Theropod (Dinosauria) diversity from the Potiguar Basin (Early-Late Cretaceous Albian-Cenomanian), northeast Brazil

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Cretaceous Research

THEROPOD (DINOSAURIA) DIVERSITY FROM THE POTIGUAR BASIN (EARLY - LATE CRETACEOUS), NORTHEAST BRAZIL

--Manuscript Draft--

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Abstract:	The theropod record from the Cretaceous of northeastern Brazil are rare and consist mostly of isolated and incomplete remains, with only four species described. Here we describe, identify and evaluate the diversity of theropod materials from the Albian-Cenomanian Açu Formation, Potiguar Basin. The material consists of nine isolated vertebrae and a tooth. The vertebrae have been identified as belonging to four theropod groups: Abelisauria, Carcharodontosauria, Spinosauridae, Megaraptora, and Maniraptora. The isolated tooth was classified as belonging to a spinosaurid. One of the significant results so far is the occurrence of Megaraptora in the Potiguar Basin, based on the general morphology, the bones are very similar to Aerosteon and Megaraptor. Another unexpected result is the identification and presence of a maniraptoran caudal vertebrae, very rare in Brazil, with few fossils described. Besides this, other groups already found on isochronous basins of the Northeast region of Brazil and Africa as Carcharodontosauria and Spinosauridae. The presence of these theropod groups in the Açu Formation reveals a dinosaur richness in in the Potiguar Basin similar to isochronous basins in Northern Africa and increases the knowledge about the diversity of South American dinosaurs.
Suggested Reviewers:	Manuel Alfredo Medeiros manuel.alfredo@ufma.br Extensive knowledge and experience with brazilian dinosaurs fauna
	Juan Canale juanignaciocanale@hotmail.com Interest and great knowledge of theropoda fauna in south america
	Rafael Matos Lindoso rafael.lindoso@ifma.edu.br Has experience with Theropoda materials from Brazil
Opposed Reviewers:	

The suggestions were taken into consideration during the reviewing process and were a valuable contribution for the improvement of the paper.

Almost all the specific revisions and suggestions from reviewer 02 and 03 were made with no exception and are highlighted in red color in the text (in the “with highlights” version). Bellow we answer some of the edito/reviewers question and suggestions.

Editor: Place your Figure captions at the end of the manuscript file, after References.

A: Done

Editor: As the reviewers have commented below, the English of the manuscript needs to be improved (grammar, syntax, structure of sentences, odd phrasing, etc.). It is the authors' responsibility to proof their manuscript for English problems. The revised version should be carefully proofed before you resubmit it. You should seek help from your co-author, Prof. Steve Busatte, to carefully go through the manuscript before submission. This would help to remove the linguistic problems and in dealing with all the key issues mentioned by the reviewers.

A: Done. The English was improved. Prof. Steve Busatte read carrefuly the manuscript.

Editor: Order of Figures: All figures must to be presented in the same sequence that have their first citations in the manuscript text. Please check and correct carefully the order of figures in the manuscript and their corresponding first citations. Delete out-of order citations and/or rearrange them if necessary. Check also for missing citations

A: Done.

Reviewer 01: All revision in the abstract.

A: All the revisions were accepted.

Reviewer 01: I recommend to change the title for a more realistic one, for example: "Theropod dinosaur remains from..."

A: We understoood the statement of Revisor 01, but we prefered to keep the original title, as it summarizes the results seen in the manuscript.

Reviewer 03: Five theropod species only in the northeast, or in all Brazil?

A: The four specimens are only from northeastern Brazil. This detail is better explained in the second paragraph of the Introduction.

Reviewer 03: Spinosauridae was recognized by a tooth, not a vertebra

A: done

Reviewer 03: I suggest to end this sentence with something more "… about the diversity of dinosaursxxx…"

A: Done

Reviewer 01: Please, restrict to Cretaceous record, to address the relevance of the materials here reported.

A: We choose to keep this part of the text to preserve the coesion within of the Introduction, featuring the first works and discoveries on theropod paleontology of Brazil. The next paragraph has a small summary of the Cretaceous northeastern theropoddinosaurs of Brazil.

Reviewer 01: Please, restrict to Cretaceous record
A: Done

Reviewer 01: Confuse

A: We rewrite this paragraph.

Reviewer 03: To this list should be added the recently described *Vespersaurus paranaensis* Langer et al., 2019 and *Gnathovorax cabreirai* Pacheco et al., 2019.

A: We choose to limit this list to the northeastern Brazil's theropod record only to make the text more easy to read/understand

Reviewer 03: The authors do not describe any osteoderm in the text.

A: Done

Reviewer 01: Do you mean the sedimentary infilling is divided into three groups?

A: Yes, we are following the terminology and geological description of the Basin.

Reviewer 03: I suggest to add its collection number

A: Done

Reviewer 03: They were described only five morphotypes in the text.

A: Done

Reviewer 01: This is not necessary to say. Anatomy is based on morphology. Avoid the use of "morphotypes", as if they were discrete biological units. Based on morphology, you identify vertebrae as corresponding to such section of the column, and to which theropod clade it may belong. Identification of "morphotypes" is useless.

A: We agree. We decided to remove the word “morphology” to avoid confusion.

Reviewer 01: Considering that this is not a ms devoted to analyze theropod teeth as a whole, and taking into account that just only one tooth is described, I suggest to remove all these considerations.

A: Done.

Reviewer 03: I suggest to b econsistent with the abbreviations, using their English verisions as is usual besides FABL: CBW: crown basal width (rather than EST), CH: crown height (rather than ALT), etc. See Hendrickx et al 2015. The dentition of megalosaurid theropods . Acta Paleontologica Polonica 60 (3): 627-642.

A: We followed the reviewer 01 and removed this part.

Reviewer 03: The values of most of these parameters were not specified in the analysis of the tooth recovered. I suggest to add them.

A: We followed the reviewer 01 and removed this part.

Reviewer 03: This measurement has a big fault, given there covered tooth lacks most of its tip.

A: Done. We didn t use this measurement any more.

Reviewer 03: Other abbreviation was used in Material and methods

A: We followed the reviewer 01 and removed this part.

Reviewer 01: Remove this and replace for "Systematic Paleontology"

A: Done

Reviewer 03: I suggest that, before comparing this material with other spinosaurids, the authors should add a summary of characters that allow to asign it to Spinosauridae.

A: Done. We summarize the characteristics of spinosaurids in the Discussion.

Reviewer 03: Given there are two morphotype sassigned to Megaraptora, both showing similar characteristics, the authors should explain why there are not included in a single morphotype.

A: Done. We reorganized the material in the groups and removed the division “Morphotypes”

Reviewer 03: The word “expressive” seems wrong in this context.

A: Done.

Reviewer 01: Which is the systematic relevance of all these ratios?

A: We strongly suggest that the reviewer read the articles about the use of quantitative analysis in the identification of theropod teeth:

-HENDRICKX, C. & MATEUS, O. 2014. Abelisauridae (Dinosauria: Theropoda) from the Late Jurassic of Portugal and dentition-based phylogeny as a contribution for the identification of isolated theropod teeth. Zootaxa, 3751, 1–74.

-HENDRICKX, C., MATEUS, O., ARAÚJO, R. 2015. A proposed terminology of theropod teeth (Dinosauria, Saurischia). Journal of Vertebrate Paleontology 35 (5), e982797. http://dx.doi.org/10.1080/02724634.2015.982797.HENDRICKX, C. & MATEUS, O. 2014. Abelisauridae (Dinosauria: Theropoda) from the Late Jurassic of Portugal and dentition-based phylogeny as a contribution for the identification of isolated theropod teeth. Zootaxa, 3751, 1–74.

-HENDRICKX, C., MATEUS, O., ARAÚJO, R., AND CHOINIERE, J. 2019. The distribution of dental features in non-avian theropod dinosaurs: Taxonomic potential, degree of homoplasy, and major evolutionary trends. Palaeontologia Electronica 22.3.74 1– 110. https://doi.org/10.26879/820palaeo-electronica.org/content/2019/2806-dental-features-in-theropods.

-SMITH, J.B., VANN, D.R., DODSON, P. 2005. Dental morphology and variation in theropod dinosaurs: implications for the taxonomic identification of isolated teeth. The Anatomical Record Part A285: 699-736.

-SANKEY, J.T., BRINKMAN, D.B., GUENTHER M., CURRIE, P.J. 2002. Small theropod and bird teeth from the Late Cretaceous (Late Campanian) Judith River Group, Alberta. Journal of Paleontology, 76, 751–763.

Reviewer 01: "Which are the anatomical bases to refer these elements as to Neovenatoridae/Megaraptora? The present manuscript suffers of the lack of anatomical descriptions and comparissons allowing the reader to understand why present authors conclusions.";

"Please, provide morphological bases to support this referral.";

"Please, give reasons for referring these elements as to Abelisauroidea"

"Please, explain why this element is referred as to Maniraptora"

"Please, explain why this element is referred as to Carcharodontosauria"

"Please, explain why this element is referred as to Megaraptora";

A: These parts have been rewrite to increase cohesion and make it clearer to understand. The first paragraph of the "comparisons" part has the characteristics used to allocate the fossil in the specific theropod group and the corresponding bibliography.

Reviewer 01: Please, obviate this detail. It is not morphological!

A: We removed the measurements.

Reviewer 01: Please, clarify

A: Done

Reviewer 01: Before description of any dinosaur bone, it must be glued.

A: Done. Material have been found associated, but there is no clear point of junction between both pieces, with most of the middle portion being lost.

Reviewer 03: Sem-spherical or semicircular?

A: Done. Semicircular

Reviewer 03: The authors should describe (and figure) the materials as a single vertebra, not as two different fragments. It is confusing and does not help with interpretation of the materials.

A: Ok. Done

Reviewer 03: At the beginning of this morphotype description the authors suggest that they are possibly caudal vertebrae.

A: Ok. Done

Reviewer 03: Why anterior? It could not be posterior?

A: We removed this fragment because it is not significant or relevant for this manuscript.

Reviewer 03: Why the authors assign this material to morphotype 1? They only suggest that it belongs to a theropod.

A: We removed this fragment because it is not significant or relevant for this manuscript.

Reviewer 01: I am surprised with this statement: Ceratosauria as members of Tetanurae. This is not a serious manuscript.

A: It was just a confusion when we were arranging the morphotypes. We know that Ceratosauria is not inside Tetanurae. Thanks for the revision…

Reviewer 03: This character used for differentiate this morphotype is clearly related to the position of the vertebra inside the vertebral series; This character is used for differentiate this morphotype is also present in morphotype 1; I suggest to look for other more specific characters to differentiate this morphotype.

A: We revised the attribution of this morphotype in Abelisauria and not found any solid characteristic to sustain this classification. We decided to follow the reviewers and be conservative and put these material at Theropoda indet.

Reviewer 03: I think both are synonyms

A: Done.

Reviewer 03: This sentence is confusing.

A: Done.

Reviewer 03: Think the authors should specify which transition point are referring here (I suppose that proposed by Russel (1972), but this is my guess)

A: Done

Reviewer 03: The shape of the articular face of caudal vertebrae is so variable, it show differences inside the same taxonomic group. For example inside Abelisauridae, Carnotaurus shows semicircular articular surface, and Majungasaurus show oval articular surface, as the authors clearly show in the figure 8. This makes this character not useful for separating morphotypes.

A: We don’t use anymore this ratio type of character on the description.

Reviewer 03: The articular surfaces shown in the figure 4 has ovoidal articular faces.

A: Done.

Reviewer 03: hourglass-shaped

A: Done.

Reviewer 03: The lateral surfaces are slightly concave in these taxa, not very.

A: Done

Reviewer 03: Please seeAranciaga-Rolando et al (2018) A supposed Gondwanan oviraptorosaur from the Albian of Brazil represents the oldest South American megaraptoran. Cretaceous Research 84: 107-119.

A: Done

All the reviewers: All the revisions in the discussion.

A: We followed the suggestion of the reviewer 01 and reorganized the discussion. We replaced the most part to results in the comparative morphology and rewrite the discussion based on the importance of the Potiguar’s fossils.

FIGURES

We done all the revisions requested by the reviewers and improved the figures.

Highlights – article: THEROPOD (DINOSAURIA) DIVERSITY FROM THE POTIGUAR BASIN (EARLY - LATE CRETACEOUS), NORTHEAST BRAZIL

- These are the first described theropod materials from the Potiguar Basin, Brazil.
- Four morphotypes were described based on morphological and/or diagnostic characters.
- Carcharodontosauria and Spinosauridae were groups identified.
- Rare Megaraptora, and Maniraptora materials were also identified.

THEROPOD (DINOSAURIA) DIVERSITY FROM THE POTIGUAR BASIN (EARLY-LATE CRETACEOUSALBIAN – CENOMANIAN), NORTHEAST BRAZIL

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Abstract

The theropod record from the Cretaceous of northeastern Brazil are rare and consist mostly of isolated and incomplete remains, with only four species described. Here we describe, identify and evaluate the diversity of theropod materials from the Albian-Cenomanian Açu Formation, Potiguar Basin. The material consists of seven isolated theropod vertebrae and a tooth. We identify the material as belonging to four theropod

groups: Spinosauroidea, Carcharodontosauria, Megaraptora, and Maniraptora. One of the significant results is the occurrence of Megaraptora in the Potiguar Basin; based on the general morphology, some of the bones we describe are very similar to those of *Aerosteon* and *Megaraptor*. Another unexpected result is the identification and presence of a maniraptoran caudal vertebrae; these dinosaurs are very rare in Brazil, with few fossils previously described. Furthermore, we identify other groups that have already been found in isochronous basins of the Northeast region of Brazil and Africa, including Carcharodontosauria and Spinosauroidea. The presence of these theropod groups in the Açu Formation reveals a dinosaur richness in in the Potiguar Basin similar to isochronous basins in Northern Africa and increases knowledge about the diversity of South American dinosaurs.

Keywords: Dinosauria, Potiguar Basin, Theropoda, faunistic richness, Carcharodontosauria, Megaraptora, Spinosauridae, Maniraptora.

Introduction

The first studies in Brazil that attributed vertebrate fossil remains to dinosaurs were published in the nineteenth and mid-twentieth centuries (Marsh, 1869; Derby, 1890; Mawson and Woodward, 1907; Price, 1960, 1961). Since that time, dinosaur fossils have been recorded from three principal localities and ages in Brazil: the Triassic of the Santa Maria and Caturrita formations (Langer et al., 2007a), the mid-Cretaceous of the Araripe, Triufo and São Luís-Grajaú basins (Frey and Martill 1995; Kellner 1996a, b, 1999; Medeiros *et al*., 2007; Carvalho *et al*., 2017), and the Late Cretaceous of the Bauru and Parecis groups (Franco-Rosas *et al*., 2004; Kellner *et al*., 2004; Brusatte *et al*. 2017).

There are eight theropod dinosaur species formally described from Brazil so far, four from the northeastern region: *Santanaraptor placidus* Kellner, 1999, *Irritator challengeri* Martill, Cruikshank, Frey, Small and Clarke, 2002 and *Mirischia asymmetrica* Naish, Martill and Frey 2004 from the Araripe Basin; and *Oxalaia quilombensis* Kellner, Azevedo, Machado, Carvalho and Henriques, 2011 from the São Luís-Grajaú Basin.

A promising area for new dinosaur discoveries is the rocks of the Açu Formation, in the Portiguar Basin. Until now, the macrofossils of the Açu Formation consisted of bivalve molluscs, small crustaceans, fish scales, and plant remains (Duarte and Santos, 1961). However this changed in the 2000s, when researchers from the Group of Analogs to Oil Reservoirs of the Department of Geology of the Federal University of Rio Grande do Norte, in geological mapping of the Açu 4 operational unit, found large vertebrate fossils.

In the decade after the discovery of these first continental vertebrate fossils in the formation (Santos *et al*., 2005), no other fieldwork was conducted. However, in 2015 and 2016, this area was again prospected by Laboratório de Macrofósseis of the Universidade Federal do Rio Janeiro and dozens of fossils were found. The aim of the present work is to describe and identify the collected materials attributed to theropod dinosaurs, showing that the Potiguar Basin preserves a large diversity of species and has great potential for future discoveries and studies about the mid-Cretaceous paleoenvironments of the Atlantic margin of Brazil.

Geological Setting and Lithostratigraphy

The Potiguar Basin is located at the eastern continental margin of northeastern Brazil, cropping out in the states of Rio Grande do Norte and Ceará (Fig. 01), with a total estimated area of 60,000 km^2, of which 22,000 km^2 is interpreted as continental (Cassab, 2003). The Potiguar Basin is bounded to the east by Alto de Touros, which separates it from the Pernambuco-Paraíba Basin, to the northwest by the Alto de Fortaleza, which separates it from the Ceará Basin, and to the south and west by crystalline basement rocks (Pessoa-Neto *et al*., 2007).

The sedimentary units of the Potiguar Basin are divided into three groups: Areia Branca (Pendência and Alagamar formations), Apodi (Açu, Quebradas and Jandaíra formations) and Agulha (Ubarana, Guamaré and Tibau formations) (Araripe and Feijó, 1994). The Açu formation is divided into four subunits according to electric logs, identified from bottom to top as Açu 1, Açu 2, Açu 3 and, Açu 4 (Vasconcelos *et al*., 1990). The material described here comes from the Açu 4 subunit, which corresponds to a transgressive, coastal-estuarine system.

The Açu-4 Unit consists of sixteen facies, fourteen being siliciclastic and two being hybrid. The siliciclastic facies are grouped into nine associations, namely: (1) lag residual deposits, (2) channel fill deposits, (3) crevasse-splay deposits, (4) floodplain deposits, (5) abandoned channel deposits, (6) upper-flow regime sandflat deposits, (7) lower-flow regime sandflats, (8) sandflat/mudflat deposits of restricted environment, and (9) mudflat deposits. The first five facies associations represent a meandering fluvial system with tidal influence, and the remaining integrate the intermediate and distal sectors of an estuarine complex dominated by tides. The hybrid facies were deposited in a shallow platform adjacent to an estuary (Costa et al., 2014).

The Açu Formation has been suggested to be Albian-Cenomanian in age (Early–Late Cretaceous), based on palynological data (Araripe and Feijó, 1994).

