



PALEONTOLOGY

The first Jurassic theropod from the Sergi Formation, Jatobá Basin, Brazil

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Abstract: Archosaur osteological remains are abundant in Brazil, particularly from the Triassic and Cretaceous strata, but in Jurassic, the record is predominantly represented by ichnofossils. The Upper Jurassic archosaur records comprise the Paralligatoridae *Batrachomimus pastosbonensis*, from the Pastos Bons Formation (Parnaíba Basin), remains of Mesoeucrocodylia from the Aliança Formation (Jatobá Basin), and fragments of Dinosauria from the Brejo Santo Formation (Araripe Basin) with a dubious assignment. Here, we present the first undoubted Dinosauria record for the Jurassic of Brazil, MCT 2670-LE, a middle to distal caudal vertebra belonging to a theropod. MCT 2670-LE was excavated in the 60s by prof. Ignacio Machado Brito, being primarily attributed to strata of the Aliança Formation but the rock matrix involving the specimen allows us to correlate MCT 2670-LE to Sergi Formation, marking this specimen as the first archosaur record of this unit. The caudal vertebra is assigned to Carcharodontosauria based on the hourglass shaped centrum and the deep and narrow ventral groove. The specimen provides new data to the paleogeographic distribution of carcharodontosaurians before the South America-Africa break-up, as well as understanding the theropod faunal turnover of paleoenvironments during the Jurassic-Cretaceous transition in Brazil.

Key words: Theropoda, Carcharodontosauria, Caudal Vertebra, Upper Jurassic, Sergi Formation, Jatobá Basin.

INTRODUCTION

In Brazil, archosaur remains are well-known, especially those dating from the Mesozoic Era, and the Triassic and Cretaceous deposits are the main fossiliferous ones (Bittencourt & Langer 2011). The Cretaceous represents the most expressive interval with abundant vertebrate fossil record (Bittencourt & Langer 2011, Brusatte et al. 2017), both on the Lower (e.g. Pereira et al. 2020a, b) and Upper levels (e.g., Pinheiro et al. 2018, Bandeira et al. 2019, Delcourt et al. 2020). Archosaurs are the predominant fossil records especially on the Upper Cretaceous strata (Bandeira et al. 2018). However, rock exposures from the Brazilian Jurassic are scarce (Bittencourt

& Langer 2011), due to the sedimentation and tectonic conditions unfavorable to the preservation of bone elements (e.g., Milani 2007).

This scenario makes challenging the study and the consequent interpretations of Jurassic fossil data on Brazil (e.g., Gallo & Brito 2004, Gallo 2005, Bittencourt & Langer 2011). Thus, the Jurassic record for Brazil is best represented by the ichnofossils (e.g., Leonardi et al. 2007, but see Table I), while the Araripe Basin (Brejo Santo Formation and Missão Velha Formation), the Parnaíba Basin (Pastos Bons Formation) and the Jatobá Basin (Aliança Formation), all from Upper Jurassic, are the only units with tetrapod bone elements - mostly, archosaurs. The Paralligatoridae *Batrachomimus pastosbonensis*

Montefeltro et al. 2013, from the Pastos Bons Formation, is the only archosaur species described so far for the Brazilian Jurassic (Montefeltro et al. 2013).

Other records consist of small axial elements (about 3-4 cm) found in the Brejo Santo Formation (Melo & Carvalho 2017), along with Mesoeucrocodylia teeth. These axial elements (which do not have a collection number) were proposed as the first Dinosauria record for the Brazilian Jurassic (Melo & Carvalho 2017). However, the authors provided no diagnostic feature for this classification, and the description of these elements is superficial. The specimen images also depict just a ventral view of the material, and more detailed comparisons become impossible. Due to the difficulty of knowing the origin in which institution these specimens are allocated, as well as unclear diagnostic characteristics that allow a more accurate systematic assignment, we assume here that the attribution to Dinosauria of these specimens is doubtful. The Missão Velha Formation has a rich fossil assemblage, including anurans, lizards, turtles, mesoeucrocodylians and even nonavian dinosaurs (*sensu* Brito et al. 1994), but most elements require a formal description and systematic review.

Finally, for the Upper Jurassic of Aliança Formation, there is a brief report of some Mesoeucrocodylia remains (Silva et al. 2011) which are more recently reviewed and described together with new mesoeucrocodylian findings (Carvalho et al. 2021). Thus, we present the first confirmed Dinosauria record for the Jurassic of Brazil, MCT 2670-LE, collected in 1962 by prof. Ignacio Machado Brito at São Francisco riverbank (see Geological Settings). MCT

2670-LE is identified as a middle caudal vertebra of a carcharodontosaurian theropod. The new specimen improves the understanding of the rare archosaur remains from the Jurassic period in Brazil. It is also possible to link MCT 2670-LE to theropods of other basins with Jurassic outcrops, allowing an evaluation of the paleogeographic distribution of tetrapods recognized in these formations, as well as the evolutionary and faunal changes of paleoenvironments during the Jurassic-Cretaceous transition in Brazil.

HISTORICAL REMARKS

We describe a new fossil material collected close to the municipality of Petrolândia (Pernambuco) in 1962 by Prof. Dr Ignacio Machado Brito. In the notes associated with the specimen, Brito mentioned that it was recovered in the margins of the São Francisco River upstream the Petrolândia municipality.

This contribution is a tribute to Diogenes de Almeida Campos, the paleontologist of the Museu de Ciências da Terra (Serviço Geológico do Brasil – CPRM), who had prof. Ignacio as advisor and paleontology undergraduate professor. Ignacio led Diogenes to his first collecting fossils fieldwork at this same region. Besides this, Diogenes made a prospect in the area in the 1980s aiming for the rescue of paleontological material prior to the construction of the Luis Gonzaga hydroelectric plan. Therefore, the material here described connects Diogenes with his past advisor and to a region on which he had important historical action.

Table I. Jurassic sedimentary basins in Brazil, and their respective fossil contents, (when found). Abbreviations: Fm, Formation, Mb, Member.

geological unit	lithology and depositional context	distribution	fossil record	age	references
Parecis Basin					
Fm. Anari	fine-grained to aphanitic basalts, with subordinate coarsed diabase bodies. Volcanic flows	southeast of Rondônia (RO) to the Northwest of Mato Grosso (MT) state	no fossils related	Lower Jurassic - Hettangian	Schobbenhaus et al. 1984, Marzoli et al. 1999, Silva et al. 2003. Pedreira & Bahia 2004
Fm Tapirapuã	similar to basalts from Anari Formation, with columnar disjunction and spheroidal exfoliation	comprises the Tapirapuã massif in Mato Grosso (MT) state	no fossils related	Lower Jurassic - Hettangian	Schobbenhaus et al. 1984, Marzoli et al. 1999, Silva et al. 2003. Pedreira & Bahia 2004
Fm Rio Ávila	reddish, friable and eolic sandstones with rounded grains, well to poorly selected	Outcrops in north of General Carneiro, in the valley of the Culuene river and northwest of Vilhena, Mato Grosso (MT) state	no macrofossils related	Jurassic	Silva et al. 2003, Bahia, 2007
Fm. Botucatu	large scale cross-bedded bimodal sandstones. Aeolian dunes	Outcrops in West of Rondônia (RO) and small exposures in southeast of Mato Grosso (MT)	no macrofossils or ichnofossils related	Jurassic	Pedreira & Bahia 2000, 2004
Parnaíba Basin					
Fm Mosquito	tholeiitic flood basalts, interbedded with sandstones	around the municipality of Fortaleza dos Nogueiras, Maranhão (MA) state	no macrofossils related	Lower–Middle Jurassic	Schobbenhaus et al. 1984, Bellieni et al. 1992, Santos & Carvalho 2004
Alparcata Basin					
Fm Pastos Bons	for the base, sequences of siltstone, dark shale, and greenish and brownish mudstones. The upper strata consist of gray to green shales with wavy lamination	occurs as a south-central belt in Maranhão (MA) state, with some exposure in west of Piauí (PI)	ostracods; conchostracans; palynomorphs; plant cuticles; fishes (<i>Lepidotus piauihyensis</i> , probable <i>Semionotus</i> and pleuropholids); Crocodyliformes (i.e., <i>Batrachomimus pastosbonensis</i>);	Upper Jurassic - Oxfordian–Kimmeridgian	Schobbenhaus et al. 1984, Gallo, 2005, Montefeltro et al. 2013

