inclined towards the lingual portion. The distal carina has no visible displacement in all its extension. In distal view, the distal carina is almost straight. It's not possible to determine if the mesial or distal carina extends farther than the other, as the basalmost portion of both are damaged. Yet, judging by the gradual size reduction of the denticles it can be expected that the distal carina ended at an almost equal height to the mesial carina. The mesial and distal denticles extend up to the apex of the distal carina in this specimen.

MCT.R.514 has mesial and distal denticles of subequal size (DSDI = 1; Table I), with approximately 11 denticles per 5 millimeters at the midpoint of both mesial and distal carina

**Table I. Measurements of the tooth crown from Nova Olinda (MCT.R.514). Measurements in millimeters, number of denticles per five mm and crown angle (CA) in degrees. Asterisk (\*) signaling incomplete measurements.**

Tooth	CBL	CBW	CH	AL	CBR	CHR	MCL	MCW	MCR	MSL	CA
MCT.R.514	14,57*	7,65*	26,18*	28,08*	0,52*	1,79*	10,86	5,9	0,54	21,21*	67,33°
	LAF +1	LIF +1	MDL	DDL	MA	MC	MB	DA	DC	DB	DSDI
	1	1	0,33	0,41	12	11	11	13	11	11,5	1



**Figure 3. Details on MCT.R.514 morphology, with a close caption of its mesiocentral (a) and distocentral (b) denticles, and its overall irregular enamel texture (c).**

(MC and DC; Table I). There is a gradual change of denticle size on both carinae, with mesioapical denticles being smaller than the mesiocentral and mesio basal denticles, those being almost equal in size (Table I). A similar pattern can be seen in the distal carina (Table I).

The mesial denticles are subquadrangular in shape (Figure 3a), almost as wide as tall, with a parabolic and symmetrical mesial surface. These denticles do not show any inclination towards the apex of the crown, being perpendicular to the mesial margin. Some of the centrodial denticles are slightly worn, while the rest of the denticles are relatively well preserved. The distal denticles are subquadrangular, being as tall as wide, with symmetrical and straight distal margins (Figure 3b). The distobasal denticles show a weak inclination towards the apex, while the mesodistal and apicodistal denticles are mostly perpendicular to the distal margin. There are interdenticular sulci in both mesial and distal denticles (Figure 2a and 2b), with the mesial sulci present mostly in the mesioapical denticles, those being shorter and less developed than the distal sulci. The distal interdenticular sulci are more developed in the distobasal denticles. There are shallow interdenticular slits between the distobasal denticles.

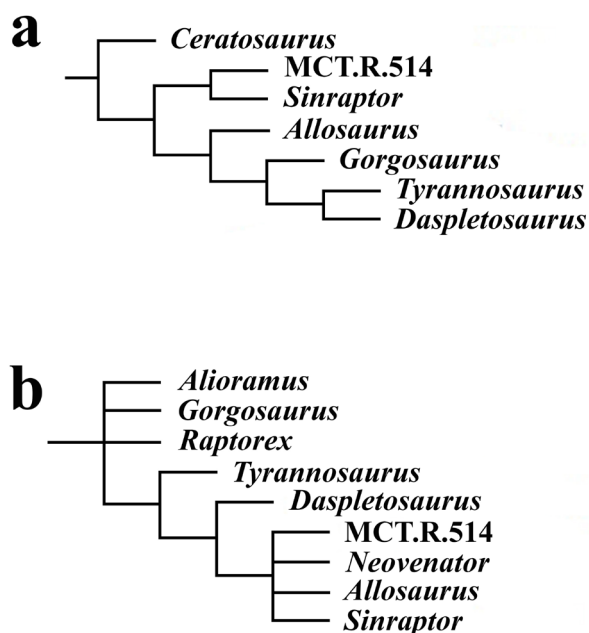
The external enamel surface is irregular (Figure 3c) and has smooth marginal undulations extending throughout the distolabial and distolingual margins of the crown (Figure 3a). These undulations are positioned diagonally to the distal margin. Other than this, there are no other observable enamel ornamentations. There are no wear facets or spalled surfaces on the crown's apex or in its carinae.