Material and Methods

The fossils were collected from outcrops of the Açu Formation, Potiguar Basin (Ceará state, noutheastern Brazil) and are deposited at the Fossil Reptile Collection of the Departamento de Geologia (DG), Universidade Federal do Rio de Janeiro (UFRJ). The material consists of seven isolated theropod vertebrae (UFRJ-DG 521-R, 523-R, 524-R, 528-R, 558-R, 575-R, and 634-R) and a tooth (619-Rd)

The following tooth characteristics were assessed, following the nomenclature proposed by Hendrickx *et al*. (2015): general morphological traits of the dental crown (its overall shape, curvature, ornamentations in the enamel), denticles (presence, size and shape) cross section (compression and shape), orientation of the tooth (lingual, labial, mesial and distal) and measurements.

Systematic paleontology

SAURISCHIA Seeley, 1888

THEROPODA Marsh, 1881

Referred material: UFRJ-DG 532-R and 575-R.

Description:

UFRJ-DG 528-R

Specimen 528-R is a theropod vertebral centrum (Fig. 02, C-E). It is amphicoelous, and slightly higher than long. Its lateral surface is smooth and slightly concave, without marks or other remarkable characteristics, giving the vertebra a straight and somewhat featureless appearance. The ventral surface smooth with no groove or keel and it is slightly concave in lateral view.

The dorsal surface possesses a distinct longitudinal groove extending from one articular facet to the other that can be identified as the neural canal. The articular faces have nearly straight margins. The anterior facet is somewhat concave, and the posterior is slightly convex and slightly oval in shape; both articular facets have the same general proportions (height longer than length). The anterior articular face presents a deeper concavity, and is slightly larger in size, than the posterior face, which is very flat and without deep depressions.

UFRJ-DG 575-R

Specimen 575-R (Fig. 02, A-B) is a theropod vertebral centrum broken in two: a smaller anterior piece and a larger posterior section. Although the material was found associated there is no clear point of junction between both pieces, as most of the middle portion has been lost. The anterior fragment exhibits a very concave articular face of semi-circular shape and slightly forward-protruding margins.

On the lateral surface of the anterior fragment there is a deep perforation close to the dorsal region that reaches the other lateral surface, which can be described as a pleurocoel. The ventral surface of the anterior fragment is smooth and concave in anterior view. The dorsal surface of the anterior fragment is broken, missing most of the surface above the pleurocoel.

The posterior fragment has a slightly smaller articular surface, which is broken on the anterior portion; it is also concave and of semi-circular shape, with slightly backwards-protruding margins. Its dorsal surface and the dorsal half of the left lateral surface are broken, while the right lateral surface is broken in a slightly more dorsal region in comparison to the left one. The ventral surface of the fragment is smooth and concave in lateral view. Due to the highly fragmentary state of UFRJ-DG 575-R, it is possible to see multiple small pervasive pneumatic chambers, the camellae, in the internal bone.

Comparisons:

The highly pneumatized camellate bone seen in UFRJ-DG 575-R is a characteristic seen in many groups of theropods, from the basal *Ceratosaurus* to tetanuran groups such as carcharodontosaurids and coelurosaurs mainly in its presacral vertebrae (Carrano and Sampson, 2008). This feature, together with the poor preservation of this specimen, which prevents the identification of other more diagnostic characteristics, hinders the classification of this specimen beyond Theropoda.

THEROPODA Marsh, 1881

TETANURAE Gauthier, 1986

? SPINOSAUROIDEA Stromer, 1915

Referred material: UFRJ-DG 619-Rd.

Description:

UFRJ-DG 619-Rd (Fig. 03) is a fragment of a large isolated tooth crown, probably belonging to the middle to almost apical portion of the tooth. The specimen lacks any form of enamel, as it has dentine exposed, what prevents description of external ornamentation such as transversal undulations, flutes and denticulation. The crown is almost completely straight with only a subtle curvature in its lingual surface, while the labial surface remains slightly convex.

The crown fragment has an overall cone-like shape with an almost ovoid cross section. In basal view, it is possible to see concentrically deposited rings of dentine surrounding a small depression, which probably represents the apical-most portion of the dental pulp cavity.

Comparisons:

UFRJ-DG 619-Rd have some characteristics that it shares with the highly specialized teeth of spinosauroid theropods. The most salient of these is the almost straight conical shaped crown, with an ovoid cross section, a feature often seen in piscivorous animals (Mateus, 2011; Hendrickx and Mateus, 2014).

THEROPODA Marsh, 1881

TETANURAE Gauthier, 1986

MANIRAPTORA Gauthier, 1986

Referred material: UFRJ-DG 521-R

Description:

UFRJ-DG 521-R

Specimen UFRJ-DG 521-R (Fig. 04) is an almost complete distal caudal vertebrae of a maniraptoran theropod. It is amphicoelous with a length to height ratio of almost 2.5, making it a least twice longer than tall. The dorsal surface of the centrum is almost complete with half of a dorsal midline ridge reminiscent of reduced neural spine, a well preserved and more dorsally positioned prezygapophysis, and a lost postzygapophysis. The prezygapophysis articular surface is ellipsoid and is reclined 45° laterally. The neural canal is almost completely preserved, having lost only its posterior half .

The lateral surfaces of the centrum are mostly smooth, marked only with a midline ridge reminiscent of a reduced transverse processes. The ventral surface of the centrum has a shallow groove that extends from one articular facet to the other. In the lateral view the ventral surface is slightly concave.

The articular facets of the centrum are both concave, with the anterior facet being more excavated than the posterior facet, and have a semi-circular shape. The articular margins are almost straight, with the anterior margin being larger than the posterior margin.

Comparisons:

UFRJ-DG 521-R has characteristics of a maniraptoran centrum positioned after the transition point in the tail (Russell, 1972, Gauthier, 1986; Tykoski, 2005), as it is longer than high and possesses a large reduction in both its neural spine and transverse processes, with those structures becoming midline ridges (Senter *et al*., 2011; Motta *et al*., 2018). Thus, it is possible to deduce that it is positioned after vertebra 11 of the caudal series as seen in *Buitreraptor*, *Rahonavis*, Dromaeosauridae and Troodontidae (Ostrom, 1969; Forster *et al*., 1998; Senter *et al*., 2012; Xu *et al*., 2017).

The presence of a reduced transverse process forming a midline ridge after the transition point is seen in the distal caudal vertebrae of *Rahonavis* and *Buitreraptor* (Forster *et al*., 1998; Novas *et al*., 2017), a characteristic also seen in UFRJ-DG 521-R, which differentiates it from most other paravians as dromaeosaurids, *Archaeopteryx*, *Jeholornis* and *Anchiornis*.

In addition, the 521-R specimen also has dorsally positioned pre-zygapophyses in the same way as in *Buitreraptor, Rahonavis* and *Anchiornis* (fig. 05) (Motta *et al*., 2018). The vertebral centrum has a length-to-height ratio between close to 2.5, a ratio usually seen in dromaeosaurids with exception to *Buitreraptor* but not seen in other maniraptorans as troodontids and microraptorians whose ratio can reach up to 5.0 to 6.0.

THEROPODA Marsh, 1881

TETANURAE Gauthier, 1986

ALLOSAUROIDEA Marsh, 1878

CARCHARODONTOSAURIA Benson, Brusatte and Carrano, 2010

Referred material: UFRJ-DG 523-R and 524-R.

Description:

UFRJ-DG523-R

Specimen 523-R (Fig. 06, D-F) is a theropod vertebral centrum, with the following characteristics: it is amphicoelous, and slightly longer than high. Its lateral surface is very concave and smooth on both sides, with the shape of an hourglass in dorsal view. The ventral surface is mostly smooth on the anterior part, with marks that possibly indicate the articulation with the hemal arch on the posterior part.

The dorsal surface is marked by a long and deep longitudinal canal from one articular face to the other, which widens on the extremities and tapers in the middle. This canal was possibly the space of the neural canal of the vertebra, given the marks of fusion with the neural arch that meet on its borders.

The articular faces are ovoid in shape and have slightly forward-protruding margins, the anterior facet being higher in comparison to the posterior facet. The anterior articular face has a concavity deeper than the posterior one, being also slightly larger in its proportions.

UFRJ-DG524-R

Specimen 524-R (Fig. 06, A-C) is a centrum of a theropod caudal vertebra. It is amphicoelous and is slightly longer than high, which indicates a more proximal position in the caudal series. The lateral surface is smooth and marked by two deep concavities on both lateral faces, giving it an hourglass-like shape.. Additionally, on the most dorsal region of the lateral surface there is a small and shallow longitudinal depression on each side.

The ventral surface is a double keel marked by a very superficial groove extending from the anterior part up to the posterior part. The dorsal surface is marked by the neural canal of the vertebra. Above the anterior part of this canal the entire upper portion of the neural tube is preserved, forming a small arch filled by sediment positioned slightly above the anterior articular face.

The articular faces are semi-circular and somewhat oval, with the anterior one being slightly larger than the posterior, and their margins slightly protrude forward. The anterior articular face has a concavity slightly deeper than the posterior.

Comparisons:

Both UFRJ-DG 523 and 524 present characteristics commonly found in carcharodontosaurids (Fig. 07). For instance, depressions in the most dorsal part of the lateral surface are found in *Giganotosaurus*, *Mapusaurus* and *Tyrannotitan* and in the mid-caudal vertebra Vb-870 found in the Wadi Milk Formation (Coria and Salgado, 1995; Coria and Currie, 2006; Novas *et al*., 2005a; Canale *et al*., 2015; Rauhut, 1999). This condition is different from that in *Carcharodontosaurus*, which has pleurocoels in its anterior caudal vertebrae (Stromer, 1931). Furthermore, the strongly waisted centrum morphology, a double keel cut by a longitudinal groove and offset articular facets (although it is a plesiomorphic feature found in *Allosaurus* Gilmore, 1920; Madsen, 1976) are also found in specimens such as the carcharodontosaurid material from Sudan (Rauhut, 1999) and in *Tyrannotitan*, *Mapusaurus* and *Acrocanthosaurus* (Canale *et al*., 2015; Harris, 1998; Coria and Currie, 2006; Currie and Carpenter, 2000).

THEROPODA Marsh, 1881

NEOVENATORIDAE Benson, Carrano and Brusatte, 2010

MEGARAPTORA Benson, Carrano and Brusatte, 2010

Referred material: UFRJ-DG 558-R e 634-R

Description:

UFRJ-DG 558-R

Specimen 558-R is a centrum of a theropod caudal vertebra, damaged by various cracks (Fig. 08, D-F). It is amphicoelous, and slightly longer than high, indicating a somewhat proximal position within the caudal series. Its ventral surface is very smooth and convex in lateral view, but is very damaged in the region where the base of the posterior articular face would be.

The dorsal surface is marked by a great depression extending longitudinally from one articular face to the other, wider in the extremities, denoting the neural canal. The lateral surfaces are marked by a longitudinal elliptic depression on their medial parts, where there is a pleurocoel on each side. The left lateral pleurocoel is deeper and better defined than the right lateral one.

Its articular faces are semi-circular and have very straight margins. The anterior articular face possesses a more distinctive depression of a slightly greater size than the posterior face and is also in a better state of preservation. The posterior articular face possesses a very slight concavity, making it almost straight, and is in a much more damaged state, presenting cracks and breaches on the ventral base of the face.

UFRJ-DG 634-R

This material is in a worse state of preservation than UFRJ-DG 558-R(Fig. 08, A-C). The ventral centrum portion and anterior articular face are fragmented. On its lateral surface, there is what appears to be the border of the pleurocoel in the same position seen in specimen 558-R.

Different from the other vertebra of this group, part of the neural arch and the transverse process are preserved on the right side of the specimen. The transverse process is positioned upwards at an angle of approximately 45º degrees.

Comparisons

The presence of pleurocoels in the caudal vertebrae is characteristic of megaraptoran neovenatids (Benson *et al*., 2010). Pneumaticity in the caudal vertebrae is rare in Theropoda, present only in some groups: Megaraptora, Oviraptorosauria, Therizinosauria, and Carcharodontosauridae (Benson *et al*., 2012). As far as is known, no fossils of therizinosaurs have been found in South America and South American fossils attributed to oviraptorosaurs have been reassigned to other taxa, including to Maniraptora (*e.g* Agnolín and Martinelli, 2007, Aranciaga-Rolando *et al*., 2018). In addition, the caudal vertebrae of Oviraptorosauria have, on the ventral surface, a medial groove delimited by two longitudinal elevations (e.g., Sues, 1997; Xu *et al*., 2007). Specimen UFRJ-DG 558-R does not have this feature (Fig. 09).

South American carcharodontosaurids (e.g., *Giganotosaurus*, *Mapusaurus*, *Tyrannotitan*) show slightly concave lateral sides in the caudal vertebrae, but do not bear actual pneumatic foramina. Stromer (1931) described an anterior caudal vertebra from northern Africa, which he identified as *Carcharodontosaurus*, which had pneumatic characteristics, including a pleurocoel. However, that vertebra has a different general morphology and proportions when compared with the megaraptorid vertebrae from the Potiguar Basin (length-height ratio is 1 in *Carcharodontosaurus* and approximately 1.48 in UFRJ DG 558-R) and other members of Megaraptora.

Among the Megaraptora group, only *Aerosteon*, *Aoniraptor*, *Orkoraptor* and *Megaraptor* have preserved caudal vertebrae (Fig. 10) (Sereno *et al*., 2008; Benson *et al*., 2010; Motta et al., 2016). The height/length ratio of UFRJ DG 558-R is 1.4, consistent with a median tail position, compared to the ratios of 1.2 and 1.3, respectively, of the medial caudal vertebrae of *Aerosteon* and *Orkoraptor* (Novas *et al*., 2008). The Potiguar Basin specimens resemble those of *Aoniraptor* (Fig. 07, F) due to the absence of a keel in the ventral region, but are distinguished by the presence of a pair of pneumatic troughs in the lateral region, separated by a septum. Only the first caudal vertebra of *Aoniraptor* presents such fossae, a characteristic present in the other megaraptorans (e.g., Novas *et al*., 2008; Sereno *et al*., 2008).

Comparing the morphology of pneumatic foramina, UFRJ DG 558-R (Figure 10, A) is very similar to *Aerosteon* (Figure 10, C), *Megaraptor* (Figure 10, H) and *Orkoraptor* (Figure 10, G) in the presence of a large elliptic foramen and a second smaller circular shaped foramen. In addition, UFRJ-DG 558-R and 634-R has its cavities located on the lateral surface of the vertebral centrum near the base of the neural arch, which does not occur in the other species observed.

UFRJ-DG 558-R and 634-R also presents extensive pneumatization in the vertebral centrum, composed of a camerate internal microstructure (Britt, 1993), with several small chambers, similar to other megaraptorans (e.g., *Aerosteon*, *Megaraptor*; Martinelli *et al*., 2013).

Discussion

The Açu Formation material and its importance

The fossil potential of Açu Formation was poorly known, with only a few fossils recovered (Duarte and Santos, 1962; Silva-Santos, 1963; Mussa et al., 1984), until the discovery of vertebrae and teeth identified as belonging to Theropoda indet. and Titanosauria (Santos et al., 2005).

No further work was conducted until 2018, when the materials described here were studied in more detail. Thus far, the dinosaur fauna of the Potiguar Basin includes two groups of Sauropoda (Diplodocoidea: Rebbachisauridae, Pereira et al., in press; Titanosauriformes, Barbosa et al., 2018; Titanosauria, Pereira et al., 2018) and four groups of Theropoda (Spinosauroidea, Carcharodontosauridae, Megaraptora and Maniraptora, present work).

The occurrence of these groups (except Megaraptora) in the Potiguar Basin is yet another similarity between the faunas of northeastern Brazil and multiple North Africa Cretaceous units (e.g. Medeiros and Schultz, 2001a, 2002; Sereno and Brusatte, 2008; Contessi, 2009; Candeiro et al., 2011; Candeiro, 2015). Except for the Elrhaz (Niger); Douiret and Ain El Guettar (both in Tunisia) and Chicla (Libya) formations, which were dated to the Early Cretaceous, all other Cretaceous formations from Northern Africa are Albian-Cenomanian in age, roughly equivalent to the Açu Formation (Werner, 1994; Rossetti, 1997; Rossetti and Truckenbrodt, 1997; Smith et al., 2001; Anderson et al., 2007; Sereno and Brusatte, 2008; Cavin et al., 2010). Among the formations, the Alcântara Formation (Brazil), Bahariya Formation (Egypt), Echkar Formation (Niger) and the Waldi Milk Formation (Sudan) have similarities with the Açu Formation's dinosaur fauna.

According to paleobiogeographic models, South America and Africa started separating from each other in the Valanginian (Early Cretaceous), leading to the formation of the South Atlantic Ocean (Viramonte et al., 1999; Jokat et al. 2003; Macdonald et al., 2003). Although the ocean turned into one of the most important continental barriers of the southern hemisphere, faunal interchange among the terrestrial landmasses of western of Gondwana definitely occurred up to the Albian, and possibly until the Cenomanian (e.g. Petri, 1987; Reyment and Dingle, 1987; Pletsch et al., 2001, Tello Saenz et al., 2003, Guedes et al., 2005, Bodin et al., 2010).

Based on the proposed age and geographic position, the fossil vertebrates of the Açu Formation may have lived during some of the last intervals of continental connection between South America and Western Africa, before the complete formation of the South Atlantic Ocean (Arai, 2009; Castro et al., 2012). This makes them exceedingly important for understanding biogeography and faunal evolution.

More extensive comparisons are still limited by the lack of completeness of the Açu material and the absence of formally described taxa. The continuation of studies on previously collected material (like that described in this paper) and prospecting for new fossils is important in this basin which, while still the subject of only recent research, already exhibits among the greatest diversity of dinosaur groups in Brazil.

Conclusion

In the present work we assigned the material from Açu Formation, Potiguar Basin, to four groups: Spinosauroidea, Carcharodontosauria, Maniraptora and Megaraptora (Fig. 11), the two last groups being relatively rare in Brazil. All this groups have already been found in isochronous formations in both Northeastern Brazil and Northern Africa, leading further support for faunal similarities in the “mid”-Cretaceous western Gondwana. These fossils provide the first theropod record from Potiguar Basin and an important opportunity to increase the knowledge on the diversity of this still poorly known basin.

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Figure captions

Figure 01: Geological map of the continental part of the Potiguar Basin with the region near the Limoeiro do Norte municipality (Ceará state) where the material were discovered (dark star). CE, Ceará state; RN, Rio Grande do Norte state and its capital, Natal. Modified from Cassab (2003).