Table I. Continuation

Paraná Basin					
Fm Botucatu	mostly composed of fine-to medium-grained quartz sandstones. Friable, rounded and with large-scale cross-bedding related to a wide eolian dunes field. Sand sea of large eolian dunes	widespread occurrence in the Paraná Basin, which cover great áreas of São Paulo (SP), Paraná (PR), Santa Catarina (SC), Rio Grande do Sul (RS), Mato Grosso (MT) and Mato Grosso do Sul (MS) states, with some portions in Goiás (GO) and Minas Gerais (MG) states	abundant ichnofossils: as footprints and tracks produced by invertebrates (arachnids and insects) and tetrapods (small to medium dinosaurs [<i>i.e.</i> , ceratosaurid theropods, ornithopods?] and mammals [<i>e.g.</i> , <i>Brasilichnium elusivum</i>]), also urolites attributed to dinosaurs.	Upper Jurassic - Lower Cretaceous	Schobbenhaus et al. 1984, Scherer, 2000, Fernandes et al. 2004, Scherer & Lavina 2006, Leonardi et al. 2007
Fm Guará	composed of fine-to coarse-grained sandstones and rare mudstones of fluvial and eolian depositional systems	south region of Rio Grande do Sul state (RS)	ichnoassemblage formed by theropod, ornithopod and sauropod tracks	Upper Jurassic-Kimmeridgian-Tithonian	Scherer & Lavina 2005, 2006, Francischini et al. 2017
Almada Basin					
Fm Sergi	fluvial and eolic deposits. Mostly composed by sandstones, but with conglomerates in a fining upward granulometry	south-central coast of Bahia state (BA)	no macrofossils related	Upper Jurassic (Tithonian, Dom Joao local age)	Scherer et al. 2007, Bongiolo & Scherer 2010, Adegas et al. 2012
Camamu Basin					
Fm Sergi	similar as above	central coast of Bahia state (BA)	no macrofossils related	Upper Jurassic (Tithonian, Dom Joao local age)	Ferreira et al. 2009, Kuchle et al. 2011,
Recôncavo Basin					
Fm Sergi	similar as above	central-eastern of the State of Bahia (BA)	ostracods (<i>e.g.</i> , <i>Bisulcoypris pricei</i>); silicified wood attributed to coniferous <i>Dadoxylon benderi</i>	Upper Jurassic (Tithonian, Dom Joao local age)	Pedreira, 2000, Kuchle et al. 2011, Guzmán et al. 2015, Vilas Boas et al. 2018

Table I. Continuation

Fm Aliança	formed by Capianga e Boipeba members. A gondwanic pre-rift sequence	central-eastern of the State of Bahia (BA)	permineralized wood reported (from Tucano and Jatobá deposits) ostracods (<i>e.g.</i> , <i>Darwinula</i> , <i>Bisulcocypris pricei</i> , <i>B. uninodosa</i>) conchostracans (<i>e.g.</i> , <i>Cyzicus brauni</i>); fish remains (<i>e.g.</i> , hybodontid sharks, coelachants [<i>e.g.</i> , <i>Mawsonia gigas</i>], <i>Lepidotes</i> and ceratodontid dipnoics); mesoeucrocodylian remains	Upper Jurassic (Tithonian, Dom Joao local age)	Netto & Oliveira, 1985, Ricardi-Branco 2004 Kuchle et al. 2011, Silva et al. 2011, Guzmán et al. 2015, Vilas Boas et al. 2018, Carvalho et al. 2021
Mb Capianga	lacustrine mudstones. A gondwanic pre-rift sequence	central-eastern of the State of Bahia (BA)	no macrofossils related	Upper Jurassic (Tithonian, Dom Joao local age)	Scherer et al. 2007, Kuchle et al. 2011, Vilas Boas et al. 2018
Mb Boipeba	fluvial sandstones, compacted and cemented by quartz, anhydrite and calcite toward the base. A gondwanic pre-rift sequence	central-eastern of the State of Bahia (BA)	no macrofossils related	Upper Jurassic (Tithonian, Dom Joao local age)	Salem et al. 2000, Scherer et al. 2007, Kuchle et al. 2011, Vilas Boas et al. 2018
Tucano Basin					
the same depositional units as observed for Recôncavo Basin	the same lithostratigraphy as observed for Recôncavo Basin units (<i>sup. cit.</i>)	Observations: Subdivided in North-Jatobá-Tucano and South-Central Tucano. Synchronic depositional sequence with Reconcavo and Jatobá units as consequence of Recôncavo-Tucano-Jatobá aborted intracontinental rift			Vita & Cupertino 1988, Milani et al. 2007, Costa et al. 2007a, Kuchle et al. 2011
Jatobá Basin					
except by Boipeba Member, the same depositional units as observed for Recôncavo and Tucano basins	expected by Boipeba Member, the same lithostratigraphy as observed for Recôncavo and Tucano depositional units (<i>sup. cit.</i>)	Observations: Synchronic depositional sequence with Reconcavo and Tucano units as consequence of Recôncavo-Tucano-Jatobá aborted intracontinental rift			Vita & Cupertino 1988, Milani et al. 2007, Costa et al. 2007b, Kuchle et al. 2011
Sergipe Basin					

Table I. Continuation

Fm Serraria	coarse grained, poorly sorted, kaolinitic sandstones of fluvial braided depositions	coastal margin of Sergipe state (SE)	no macrofossils related	Upper Jurassic (Tithonian, Dom Joao local age)	Azambuja Filho 1998, Melton 2008, Borba et al. 2011, Kuchle et al. 2011, Freitas & Silveira 2017, Franco 2018
Fm Bananeiras	lacustrine red shales	coastal margin of Sergipe state (SE)	no macrofossils related	Upper Jurassic (Tithonian, Dom Joao local age)	Azambuja Filho, 1998, Melton 2008, Borba et al. 2011, Kuchle et al. 2011, Freitas & Silveira 2017
Alagoas Basin					
Bananeiras and Serraria formations are same depositional units as observed for Sergipe Basin	the same lithostratigraphy as observed for Bananeiras and Serraria sequences (<i>sup. cit.</i>)	coastal margin of Alagoas state (AL)	same as Sergipe Basin		Azambuja Filho, 1998, Melton 2008, Borba et al. 2011, Kuchle et al. 2011, Freitas & Silveira 2017
Fm Candeiro	interbedding of fine to medium-grained sandstones with reddish siltstones and shales	coastal margin of Alagoas state (AL)	no macrofossils related	Upper Jurassic (Tithonian, Dom Joao local age)	Azambuja Filho, 1998, Freitas & Silveira 2017
Araipe Basin					
Fm Missão Velha	consists of quartz sandstones, sometimes feldspar and/or kaolinitic, locally conglomeratic. River plains of interlaced systems characterized by shallow, high-energy channels. A gondwanic pre-rift sequence	south of Ceará state (CE)	abundant silicified wood, attributed to coniferous <i>Dadoxylon benderi</i>	Upper Jurassic (Tithonian? Dom Joao local age)	Assine, 1992, 2007, Fambrini et al. 2009, Kuchle et al. 2011