## RESULTS

### Cladistic analyses

The two unconstrained cladistic analyses conducted on MCT.R.514 assigned it as a metriacanthosaurid or as a non carcharodontosaurid allosauroid, while the constrained analysis placed MCT.R.514 in a polytomy composed by most neotheropod clades. The constrained analysis (Figures S1 and S2) retrieved 11 trees with 1315 steps (CI = 0,204; RI = 0,451; Table SV). The addition of MCT.R.514 in the matrix resulted in a large polytomy within Neotheropoda, with most allosauroid branches (Metriacanthosauridae, Allosauridae and Carcharodontosauridae) being completely imploded. Ceratosauridae, Abelisauridae and Megalosauridae were partially recovered, with few taxa being placed within the polytomy (*Berberosaurus*, *Rugops*, *Kryptops*, *Abelisaurus*, and *Sciurumimus*). Most theropod clades, such as Noasauridae, Spinosauridae, Neovenatoridae and Coelurosauria maintained their topologies as normally seen in literature (*sensu* Carrano et al. 2012, Rauhut et al. 2012, 2016, Brusatte and Carr 2016, Rauhut & Carrano 2016, Cau et al. 2017, Wang et al. 2017).

The dentition based unconstrained analysis (Figures 4a, S3 and S4) retrieved 170 trees with 1068 steps (CI = 0,251; RI = 0,581; Table SV). It is mostly unresolved, with most clades being either recovered in odd arrangements (such as Abelisauridae with the inclusion of *Erectopus*, and part of Carcharodontosauridae, Tyrannosauridae, and Therizinosauria) or totally imploded within large polytomies. The sole theropod clades fully recovered in this analysis were Abelisauridae and Spinosauridae, yet, still presenting an odd topology. MCT.R.514 was recovered as the sister taxon of the metriacanthosaurid *Sinraptor* due to its denticles being contiguous to the apex of the tooth (character 61.0). This clade belonged in



**Figure 4.** Simplified phylogenetic trees showing the strict consensus trees: a, unconstrained dentition based analysis (a; consensus of 170 MPTs); b, unconstrained crown based analysis (consensus of 201 MPTs). For complete trees, see S1 to S6.

a larger branch composed mainly of alioramine Tyrannosauridae, *Allosaurus* and *Ceratosaurus*.

The “crown based” unconstrained analysis (Figures 4b, S5 and S6 ) retrieved 201 trees with 641 steps (CI = 0,251; RI = 0,624; Table SV). It also resulted in a polytomy, although better resolved when compared to the dentition analysis, with few groups being recovered, such as Ceratosauridae Abelisauridae and Carcharodontosaurinae. Specimen MCT.R.514 was nested within a polytomy with the non carcharodontosaurid allosauroids *Sinraptor*, *Allosaurus* and *Neovenator*, all united by having a straight distal margin in its mesial teeth (Character 44. 1). This clade groups with most tyrannosaurids present on the sample.

### Morphometric analyses

The morphometric results, summarized in Tables II and III and detailed in Table SVI and Figures S7 to

S13, varied throughout the various analyses. The LDAs identified MCT.R.514 either as an abelisaurid or as the Asian tyrannosaurid *Alioramus* (Table III), with only one analysis assigning it as a non-megalosauran megalosauroid, probably as a piatnitzkysaurid (Table III). Abelisauridae and Tyrannosauridae were the most recovered clades by the quantitative analyses, with MCT.R.514 being assigned to each of those groups in four different searches.

## DISCUSSION

### Remarks and comparisons

The results of the cladistic analyses assign MCT.R.514 mostly to allosauroid taxa (e.g. *Sinraptor*, *Allosaurus* and *Neovenator*) with both unconstrained analyses also pointing possible similarities between it and non alioramine tyrannosaurids. The quantitative analyses obtained a diverse array of results, with half of the LDAs assigning MCT.R.514 as an abelisaurid, while the other three suggesting either alioramine or piatnitzkysaurid affinities (Table III).