Figure 02: The theropod vertebrae UFRJ-DG 528-R (A-C) and UFRJ-DG 575-R (D-E). UFRJ-DG 575-R: A, lateral view; B, the anterior articular facet. UFRJ-DG 528-R: C, the lateral view; D, the ventral view; E, anterior articular facet. Note the large pneumatic

foramen on the side of the anterior fragment of UFRJ-DG 575-R. pfr = pneumatic foramen. Scale bar: 2 cm.

Figure 03: Spinosauroid tooth (UFRJ-DG 619-R): A, the labial view; B, the lingual view; and C, the cross section. Scale: 1 cm

Figure 04: Maniraptoran caudal vertebrae (UFRJ-DG 521-R): A, Lateral view; B, ventral view; C, anterior articular facet. Prz, prezygophysis; Nc, neural canal. Scale: 1cm.

Figure 05: Comparison of UFRJ-DG 521-R and other maniraptorans. A, Potiguar's material; B, *Rahonavis*; C, *Buitreraptor*; D, *Anchiornis*. Pr, prezygapophysis; lg, Longitudinal groove. Modified from Motta et al., (2018).

Figure 06: Carcharodontosaurid caudal vertebrae UFRJ-DG 523(A-C) and UFRJ-DG 524-R (D-F). UFRJ-DG 524-R: A, ventral view; B, lateral view; C, anterior articular facet. UFRJ-DG 523-R: D, ventral view; E, lateral view; F, anterior articular facet. Nc, neural canal. Scale: 1cm.

Figure 07: Comparison of UFRJ-DG 523-R and 524-R and other carcharodontosaurids. A and B, UFRJ DG 523-R; C and D, UFRJ DG 524-R; E and F, Kem Kem beds material (from Rauhut, 1999); G, *Tyrannotitan chubutensis* MPEF-PV 1156 (Modified from Canale et al., 2015); H, *Mapusaurus roseae* MCF-PVPH-108.81 (Modified from Coria and Currie, 2006) ; I, *Acrocanthosaurus atokensis* NCSM 14345 (Modified from Currie and Carpenter, 2000). Scale bar = 5 cm.

Figure 08: Caudal vertebrae UFRJ-DG. UFRJ-DG 558-R: A, posterior articular facet; B, lateral view; C, ventral view. UFRJ-DG 634-R: D, anterior articular facet; E, lateral view; F, ventral view. Pfr, Pneumatic foramen. Scale bar: 1cm.

Figure 09: Brazilian megaraptoran vertebrae findings. A and B, UFRJ DG 558-R; C and D, MPMA 08-003-94 (Méndez et al., 2012); E and F, CPPLIP 1324 (Martinelli et al., 2013).A, C e E, lateral view; B, D e F, ventral view. Pfr, Pneumatic foramen. Scale bar = 1cm.

Figure 10: Megaraptoran caudals vertebrae. A and B, UFRJ DG 558-R; C and D, *Aerosteon*; E and F, *Aoniraptor*; G, *Orkoraptor*. H, *Megaraptor*. A, C, E, G e H, lateral view; B, D e F, ventral view. Pfr, pneumatic foramen. Scale bar = 5cm.

Figure 11: Reconstruction of the theropods groups from Açu Formation, Potiguar Basin. In the center, a group of megaraptorans slaughtering a titanosaur; on the right a carcharodontosaurid awakens from its sleep; in the top center, a maniraptoran just watches. Art by Luciano da Silva Vidal.

Figure

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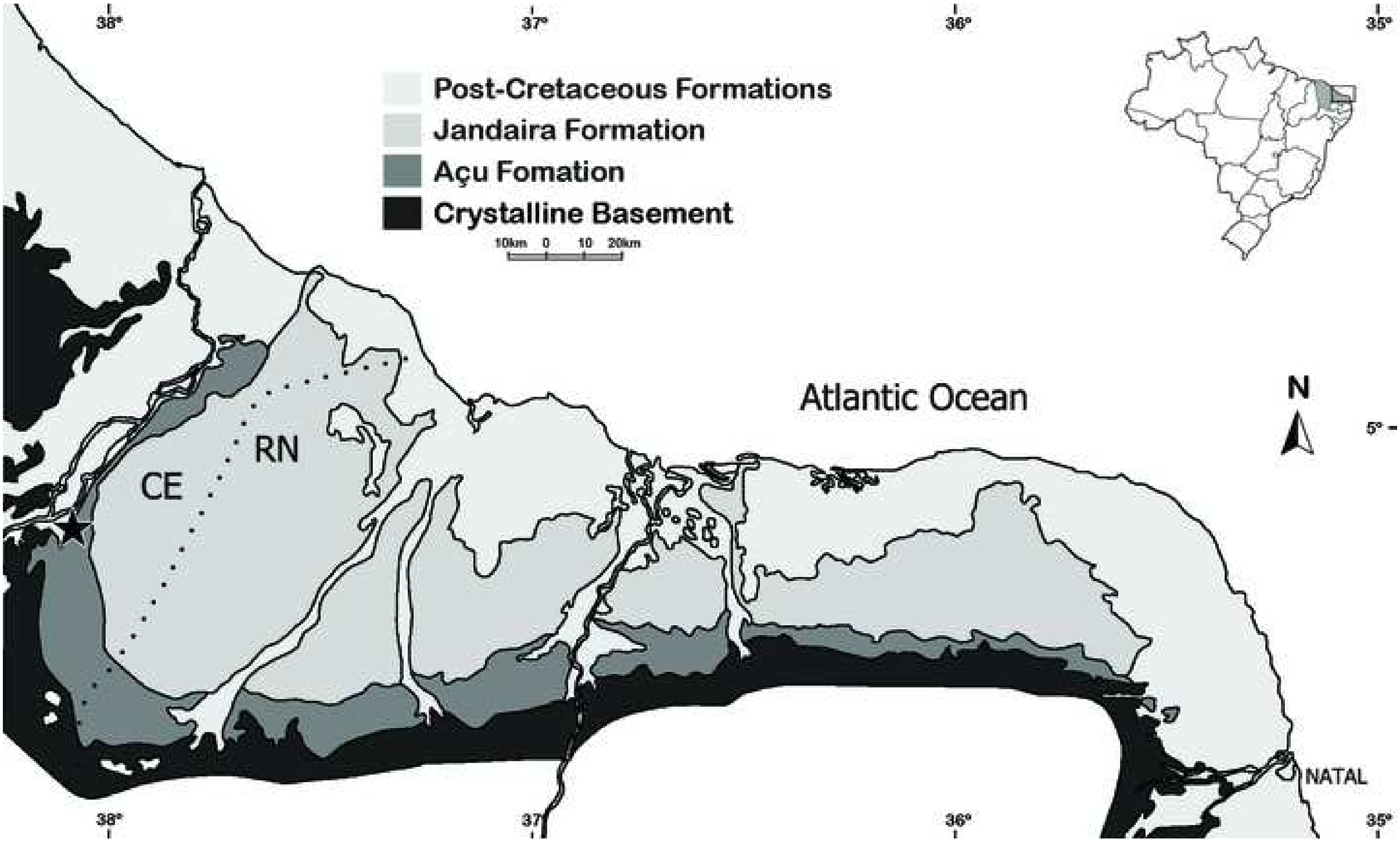

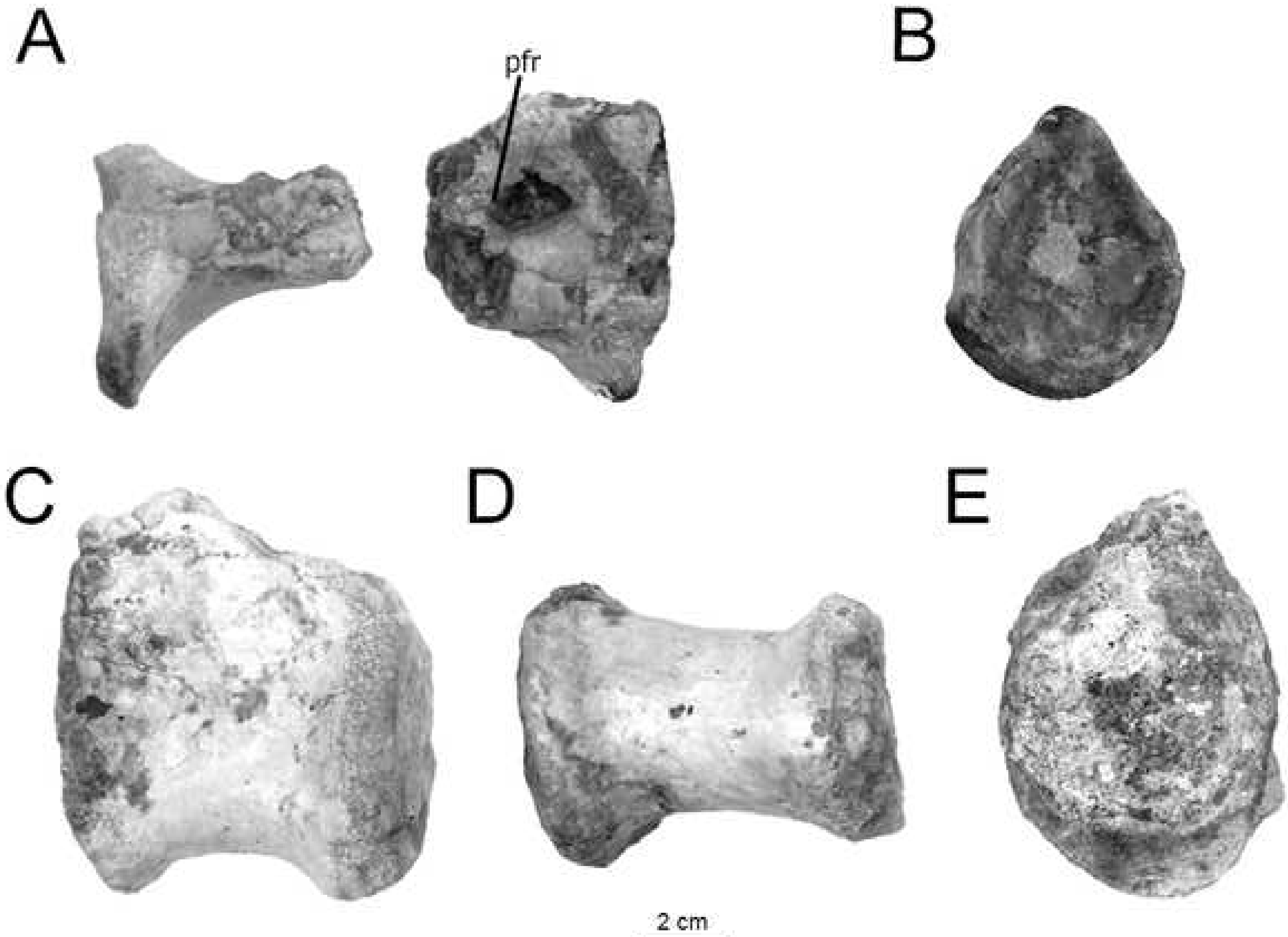
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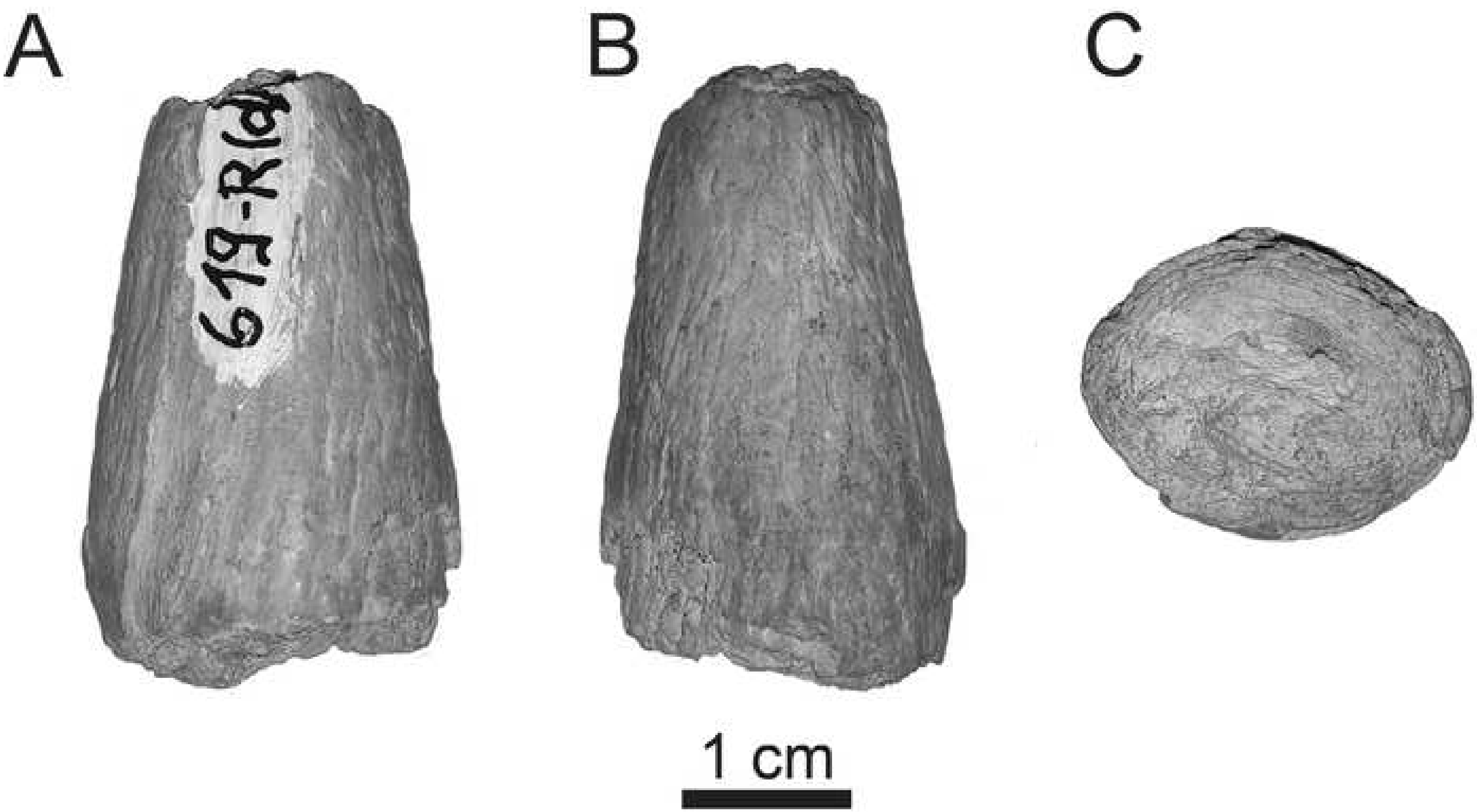
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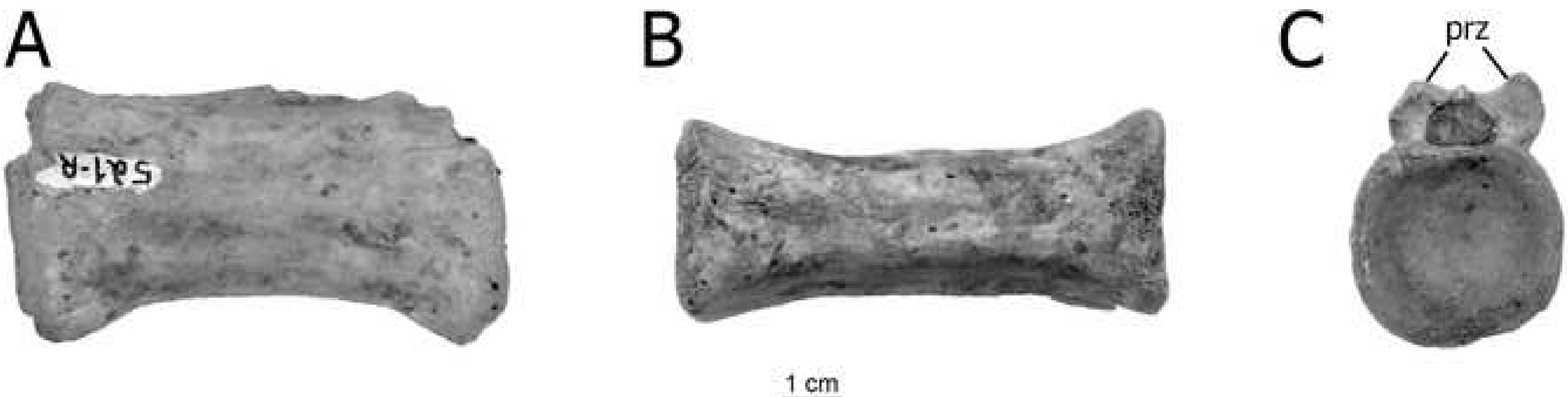
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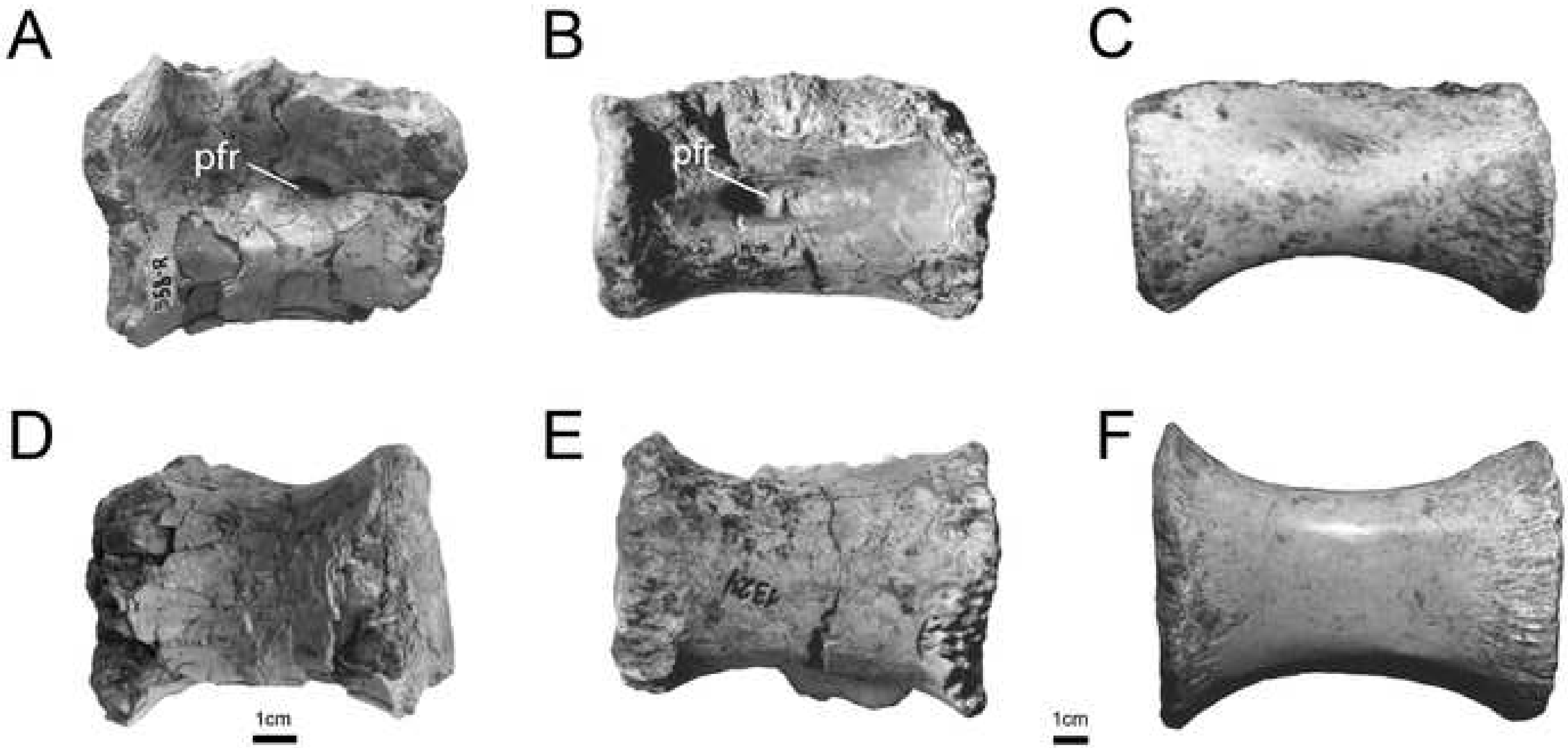