Table I. Continuation

Fm Brejo Santo	shales and red lamitos from a lacustrine deposition. A gondwanic pre-rift sequence	south of Ceará state (CE)	ichnofossils; continental ostracodes (<i>e.g.</i> , <i>Bisulcopypris pricei</i> , <i>Darwinula oblonga</i> , <i>Theriosynoecum miritiensis</i>); conchostraceans (<i>i.e.</i> , <i>Cyzicus pricei</i>); gastropods; bivalves; fishes (<i>i.e.</i> , <i>Mawsonia gigas</i> , <i>Lepidotes</i> sp.); crocodyliforms teeth and dinosaurians remains	Upper Jurassic (Tithonian? Dom Joao local age)	Assine 1992, 2007, Kuchle et al. 2011, Vieira de Melo & Carvalho 2017
Tacutu basin					
Fm Pirara	consists of halites in the areas central for granite and laterally interdigitated schists and, less frequently, siltstones and carbonates	central-northeast sector of Roraima state (RO). The Tacutu hemigraben deposits extends between Brazil and Guyana	no macrofossils related	Upper Jurassic	Crawford et al. 1984, Eiras & Kinoshita 2006, Vaz et al. 2007
Fm Manari	siltstones, shales and, locally, calcisiltites and dolomites, produced by a lake sedimentary environment	central-northeast sector of Roraima state (RO). The Tacutu hemigraben deposits extends between Brazil and Guyana	no macrofossils related	Upper Jurassic	Crawford et al. 1984, Eiras & Kinoshita 2006, Vaz et al. 2007
Fm Apoteri	massive tholeiitic basalts to amigdaloidals, occasionally interspersed with sandstones at the base of Takutu basin; diabase dikes	central-northeast sector of Roraima state (RO). The Tacutu hemigraben deposits extends between Brazil and Guyana	no macrofossils related	Upper - Jurassic	"BRASIL, Radambrasil Project"1975, Crawford et al. 1984, Schobbenhaus et al. 1984, Eiras & Kinoshita 2006, Milani, et al.2007, Vaz et al. 2007
Mangabeira, Lavras da Mangabeira and Iborepi					

Table I. Continuation

Fms Serrote do Limoeiro and Iborepi	fluvial depositions, generally formed by conglomeratic layers to the base, with fining upward red sandstones with interbedded pelites to the top	three small basins (63km ² total area) for the south of Ceará state (CE)	rhizolites and ichnofossils related to invertebrates (<i>e.g.</i> , <i>Skolithos</i> sp.); conchostraceans (<i>i.e.</i> , " <i>Pseudestheria pricei</i> "); and fragments of other invertebrates (<i>e.g.</i> , <i>Anodontites</i>), plants, and vertebrates (indet.)	Lower Jurassic (Iborepi and Serrote do Limoeiro [?] formations) / Upper Jurassic ? (Lavras da Mangabeira)	Carvalho 1993, Carvalho & Fernandes 1993, Rocha et al. 2008 Hessel, 2014
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Geological settings

The Recôncavo-Tucano-Jatobá (or RTJ System, Santos et al. 1990, Costa et al. 2007) is a well-known rift system in Northeastern Brazil (Almeida, 1967, Magnavita & Cupertino 1988, Guzmán et al. 2015). The RTJ System is part of the Borborema Province (Almeida et al. 1977) which strata records the intracontinental evolution of the Gondwana break up in South America and Africa continents (Guzmán et al. 2015, Guzmán-González et al. 2016). The Jatobá Basin - the northern end of the RTJ System - marks the inflection of the general orientation of the aborted intracontinental rupture in the referred system from NS to N70°E (Magnavita & Cupertino 1988, Magnavita et al. 2012). The Jatobá Basin (Figure 1) has an expressive sedimentary record known since last century (e.g., Derby 1879), where the rift phase is much less pronounced than the other rift Northeastern Basins (Guzmán-González et al. 2016).

The Jatobá Basin is divided into its three major sedimentation phases: syncline (Silurian to Devonian); rift (Upper Jurassic-Lower Cretaceous) and post-rift (Lower Cretaceous; Costa et al. 2007, Guzmán et al. 2015, Guzmán-González et al. 2016). The Brotas Group (Figure 1) represents the rift and post-rift phases and is present in the entire RTJ rift system (Cota et al. 2007, Silva et al. 2011, Guzmán et al. 2015), consisting of the Aliança and Sergi formations.

The Aliança Formation is composed mainly by packages of massive reddish laminated claystone, interbedded with limestone (Leite et al. 2001, Guzmán-González et al. 2016). Normally the claystone packages are also interbedded with sandy limestone or calcareous quartz-arenite with a minor proportion of greenish-grey claystone and thin evaporate layers (Leite et al. 2001, Guzmán-González et al. 2016). The Aliança Formation was dated to the Tithonian based on biostratigraphic zones (Viana et al. 1971, Brito 1987, Magnavita & Cupertino 1988, Silva et al. 2011, Guzmán et al. 2015, Guzmán-González et al. 2016).

Despite more than a century of exploration, few is known about the vertebrate fauna of the Jatobá Basin as a whole. Most of the reports are fish remains (Silva et al. 2011), predominantly coelacanths and *Lepidotes*, dorsal fin spines and isolated teeth from hybodontid sharks, as well as dipnoic dental plates (Silva et al. 2011) and some mesoeucrocodylian remains (Silva et al. 2011, Carvalho et al. 2021). Finally, from the limestone strata came most of the ostracods record (e.g., Guzmán-González et al. 2016).

Nevertheless, little was given about the exact layer where MCT 2670-R was collected, albeit the specimen was previously encased in a massive clast supported conglomerates, fashioned in pebble granules with sub-rounded to rounded clasts, moderately selected. As

said before, the personal annotations of prof. Ignacio Brito pointed out that the specimen came from riverbanks of the São Francisco River, in Petrolândia (Pernambuco state). He set this place as belonging to Aliança Formation (Brito 1987), whose lithological composition is distinct from the rock matrix in the specimen. However, coarse to fine-grained sandstones intercalated with massive clast supported conglomerates, as described above, are typical of other Jurassic strata from Brotas Group: the almost unknown Sergi Formation (Viana et al. 1971, Rocha 2011,

Adegas et al. 2012, Guzmán et al. 2015). It is also known that the contact between the Aliança and the Sergi formations is transitional (Rocha 2011, Guzman et al. 2015), which may have misleading the original geological assignment made by Brito

Finally, the Sergi Formation is interpreted as a braided river system (Rocha 2011, Adegas et al. 2012), in an environment characterized by climatic changes, where extensive forests developed after reworked under more dry conditions (Rocha 2011). The extensive wood