The overall morphology of MCT.R.514 differs it from most groups identified by the LDAs, such as Piatnitzkysauridae and Tyrannosauridae. Piatnitzkysaurids are a megalosauroid group commonly found in Jurassic outcrops from South America, North America and Asia (Carrano et al. 2012). The dentition of those theropods can be distinguished from MCT.R.514 it lacks the hook shaped distal denticles, has mesial and distal denticles of a similar size instead of larger distal denticles (DSDI = 1; Table I) and has an irregular enamel texture instead of a braided texture (Madsen 1976, Hendrickx et al. 2014, 2019).

Tyrannosaurid affinities were suggested by two of the taxon level searches in the LDAs , and on both unconstrained analyses, pointing morphometric and phylogenetic similarities



**Table II.** Results of the seven LDAs performed on MCT.R.514.

Dataset	RR (%)	Axis 1 (%)	Eigenval 1	Axis 2 (%)	Eigenval 2
<b>Complete (Clade)</b>	60,76	52,24	6,34	18,06	2,19
<b>Complete (Taxon)</b>	59,52	43,49	18,91	16,19	7,04
<b>Large teeth (Clade)</b>	59,12	37,95	1,9	30,79	1,54
<b>Large teeth (Taxon)</b>	57,46	35,5	6,27	27,82	4,91
<b>South American (Clade)</b>	73,93	61,04	6,88	19,41	2,18
<b>South American (Taxon)</b>	69,18	45,62	17,26	20,21	7,64
<b>South American – Delcourt et al. (2020, 2024) variables (Clade)</b>	74,74	71,41	6,78	16,14	1,53

**Table III.** Taxonomic identity obtained from the LDAs performed on MCT.R.514.

Analysis	Inferred identification
<b>LDA - Complete (Clade)</b>	Non-megalosauran Megalosauroidea
<b>LDA - Complete (Taxon)</b>	<i>Alioramus</i>
<b>LDA- Large teeth (Clade)</b>	Abelisauridae
<b>LDA - Large teeth (Taxon)</b>	<i>Alioramus</i>
<b>LDA - South American (Clade)</b>	Abelisauridae
<b>LDA - South American (Taxon)</b>	Abelisauridae indet.
<b>LDA - South American – Delcourt et al. (2020, 2024) variables (Clade)</b>	Abelisauridae

between MCT.R.514 and this coelurosaur clade. In those LDAs, the amazonian specimen was recovered as only as *Alioramus* (Table III), a tyrannosaurid with a zipodont dentition, similar to early tyrannosauroids and juvenile tyrannosaurids (Hutt et al. 2001, Rauhut et al. 2010, Brusatte et al. 2012, Voris et al. 2021).

Even though MCT.R.514 has a similar tooth morphology to alioramines and juvenile tyrannosaurids, it also shows a series of clear differences that can easily distinguish it from that clade. One of those differences is the lack of a “8” shaped cross section, which is present in some juvenile tyrannosaurids (Hendrickx et al. 2019), and in zipodont alioramines (Brusatte et al. 2012). MCT.R.514 also lacks a highly labially

deflected distal carina, normally present in the mesial and the mesialmost lateral teeth of most tyrannosaurids (Brusatte et al. 2012, Hendrickx et al. 2019). Lastly, most of the tyrannosaurid taxa (e.g., *Alioramus* and *Gorgosaurus*) have a braided enamel texture, different from the irregular texture seen in MCT.R.514 (Hendrickx et al. 2019). Although there are few tyrannosaurids that also display a similar irregular texture, all of those representatives usually also have a pachyodont dentition (e.g., *Tyrannosaurus* and *Zhuchengtyrannus*; Hendrickx et al. 2019). The sum of these features makes the assignment of MCT.R.514 as a tyrannosaurid quite unlikely.