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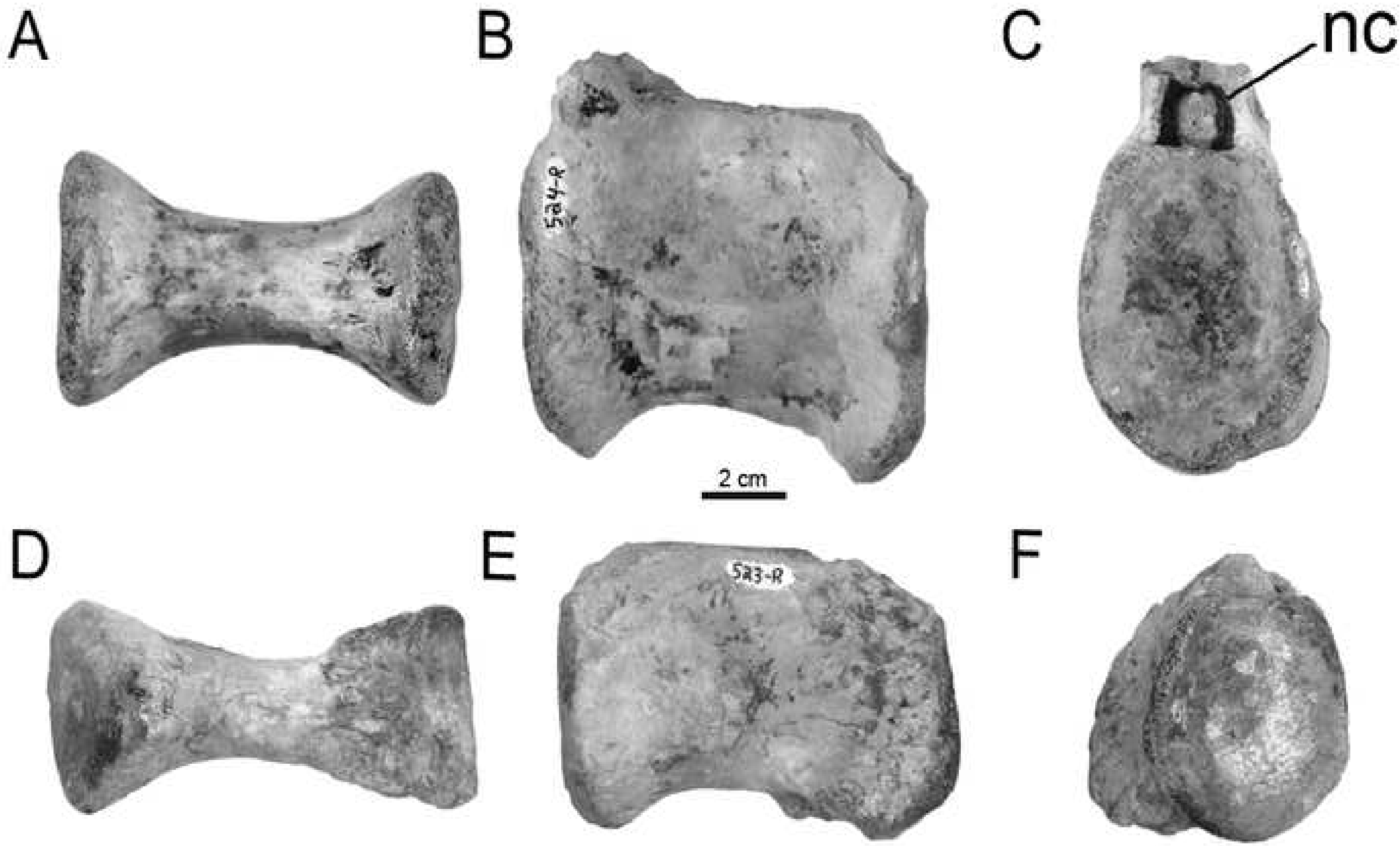

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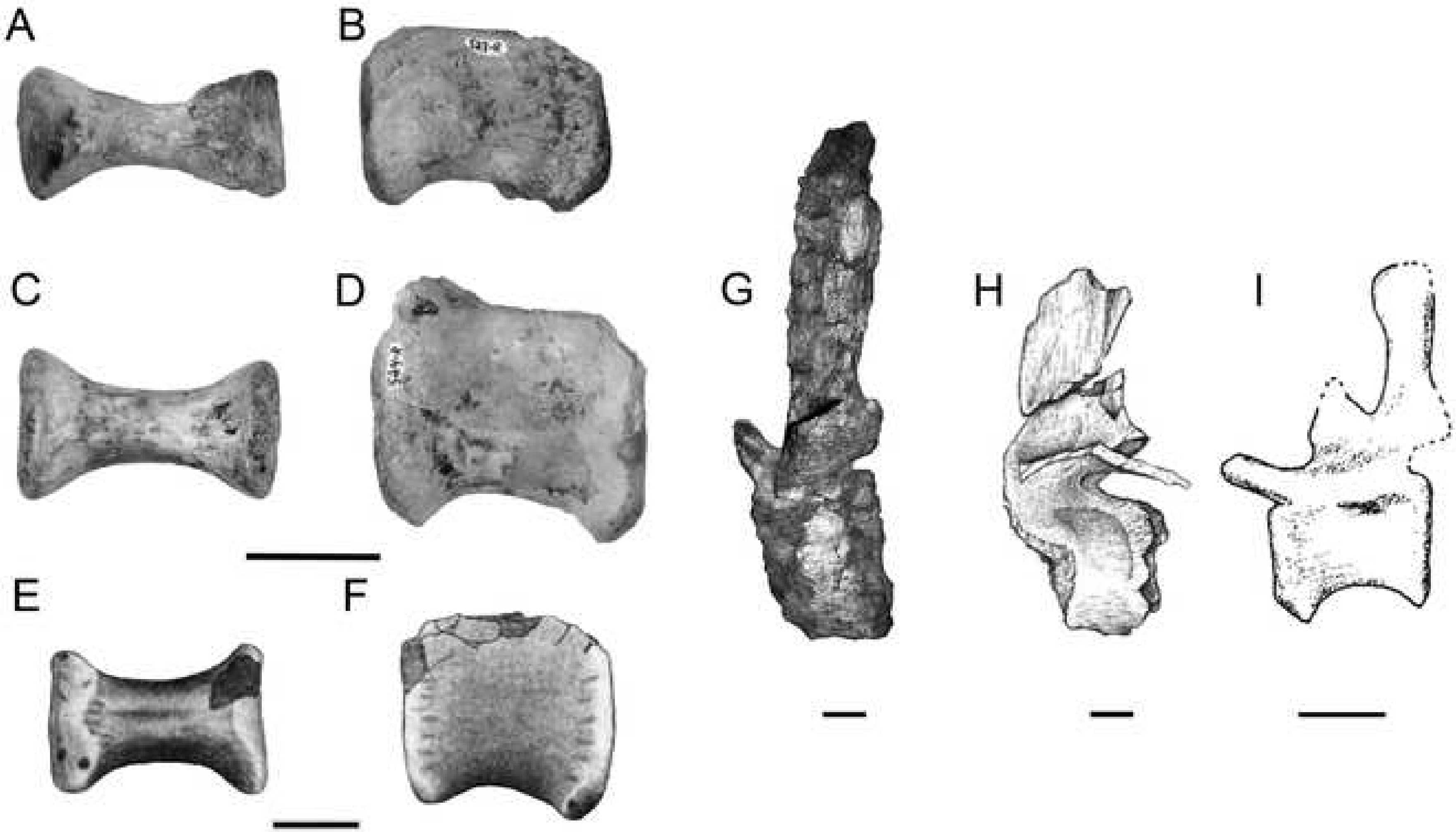

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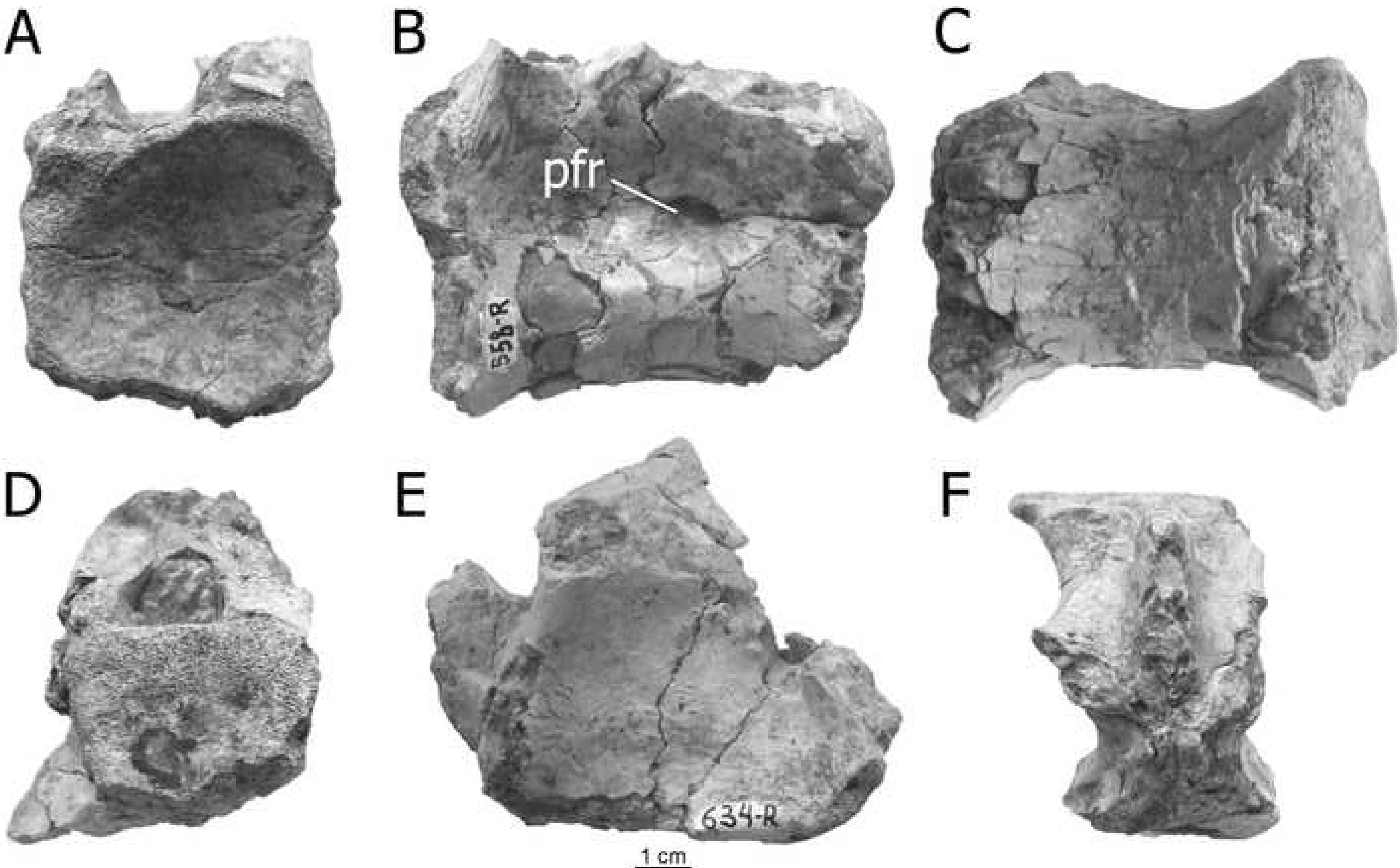

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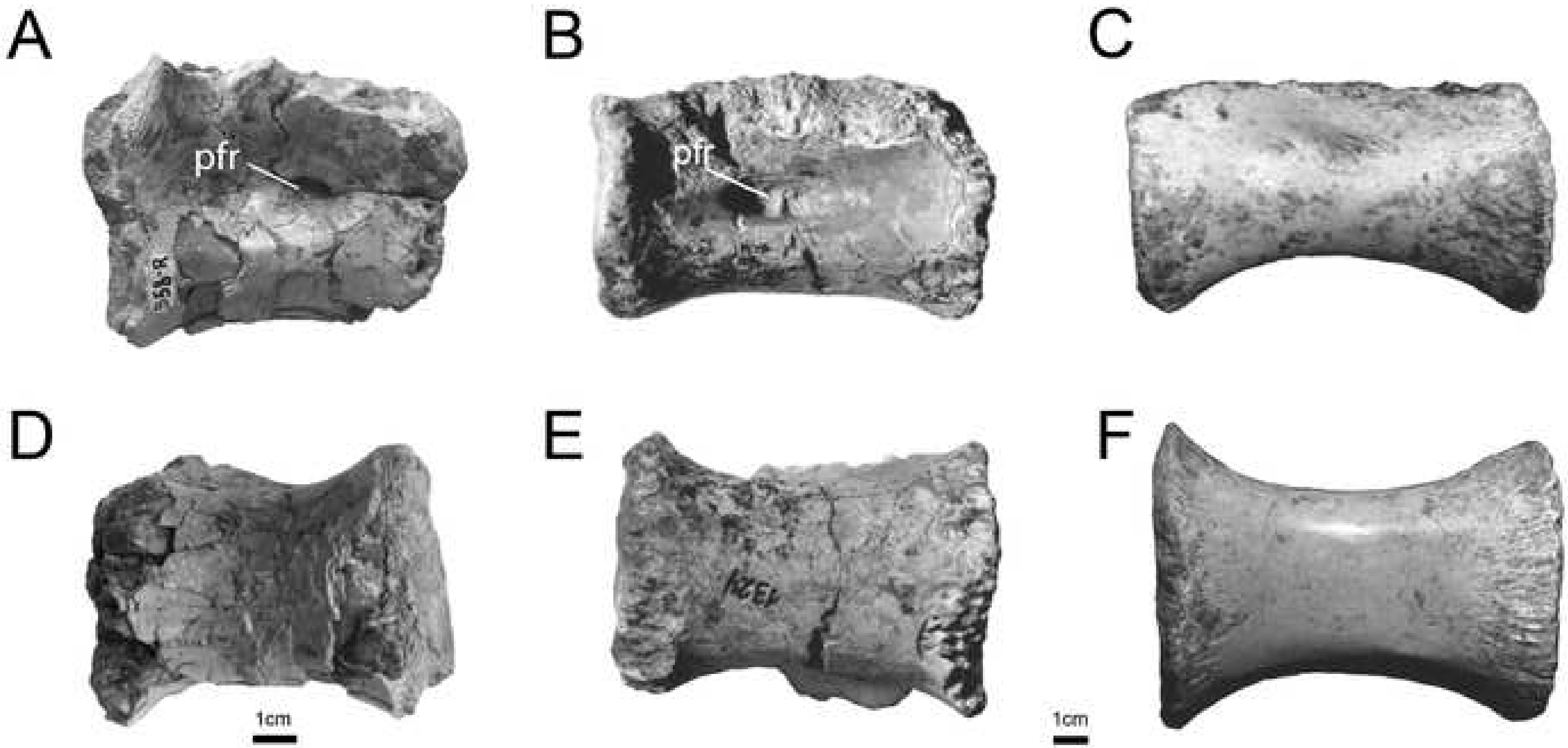


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Declaration of interests

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

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Author Statement

<u>Paulo Victor Luiz Gomes da Costa Pereira:</u> Conceptualization, Investigation, Writing - Original Draft, Writing - Review & Editing, Supervision, Funding acquisition.

<u>Theo Baptista Ribeiro:</u> Investigation. Writing - Original Draft, Writing - Review & Editing, Visualization.

<u>Stephen Louis Brusatte:</u> Validation, Writing - Review & Editing, Supervision

<u>Carlos Roberto dos Anjos Candeiro:</u> Writing - Original Draft, Writing - Review & Editing, Supervision.

<u>Thiago da Silva Marinho:</u> Investigation, Writing - Review & Editing

<u>Lilian Paglarelli Bergqvist:</u> Resources, Writing - Review & Editing, Supervision, Project administration, Funding acquisition.

Dear Editor

I, Dr. Paulo Victor Luiz Gomes da Costa Pereira, the first author of this manuscript, send this letter in order to request the change of the reviewer 01. I know that such a change can cause a delay in publication, but I believe that is important. We consider all the changes requested by you and the other reviewers and I am absolutely sure that the manuscript improved a lot with the changes proposed by you all. But I have to point out that the criticisms made by the reviewer 01 were often disrespectful and arrogant, a role that does not compete with the duties of a reviewer in a major international magazine.