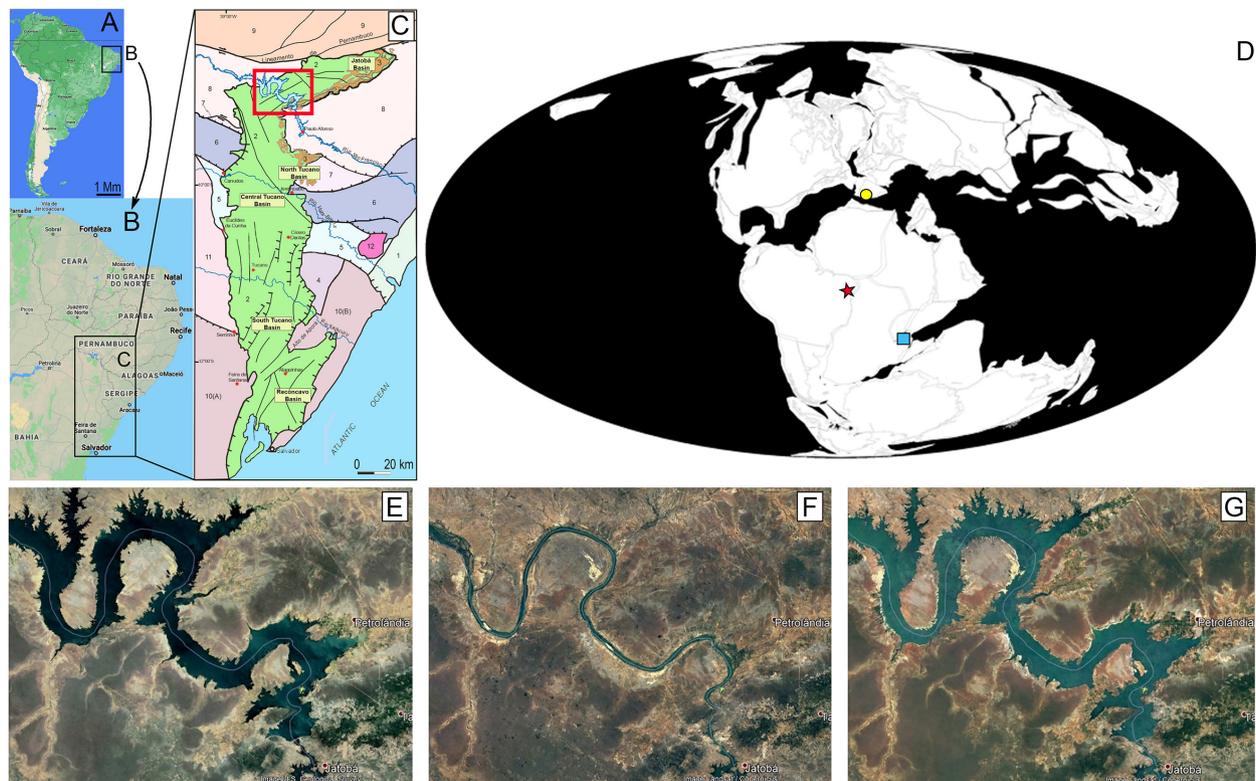


Figure 1. Geological setting. Map of South America (A), close-up of Northeastern Brazil (B), and a close-up of the Tucano-Recôncavo-Jatobá Basins system (C). World map (Tithonian) showing localities of Upper Jurassic carcharodontosaurians (D): MCT 2670-LE (red star), *Veterupristisaurus* (blue square), and *Lusovenator* (yellow circle). Surroundings of Petrolândia (corresponding to the red square in C), showing the São Francisco River dam in function in 1969, possibly where the specimen was collected (see text for discussion) in (E), deactivated in 1984, exhibiting greater area of the Sergi Formation along the river in (F), and activated in 2020, flooding a good part of the fossiliferous areas in (G). (A) and (B) extracted from Google Maps; (C) modified from the CPRM database; (D) modified from Palaeobiology Database; (E-G) extracted from Google Earth. Numbers in (C): 1, Sergipe-Alagoas Basin; 2, Recôncavo-Tucano-Jatobá system; 3, Paleozoic Formations; 4, Estância and Palmares Basins; 5, Sergipana Range (Sub-Domain Vaza-Barris); 6, Sergipana Range (Sub-Domain Macururé); 7, Canindé-Marancó Terrain; 8, Pernambuco-Alagoas Terrain; 9, Alto Pajeú and Alto Moxotó Terrains; 10(A), Salvador-Curaçá Orogen; 10(B) Salvador-Esplanada Belt; 11, Serrinha Block.

fossil record, mainly on Petrolândia (Braun 1966, Silva et al. 2003, Guzmán et al. 2015), also corroborates this scenario. Most of the wood fossil is assigned to gymnosperms, vastly *Dadoxylon benderi* Mussa, 1959 (Mussa & Muniz 1985). The Jurassic age for the Sergi Formation is based on the similar occurrence of *D. benderi* on the Missão Velha Formation (Braun 1966, Mussa & Muniz 1985). The abundant remains of *D. benderi* on strata of Sergi Formation suggests an extensive tree cover in the marginal areas of higher regions of the Brazilian northeast at that time (Freitas et al. 2008). This made MCT2670-LE as the first vertebrate remain collected on the Sergi Formation, expanding our information about the fauna of the Jatobá Basin.

MATERIALS AND METHODS

Material

The specimen MCT 2670-LE comprises a theropod mid caudal vertebra. Our dataset (Supplementary Appendix) was compiled from the literature and comprises 25 abelisaurid (six specimens; Méndez 2014, O'Connor 2007); 10 megalosauroid (five specimens; Benson 2010, Malafaia et al. 2017, Mateus et al. 2011, Rauhut et al. 2016), 18 allosauroid (six specimens; Brusatte et al. 2008, Rauhut 2011, Malafaia et al. 2019, Coria et al. 2020, Pereira et al. 2020b); six megaraptoran caudal vertebrae (five specimens; Martinelli et al. 2013, Méndez et al. 2012, Motta et al. 2016, Pereira et al. 2020b) and one indeterminate theropod material (Pereira et al. 2020b). We focused in large theropod taxa that present some degree of constriction in the mid region of the centrum to observe the distribution of this feature among these groups and if it is possible so distinguish them.

Mechanical Preparation

The specimen MCT 2670-LE was still fixed to the rock matrix since the specimen was collected, which led one of us (PVLCP) to mechanical preparation using specialized pneumatic tools at the preparation lab (DEGEO/UFRJ). Once the matrix was removed, the fragile specimen was treated with a 10% paraloid solution to confer resistance. After this step, the specimen was able to be handled for diagnosis statements.

Institutional abbreviations

BMNH, Natural History Museum, London, UK; **CPPLIP**, Centro de Pesquisas Paleontológicas “Llewellyn Ivor Price”, Uberaba, MG, Brazil; **DGM or MCT**, Museu de Ciências da Terra (ancient Companhia de Pesquisa de Recursos Minerais (CPRM) and now Agência Nacional de Mineração (ANM)), Rio de Janeiro, RJ, Brazil; **MACN-PV-RN**, Museo Argentino de Ciencias Naturales “B. Rivadavia”, Paleontología de Vertebrados, Buenos Aires, Argentina (RN, colección Río Negro); **MB**, Museum für Naturkunde, Berlin, Germany; **MIWG**, Isle of Wight Museum Service, Sandown, UK; **ML**, Museu da Lourinhã, Lourinhã, Portugal; **MLL-Pv**, Museo Municipal de Las Lajas, Las Lajas, Neuquén Province, Argentina; **MPMA**, Museu de Paleontologia de Monte Alto “Prof. Antonio Celso de Arruda Campos”, Monte Alto, SP, Brazil; **SNH**, Sociedade de História Natural, Torres Vedras, Portugal; **UFRJ-DG**, Departamento de Geologia da Universidade Federal do Rio de Janeiro, Rio de Janeiro, RJ, Brazil; **Vb**, Institut für Palaontologie of the Free University, Berlin, Germany.

Anatomical and systematic terms

Following Wilson (2006), we use the “Romerian” anatomical terms and their respective orientations (e.g., “anterior” instead of “cranial”). All measurements of the specimen are provided in Table II. For brevity and clarity, MCT 2670-LE is

mainly compared with theropod taxa: *Aerosteon riocoloradensis* Sereno et al. 2008; *Allosaurus fragilis* Marsh 1877; *Acrocanthosaurus atokensis* Stovall & Langston 1950; *Baryonyx walkeri* Charig & Milner, 1986; *Concavenator corcovatus* Ortega et al. 2010; *Dilophosaurus wetherilli* (Welles 1954); *Giganotosaurus carolinii* Coria & Salgado 1995; *Lajasvenator ascheriae* Coria et al. 2020; *Lusovenator santosi* Malafaia et al. 2020; *Majungasaurus crenatissimus* (Depéret 1896); *Mapusaurus roseae* Coria & Currie 2006; *Megalosaurus bucklandi* Mantell, 1827; *Neovenator salerii* Hutt et al. 1996; *Siamraptor suwati* Chokchaloemwong et al. 2019 and *Veterupristisaurus milneri* Rauhut, 2011. Additional comparisons are made with the following specimens: the Bajo de La Carpa Formation (Neuguén Group) abelisaurid material (MACN-PV-RN 1012; Ezcurra & Méndez 2009); the Açu Formation carcharodontosaurian remains (UFRJ-DG523-R and UFRJ-DG524-R; Pereira et al. 2020b); the Freixial Formation (Lusitanian Basin) carcharodontosaurid remains (SNH.019/4; Malafaia et al. 2019); the Wadi Milk Formation caudal (Vb-871, Rauhut 1999) and the Bauru Group megaraptoran material (CPPLIP 1324 and MPMA 08-003-94; Méndez et al. 2012, Martinelli et al. 2013). For systematic terminologies, we follow Padian et al. (1999), which consider Neotheropoda the least inclusive clade containing *Coelophysis bauri* and extant birds, and Tetanurae the most inclusive clade containing extant birds but not *Ceratosaurus nasicornis*.