The crown only unconstrained analysis pointed out similarities between MCT.R.514 and

different non carcharodontosaurid allosauroid taxa (Figure 5B), among those, the basal neovenatorid *Neovenator* (Carrano et al. 2012). Even though there is no known erupted *in situ* teeth in the holotype, several isolated teeth were found associated with the specimen (Brusatte et al. 2008). Those isolated crowns differ clearly from MCT.R.514 as they share many features seen in other neovenatorids such as an incomplete mesial carina, whose serrations don't reach the crown base, and a braided enamel texture (Brusatte et al. 2008, Hocknull et al. 2009, Coria & Currie 2016).

The overall tooth morphology of MCT.R.514 is also seen in abelisaurids, and non-carcharodontosaurid allosauroids such as metriacanthosaurids and allosaurids, three theropod clades that with greatly similar dentitions (Hendrickx et al. 2020b) to which the specimen was either assigned or at least showed some phylogenetic affinities. These similarities are particularly strong between the mesial teeth of Abelisauridae and Metriacanthosauridae, as allosaurids usually have thick pachidont teeth that distinguish it from those two clades (Hendrickx et al. 2019, 2020b).

Features such as an irregular enamel texture, well developed interdenticular sulci, a salinon shaped/biconcave cross section and an almost straight distal margin are homoplastic between abelisaurid and metriacanthosaurids, making at first difficult to distinguish both clades (e.g., Fanti & Therrien 2007, Hendrickx & Mateus 2014, Hendrickx et al. 2020a, b). Yet, there are some differences that can help us discern the mesial dentition of those theropods.

The absence of a spiraling mesial carina, a strongly labially displaced distal carina and a well-marked mesiolingual longitudinal groove distinguish MCT.R.514 from the mesial teeth of metriacanthosaurids such as *Sinraptor* (Hendrickx et al. 2020a, b). This, together

with the exclusively laurasian distribution of Metriacanthosauridae (Currie & Zhao 1993, Carrano et al. 2012, Hendrickx et al. 2020b) and the probable "Mid" Cretaceous age of the Alter do Chão Formation (Daemon 1975, Dino et al. 1999), makes the assignment of MCT.R.514 as an abelisaurid more parsimonious than the results recovered by the cladistic analysis.

Lastly, even though not recovered in none of the cladistic or morphometric analyses, we compare MCT.R.514 with one of the most prolific theropod lineages in "Mid" Cretaceous South America, Carcharodontosauridae (Novas et al. 2013). There are clear differences between MCT.R.514 and the mesial dentition of this clade, as carcharodontosaurids such as *Acrocanthosaurus*, *Giganotosaurus* and *Mapusaurus* display a strongly labially displaced mesial carina, which forms a wide lenticular/lanceolate cross section that distinguishes itself from the Nova Olinda specimen (Hendrickx et al. 2019). Other than this, carcharodontosaurids also have mesial denticles larger than the distal ones (DSDI < 0,9; *sensu* Hendrickx et al. 2015) and a braided enamel texture (Hendrickx et al. 2019), both features not seen in MCT.R.514.

### Remarks on the discriminant analyses results

The RRs obtained by the six LDAs (Table II) is generally congruent to results previously seen in literature that used similar methods and datasets (e.g., Delcourt et al. 2020, 2024, Hendrickx et al. 2020a, Brum et al. 2021, Meso et al. 2021a, b, Table SVII), albeit with some particularities. Our results of the clade level search with a complete dataset showed better RRs than the ones obtained by Meso et al. (2021a, 2021b) and Brum et al. (2021) while still being lower than the one obtained by Hendrickx et al. (2020a). A similar pattern is also seen in the taxon level searches with the same dataset (Table SVII).

As occurred with the complete dataset, the “large teeth” dataset also obtained better RRs compared to both Meso et al. (2021a, 2021b) LDAs in the clade level search while still being lower than the one obtained by Hendrickx et al. (2021a). Different from the complete dataset results, the taxon level searches with the “large tooth” dataset attained the same results from Hendrickx et al. (2021a) (RR = 57,66%; Table SVII). Both taxon level searches from Meso et al. (2021a, 2021b) were significantly higher when compared to our results (Table SVII).