His comments, did not contribute much to our work, since the reviewer limited himself to not agreeing with our classifications, always without presenting actual arguments or presenting bibliography that disagreed with our results, a totally different behavior when compared to the other two reviewers.

Our work is based on morphological description and comparison between materials, based on several similar articles with African and European fossils that have already been published, including by Cretaceous Research.

The role of our manuscript (and science in general) is to contribute as much as possible with the fossils collected. Nothing prevents better preserved fossils from disagreeing with our considerations in the future.

I'm really upset that I had to wait more than 8 months for a review that did not seek to improve the manuscript at all.

I thank you very much for the attention given by you and the other reviewers to our manuscript. Be sure that our work has improved a lot with your contributions!

Yours sincerely,

Dr. Paulo Victor Luiz Gomes da Costa Pereira

THEROPOD (DINOSAURIA) DIVERSITY FROM THE POTIGUAR BASIN (EARLY-LATE CRETACEOUSALBIAN – CENOMANIAN), NORTHEAST BRAZIL

Paulo Victor Gomes da Costa Pereira[1*]; Theo Baptista Ribeiro[1]; Stephen Louis Brusatte[2]; Carlos Roberto Dos Anjos Candeiro[3,] Thiago da Silva Marinho[4]; Lilian Paglarelli Bergqvist[1]

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Abstract

The theropod record~~s~~ from the Cretaceous of northeastern ~~Northeast of~~ Brazil are rare and consist mostly of isolated and incomplete remains, with only four~~ive~~ species described. Here we describe, identify and evaluate the diversity of theropod materials from the Albian-Cenomanian Açu Formation, Potiguar Basin. The material consists of seven ~~nineten~~ isolated theropod vertebrae ~~(UFRJ-DG 521-R, 523-R, 524-R, 528-R, 532-~~

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~~R, 547-R, 558-R, 575-R, 587-R and 589-R)~~ and a tooth ~~(UFRJ-DG 653-R)~~. ~~T~~We identify the material ~~have been identified~~ as belonging to four theropod groups: ~~Abelisauria, Carcharodontosauria,~~ Spinosauroidea, Carcharodontosauria~~idae~~, Megaraptora, and Maniraptora. ~~The vertebrae were classified into five~~ four ~~morphotypes based on morphological form and/or diagnostic characters and comprised~~ representedat ~~this moment by five~~ four ~~groups: Abelisauria, Carcharodontosauria, Spinosauridae, Megaraptora, and Maniraptora.~~ We classify the ~~The isolated tooth was classified as belonging to a spinosaurid~~ One of the significant~~great~~ results ~~so far~~ is the occurrence of Megaraptora in the Potiguar Basin~~,~~; based on the general morphology, some of the bones~~elements described~~ we describe are very similar to those of *Aerosteon*~~m~~ and *Megaraptor*. Another unexpected~~remarkable~~ result is the ~~description~~ identification and presence of a maniraptoran ~~a~~ caudal vertebra~~e of a maniraptora~~,; these dinosaurs are very rare in Brazil, with few fossils~~remnants~~ previously described. ~~Besides this~~Furthermore, we identify other groups that have already been found ~~on~~ in isochronous basins of the Northeast region of Brazil and Africa, including ~~as~~ Carcharodontosauria and Spinosauroid~~ae~~a. The presence of these theropod groups in the~~at~~ Açu Formation reveals an ~~unexpected~~ dinosaur richness ~~fauna~~in ~~the~~at in the Potiguar Basin similar to isochronous basins in Northern Africa and ~~opens up an important opportunity to~~ increases ~~the~~ knowledge about the~~the~~ diversity of South American dinosaurs.

Keywords: Dinosauria, Potiguar Basin, Theropoda, faunistic richness, ~~Abelisauria,~~ Carcharodontosauria, Megaraptora, Spinosauridae, ~~and~~ Maniraptora.

Introduction

The first ~~works~~ studies in Brazil that attributed vertebrate fossil remains to

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Formatted: No underline, Font color: Auto dinosaurs were ~~conducted~~ published into the nineteenth and mid-twentieth centuries (Marsh, 1869; Derby, 1890; Mawson ~~&~~and Woodward, 1907; Price, 1960, 1961). Since that time, dinosaur fossils have been recorded ~~in~~ from three principal localities~~/~~ and ages in Brazil: the Triassic of the Santa Maria and Caturrita formations (Langer et al., 2007a), the mid-Cretaceous of the Araripe, Triufo and São Luís-Grajaú basins (Frey ~~&~~and Martill 1995; Kellner 1996a, b, 1999; Medeiros *et al.*, 2007; Carvalho *et al.*, 2017), and the Late Cretaceous of the Bauru and Parecis groups (Franco-Rosas *et al.*, 2004; Kellner *et al.*, 2004; Brusatte *et al.* 2017).

~~As of now, there have been five theropod dinosaur species formally described from Brazil: *Staurikosaurus pricei* Colbert, 1970 and *Guaibasaurus candelariensisai* Bonaparte, Ferigolo & Ribeiro, 1999 from the Caturrita Formation; *Angaturama limai* Kellner & Campos, 1996, *Santanaraptor placidus* Kellner, 1999, *Irritator challengeri* Martill, Cruikshank, Frey, Small and Clarke, 2002 and *Mirischia asymmetrica* Naish, Martill & Frey 2004 from the Araripe Basin; *Oxalaia quilombensis* Kellner, Azevedo, Machado, Carvalho & Henriques, 2011 from the São Luís-Grajaú Basin, and *Pycnonemosaurus nevesi* Kellner & Campos, 2002 from the Bauru Group.~~ There are eight theropod dinosaur species formally described from ~~for~~ Brazil so far, four ~~of those described for its~~ from the northeastern region: *Santanaraptor placidus* Kellner, 1999, *Irritator challengeri* Martill, Cruikshank, Frey, Small and Clarke, 2002 and *Mirischia asymmetrica* Naish, Martill and Frey 2004 from the Araripe Basin; and *Oxalaia quilombensis* Kellner, Azevedo, Machado, Carvalho and Henriques, 2011 from the São Luís-Grajaú Basin.

A promising area for new dinosaur discoveries is the rocks of the Açu Formation, in the Portiguar Basin. ~~Recently~~Until now, the macrofossils of the Açu Formation ~~(in this~~

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A: We choose to keep this part of the text to preserve the cohesion within of the Introduction, featuring the first works and discoveries on theropod paleontology of Brazil. The next paragraph has a small summary of the Cretaceous northeastern theropod dinosaurs of Brazil.

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~~area were restricted to a few occurrences from outcrops on the western border of the basin (Russas and Tabuleiro do Norte municipalities, Ceará state),~~ consisted~~ing~~ of bivalve molluscs, small crustaceans, fish scales, and plant remains (Duarte ~~&~~and Santos, 1961~~2~~). ~~This situation lasted until~~However this changed in the 2000s, when researchers from the Group of Analogs to Oil Reservoirs of the Department of Geology of the Federal University of Rio Grande do Norte, in geological mapping of the Açu 4 operational unit, found large vertebrate fossils. ~~These fossils were attributed to Titanosauria and Theropodaindet., but~~ were ~~not described in detail (Santos et al., 2005).~~

In the decade after the discovery of these first continental vertebrate fossils in the formation (Santos *et al*., 2005), no other fieldwork was conducted. However, in ~~the years~~ 2015 and 2016, this area was again prospected by Laboratório de Macrofósseis of the Universidade Federal do Rio Janeiro and dozens of fossils were ~~collected~~found. The aim of the present work is to describe and identify the collected materials attributed to theropod dinosaurs, showing that the Potiguar Basin preserves a ~~great~~ large diversity of species and has great potential for future discoveries and studies about the mid-Cretaceous paleoenvironments of the Atlantic margin of Brazil.

Geological Setting and Lithostratigraphy

The Potiguar Basin is located at the eastern continental margin of northeastern Brazil, cropping out in the states of Rio Grande do Norte and Ceará (Fig. 01), with a total estimated area of 60,000 km^2, of which 22,000 km^2 is interpreted as continental (Cassab, 2003). The Potiguar Basin is bounded to the east by Alto de Touros, which ~~which~~ separates it from the Pernambuco-Paraíba Basin, to the northwest by the Alto de

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Fortaleza, which ~~bordering~~ separates it from the Ceará Basin, and to the south and west by crystalline basement rocks (Pessoa-Neto *et al*., 2007).

~~Figure 01: Geological map of the continental part of the Potiguar Basin with the region near the Limoeiro do Norte municipality (Ceará state) where the osteoderm~~ were ~~was discovered (dark star). CE, Ceará state; RN, Rio Grande do Norte state (Capital is Natal). ModifiedfromCassab (2003).~~

The sedimentary units of the Potiguar Basin ~~is~~ are divided into three groups: Areia Branca (Pendência and Alagamar formations), Apodi (Açu, Quebradas and Jandaíra formations) and Agulha (Ubarana, Guamaré and Tibau formations) (Araripe ~~&~~ and Feijó, 1994). The Açu formation is divided into four subunits according to electric logs, identified from bottom to top as Açu 1, Açu 2, Açu 3 and, Açu 4 (Vasconcelos *et al*., 1990). The material described here comes from the Açu 4 subunit, which corresponds to a transgressive, coastal-estuarine system.

The A~~ce~~çu-4 Unit consists of sixteen facies, fourteen being siliciclastic and two being hybrid. The siliciclastic facies ~~were~~ are grouped into nine associations, namely: (1) lag residual deposits, (2) channel fill deposits, (3) crevasse-splay deposits, (4) floodplain deposits, (5) abandoned channel deposits, (6) upper-flow regime sandflat deposits, (7) lower-flow regime sandflats, (8) sandflat/mudflat deposits of restricted environment, and (9) mudflat deposits. The first five facies associations represent a meandering fluvial system with tidal influence, and the remaining integrate the intermediate and distal sectors of an estuarine complex dominated by tides. The hybrid facies were deposited in a shallow platform adjacent to an estuary (Costa et al., 2014).

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The Açu Formation has been suggested to be Albian-Cenomanian in age (Early–Late Cretaceous), based on palynological data (Araripe ~~&~~and Feijó, 1994).

Material and Methods

The fossils were collected from outcrops of the Açu Formation, Potiguar Basin (Ceará state, noutheastern Brazil) and are deposited at the Fossil Reptile Collection of the Departamento de Geologia (DG), Universidade Federal do Rio de Janeiro (UFRJ). The material consists of ~~10~~ seven isolated theropod vertebrae (UFRJ-DG 521-R, 523-R, 524-R, 528-R, ~~532-R, 547-R,~~ 558-R, 575-R, ~~587-R~~ and ~~589~~634-R) and a tooth (619-Rd) ~~tooth~~. ~~The vertebrae were classified into fivesixmorphotypes based on morphological form and/or diagnostic characters.~~

The following tooth characteristics were ~~analyzed~~assessed, ~~according~~following ~~to~~ the nomenclature proposed by Hendrickx *et al.* (2015): ~~–describing:~~ general morphological traits~~ogy~~ of the dental crown (~~geometric shape, relative curvature and surface ornamentation~~its overall shape, curvature, ornamentations in the enamel), denticles (presence, size and shape)~~ and~~, cross section (compression and shape), orientation of the tooth (lingual, labial, mesial and distal) and measurements~~) and blood grooves (presence and visibility) (Currie et al., 1990; Sankey et al., 2002; Smith et al., 2005; Candeiro, 2007):~~.

~~– AL: Maximum apicobasal extent, of the tooth crown mesial base, measured from the mesial portion at the level of the cervix to the apical-most point of the crown (Smith et al., 2005).~~

~~– CBL: Maximum mesiodistal extent of the tooth crown at the level of the cervix (Smith *et al.*, 2005). Equivalent to FABL used by some authors (Currie *et al.*, 1990; Farlow *et al.*, 1991; Sankey *et al.*, 2002).~~

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- CBW: Maximum labiolingual extent of the tooth crown base, perpendicular to the CBL and at the level of the cervix. (Smith *et al*., 2005).

- CBR: Ratio expressing the narrowness, the lateral compression of the base of the crown, corresponding to the quotient of CBW by CBL (CBR=CBW/CBL, Smith *et al*., 2005). A strongly labiolingually narrow crown has a quotient of less than 0.4; a moderately narrow tooth is around 0.5-0.6; a weakly narrow crown, with an ovoid cross-section, has a ratio fluctuating between 0.6-0.7; and a tooth with a subcircular transversal section has a ratio between 0.9 and 1.1 (Smith *et al*., 2005).

- CH: Maximum apicobasal extent of the distal margin of the crown (Smith *et al*., 2005). Equivalent to the TCH proposed by Farlow *et al*. (1991).

- CHR: Ratio expressing elongation, the relative size of the tooth, equivalent to the quotient of CH by CBL (CHR=CH/CBL, Smith *et al*.,2005). A short crown tooth has a quotient less than 1.5; a medium crown tooth has a quotient varying from 1.5-2.5 and a strongly elongated crown has a ratio above 2.5.

- DC: Number of denticles on the distal carina at mid-crown per 5mm (Smith *et al*., 2005). Equivalent to five times the posterior medial carina denticles per millimeter (Buckley *et al*., 2010).In this study, teeth with less than 20mm had their denticles measured over 1mm, with this value then multiplied by five.

- MC: Number of denticles on the medial part of the mesial carina per5mm (Smith *et al*., 2005). Corresponds to five times the number of denticles of the medial part of the mesial carina per millimeter (Buckley *et al*., 2010).In this study, teeth smaller than 20mm had their denticles measured over 1mm, and this value was then multiplied by five.

• Anteroposterior basal length – commonly referred to as FABL (fore-aft basal length) – a measure taken between the most extreme points of the tooth at its base. It is conceptually represented by a straight line.

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• Total crown height - ALT - the distance between the apex and the base of the crown.

• Relative crown height - IAR - division of the total crown height by baselineanteroposterior length (ALT/FABL).

• Transverse section thickness - EST - measure of the labial-lingual thickness of the basal cross section of the tooth.

• Density of denticles - DDA (anterior carina, also known as mesial carina) - DDP (posterior carina, also known as distal carina). Measurement of the number of denticles per 1 mm on the medial part of the crown, in both carinae.

Terminology

In the present work, the terminologies proposed by Smith et al., (2005) were used to refer to both the dental structures and the positioning of the analyzed teeth. According to these authors, the dental crown is divided into three parts: apical (the most distal part of the tooth), medial (region between the apical and basal), and basal (lower part of the tooth, closer to the root). The authors defined as the labial surface the surface that was in contact with the animal's lips, and the lingual surface to that which faced the tongue of the animal.

Results

Dental element:

SistematicSystematic paleontology

Tooth

THEROPODA Marsh, 1881

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Commented [21]: I suggesttobeconsistentwiththeabbreviations, usingtheir English verisions as is usual besides FABL: CBW: crown basal width (ratherthan EST), CH: crownheight (ratherthanALT), etc. SeeHendrickx et al 2015. The dentitionofmegalosauridtheropods. Acta PaleontologicaPolonica 60 (3): 627-642.

Commented [LM22]: Done. We updated the method and nomenclatures according to Hendrickx et al., 2015 **A proposed terminology of theropod teeth (Dinosauria, Saurischia).**
We also cut some redundant parts of the methods, such as the terminology.

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TETANURAE Gauthier, 1986

SPINOSAURIDAEStromer, 1915

Referred material:UFRJ-DG 653-R, a tooth.

Description and comparisons:

The material consists of an incomplete Spinosauridae crown (Fig. 02, A and B) whose apex has been lost. The crown has a high relative height (HIR = 2.4) and is lingually curved. Its cross section is rounded with a Crown Base Ratio (CBR) of 7.8 (Smith et al., 2005).

This crown does not have denticulation in any of its carinae is shared with *Irritator challengeri* and *Spinosaurus aegyptiacus* but differs from the denticulated carinae of *Baryonyxwalkeri* (Mateus et al., 2011). On the labial surface, there are no striations, while on the lingual surface there are ca.? nine well-defined striations that bifurcate near the base of the crown.

UFRJ-DG 653Rd shares many characteristics seen in other spinosaurines as a conical teeth crown with a ovoid-shaped crown base, feature usually seen in piscivorous animals; the non-serrated carinae, which differentiates it from the other spinosauroid family, the Baryonychinae, whose teeth features a large number of small sized serrations on both of its carenae; *flutes* (Must see the material again)?

Axial elements:

Commented [25]: This measurement has a big fault, given the recovered tooth lacks most of its tip.
A: Done. We added to the text that we estimated the total height of the crown based on the works of (CITE)

Commented [26]: Other abbreviation was used in Material and methods
A: Done

Commented [27]: This ratio was not mentioned in Materials and methods
A: Done

Commented [28]: I suggest that, before comparing this material with other spinosaurids, the authors should add a summary of characters that allow to asign it to Spinosauridae.
A: Done. We summarize the characteristics of spinosaurids in the Discussion.

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A: Done.

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Commented [PP30]: A: Review the tooth description and explain why

SAURISCHIA ~~Cite~~Seeley, 1888~~year~~~~Morphotype 1:~~

THEROPODA Marsh, 1881

AVEROSTRA Paul, 2002

TETANURAE Gauthier, 1986

NEOVENATORIDAE Benson, Carrano & Brusatte, 2010

? MEGARAPTORA Benson, Carrano & Brusatte, 2010

Referred material: UFRJ-DG 532-R and 575-R.~~ and 587-R~~

Description~~ and comparisons~~:

~~Morphotype 1 consists of two specimens (Fig. 02, C-F) based on partial centra and is characterized by semicircular articular surfaces and high pneumaticity. They are possibly caudal vertebrae, but a more conclusive description is difficult because of the poor preservation of the material.~~

~~Figure 02: Tooth and vertebrae attributed to Morphotype 01: Spinosauridae tooth, A; tooth cross section, B; Articular view, C(UFRJ-DG 587-R); D (UFRJ-DG 575-R). Lateral view, E and F(UFRJ-DG 575-R). Note the large pneumatic foramen on the side of the anterior fragment. pfr = pneumatic foramen. Scale bar: 1cm.~~

UFRJ-DG 528-R

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Commented [32]: Which view?