Phylogenetic inference

In this work, we present a phylogenetic inference based on a data matrix modified from Malafaia et al. (2020). Two new characters (i.e., unpublished) relative to mid-caudal centrum anatomy are proposed: character 359 (Mid and posterior caudal vertebrae, centrum, mid-width: 0 – over half of articular facets width; 1 – half or less);

Table II. Selected measurements of MCT 2670-LE.

Anatomical measurements of the centrum	Measurements expressed in mm
maximum length	44
width at mid-length	15
proximal facet height	29
proximal facet width	31
distal facet height	30
distal facet width	32

and character 360 (Mid and posterior caudals, centrum, ventral surface: 0 – flat, 1 – with a thin sulcus, 2 – with a broad groove). Furthermore, we have added four taxa: *Veterupristisaurus*, *Siamraptor*, UFRJ DG 524-R, and MCT 2670-LE. The analysis itself was performed using the free software TNT v. 1.5 (Goloboff & Catalano 2016). To heuristic search, we followed the same protocol (default New Technology Search, driven search stabilizing consensus twice by a factor of 25) as employed by Malafaia et al. (2020), though we highlight that revisions of both matrix and protocol may be welcome in future contributions.

Linear morphometrics

We performed a linear morphometrics to the mid caudal vertebrae (from 8th to 23rd caudal) with the parameters adapted from Welles (1952) and Brown (1981), which are: height/length ratio ($HI = 100 \cdot H/L$); breadth/length ratio ($BI = 100 \cdot B/L$); and rate of vertebral elongation ($VLI = 2 \cdot 10^2 L / (H+B)$). We also added mid centrum width/breadth ratio ($MBI = 100 \cdot M/B$) to observe the variation and segregation among the analyzed neotheropod groups. The measurements were compiled from literature and/or taken from images via ImageJ v. 1.46r (Schneider et al. 2012).

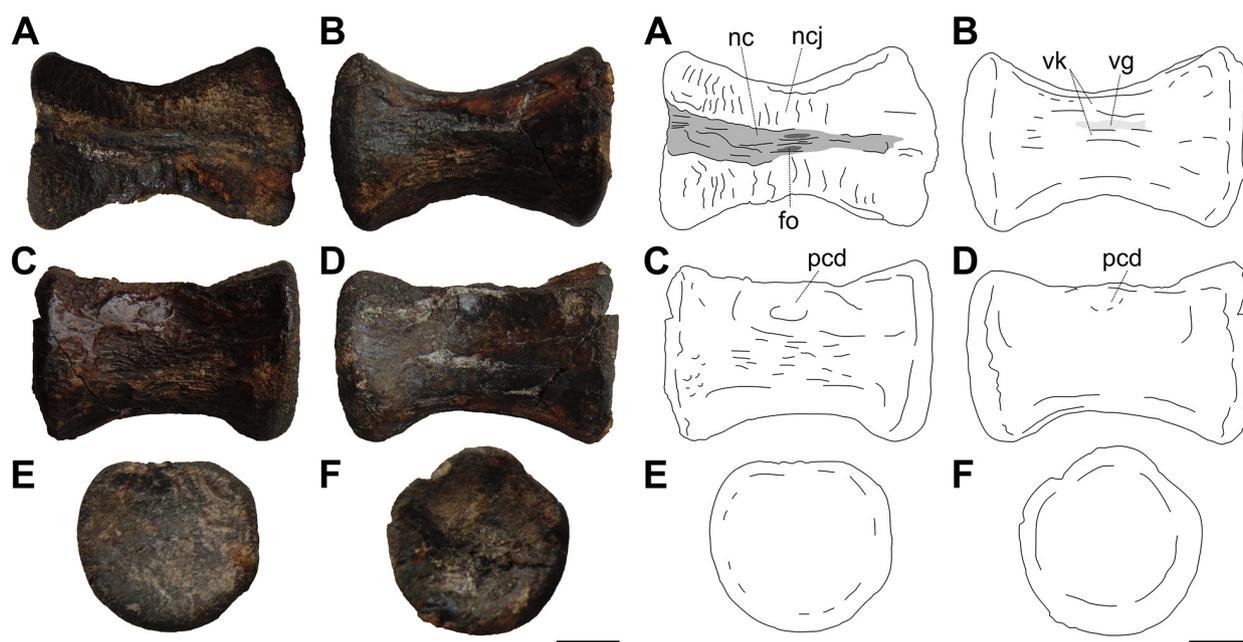


Figure 2. Plate of the allosauroid specimen MCT 2670-LE, a putative carcharodontosaurian, in dorsal (a), ventral (b), right (c) left (d), anterior (e) and posterior views (f), with a scheme on the right. Abbreviations: fo, foramen; nc, neural canal; ncj, neurocentral junction; pcd, pleurocentral depression; vk, ventral keel; vg, ventral groove. Scale bar equals 10 mm.

We used the linear bivariate regressions to test the correlation between parameters and, subsequently, linear discriminant (LDA) and principal component analyses (PCA). Due to the low sample sizes, we considered nonparametric tests to verify the significance between group means with Kruskal-Wallis, followed by Mann Whitney pairwise tests. All statistical analyses were performed in the software PAST v. 4.02 (Hammer et al. 2001), considering *p*-value of 0.05 as significant.

RESULTS

Systematic paleontology

Dinosauria Owen, 1842

Theropoda Marsh, 1881

Tetanurae Gauthier, 1986

Avetheropoda Paul, 1988

Allosauroidea Marsh, 1878

cf. Carcharodontosauria Benson, Carrano and Brusatte, 2010

Description

The specimen MCT 2670-LE (Figure 2) comprises an isolated vertebral caudal centrum. Although the neural arch is not preserved, the neurocentral junction exhibits a rugose surface, which indicates that the neurocentral junction was unfused and the neurocentral suture was visible. The amphicoelous vertebral centrum is elongated (Table II) and transversely constricted in its middle length showing an hourglass shape, as it is in several allosauroids middle and posterior caudal centra (e.g., Madsen 1976, Britt 1991, Rauhut 1999, Chure 2000) but especially carcharodontosaurian ones (e.g., Malafaia et al. 2019, Chokchaloemwong et al. 2019, Pereira et al. 2020b). The articular facets are subcircular, with the anterior facet being mostly flat and the posterior smoothly concave (Figure 2). MCT 2670-LE shows a slight offset between articular