These results showed that the addition of new avian theropod taxa in the complete dataset, as proposed by Brum et al. (2021), caused few alterations to the both clade and taxon level searches when compared to analyses made with a similar number of unknown specimens (i.e. Hendrickx et al. 2021a that also tested only one specimen). The lower RR values found in Meso et al. (2021a, b) can thus be explained by the larger number of tested specimens ( $n = 12$  and  $n = 10$ ) which in turn could hinder the correct classification of those teeth with the increase in volume of unknown data. However, the increase in RRs found in the taxon level searches with the “large teeth” dataset in those studies suggest that this could not be the sole explanation for this pattern.

The RRs attained with the clade level search with the “South American” datasets were almost equal to those obtained in their original sources (Delcourt et al. 2020, 2024; Table SVII), even though different variables were used. While this study used all the twelve measurements from the Hendrickx et al. (2020a) protocol, both Delcourt et al (2020) and Delcourt et al. (2024) used only six of those linear measurements (CBL, CBW, CH, AL, MCL, MCW) together with denticle density values (MC and DC). The usage of more variables than those two previous studies had little impact in the reclassification

rates obtained in our LDA, with somewhat lower, yet similar results being obtained (Table SVII).

The influence of the extra variables (CA, DDL, LIF, LAF, MDL, MSL) in the biplot was almost minimal (Figure S11B), with AL, CBL, CBW, and CH contributing similarly to the direction of axis 2 as seen in Delcourt et al. (2020, 2024). While at first these results could suggest that focusing on these variables could be more beneficial for the LDAs, the biplots obtained from the LDAs scored with the two other databases showed how some of those variables, DDL, LAF, LIF, and MDL in particular, were influential in most searches, especially in the “large teeth” dataset (Figures S9b and S10b). Because of this, we suggest that the employment of different variables should be used in order to test their value in this kind of analysis. Further studies focusing on refining and testing those variables can help us improve the usage of such morphometric methods in the future. When tested with the same eight variables employed by Delcourt et al. (2020, 2024) it is possible to see that our analysis obtained slightly better RR results than those found in these studies (Table II; Table SVII). This small increase in the reclassification quality might be related to the lesser number of unknown specimens being processed by the analysis, a trend that can be observed in Delcourt et al. (2020, 2024). However, even with a substantially larger sample ( $n = 18$  and  $n = 179$ ; Table SVII), the decrease in RRs is rather too small, possibly implying that the number of tested specimens plays only a small part in the quality of the classifier function.

Lastly it is important to comment on the usage of taxon level searches in morphometric analyses. Some previous studies have already stopped the employment of taxon level searches (e.g., Delcourt et al. 2020, 2024), although with no in depth discussion on that matter. As previously observed in literature, most isolated theropod

teeth are usually identifiable only down to a family level classification, with few exceptions such as the teeth from spinosaurids and some dromaeosaurids (Hendrickx et al. 2019, 2020a). This pattern is reflected by the lower RRs obtained in most taxon level searches done in literature, with few exceptions (Tables II and SVII), as it further expands the overlap found in between the analyzed taxa. In this manner, it is more recommendable to rely mostly on clade level searches in order to obtain more robust results with LDAs.

### Fossil record on the Amazon Rainforest

Northern Brazil is mostly occupied by the Amazon Rainforest. Mesozoic fossils for this region and

the Legal Amazon as a whole, including other countries, are scarce (Table IV) with the Amazon and Acre basins being majoritarily represented by cenozoic remains such as invertebrates (Klaus et al. 2017), amphibians, mammals, and various reptiles like birds, crocodiles and squamates (Price 1953, Latrubesse et al. 2010, Haag & Henriques 2016).