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Commented [33]: In the figure there is a black circle, I strongly suggest to add the real basal cross-section picture.

A: FAZER

Commented [34]: Those are lateral views of the same fragment, or one of each fragment?

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Specimen 528-R is a theropod vertebral centrum (Fig. 02~~3~~, C~~A~~-E~~B~~~~C~~). It is amphicoelous, and slightly higher than long. Its lateral surface is smooth and slightly concave, without marks or other ~~remarcable~~remarkable ~~–~~characteristics, giving the vertebra a straight and ~~clean~~somewhat featureless appearance. The ventral surface smooth with no groove or keel and ~~is not very concave~~it is slightly concave in lateral view.~~, being smooth on the medial region and presenting a groov eon the posterior region close to the articular face margin.~~

The dorsal surface possesses a distinct longitudinal groove extending from one articular facet~~end~~ to the other that~~, and this groove~~ can be identified as the neural canal. ~~The anterior part of this groove is covered, but this covering is lost from the medial part further posteriorly, exposing the neural canal of this region in dorsal view.~~ The articular faces have ~~almost~~nearly straight margins. The anterior facet is somewhat concave, and the posterior is slightly convex and slightly oval in shape; both articular facets have the same general proportions (height longer than length). The anterior articular face presents a deeper concavity, and is slightly larger in size, than~~,~~ the posterior face, which is very flat and without deep depressions.

UFRJ-DG 575-R

Specimen 575-R (Fig. 02, A~~C~~-B~~E~~~~D-F~~) is a theropod vertebral centrum broken in two: a ~~4,5cm long~~ smaller anterior piece and a~~ 5,2cm long~~ larger posterior section. Although the material ~~have been~~was found associated there is no clear point of junction between both pieces, ~~with~~as most of the middle portion ~~being~~has been lost. The anterior fragment ~~presents ~~exhibits a very concave articular face of semi-circular shape and slightly forward-protruding margins.

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Commented [PP36]: Revisor 01: Before description of any dinosaur bone, it must be glued.
A: Done.

On the lateral surface of the anterior fragment there is a deep perforation close to the dorsal region that reaches the other lateral surface, which can be described as a pleurocoel (=pneumatic foramen) (=pneumatic foramen). (asthe left lateral surface close to the dorsal surface is missing a piece, exposing the internal part of thebone). The ventral surface of the anterior fragment is smooth and concave in anterior view. The dorsal surface of the anterior fragment is broken, missing most of the surface above the pleurocoel.

The posterior fragment has a slightly smaller articular surface, which is broken on the anterior portion; it is also concave and of semi-spherical circular shape, with slightly backwards-protruding margins. Its dorsal surface and the dorsal half of the left lateral surface are broken, while the right lateral surface is broken in a slightly more dorsal region in comparison to the left one. The ventral surface of the fragment is smooth and concave in lateral view. Due to the highly fragmentary state of UFRJ-DG 575-R, itsit is possible to see multiple small pervasive pneumatic chambers, the camellae, in the internal bone.

When both fragments are joined, it is clear that the length of the centrum is even larger than the height on its most complete point, in this case the anterior articular face. This is common in anterior dorsal vertebrae of Allosauroidea (measured next to the pleurocoels, which confirms the more anterior location). Furthermore, the margins of the articular facets have forward protrusions like those found in this group (Gilmore,1920; Madsen, 1976).

Comparisons:

Commented [37]: Sem-spherical or semicircular? Done.

Commented [38]: The authors should describe (and figure) the materials as a single vertebra, not as two different fragments. It is confusing and does not help with interpretation of the materials.

Commented [39]: At thebeginningofthismorphotype description theauthors suggest thatthey are possibly caudal vertebrae.

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The highly pneumatized camellate bone seen in UFRJ-DG 575-R is a characteristic seen in many groups of theropods, from the basal *Ceratosaurus* to tetanuran groups such as carcharodontosaurids and coelurosaurs mainly in its presacral vertebrae (Carrano &and Sampson, 2008). This feature, together with the poor preservation of this specimen, which prevents the identification of other more diagnostic characteristics, hinders the classification of this specimen beyond AverostraTheropoda.

UFRJ-DG587-R

Specimen 587-R is the anterior articular face of a theropod vertebra (Fig. 02, C). It has an semicircular shape, is slightly taller (9,5 cm) than wide (8cm), and has a shallow concavity on its articular surface, possibly indicating it is the anterior face of an amphicoelous vertebra, characteristic of Theropoda. The dorsal surface is indented with a concavity representing the beginning of the neural canal.

Morphotype 2:

THEROPODA Marsh, 1881

TETANURAE Gauthier, 1986

CERATOSAURIA Marsh 1884

NEOCERATOSAURIA Novas 1989

ABELISAURIANovas 1992

Referred material: UFRJ-DG 528-R and 532-R.

Description: and comparisons:

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Commented [40]: Why anterior? It could not be posterior?

Commented [41]: Why the authors assign this material to morphotype 1? They only suggest that it belongs to a theropod.

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Morphotype 2 (Fig. 03) includes two vertebrae with a low length/height ratio and semicircular articular faces with little lateral compression.

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Commented [43]: This character is used for differentiate this morphotype is also present in morphotype 1

Commented [44]: I suggest to look for other more specific characters to differentiate this morphotype

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UFRJ-DG528-R

Specimen 528-R is a theropod vertebral centrum (Fig. 03, A-C). It is amphicoelous, and slightly higher than long (8,5 vs. 6cm). Its lateral surface is smooth and slightly concave, without marks or characteristics of note, giving the vertebra a straight appearance. The ventral surface is not very concave in lateral view, being smooth on the medial region and presenting a breach grooveon the posterior region close to the articular face margin.

Commented [45]: This sentence seems wrong, please rephrase
A: Done.

The dorsal surface possesses a distinct longitudinal groove extending from one articular end to the other, and this groove can be identified as the neural canal. The anterior part of this groove is covered, but this covering is lost from the medial part further posteriorly, exposing the neural canal of this region in dorsal view.

The articular faces have almost straight margins. The anterior face is somewhat concave, and the posterior is slightly convex and slightly oval in shape; both articular faces have the same general proportions (height longer than length). The anterior articular face presents a more expressive concavity, and is slightly larger in size than, the posterior face, which is very flat and without deep depressions.

Commented [46]: The word “expressive” seems wrong in this context.
A: Done.

UFRJ-DG532- R

It is a fragment of a theropod vertebral? articular facet (Figure reference?). Its oval shape in the dorso-ventral direction, due to its height being longer than its length (8cm vs. 6cm), indicates a position in the most proximal region of the caudal vertebrae. The articular surface is slightly concave, presenting only a small depression, which indicates it is the

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~~posterior articular face of the centrum (Bonaparte,1985; Sampson et al. 1998; Coria et al. 2002, Méndez, 2014 year?). The articular surface is slightly damaged on its lower right part, missing a fragment that goes almost up to the medial part of the articular face.~~

THEROPODA Marsh, 1881

TETANURAE Gauthier, 1986

? SPINOSAUROIDEA Stromer, 1915

Referred material: UFRJ-DG 619-Rd.

Description:~~:~~

UFRJ-DG 619-Rd (Fig. 03) is a fragment of a large~~r~~ isolated tooth crown, probably belonging to the middle to almost apical portion of the tooth. The specimen lacks any form of enamel, ~~having~~as it has ~~all its~~ dentine exposed, what prevents ~~the possibility to~~description of ~~describe any kind of~~ external ornamentation ~~as~~such as transversal undulations, ~~and~~ flutes and denticulation. The crown is almost completely straight with only a subtle curvature in its lingual surface, while the labial surface remains slightly convex.

The crown fragment has an overall cone-like shape with an almost ovoid cross section. In ~~the~~ basal view, ~~it's~~it is possible to see concentrically deposited rings of dentine surrounding a small depression, which probably represents the apical-most portion of the dental pulp cavity.

Comparisons:

UFRJ-DG 619-Rd have some characteristics that it shares with the highly specialized teeth ~~seen in~~of spinosauroid theropods. The most salient of these is the a~~a~~lmost straight

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conical shaped crown, with an ovoid cross section shape, a feature usuallyoften seen in piscivorous animals (CITEMateus, 2011; Hendrickx &and Mateus, 2014) being the most remarkable of those.

The lack of denticulation inon any of its carina is a characteristic seen in spinosaurines such as *Irritator challengeri* and *Spinosaurus aegyptiacus* (citeStromer, 1915; Martill et al., 1996) while the highly denticulated carina is characteristic of baryonychines as *Baryonyx walkeri* (Charig & Milner, 1986; Mateus et al., 2011). However, due to the lack of enamel in this material it is not possible to distinguish between Baryonychinae and Spinosaurinae nor its possible.

Morphotype 3:

THEROPODA Marsh, 1881

TETANURAE Gauthier, 1986

MANIRAPTORA Gauthier, 1986

Referred material: UFRJ-DG 521-R

Description: and comparisons:

Morphotype 3 (Fig. 03, E? F-G) consists of one vertebra whose ratio betweenheight and its length somewhat greater than six and dorsally positioned prezygapophyses.

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~~length is more than twice its height, and which lacks any processes, indicating to be a distal caudal vertebra.~~

UFRJ-DG 521-R

Specimen UFRJ-DG 521-R (Fig. 04) is an almost complete distal caudal vertebrae of a ~~paravian~~maniraptoran theropod. It is amphicoelous with a length to height ratio of almost 2.5, making it a least twice longer than tall. The dorsal surface of the centrum is almost complete with half of a dorsal midline ridge reminiscent of reduced neural spine, a well preserved and more dorsally positioned pre-zygapophysis, and a lost post-zygapophysis. The pre-zygapophysis articular surface is ellipsoid and is reclined 45° laterally. The neural canal is almost completely preserved, -having lost only its posterior half .

The lateral surfaces of the centrum are mostly smooth, marked only with a midline ridge reminiscent ~~from~~of ~~the~~a reduced transverse processes ~~of the vertebrae~~. The ventral surface of the centrum has a~~n~~ shallow groove that ~~goes~~extends from one articular facet to the other. In the lateral view the ventral surface is slightly concave.

The articular facets of the centrum are both concave, with the anterior facet being more excavated than the posterior facet, and have a semi-circular shape. The articular margins are almost straight, with the anterior margin being larger than the posterior margin.

~~Specimen 521-R is a distal caudal vertebra of a theropod. It is almost complete, damaged only in the postzygapophysis region. It is abiconcave, amphicoelous vertebrae with a centrum slightly shorter anteroposteriorly than twice the height near the neural spine remnant and diapophysis, which confirms its more distal position within the caudal series (but not so distant from a medial position).~~

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Commented [BS50]: A paravian? Can you be this specific? If so, this should go in the Systematic Palaeontology section. If not, then just call it a maniraptoran here.

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On the dorsal surface, the neural canal and the prezygapophyses are well preserved on the anterior part of the vertebra, being damaged only on in medial-posterior portion. The prezygapophyses are intact. The lateral surfaces of the centrum?are smooth and present only a pair of small depressions on the part close to the dorsal surface. The ventral surface is intact and is very smooth and concave in lateral view.

The articular faces are biconcave; i.e. both present very expressiveconcavities on their surfaces, the anterior being much deeper than the posterior. Their margins are very straight and have a semi-circular shape, the anterior one being slightly larger than the posterior

.*Comparisons:*

UFRJ-DG 521-R has characteristics of a paravianmaniraptoran centrum , positioned after the transition point in the tail (Russell, 1972, Gauthier, 1986; Tykoski, 2005), as it is being longer than high and possessingpossesses a large reduction in both its neural spine and transverse processes, with those structures becoming midline ridges (Senter *et al.*, 2011; Motta *et al.*, 20187). This way it isThus, it is possible to deduce that it is positioned at least after the vertebra 11 of the caudal series as seen in *Buitreraptor*, *Rahonavis*, Dromaeosauridae and Troodontidae (Ostrom, 1969; Forster *et al.*, 1998; Senter *et al.*, 2012; Xu *et al.*, 2017).

The presence of a reduced transverse process forming a midline ridges after the transition point is seen seen in some paravians, such as *Microraptor*, *Rahonavis*, *Buitreraptor*, and Archeaopteryx. but it is seen in specimens ofin the distal caudal vertebrae of *Microraptor*, *Rahonavis* ,and *Buitreraptor*, *Anchiornis* and *Archaeopteryx* (Hwang et al., 2002; Hu et al., 2009; Han et al., 2014Forster *et al.*, 1998; Novas *et al.*, 2017), a characteristic also seen in UFRJ-DG 521-R, which differentiates it from most other paravians as dromaeosaurids, *Archaeopteryx*, *Jeholornis* and *Anchiornis*. .

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Commented [53]: I think the authors should specify which transition point are referring here (I suppose that proposed by Russel (1972), but this is my guess)
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Commented [BS54]: I don't agree with this taxonomy. Microraptor and Buitreraptor are dromaeosaurids, at least in most phylogenetic analyses. Rahonavis probably too. Anchiornis may

be a troodontid. The Agnolin and Novas phylogeny has many strange results and is not widely accepted.

So instead, just say that:

'The presence of a transverse process after the transition point is seen in some paravians, such as Microraptor, Rahonavis, Buitreraptor, and Archeaopteryx.'

Don't use the term Averaptor.

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The presence of the transverse processes after the transition point of the tail is not observed in more basal paravian groups of like dromaeosaurids and troodontids that have smooth lateral surfaces in their centra (Ostrom, 1969; Norell & Makovicky, 1999; Currie & Dong, 2001; Xu et al., 2012), but it is seen in specimens of *Microraptor*, *Rahonavis*, *Buitreraptor*, *Anchiornis* and *Archaeopteryx* (Hwang et al., 2002; Hu et al., 2009; Han et al., 2014; Novas et al., 2017), all belonging to the group Averaptora.

In addition, the 521-R specimen also has the dorsally positioned pre-zygapophyses more dorsally positioned in the same way as in *Buitreraptor*, *Rahonavis* and *Anchiornis* (fig. 059) (Motta *et al*., 20188). The vertebral centrum has a length-to-height ratio between its height and its length is close to 2.5, a ratio usually seen in dromaeosaurids with exception to *Buitreraptor* but not seen in other maniraptorans as troodontids and microraptorians whose ratio can reach up to 5.0 to 6.0. a ratio seen in more basal paravians such as dromaeosaurids, in contrast to troodontids and more derived averaptorans whose ratio can be as much as 6.0.

Figure 03: Caudal vertebrae attributed to Morphotype 02 (A-D) and Morphotype 03 (E-G). UFRJ-DG 528-R: A, ventral view; B, Lateral view; C, anterior articular facet. UFRJ-DG 532-R: D, anterior articular facet. UFRJ-DG 521-R: E, Lateral view; F, ventral view; G, anterior articular facet. Prz, prezygophysis; Nc, neural canalhannel. Scale: 1cm.

Morphotype 4:

THEROPODA Marsh, 1881

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So instead, just say that:

'The presence of a transverse process after the transition point is seen in some paravians, such as Microraptor, Rahonavis, Buitreraptor, and Archeaopteryx.'

Don't use the term Averaptor.

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Commented [BS56]: Again, don't use averaptorans. Instead, just say that long vertebrae like these are seen in some, but not all, paravians.

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TETANURAE Gauthier, 1986

ALLOSAUROIDEA Marsh, 1878

CARCHARODONTOSAURIA Benson, Brusatte and Carrano, 2010

Referred material: UFRJ-DG 523-R and 524-R.

Description:~~:and comparisons:~~

~~Morphotype 4 (Fig. 04) is formed by two vertebrae with low length/height ratio, close to morphotype 1, and oval articular facet.with strongly waisted centra withlateral depressions in the dorsal half of the lateral surface, a double keel cut by a longitudinal groove and offset articular facets~~

~~Figure 04: Caudal vertebrae attributed to Morphotype 4. UFRJ-DG 524-R: A, ventral view; B, lateral view; C, anterior articular facet. UFRJ-DG 523-R: D, ventral view; E, lateral view; F, anterior articular facet. Nc, neural canalhannel. Scale: 1cm.~~

UFRJ-DG523-R

Specimen 523-R (Fig. 06~~4~~, D-F) is a theropod vertebral centrum, with the following characteristics: it is amphicoelous, and slightly longer than high~~ (8,9 cm vs. 6,5cm)~~. Its lateral surface is very concave and smooth on both sides, with the shape of an hourglass in dorsal view. The ventral surface is mostly smooth on the anterior part, with ~~breaches and ~~marks that possibly indicate the articulation~~fusion of~~ with the hemal arch on the posterior part.

The dorsal surface is marked by a long and ~~expressive~~deep longitudinal canal from one articular face to the other, which widens~~r~~ on the extremities and tapers~~ed~~ in the

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Commented [58]: Again, this character varies with the position inside the caudal series.

Commented [59]: The shape of the articular face of caudal vertebrae is so variable, it show differences inside the same taxonomic group. For example inside Abelisauridae, Carnotaurus shows semicircular articular surface, and Majungasaurus show oval articular surface, as the authors clearly show in the figure 8. This makes this character not useful for separating morphotypes.

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middle. This canal was possibly the space of the neural canal of the vertebra, given the marks of fusion with the neural arch that meet on its borders.

The articular faces are ovoid~~al~~ ~~semi-circular~~ in shape and ~~with~~have slightly forward-protruding margins~~ of the articular faces~~, the anterior facet being higher in comparison to the posterior facet. The anterior articular face has a concavity deeper than the posterior one, being also slightly larger in its proportions.

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UFRJ-DG524-R

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Specimen 524-R (Fig. 06~~4~~, A-C) is a centrum of a theropod caudal vertebra. It is amphicoelous and is slightly longer than high~~ (7,5 cm vs. 8,5 cm)~~, which indicates a more proximal position ~~between the~~in the caudal ~~vertebrae~~series. The lateral surface is smooth and marked by two deep~~expressive~~ concavities on both lateral faces, giving ~~to~~ it ~~a~~an hourglass-like shape.~~with a shape like an hourglass~~. Additionally, on the most dorsal region of the lateral surface ~~it is possible to notice~~there is a small and shallow longitudinal depression on each side.

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The ventral surface is a double keel marked by a very superficial groove extending from the anterior part up to the posterior part. The dorsal surface is marked by the neural canal of the vertebrae. Above the anterior part of this canal the entire ~~cover~~ upper portion~~art~~ of the neural tube is preserved, forming a small arch filled by sediment positioned slightly above ~~of~~ the anterior articular face.