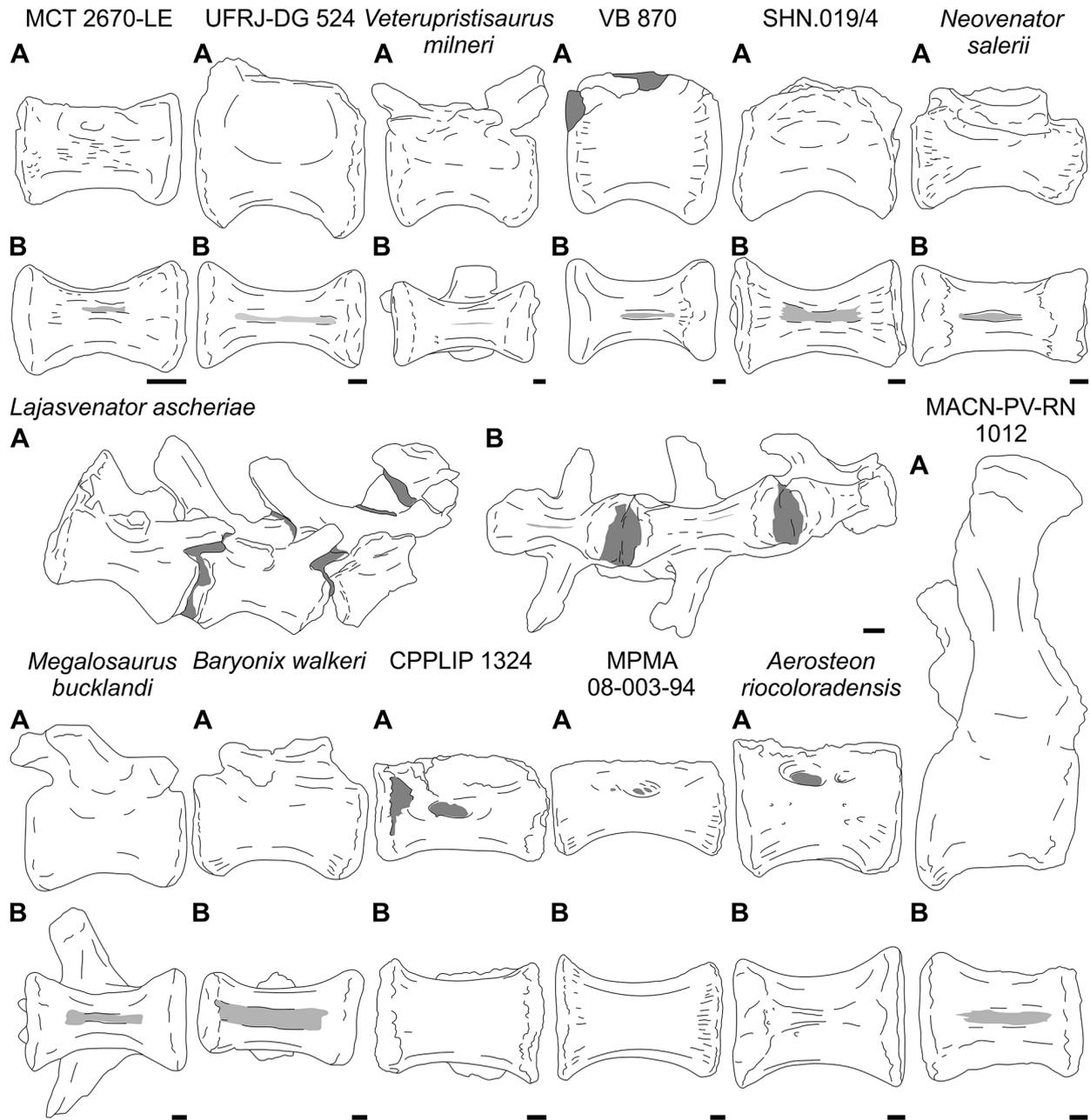


Figure 3. Comparative left lateral (a) and ventral (b) views between MCT 2670-LE and other caudal vertebrae from allosauroid specimens: UFRJ-DG524-R (modified from Pereira et al. 2020b); *Veterupristisaurus milneri* (MB R 2166, modified from Rauhut 2011); Vb-607, Wadi Milk Formation caudal (modified from Rauhut 1999); referred specimen of *Lusovenator santosi* (SHN.19/04, modified from Malafaia et al. 2019); *Neovenator salerii* (MIWG 6348, modified from Brusatte et al. 2008), *Lajasvenator ascheriae* (MLL-Pv-005, modified from Coria et al. 2020); *Megalosaurus bucklandi* (BMNH R9672, modified from Benson 2010); *Baryonyx walkeri* (ML 1190, modified from Mateus et al. 2011); CPPLIP 1324 (modified from Martinelli et al. 2013); MPMA 08-003-94 (modified from Méndez et al. 2012); *Aerosteon riocoloradensis* (MACN-PV-3137, modified from Méndez et al. 2012); and MACN-PV-RN-1012 (modified from Ezcurra & Méndez 2009). Scale bars equal 10 mm.

facets. In lateral view, the specimen MCT 2670-LE exhibits a slight concavity in its ventral surface. Close to the neurocentral joint, in the mid-region of the centrum, the neurocentral depressions are shallow. The ventral surface of the centrum has a narrow longitudinal groove extending along its anteroposterior length. This longitudinal groove is bounded by faint paired keels, which are slightly eroded. In ventral view, the facets for chevrons joints are quite visible next to the posterior face.

Comparisons

The offset between articular facets is a feature spread among basal Neotheropoda, being observed in *Dilophosaurus* (Welles 1984), abelisaurids (Méndez 2014), *Allosaurus* (Madsen 1976), *Acrocanthosaurus* (Stovall & Langston 1950) as well as in other carcharodontosaurian mid and posterior caudal vertebrae (e.g., Rauhut 1999, Coria & Currie 2006, Malafaia et al. 2019). However, MCT 2670-LE does not show the ventrolateral ridges (Figure 3) that normally seems to accompany this ventral pronounced offset (e.g., present in *Dilophosaurus* Welles, 1984 and several abelisaurids, Méndez et al. 2012). The hourglass shaped centrum is typical to the middle and posterior caudal centra of several allosauroids (e.g., Madsen 1976, Britt 1991, Rauhut 1999, Chure 2000) but especially carcharodontosaurian ones (e.g., Malafaia et al. 2019, Chokchaloemwong et al. 2019, Coria et al. 2020, Pereira et al. 2020b, Figure 3). Such feature is distinct in the caudal observed in abelisauroids (e.g., MACN-PV-RN 1012; see Ezcurra & Méndez 2009) The narrow longitudinal groove in the ventral surface, bounded by faint keels in the caudal centrum is also commonly found in Abelisauroida, Allosauroida, especially carcharodontosaurids and Megalosauroidea (Ezcurra & Méndez 2009, Benson 2010, Mateus et al. 2011, Carrano et al. 2012, Rauhut et al.

2016, Malafaia et al. 2017, 2020, Coria et al. 2020). The absence of the ventrolateral ridges when the ventral pronounced offset is present could be a character that can be ascertained in the future phylogenetic approaches. Such feature is something putatively present in Avetheropoda, suggesting a secondary loss of these ventrolateral ridges at least within Allosauroida, as observed in MCT 2670-R and carcharodontosaurids. Although the hourglass shape is observed in megaraptorans, as *Aerosteon* (see Sereno et al. 2008) and in the specimens CPPLIP 1324 (see Martinelli et al. 2013), MPMA 08-00394 (see Méndez et al. 2012), they have pneumatic foramina and/or lack a ventral groove. Therefore, the hourglass shaped centrum and the presence of a narrow longitudinal groove, bounded by ventral keels along its ventral surface allows referral of the specimen MCT 2670-LE to Allosauroida.

The phylogenetic placement of Megaraptora is uncertain, as the group may fall within neovenatorids (as after the dataset Malafaia et al. 2020, which we have utilized here) or as basal coelurosaurs (e.g., Delcourt & Grillo 2018). We highlight that the phylogenetic placement of Megaraptora within or outside the Carcharodontosauria has no bearing on the taxonomic referral of MCT 2670-LE, which differs from megaraptorans (as expressed above) whether they are considered as carcharodontosaurians or not.