There are few studies reporting fossils of mesozoic origins in the BLA, with most evidence coming from palynological and ichnological data (Mabesoone & Neumann 2005, Mendes et al. 2012, Silva 2020). The Alter do Chão Formation is a rare exception, displaying the sole record for terrestrial vertebrates in the whole region, those being represented by the two theropod

**Table IV. Dinosaur record from the Northern portion of South America.**

Taxa	Specimen	Clade	Type	Locality	Unit (Age)	Reference
<b>Dinosauria indet.</b>	MBLUZ P1504	Dinosauria	Left postorbital	Venezuelan Andes - Venezuela	La Quinta Formation (Hettangian)	Barret et al. (2008)
<b>Dinosauria indet.</b>	MBLUZ P1100A, P1340, P1341, P 1352, P1515, P1555(2),		Caudal vertebrae			
<b>Dinosauria indet.</b>	-		Femur			
<b><i>Laquintasaura venezuelae</i></b>	MBLUZ P-4882	Ornithischia	Premaxillary	Rio Batá - Colombia	Batá Formation (Early Cretaceous)	Herrera-Castillo et al. (2021)
<b>Ornithischia indet.</b>	MBLUZ P962, P1062, P1072, P1085, P1094, P1098, P1337, P1395, P1396, P1397, P1398, P1400, P1401, P1434, P1555(1)		Isolated teeth			Barret et al. (2008)
<b>Ornithischia indet</b>	MBLUZ P-1095		Tibia			
<b>c.f. Hadrosauria (?)</b>	-		Caudal vertebra			-
<b><i>Iguanodontipus burreyi</i></b>	DF1-DF6		Tracks			Noè et al. (2020)
<b>Ornithischia indet.</b>	-		Trackways	Boyacá - Colombia	Arcabuco Formation (Late Jurassic-Early Cretaceous)	Moreno-Sánchez (2011)

Table IV. Continuation.

Taxa	Specimen	Clade	Type	Locality	Unit (Age)	Reference
<b>Saurischia indet.</b>	MBLUZ P1443	Saurischia	Ilium	Venezuelan Andes - Venezuela	La Quinta Formation (Hettangian)	Barret et al. (2008)
<b>Padillasaurus leivaensis</b>	JACVM 0001	Sauropoda	Axial bones	Ricaurte Province - Colombia	Paja Formation (Barremian-Aptian)	Carballido et al. (2015), Mannion et al. (2017)
<b>Perijasaurus lapaz</b>	UCMP 37689	Sauropoda	Dorsal vertebra	La paz - Colombia	La Quinta Formation (Early Aptian)	Langston & Durham (1955), Ricón et al. (2022)
<b>Amazonsaurus maranhensis</b>	MN 4558- V, UFRJ- DG 58R/9, MN 4559- V; MNS/nº- V, UFRJ- DG 58R/7, MN 4555- V, 4556- V, 4560- V, UFRJ- DG 58R/2; 58R/3; 58R/4; 58R/5, MN 4564- V, UFRJ- DG 58- R/1, MN s/nº- V, MN 4562- V	Sauropoda	Axial and appendicular bones	Itapecuru-mirim - Brazil	Itapecuru Formation (Aptian-Albian)	Carvalho et al. (2003)
<b>Yamasaurus lojaensis</b>	YM-UTPL_002, YM-INPC-014, YM- INPC-016, YM- INPC-015, YM- INPC-017	Sauropoda	Sacrum	Loja Province - Ecuador	Río Playas Formation (Late Cretaceous)	Apesteuguía et al. (2020)
<b>Titanosauria indet.</b>	CCC 005, CCC 010, 053, 074	Sauropoda	Axial and appendicular bones	Coroatã - Brazil	Itapecuru Formation (Aptian-Albian)	Castro et al. (2007)
Taxa	Specimen	Clade	Type	Locality	Unit (Age)	Reference
<b>Diplodocoidea indet.</b>	CCC 017, 030, 060	Sauropoda	Neural arches	Itapecuru Formation (Aptian-Albian)	Itapecuru Formation (Aptian-Albian)	Castro et al. (2007)
<b>Sauropoda indet.</b>	-		Trackways	Boyacá - Colombia	Arcabuco Formation (Late Jurassic-Early Cretaceous)	Moreno-Sánchez (2011)
<b>Theropoda indet.</b>	-	Theropoda	Isolated teeth	Itapecuru-mirim - Brazil	Itapecuru Formation (Aptian-Albian)	Ferreira et al. (1992)
<b>Theropoda indet.</b>	-		Isolated teeth	Coroatã - Brazil		Ribeiro et al. (2003)
<b>Theropoda indet.</b>	-		Isolated tooth	Nova Olinda - Brazil	Alter do Chão Formation (Aptian-Turonian)	Price (1960)
<b>Tachiraptor admirabilis</b>	IVIC-P-2867, IVIC-P-2868		Tibia and ischium	Jáuregui municipality -Venezuela	La Quinta Formation (Hettangian)	Langer et al. (2014)
<b>Abelisauridae indet.</b>	UCMP 39649a		Isolated teeth	Colombia	Girardot Sub-basin (Maastrichtian)	Ezcurra (2009).