The articular faces are semi-circular and somewhat oval, with the anterior one being slightly larger than the posterior, and their margins slightly protrude forward. The anterior articular face has a concavity slightly deeper than the posterior~~, which is more superficial.~~.

Comparisons:

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Both ~~vertebrae of morphotype 4~~UFRJ-DG 523 and ~~AND~~ 524 present characteristics commonly found in carcharodontosaurids (Fig. 07~~10~~). For instance, depressions in the most dorsal part of ~~their~~the lateral surface are found in *Giganotosaurus*, *Mapusaurus* and *Tyrannotitan* and in the mid-caudal vertebrae Vb-870 found in the Wadi Milk Formation (Coria ~~&~~and Salgado, 1995; Coria ~~&~~and Currie, 2006; Novas *et al*., 2005a; Canale *et al*., 2015; Rauhut, 1999)~~,~~. ~~which~~This condition is different from that in *Carcharodontosaurus*, ~~that~~which has pleurocoels in ~~their~~its anterior caudal vertebrae (Stromer, 1931). Furthermore, the strongly waisted centrum morphology, a double keel cut by a longitudinal groove and offset articular facets (although it is a plesiomorphic feature found in *Allosaurus* Gilmore, 1920; Madsen, 1976) are also found in specimens such as the carcharodontosaurid material from Sudan (Rauhut, 1999) and in *Tyrannotitan*, *Mapusaurus* and *Acrocanthosaurus* (Canale *et al*., 2015; Harris, 1998; Coria ~~&~~and Currie, 2006; Currie ~~&~~and Carpenter, 2000).

~~Morphotype 5:~~

THEROPODA Marsh, 1881

NEOVENATORIDAE Benson, Carrano ~~&~~and Brusatte, 2010

MEGARAPTORA Benson, Carrano ~~&~~and Brusatte, 2010

Referred material: UFRJ-DG 558-R e 634-R

Description:~~and comparisons:~~

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Morphotype 5 (Fig. 05) includes two amphicoelous caudal vertebrae with pleurocoels and high pneumaticity.

Figure 05: Caudal vertebrae attributed to Morphotype 05. UFRJ-DG 634-R: A, posterior articular facet; B, lateral view; C, ventral view. UFRJ-DG 558-R: D, anterior articular facet; E, lateral view; F, ventral view. Pfr, Pneumatic foramen. Scale bar: 1cm.

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UFRJ-DG 558-R

Specimen 558-R is a centrum of a theropod caudal vertebra, damaged by various cracks (Fig. 085, D-F). It is amphicoelous, and slightly longer than high (6cm vs. 7cm), indicating a somewhat proximal position within the caudal series. Its ventral surface is very smooth and convex in lateral view, but is very damaged in the region where the base of the posterior articular face would be.

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The dorsal surface is marked by a great depression extending longitudinally from one articular face to the other, wider in the extremities, denoting the neural canal. The lateral surfaces are marked by a longitudinal elliptic depression on their medial parts, where there is a pleurocoel on each side. The left lateral pleurocoel is deeper and better defined than the right lateral one. The presence of pleurocoels in the caudal vertebrae is characteristic of megaraptoran neovenatorids the Megaraptora group of the Neovenatoridae family (Benson *et al.*, 2011).

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Its articular faces are semi-circular and have very straight margins. The anterior articular face possesses a more distinctive depression of a slightly greater size than the posterior face and is also in a better state of preservation. The posterior articular face possesses a very slight concavity, making it almost straight, and is in a much more damaged state, presenting cracks and breaches on the ventral base of the face.

UFRJ-DG 634-R

This material is in a worse state of preservation than UFRJ-DG 558-R (Fig. 0~~8~~5, A-C). The ventral centrum portion and anterior articular face are fragmented. On its lateral surface, there is what appears to be the border of the pleurocoel in the same position seen in specimen 558-R~~, leading to the attribution of this vertebra to this morphotype.~~.

Different~~ly~~ from the other vertebrae of this ~~morphotype~~group, part of the neural arch and the transverse process are~~is~~ preserved on the right side of the specimen. The transverse process is positioned upwards at an angle of approximately 45º degrees.

Comparisons

The presence of pleurocoels in the caudal vertebrae is characteristic of megaraptoran neovenatids (Benson *et al.*, 2010). Pneumaticity in the caudal vertebrae is rare in Theropoda, present only in some groups: Megaraptora, Oviraptorosauria, Therizinosauria, and Carcharodontosauridae (Benson *et al.*, 2012~~1~~). As far as is known, no fossils of therizinosaurs have been found in South America and South American fossils attributed to oviraptorosaurs have been reassigned to other taxa, including to Maniraptora (*e.g.*~~see~~ Agnolín ~~&~~and Martinelli, 2007, Aranciaga-Rolando *et al.*, 2018). In addition, the caudal vertebrae of Oviraptorosauria have, on the ventral surface, a medial groove delimited by two longitudinal elevations (e.g., Sues, 1997; Xu *et al.*, 2007). Specimen UFRJ-DG 558-R does not have this feature (Fig. 09).

South American carcharodontosaurids (e.g., *Giganotosaurus*, *Mapusaurus*, *Tyrannotitan*) show ~~a~~ slightly concave lateral sides in the caudal vertebrae, ~~while~~but do

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not ~~being~~bear actual pneumatic foramina. Stromer (1931) described an anterior caudal vertebra from northern Africa, which he identified as *Carcharodontosaurus*, which had pneumatic characteristics, including a pleurocoel. However, that vertebra has a different general morphology and proportions when compared with ~~morphotype~~ the megaraptorid vertebrae~~6~~ from the Potiguar Basin (length-height ratio is 1 in *Carcharodontosaurus* and approximately 1.48 in UFRJ DG 558-R) and other members of Megaraptora.

Among the Megaraptora group, only *Aerosteon*, *Aoniraptor*, *Orkoraptor* and *Megaraptor* have preserved caudal vertebrae (Fig.~~ure~~ 10~~07~~) (Sereno *et al*., 2008; Benson *et al*., 2010; Motta et al., 2016). The height/length ratio of UFRJ DG 558-R is 1.4, consistent with a median tail position, compared to the ratios of 1.2 and 1.3, respectively, of the medial caudal vertebrae of *Aerosteon* and *Orkoraptor* (Novas *et al*., ~~al.,~~ 2008). The Potiguar Basin specimens resemble those of *Aoniraptor* (Fig. 07, F) due to the absence of a keel in the ventral region, but ~~is~~are distinguished by the presence of a pair of pneumatic ~~septal~~ troughs in the lateral region, separated by a septum. Only the first caudal vertebra of *Aoniraptor* presents such fossae, a characteristic present in the other megaraptorans (e.g., Novas *et al*., 2008; Sereno *et al*., 2008).

Comparing the morphology of pneumatic foramina, UFRJ DG 558-R (Figure 10~~07~~, A) is very similar to *Aerosteon* (Figure 10~~07~~, C), *Megaraptor* (Figure ~~07~~10, H) and *Orkoraptor* (Figure 10~~07~~, G) ~~by~~in the presence of a large elliptic foramen and a second smaller circular shaped foramen. In addition, ~~morphotype 6~~ UFRJ-DG 558-R and 634-R has its cavities located on the lateral surface of the vertebral centrum near the base of the neural arch, which does not occur in the other species ~~analyzed~~observed.

UFRJ-DG 558-R and 634-R ~~The morphotype 06 vertebrae~~ also presents extensive pneumatization in the vertebral centrum, composed of a camerate internal microstructure

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(Britt, 1993), with several small chambers, similar to other megaraptorans (e.g., *Aerosteon*, *Megaraptor*; Martinelli *et al.*, 2013).

Discussion

The Açu Formation material and your its importance

The fossil potential of Açu Formation was poorly known, with only a few fossils recovered (Duarte and Santos, 1962; Silva-Santos, 1963; Mussa et al., 1984), until the discovery of vertebrae and teeth identified as belonging to Theropoda indet. and Titanosauria (Santos et al., 2005).

No further work was conducted until 2018, when the materials described here were studied in more detail. Thus far, the dinosaur fauna of the Potiguar Basin includes two groups of Sauropoda (Diplodocoidea: Rebbachisauridae, Pereira et al., in press; Titanosauriformes, Barbosa et al., 2018; Titanosauria, Pereira et al., 2018) and four groups of Theropoda (Spinosauroidea, Carcharodontosauridae, Megaraptora and Maniraptora, present work).The fossil potential of Açu Formation was poorly known, with only a few fossils recovered (Duarte & Santos, 1962; Silva Santos, 1963; Mussa *et al.*, 1984),. until the discovery of vertebrae and teeth identified as belonging to Theropoda indet. and Titanosauria (Santos *et al.*, 2005).

The occurrence of these groups (except Megaraptora) in the Potiguar Basin is yet another similarity between the faunas of northeastern Brazil and multiple North Africa Cretaceous units (e.g. Medeiros and Schultz, 2001a, 2002; Sereno and Brusatte, 2008; Contessi, 2009; Candeiro et al., 2011; Candeiro, 2015). Except for the Elrhaz (Niger); Douiret and Ain El Guettar (both in Tunisia) and Chicla (Libya) formations, which were

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dated to the Early Cretaceous, all other Cretaceous formations from Northern Africa are Albian-Cenomanian in age, roughly equivalent to the Açu Formation (Werner, 1994; Rossetti, 1997; Rossetti and Truckenbrodt, 1997; Smith et al., 2001; Anderson et al., 2007; Sereno and Brusatte, 2008; Cavin et al., 2010). Among the formations, the Alcântara Formation (Brazil), Bahariya Formation (Egypt), Echkar Formation (Niger) and the Waldi Milk Formation (Sudan) have similarities with the Açu Formation's dinosaur fauna.

According to paleobiogeographic models, South America and Africa started separating from each other in the Valanginian (Early Cretaceous), leading to the formation of the South Atlantic Ocean (Viramonte et al., 1999; Jokat et al. 2003; Macdonald et al., 2003). Although the ocean turned into one of the most important continental barriers of the southern hemisphere, faunal interchange among the terrestrial landmasses of western of Gondwana definitely occurred up to the Albian, and possibly until the Cenomanian (e.g. Petri, 1987; Reyment and Dingle, 1987; Pletsch et al., 2001, Tello Saenz et al., 2003, Guedes et al., 2005, Bodin et al., 2010).

Based on the proposed age and geographic position, the fossil vertebrates of the Açu Formation may have lived during some of the last intervals of continental connection between South America and Western Africa, before the complete formation of the South Atlantic Ocean (Arai, 2009; Castro et al., 2012). This makes them exceedingly important for understanding biogeography and faunal evolution.

More extensive comparisons are still limited by the lack of completeness of the Açu material and the absence of formally described taxa. The continuation of studies on previously collected material (like that described in this paper) and prospecting for new fossils is important in this basin which, while still the subject of only recent research, already exhibits among the greatest diversity of dinosaur groups in Brazil.

No further work was conducted until 2018, wherewhen the materials described here began to be describedwere studied in more detail. For nowThus far, the Ddinosaur fauna of the Potiguar Basin has so far includes two groups of Sauropoda (Diplodocoidea: Rebbachisauridae, Pereira *et al.* in press; Titanosauriformes, Barbosa *et al.*, 2018; Titanosauria, Pereira *et al.*, 2018) and four groups of Theropoda (Spinosauroidea, Carcharodontosauridae, Megaraptora and Paraves, present work).

The occurrence of these groups (except Megaraptora) in the Potiguar Basin is oneyet another of the numerous similaritiessimilarity between the faunas of northeastern Brazil and multiple North Africa Cretaceous units (e.g. Medeiros & Schultz, 2001a, 2002; Sereno & Brusatte, 2008; Contessi, 2009; Candeiro *et al.*, 2011; Candeiro, 2015). Except for the Elrhaz (Niger) formations; Douiret and Ain El Guettar (both in Tunisia) and Chicla (Libya) formations, which were dated to belong to the Early Cretaceous, all other Cretaceous formations from Northern Africa are Albian-Cenomanian in age, roughly equivalent to the Açu Formation (Werner, 1994; Rossetti, 1997; Rossetti & Truckenbrodt, 1997; Smith *et al.*, 2001; Anderson *et al.*, 2007; Sereno & Brusatte, 2008; Cavin *et al.*, 2010). Among the formations,, the Alcântara Formation (Brazil), Bahariya Formation (Egypt), Echkar Formation (Niger) and the Waldi Milk Formation (Sudan) may have special attention due thehave similarities with the Açu Formation's dinosaur fauna.

According to paleobiogeographic models, South America and Africa started separating from each other in the Valanginian (Early Cretaceous), leading to the formation of the South Atlantic Ocean (Viramonte *et al.*, 1999; Jokat *et al.* 2003; Macdonald *et al.*, 2003). Although the ocean turned into one of the most important continental barriers of the southern hemisphere, faunal interchange among the terrestrial landmasses of western of Gondwana definitely occurred up to the Albian, and possibly

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until the Cenomanian (e.g. Petri, 1987; Reyment & Dingle, 1987; Pletsch *et al*., 2001, Tello Saenz *et al*., 2003, Guedes *et al*., 2005, Bodin *et al*., 2010).

Based on the proposed age and geographic position, the fossil vertebrates of the Açu Formation may have lived during some of the last momentsintervals of continental connection between South America and Western Africa, before the complete formation of the South Atlantic Ocean (Arai, 2009; Castro *et al*., 2012). This makes them exceedingly important for understanding biogeography and faunal evolution.

More extensive comparisons are still limited by the lack of completeness of the Açu material and the absence of formally described taxa. The continuation of the studies on the alreadypreviously collected material (like that described in this paper) and the prospecting offor new fossils is important in this basin which, while the research still the subject of only recent research, it is already a formation that shows one ofexhibits among the greatest diversity of dinosaur groups in Brazil.

The first described megaraptoran was *Megaraptor namunhuaiquii* from the Turonian of Patagonia/Argentina (Novas, 1998). Recently, new findings have increased our knowledge about the anatomy and taxonomic diversity of these animals (Calvo et al., 2004; Novas et al., 2008; Hocknull et al., 2009; Novas, 2009).

In 2010, Benson et al. created the name Megaraptora for a newly recognized clade of theropods including taxa found in Argentina (*Aerosteon*,*Megaraptor*,*Aoniraptor* and *Orkoraptor*), Australia (*Australovenator*) and Japan (*Fukuiraptor*). One of the most striking features of the group is the presence of pneumatic anterior caudal vertebrae (Calvo et al., 2004).

Pneumaticity in the caudal vertebrae is rare in Theropoda, present only in some groups: Megaraptora, Oviraptorosauria, Therizinosauria and Carcharodontosauridae (Benson et

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~~al., 2011). As far as is known, no fossils of therizinosaurs have been found in South America and South American fossils attributed to oviraptorosaurs have been reassigned to other taxa (see Agnolín& Martinelli, 2007). In addition, the caudal vertebrae of Oviraptorosauria have, on the ventral surface, a medial groove delimited by two longitudinal elevations (e.g., Sues, 1997; Xu et al., 2007). Specimen UFRJ-DG 558-R does not have this feature.~~

~~South American carcharodontosaurids (e.g., *Giganotosaurus*,*Mapusaurus*, *Tyrannotitan*) showavery deeplyconcave lateral sides in the caudal vertebrae, but not apneumatic foramen. Stromer (1931) described an anterior caudal vertebra from northern Africa, which he identified as *Carcharodontosaurus*, which had pneumatic characteristics, including a pleurocoel. However, that vertebra has a different general morphology and proportions when compared with morphotype 6 from the Portiguar Basin (length-height ratio is 1 in *Carcharodontosaurus* and approximately 1.48 in UFRJ-DG 558-R) and other members of Megaraptora.~~

~~In Brazil, there are only two previous records (Fig. 06) attributed to Megaraptora, both in the Bauru Group. Méndez et al. (2012) described an isolated caudal vertebral centrum (MPMA 08-003-94), found in the municipality of Ibirá, São Paulo (Maastrichtian, Late Cretaceous). The authors compared their specimen with the megaraptorids *Aerosteon* and *Megaraptor*, and found important differences, such as the absence of a median longitudinal keel on the ventral surface and its more elongated proportions. Martinelli et al. (2013) described another isolated caudal vertebra found in Uberaba (Campanian, Late Cretaceous) as belonging to Megaraptora.~~

~~In a recent work, Motta et al. (2016) considered that both specimens are in fact sacral vertebrae, due to their more elongated proportions, rough articular face and anteroposteriorly expanded transverse processes. Due to this fact, a comparison with the~~

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material analyzed here becomes difficult, and the Potiguar vertebrae areis thus the first caudal vertebrae of megaraptorans from Brazil.

Figure 06: BrazilianMegaraptoran Vertebrae findings. A and B, UFRJ DG 558-R; C and D, MPMA 08-003-94 (Méndez et al., 2012); E and F, CPPLIP 1324 (Martinelli et al., 2013). A, C e E, lateral view; B, D e F, ventral view. Pfr, Pneumatic foramen. Scale bar = 1cm.

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Among the Megaraptora group, only *Aerosteon*, *Aoniraptor*, *Orkoraptor* and *Megaraptor* have preserved caudal vertebrae (Figure 07) (Sereno et al., 2008; Benson et al., 2010; Motta et al., 2016).

The height/length ratio of UFRJ DG 558-R is 1.4, consistent with a median tail position, compared to the ratios of 1.2 and 1.3, respectively, of the medial caudal vertebrae of *Aerosteon* and *Orkoraptor* (Novas et al. al., 2008). The Potiguar Basin specimens resemble those of *Aoniraptor* (Fig. 07, F) due to the absence of a keel in the ventral region, but is distinguished by the presence of a pair of pneumatic septal troughs in the lateral region, separated by a septum. Only the first caudal vertebra of *Aoniraptor* presents such fossae, a characteristic present in the other megaraptorans (e.g., Novas et al., 2008; Sereno et al., 2008).

Comparing the morphology of pneumatic foramina, UFRJ DG 558-R (Figure 07, A) is very similar to *Aerosteon* (Figure 07, C), *Megaraptor* (Figure 07, H) and *Orkoraptor* (Figure 07, G) by the presence of a large elliptic foramen and a second smaller circular shaped foramen. In addition, morphotype 6 has its cavities located on the lateral surface of the vertebral centrum near the base of the neural arch, which does not occur in the other species analyzed.