Among Allosauroida, MCT 2670-LE is quite similar to the holotypic (SHN.036, Malafaia et al. 2020) and the referred (SHN.19, Malafaia et al. 2019) mid caudal vertebrae of *Lusovenator santosi*, as it is similar to *Lajasvenator ascheriae*. The specimen MCT 2670-R, *L. santosi* and *L. ascheriae* share the moderately elongated centra. However, the Brazilian specimen differs from SHN.019 due to the development of the pleurocentral depression well visible in the

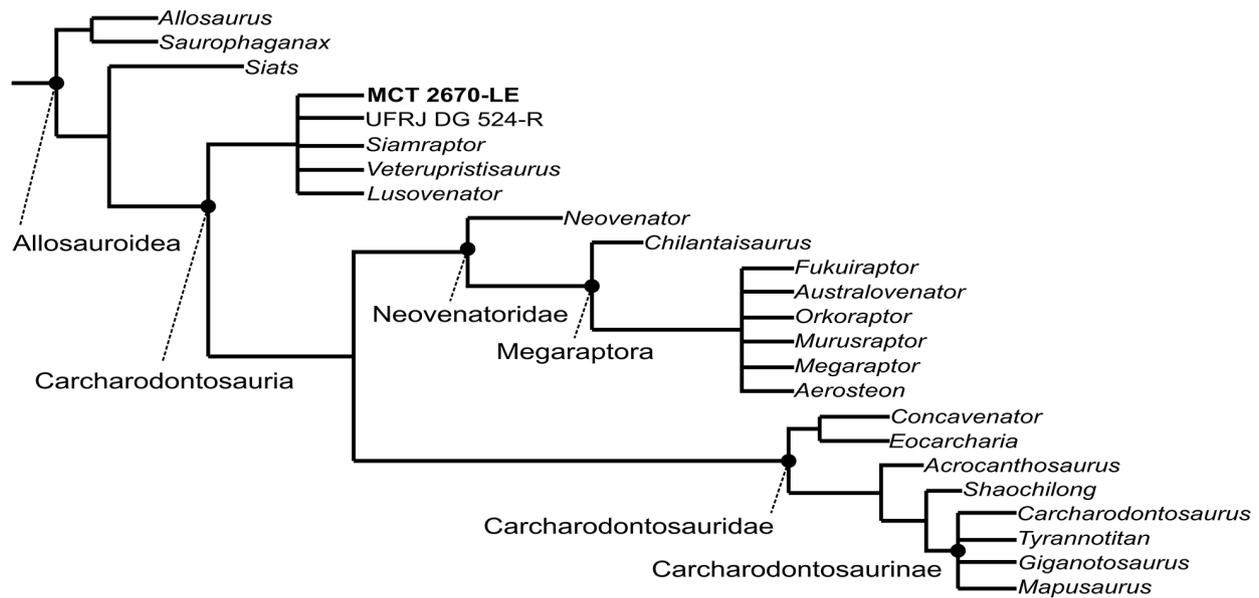


Figure 4. Consensus tree showing the assignment of MCT 2670-LE within Carcharodontosauria (Allosauroidea) (to access the full tree, see Supplementary Appendix).

European specimen. The extremely reduced pleurocentral depression is shared with the vertebra of *L. ascheriae* (Coria et al. 2020), *Veterupristisaurus milneri* (MB R 1938; Rauhut 2011), differing from the comparatively deeper depression in the derived carcharodontosaurids *Giganotosaurus carolinii* (see Coria & Salgado 1995) and expanded depression in *Acrocanthosaurus atokensis* (see Storval & Langston 1950). However, the centrum of MCT 2670-LE has a much shallower dorsolateral depression, similar to *L. ascheriae* and *Mapusaurus roseae* (see Coria & Currie 2006, Coria et al. 2020). MCT 2670-LE also differs from *L. santosi* caudal vertebrae (SHN.06 and SHN.19) for the absence of the lateral lamina in Brazilian specimen, which is also absent in *G. carolinii* (see Coria & Salgado 1995) *M. roseae* (Coria & Currie 2006) and in the carcharodontosaurian remains from Açú Formation (UFRJ-DG523-R and UFRJ-DG524-R), although those are more anterior caudal vertebrae compared to MCT 2670-LE.

The amphicoelous centra with the anterior articular surface being slightly more concave

than the posterior face is a feature shared with MB R 1938 (Rauhut 2011). The round articular surface is widely spread in the mid to posterior caudal vertebrae of *Torvosaurus* (Hanson & Makovicky 2014) and several allosauroids, such as *Allosaurus* (Madsen 1976), *Acrocanthosaurus* (Stovall & Langston 1950, Currie & Carpenter 2000), *Concavenator* (Cuesta et al. 2019) and in several carcharodontosaurids, but not in *Mapusaurus* (Coria & Currie 2006) and *Siamraptor* (Chokchaloemwong et al. 2019), which in turn shows subtriangular articular surfaces on mid to posterior caudal vertebrae (Coria & Currie 2006) - albeit *Siamraptor* has a subrectangular posterior face (Chokchaloemwong et al. 2019). MCT 2670-LE shares the ventrally pronounced border of the articular facets with Vb-871 (Rauhut 1999), MB R 1938 (Rauhut 2011), UFRJ-DG523-R and UFRJ-DG524-R (Pereira et al. 2020b) but differs from those specimens due to the less pronounced ventral keels. Such faint ventral keels, surrounding a longitudinal groove, is observed in basal carcharodontosaurids (Figure

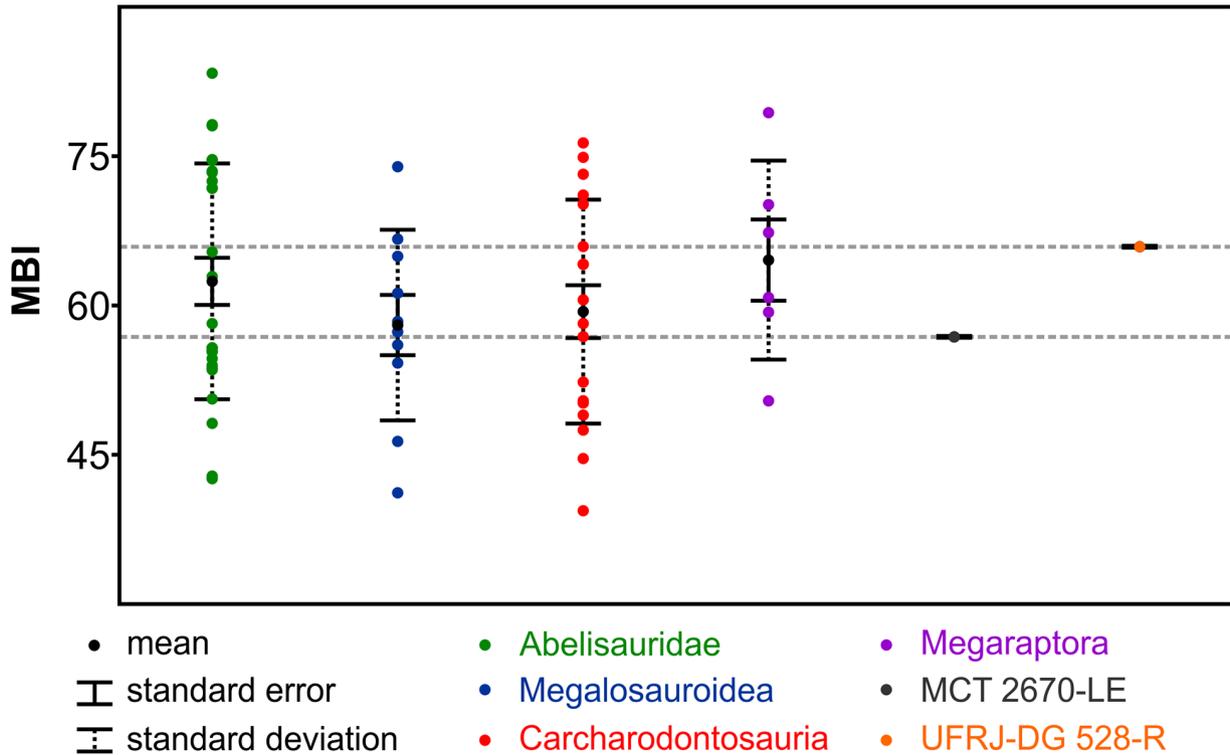


Figure 5. Mean and Whisker plot of vertebral caudal MBI values from Abelisauridae, Megalosauroidae, Allosauroidae, Megaraptora, MCT 2670-LE and UFRJ-DG 528-R.

3), as in the caudal of *Lajasvenator ascheriae* (see Coria et al. 2020).