**Table IV. Continuation.**

<b>Spinosauridae indet.</b>	-	Theropoda	Isolated teeth	Coroatá - Brazil	Itapecuru Formation (Aptian-Albian)	Ribeiro et al. (2003)
<b>Spinosauridae indet.</b>	-		Ungual phalanx			De França et al. (2021)
<b>Carcharodontosauridae indet.</b>	-		Isolated teeth			Ribeiro et al. (2003)
<b>Taxa</b>	<b>Specimen</b>		<b>Type</b>	<b>Locality</b>	<b>Unit (Age)</b>	<b>Reference</b>
<b>Unenlagiinae indet. (?)</b>	UCMP 39649b		Isolated tooth	Colombia	Girardot Sub-basin (Maastrichtian)	Ezcurra (2009).
<b>Theropoda indet. (?)</b>	-		Tracks	Oiba - Colombia	Paja Formation? (Barremian-Aptian)	Buffetaut (2000)
<b>Theropoda indet.</b>	-		Trackways	Huansala Mine - Peru	Chimu Formation (Late Jurassic-Early Cretaceous)	Moreno (2004)
<b>Theropoda indet.</b>	-		Trackways	Northern Peru	Yura Group (Late Jurassic-Early Cretaceous)	Moreno (2004)
<b>Theropoda indet.</b>	-		Trackways	Boyacá - Colombia	Arcabuco Formation (Late Jurassic-Early Cretaceous)	Moreno-Sánchez (2011)
<b>Abelisauridae indet.</b>	<b>MCT.R.514</b>		<b>Isolated tooth</b>	<b>Nova Olinda - Brazil</b>	<b>Alter do Chão Formation (Aptian-Turonian)</b>	<b>Price (1960); this study</b>

teeth from Nova Olinda (Price 1960, Bittencourt & Langer 2011, Ribeiro et al. 2023).

Due to the scant mesozoic fossil record for the Legal Amazon in general, it is difficult to properly make accurate faunal correlations between the Alter do Chão paleobiota and other closely located lithostratigraphic units (Table IV). This is further hampered by the still uncertain age of this formation, with previous studies proposing either a “Mid” Cretaceous (Aptian to Turonian; Daemon 1975, Dino et al. 1999) or a Late Cretaceous (Cenomanian-Maastrichtian; Daemon & Contreiras 1971) dating.

Following the “Mid” Cretaceous dating proposals it is possible to compare it to the Early to “Mid” Cretaceous of the Itapecuru Formation (Aptian-Albian; Pedrão et al. 1993), also located on the BLA, and other relatively isochronous

units from Northeastern Brazil such as the Açu and Alcântara formations (Ribeiro et al. 2023). Even though geographically closer, the Itapecuru Formation has no known abelisaurid fossils (Ribeiro et al. 2003, Ribeiro et al. 2023), which sets it apart from both Açu and Alcântara formations that have a scarce yet perceivable abelisaurid record, all of those also being solely described through isolated teeth (Sales et al. 2018, Ribeiro et al. 2022). In this scenario, the Nova Olinda tooth adds some information to the still rare “Mid” Cretaceous record of Abelisauridae (Ribeiro et al. 2022, 2023).