Figure 07: Megaraptorancaudals vertebras. A and B, UFRJ DG 558 R; C and D, *Aerosteonm*; E and F, *Aoniraptor*; G, *Orkoraptor*. H, *Megaraptor*. A, C, E, G e H, lateral view; B, D e F, ventral view. Pfr, pneumatic foramen. Scale bar = 5cm.

The morphotype 06 vertebrae also presents extensive pneumatization in the vertebral centrum, composed of a camerate internal microstructure (Britt, 1993), with several small chambers, similar to other megaraptorans (e.g., *Aerosteon*, *Megaraptor*; Martinelli et al., 2013). Based on the general morphology, the elements described herein possibly belong to a form closer to *Aerosteon* and *Megaraptor* than to *Aoniraptor*.

The Potiguar material is also one of the oldest records of the group in South America, together with *Aoniraptor* from the Early Cenomanian-mid-Turonian of Argentina (Motta et al., 2016).

The abelisauroid fossil record from Brazil is known from fragmentary specimens. Recently, Silva (2013) and Santucci et al. (2018) described incomplete abelisaurid cranial and postcranial Abelisauria remains from Barremian–Aptian age of Quiricó Formation (São Francisco Basin) of northern Minas Gerais state.

Brazillian noasaurids were known only by teethfrom Albian-Cenomanian of Alcântra Formation, where *Masiakasaurus*-like teeth were recorded. Howevber this changed when *Vespersaurus paranaensis*, a desert-dwelling monodactyl noasaurid, was described in the Late Cretaceous Rio Paraná Formation (Langer et al, 2019).From Albian-Cenomanian of Alcântara formation bed have produced one tooth reported as *Masiakasaurus*-like (Noasauridae) by Lindoso et al. (2012).

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Thefirst abelisaurid speecies discovered in Brazil was*Pycnonemosaurus.nevesi*wasthe first and unique specie of abelisaurid from Brazil (Kellner & Campos, 2002). Itwas described based on postcranial remains from the Upper Cretaceous of the RibeirãoBoiadeiro Group and represents the most complete collection known to Brazil. Additionally, Bittencourt and Kellner (2002) described nine Abelisauria teeth from the same locality of *Pcycnonemosaurus*. The second abelisaurid descovered in Brazil was *Thanos simonattoi* (Delcourt & Iori, 2018), whose description was based on an almost complete axis with an axial intercentrum.

The first record of Abelisauridae known to Brazil was reported by Bertini (1996) and was discovered in the Adamantina Formation, western São Paulo State. Later, other authors reported isolated teeth from the Adamantina Formation from western São Paulo state (e.g., Candeiro et al., 2004; Azevedo et al., 2007) and from Minas Gerais state (e.g., Candeiro et al., 2006; Oliveira et al., 2012). Also, there are some known postcranial records from the São José do Rio Preto and Marília formations (Méndez et al., 2014) were recently described by Méndez et al (2014) as well as other abelisaurid materials from the Adamantina Formation, São Paulo State (a partial femur, Brum et al., 2016).

However, the most abundant materials of abelisaurid are from the Marília Formation that outcrops in the region of Peirópolis, municipality of Uberaba. Innumerous teeth (Candeiro et al. 2012) and postcranial materials (Novas et al. 2008, Machado et al. 2013) from this locality were already described.

Even though most of the abelisaurid axial characteristics are mainly in their uniquely shaped transverse processes in the caudal vertebrae (e.g. Méndez, 2014), there are some characteristics that can be seen in their caudal centra.

The mid-caudal vertebrae of Abelisauria have, as basic characteristics, an amphilcoelous condition with subcircular articular facets, a centrum twice as long as tall, well-marked

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facets, and a ventral concavity in its lateral view as seen in *Majungasaurus*, *Aucasaurus*, and *Ilokelesia* (Coria & Salgado, 1998), however much these features are also seen in Abelisauroidea and even in basal ceratosaurs (Méndez, 2014). All these characteristics can be observed in the specimens of morphotype 2,with specimen 547-R standing out from the others for the presence of two small depressions on its lateral surface, a characteristic not very common within the group.

The anterior caudal vertebrae of Abelisauria present a set of striking features that can be observed in specimens of morphotype 3 (Fig. 08). First is its oval, taller than wide, facet that both the 528-R specimen and the 532 -R have.In addition, there are features found in the centrumer of specimen 528-R, such as the slight centrum? central?er constriction (Méndez, 2014) and a concave anterior margin while the posterior convex margin is seen in the first four caudal vertebrae of *Aucasaurus*, *Carnotaurus*, *Majungasaurus*, *Ekrixinatosaurus*, *Rajasaurus* and *Rahiolisaurus* (Bonaparte, 1985; Sampson et al. 1998; Coria et al. 2002). Unlike *Aucasaurus*, *Carnotaurus* and *Ekrixinatosaurus*, specimen 528-R also does not exhibit any forms of depression or pneumaticity on its lateral surface. These are the oldest record of Abelisauria at Brazil.

Figure 08: Comparison of morphotype 02 and other abelisaurids. A and B, *Majungasaurus*; C and D, *Carnotaurus*; E and F, *Ekrixinatosaurus*; G and H, *Aucasaurus*; I and J, morphotype 02. Scale bar: 5 cm.

The record of maniraptorans is rare in Brazil (see Delcourt& Grillo, 2014). It is based mostly on isolated teeth from several localities and postcranial elements, namely, a manual ungual and scapula from the Serra da Galga Member of Peirópolis, Uberaba,

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Commented [77]: None of the characters mentioned are exclusive of Ceratosauria, but they are present in other theropods. Moreover, the specimens described and figured for this morphotype are anterior caudals, not middle.

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Minas Gerais state (Marília Formation, Maastrichtian), and an unenlagiuid dorsal vertebra and fragmentary remains of an undetermined maniraptoran from the Adamantina Formation (Late Cretaceous) of São Paulo state (Novas et al., 2005; Machado et al., 2008; Candeiro et al., 2012; Delcourt& Grillo, 2014). The material here described is the first post-cranial remain of a maniraptoran outside Bauru Basin and from the mid-Cretaceous, shedding new light on the biogeography of this group in South America and western Gondwana.

Specimen 521-R has characteristics of a vertebral centrum positioned after the transition point, being longer than high possessing a large reduction in both its neural spine and transverse processes (Senter et al., 2011). This way it is possible to deduce that it is at least after the vertebra 11 of the caudal series as seen in *Buitreraptor*, *Rahonavis*, Dromaeosauridae and Troodontidae (Ostrom, 1969; Forster et al., 1998; Senter et al., 2012; Xu et al., 2017).

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The maintenance of the transverse processes is not observed in more basal groups of Paraves like dromaeosaurids and troodontids that have smooth lateral surfaces in their centra (Ostrom, 1969; Norell&Malkovicky, 1999; Currie & Dong, 2001; Xu et al., 2012), but is seen in specimens of *Microraptora*,*Rahonavis*,*Builtreraptor*,*Anchiornis* and *Archaeopterix*(Hwang et al., 2002; Hu et al., 2009; Han et al., 2014; Novas et al., 2017), all belonging to the group Averaptora. In addition, the 521-R specimen also presents the prezygapophyses more dorsally positioned in the same way as in *Buitreraptor*, *Rahonavis* and *Anchiornis* (fig. 09) (Motta et al., 2018). The vertebral centrum has a ratio between its height and its length somewhat greater than six which is seen in almost all the groups of Paraves except for Dromaeosauridae that displays a smaller ratio being the only 3 times longer than high.

Figure 09: Comparison of Morphotype 3 and other paravians. A, Potiguar's material; B, *Rahonavis*; C,*Buitreraptor*; D, *Anchiornis*. Pr, prezygapophysise; lg, Longitudinal groove. Modified from Motta et al., (2018).

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Carcharodontosaurid were amongst the largest and some of the most widespread theropods during the Kimmeridgian-Turonian (Candeiro, 2015; Delcourt& Grillo, 2017). In Brazil, carcharodontosaurids were recorded based on isolated teeth and putative remains from São Luís-Grajaú Basin (Cenomanian) and Bauru Group (Late Cretaceous) (Vilas-Bôas et al., 1999; Medeiros, 2001; Azevedo et al., 2013). The Potiguar Basin materials lie within the age range of occurrence of carcharodontosaurids and, might be related to the São Luís-Grajaú and western Africa fauna where these are common findings.

Both vertebrae of morphotype 4 present characteristics commonly found in carcharodontosaurids (Fig. 10). For instance, depressions in the most dorsal part of their lateral surface are is found in *Giganotosaurus*, *Mapusaurus* and *Tyrannotitan* and in the mid-caudal vertebrae Vb-870 found in the Wadi Milk Formation (Coria & Salgado, 1995; Coria & Currie, 2006; Novas et al., 2005; Canale et al., 2015; Rauhut, 1999), which is different from *Carcharodontosaurus*, which has pleurocoels in their anterior caudal vertebrae (Stromer, 1931). Furthermore, the strongly waisted centrum morphology, a double keel cut by a longitudinal groove and offset articular facets (although it is a plesiomorphic feature found in *Allosaurus* Gilmore, 1920; Madsen, 1976) are also found in specimens such as the carcharodontosaurid material from Sudan (Vb-870) and in *Tyrannotitan*, *Mapusaurus* and *Acrocanthosaurus* (Canale et al., 2015; Harris, 1998; Coria & Currie, 2006; Currie & Carpenter, 2000).

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Figure 10: Comparison of Morphotype 4 and Carcharodontosauriaindet. A and B, UFRJ DG 523-R; C and D, UFRJ DG 524-R; E and F, Kem Kem beds material (from Rauhut, 1999). G? H? I?. Scale bar = 5 cm.

The record of maniraptorans is rare in Brazil (see Delcourt& Grillo, 2014). It is based mostly on isolated teeth from several localities and postcranial elements, namely, a manual ungual and scapula from the Serra da Galga Member of Peirópolis, Uberaba, Minas Gerais state (Marília Formation, Maastrichtian), and an unenlagiuid dorsal vertebra and fragmentary remains of an undetermined maniraptoran from the Adamantina Formation (Late Cretaceous) of São Paulo state (Novas et al., 2005; Machado et al., 2008; Candeiro et al., 2012; Delcourt& Grillo, 2014). The material here described is the first post-cranial remain of a maniraptoran outside Bauru Basin and from the mid-Cretaceous, shedding new light on the biogeography of this group in South America and western Gondwana.

Specimen 521-R has characteristics of a vertebral centrum positioned after the transition point, being longer than high possessing a large reduction in both its neural spine and transverse processes (Senter et al., 2011). This way it is possible to deduce that it is at least after the vertebra 11 of the caudal series as seen in *Buitreraptor*, *Rahonavis*, Dromaeosauridae and Troodontidae (Ostrom, 1969; Forster et al., 1998; Senter et al., 2012; Xu et al., 2017).

The maintenance of the transverse processes is not observed in more basal groups of Paraves like dromaeosaurids and troodontids that have smooth lateral surfaces in their centra (Ostrom, 1969; Norell&Malkovicky, 1999; Currie & Dong, 2001; Xu et al., 2012), but is seen in specimens of *Microraptora*,*Rahonavis*,*Builtreraptor*,*Anchiornis* and *Archaeopterix* (Hwang et al., 2002; Hu et al., 2009; Han et al., 2014; Novas et al., 2017),

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all belonging to the group Averaptora. In addition, the 521-R specimen also presents the prezygapophyses more dorsally positioned in the same way as in *Buitreraptor*, *Rahonavis* and *Anchiornis*(fig. 10) (Motta et al., 2018). The vertebral centrum has a ratio between its height and its length somewhat greater than six which is seen in almost all the groups of Paraves except for Dromaeosauridae that displays a smaller ratio being the only 3 times longer than high.

The spinosaurid record of Brazil is known by two species: *Oxalaia quilombensis* (CITE) and *Irritator challengeri* (CITE), both spinosaurines from the "mid" Cretaceous strata from the Cenomanian Alcantra Formation and fromthe Aptian-Albian Santana Formation respectively. Other than those two species, there are many unidentified isolated spinosaurid post cranial elements and teeth that range from Berriasian–Valanginian Feliz Deserto Formation (CITE) to the "mid" Cretaceous Santana and Alcantra Formations (CITE).

There is no discussion about the recovered tooth, and the traits that allow assigning it to Spinosauridae.

Conclusion REVISARRRRR

In the present work we assigned the material from Açu Formation, Potiguar Basin, to four groups: Spinosauroidea, Carcharodontosauria, Maniraptora and Megaraptora (Fig. 11), the two last groups being relatively rare in Brazil. All this groups have already been found in isochronous formations in both Northeastern Brazil and Northern Africa, leading further support for faunal similarities in the “mid”-Cretaceous western Gondwana. These fossils provide the first theropod record from Potiguar Basin and an important opportunity to increase the knowledge on the diversity of this still poorly known basin.We describe

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several newly discovered dinosaur fossils, which constitute A a new dinosaur fauna was discovered and described from the Açu Formation (Potiguar Bbasin), Northeast region of Brazil. The vertebrae were are classified into five morphotypes based on morphological form and/or diagnostic characters and comprised at this moment bycan be assigned to five four groups: Abelisauria, Carcharodontosauria, Spinosauridae, Megaraptora, and Maniraptora. While the teeth was recovered as a SpinosauridFurthermore, a single tooth is attributed to Spinosauridae Besides tThese groups werehave already been found on in isochronous basins of the Northeast region of Brazil and Africa, lending further support for faunal similarities between these regions.

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the presence of these theropod groups at Açu FormationThe new fossils reveals an unexpected dinosaur richness fauna at from the Potiguar Basin (fig. 11) and opens up anprovide an important opportunity to increase the knowledge about on the diversity and palaeobiogeography of this important vertebrate groupthese animals during a time of Gondwanan fragmentation.

Figure 11: Reconstruction of the theropods groupsdescribed in this present study to the Açu Formation, Potiguar Basin. In the water, a Spinosauridae. On the ground, on the left an Abelisauridae; in the center, a group of megaraptoransMegaraptora and a slaughtered atitanosaurTitanosauriasauropod while to the right, a Carcharodontosauridae awakens from its sleep; in the top center, a Paraves just watches. Drawing of Luciano da Silva Vidal.

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Figure captions

Figure 01: Geological map of the continental part of the Potiguar Basin with the region near the Limoeiro do Norte municipality (Ceará state) where the material were discovered (dark star). CE, Ceará state; RN, Rio Grande do Norte state and its capital, Natal. Modified from Cassab (2003).

Figure 02: The avirostrantheropod vertebrae UFRJ-DG 52875-R (A-CB) and UFRJ-DG 57528-R (DC-E). UFRJ-DG 575-R: A, lateral view; B, the anterior articular facet. UFRJ-DG 528-R: C, the lateral view; D, the ventral view; E, anterior articular facet. Note the large pneumatic foramen on the side of the anterior fragment of UFRJ-DG 575-R. pfr = pneumatic foramen. Scale bar: 2 cm.

Figure 03: Spinosauroid tooth (UFRJ-DG 619-R): A, the labial view; B, the lingual view; and C, the cross section. Scale: 1 cm

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Figure 04: Maniraptoran caudal vertebrae (UFRJ-DG 521-R): A, Lateral view; B, ventral view; C, anterior articular facet. Prz, prezygophysis; Nc, neural canal. Scale: 1cm.

Figure 05: Comparison of UFRJ-DG 521-R and other maniraptorans. A, Potiguar's material; B, *Rahonavis*; C, *Buitreraptor*; D, *Anchiornis*. Pr, prezygapophysis; lg, Longitudinal groove. Modified from Motta et al., (2018).

Figure 06: Carcharodontosaurid caudal vertebrae UFRJ-DG 523~~4~~ (A-C) and UFRJ-DG 524~~3~~-R (D-F). UFRJ-DG 524-R: A, ventral view; B, lateral view; C, anterior articular facet. UFRJ-DG 523-R: D, ventral view; E, lateral view; F, anterior articular facet. Nc, neural canal. Scale: 1cm.

Figure 07: Comparison of UFRJ-DG 523-R and 524-R and other carcharodontosaurids. A and B, UFRJ DG 523-R; C and D, UFRJ DG 524-R; E and F, Kem Kem beds material (from Rauhut, 1999); G, *Tyrannotitan chubutensis* MPEF-PV 1156 (Modified from Canale et al., 2015); H, *Mapusaurus roseae* MCF-PVPH-108.81 (Modified from Coria ~~&~~and Currie, 2006) ; I, *Acrocanthosaurus atokensis* NCSM 14345 (Modified from Currie ~~&~~and Carpenter, 2000). Scale bar = 5 cm.

Figure 08: Caudal vertebrae UFRJ-DG. UFRJ-DG 558-R~~-634-R~~: A, posterior articular facet; B, lateral view; C, ventral view. UFRJ-DG 634-R~~558-R~~: D, anterior articular facet; E, lateral view; F, ventral view. Pfr, Pneumatic foramen. Scale bar: 1cm.

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Figure 09: Brazilian megaraptoran vertebrae findings. A and B, UFRJ DG 558-R; C and D, MPMA 08-003-94 (Méndez et al., 2012); E and F, CPPLIP 1324 (Martinelli et al., 2013).A, C e E, lateral view; B, D e F, ventral view. Pfr, Pneumatic foramen. Scale bar = 1cm.

Figure 10: Megaraptoran caudals vertebrae. A and B, UFRJ DG 558-R; C and D, *Aerosteon*; E and F, *Aoniraptor*; G, *Orkoraptor*. H, *Megaraptor*. A, C, E, G e H, lateral view; B, D e F, ventral view. Pfr, pneumatic foramen. Scale bar = 5cm.

Figure 11: Reconstruction of the theropods groups from Açu Formation, Potiguar Basin. In the center, a group of megaraptorans slaughtering a titanosaur; on the right a carcharodontosaurid awakens from its sleep; in the top center, a maniraptoran just watches. ~~Drawing~~Art by Luciano da Silva Vidal.

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Figure 05: Carcharodontosaurid caudal vertebrae UFRJ-DG 524 (A-C) and UFRJ-DG 523-R (D-F). UFRJ-DG 524-R: A, ventral view; B, lateral view; C, anterior articular facet. UFRJ-DG 523-R: D, ventral view; E, lateral view; F, anterior articular facet. Nc, neural canal. Scale: 1cm.

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