### **Difficulties related to the study of Amazonian fossils**

The Amazon Rainforest is the largest forest in the world, spanning an area of 7,008,370 km<sup>2</sup> and

encompassing territories of Brazil, Colombia, Bolivia, Ecuador, Guyana, Peru, and Venezuela (Souza Filho et al. 2006, Calegare et al. 2013). This region is engulfed in a dense closed rainforest with wide rivers that overflow during part of the year. These environmental conditions end up limiting the exposure of sedimentary rocks and, therefore, of possible fossil outcrops, making paleontological research a challenging task in those localities (Haag & Henriques 2016). These difficulties are further worsened in the few Mesozoic outcrops in the region, limiting some of those findings to unexpected oil core perforations (Price 1960).

The BLA is wide and isolated in most parts, with a population of 21 million inhabitants (about 4% of the country's population), with an average density of only 3 hab./km<sup>2</sup> (Souza Filho et al. 2006). Considering these factors, it's clear how difficult it might be to send personnel, machinery, and resources to those outcrops in order to collect and transport fossil specimens (Calegare et al. 2013, Menin 2007, Santos et al. 2019).

Another point to consider, is that the task of finding fossil material can be invasive and the BLA is rightfully protected by Brazilian Ambiental laws that prevent deforestation and excavation of most part of the area (Rorato et al. 2020). All the aforementioned factors can be seen reflected in the countries that are part of the Legal Amazon, with some also showcasing further predicaments concerning their overall investment on research (UNESCO 2023).

## CONCLUSIONS

In this study, we reviewed MCT.R.514, the sole terrestrial vertebrate ever found in mesozoic deposits from Northern Brazil, in order to assign it to a less inclusive clade through the most up to date methods available in literature. The

qualitative analyses recovered the Nova Olinda theropod as a possible metriacanthosaurid while quantitative analyses showed similarities between the specimen and both Abelisauridae and Tyrannosauridae. MCT.R.514 was then assigned as an abelisaurid due to two main reasons: one based on its overall morphology and other based on patterns of geographical distribution during the Cretaceous Period.

Even though the dentitions of Abelisauridae and Metriacanthosauridae share many similarities between themselves, which constantly provoke misidentifications (e.g., Hendrickx & Mateus 2014), there are some features that can help us distinguish both clades. The absence of features such as a spiraling mesial carina, a strongly labially displaced distal carina and a well-marked mesiolingual longitudinal groove in MCT.R.514 sets it apart from the mesial dentitions seen in most metriacanthosaurids (Hendrickx et al. 2020b), strengthening the abelisaurid affinities first conveyed by the quantitative analyzes.

These morphological features together with the known geographical and temporal distribution of Metriacanthosauridae (limited to the Late Jurassic and Earliest Cretaceous of the Laurasian landmasses, especially in Asia and Europe; Currie & Zhao 1993, Hendrickx et al. 2020b) favors the assignment of MCT.R.514 to Abelisauridae as the most parsimonious hypothesis. The identification of the Nova Olinda specimen as an abelisaurid further expands the still scarce "Mid" Cretaceous record of this clade in Brazil, being also found in other similarly aged units such as the Açu and Alcântara formations.

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## SUPPLEMENTARY MATERIAL

### Table SI-SVII.

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TBR: Conceptualization; Formal analysis; Investigation; Methodology; Visualization; Writing – original draft; Writing – review & editing. ASA: Investigation; Visualization; Writing – original draft; Writing – review & editing. TBPG: Investigation; Writing – original draft; Writing – review & editing. PVLGCP: Conceptualization; Investigation; Project administration; Supervision; Writing – original draft; Writing – review & editing.