Phylogenetic inference results

Our phylogenetic inference produced eight minimum-length trees, with 1085 steps, a consistency index of 0.399 and retention index of 0.687. Near the base of the Carcharodontosauria, we have recovered a small clade that includes *Lusovenator*, *Veterupristisaurus*, *Siamraptor*, UFRJ DG 524-R, and MCT 2670-LE (Figure 4). This small clade is recovered in a polytomy including *Siats* and the node that joins Neovenatoridae + Carcharodontosauridae. This small clade is supported by a single synapomorphy: character 359(1): mid and posterior caudals, centrum, mid-width: half or less of articular facets width.

Linear morphometrics results

The centrum width lacks correlation with all other parameters ($r^2 < 0.5$; see graphics in Supplementary Appendix). Only the elongation shows strong correlation with both height ($r^2 = 0.892$) and breadth ($r^2 = 0.799$). Therefore, the multivariate analyses lack support based on these parameters (Table S1), with LDA correctly assigning only 38.98% of the specimens. Our results could not significantly segregate the proposed groups in morphospaces based in all parameters and evaluate the mid centrum width.

We regard only the mid centrum width among the theropod groups to evaluate this feature. The specimen MCT 2670-LE is close to the mean of megalosauroids and allosauroids (Figure 5), while the indeterminate theropod UFRJ-DG 528-R is close to the mean of abelisaurids and megaraptorans. However, the Kruskal-Wallis

Table III. Pairwise Mann-Whitney test (raw *p* values, uncorrected significance) based on MBI main groups for caudal vertebrae.

	Abelisauridae	Megalosauroidae	Allosauroidae	Megaraptora
Abelisauridae	-	0.547	0.382	0.708
Megalosauroidae	-	-	0.829	0.212
Allosauroidae	-	-	-	0.368
Megaraptora	-	-	-	-

No value is significant.

shows no significant difference between the sample medians (H (chi-square) = 1.701; p = 0.637) and the Mann Whitney pairwise shows no significance (Table III). Therefore, the difference between samples regarding the mid centrum width is not significant to distinguish between groups. We also evaluate the variation along the caudal series in more complete specimens (e.g. *Majungasaurus* and *Neovenator*) with more incomplete specimens. The mid centrum width is more constricted in more posterior caudal vertebrae and we observed a wide variation along the anteroposterior caudal sequence, which contributes to the wide standard deviation observed among the samples (Figure 5 and 6).

DISCUSSION

Distribution of carcharodontosaurians among Jurassic-Cretaceous boundary

Up-to-date, most of the carcharodontosaurid record from Brazil comprises teeth from the Albian to early Cenomanian (Vilas Bôas et al. 1999, Medeiros & Schultz 2002, Medeiros et al. 2014), and some caudal vertebrae from the Albian-Cenomanian of Potiguar Basin (Pereira et al. 2020b). Although the discussion in the literature points out that the latest carcharodontosaurian fossil records are restricted to the Lower Cretaceous strata, with the decline of the lineage in the mid-Cretaceous and a niche occupation by abelisaurids (Novas et al. 2013). However,

some records of Upper Cretaceous outcrops from Bauru Group have been previously assigned to Carcharodontosauridae (Candeiro et al. 2004, 2006, 2012, Azevedo et al. 2013). The isolated teeth material was reanalyzed, as well as the unique osteological record (a partial maxilla with a tooth *in situ*; Azevedo et al. 2013) and all were reassigned to Abelisauridae (e.g., Delcourt et al. 2020). Therefore, the current data and analyses in the literature support that carcharodontosaurids were rare at the end of the Early Cretaceous and became extinct up to the Turonian (Apesteguía 2002, Coria & Salgado 2005, Novas et al. 2005, 2013).

Carcharodontosaurians are generally recognized because of global Cretaceous-age radiation of those distinctive allosauroid theropods (Serenó et al. 1996), being most present in southern landmasses (Coria & Salgado 1995, Sereno et al. 1996, Calvo & Coria 1998). Although most of the fossil record of carcharodontosaurians are mainly associated with southern landmasses, there were some exceptions. The Laurasian records consist of fragmentary materials from Upper Jurassic strata of China (Brusatte et al. 2009), Portugal (Malafaia et al. 2019, 2020), Lower Cretaceous of England (Brusatte et al. 2008) and Spain (Ortega et al. 2010, Cuesta et al. 2018). The analysis of a tooth from Romania also indicates the presence of carcharodontosaurids in the Valanginian of Laurasia, but such assignment is still dubious due

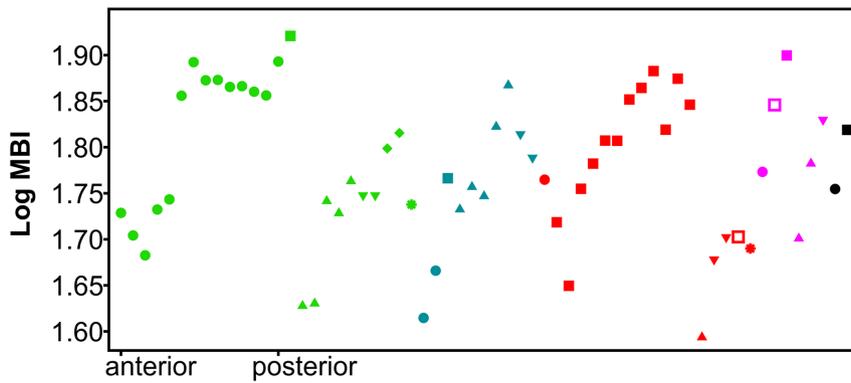


Figure 6. Plotted MBI values of caudal vertebrae from Abelisauridae, Megalosauoidea, Allosauoidea, Megaraptora, MCT 2670-LE and UFRJ-DG 528-R. When specimens show more than one preserved caudal, it follows the anteroposterior order.

Theropoda indet.

- MCT 2670-LE
- UFRJ-DG 528-R

Abelisauridae

- *Majungasaurus crenatissimus*
- *Carnotaurus sastrei*
- *Aucasaurus garridoi*
- *Ekrixinatosaurus novasi*
- *Ilokelesia aguadagrandensis*
- *Rajasaurus narmadensis*

Megalosauoidea

- *Wiehenvenator albatii*
- *Megalosaurus bucklandii*
- *Megalosauridae* indet.
- *Baryonyx walkeri*

Megaraptora

- Megaraptora indet. (MPMA)
- Megaraptora indet. (CPPLIP)
- Megaraptora indet. (UFRJ-DG 558-R)
- *Aoniraptor libertatem*
- *Aerosteon riocoloradensis*

Carcharodontosauria

- *Veterupristisaurus milneri*
- *Neovenator salerii*
- *Lajasvenator ascheriae*
- *Carcharodontosauridae* indet. (SNH)
- *Carcharodontosauridae* indet. (UFRJ 524)
- *Carcharodontosauridae* indet. (UFRJ 523)

to the fragmentary nature of the fossil material (Csiki-sava et al. 2016). The report of MCT 2670-LE is one of the oldest for Carcharodontosauria in Gondwana, after *Veterupristisaurus*, from the Kimmeridgian (Jurassic) of Tendaguru (Rauhut 2011).

From the Jurassic to the Lower Cretaceous, the sole occurrence is the allosauroid *Acrocanthosaurus* which could be a putative carcharodontosaurian from North America (Harris 1998, Currie & Carpenter 2000). Among the Gondwanan carcharodontosaurian record, is remarkable the diversification of the clade especially from South America (Patagonia, Argentina; Novas et al. 2013). This diversification probably occurred just before the Albian-Cenomanian interval, since it is markedly by the origin of carcharodontosaurines (Brusatte et al. 2009, Brusatte & Sereno 2008, Canale et

al. 2015, Carrano et al. 2012) and the subsequent occurrence of the Giganotosaurini (the last is endemic to South America; Canale et al. 2015). The oldest record of a carcharodontosaurian to South America is from the upper Valanginian (Lower Cretaceous) of Patagonia, with the species *Lajasvenator ascheriae* (Coria et al. 2020).

The MCT 2670-LE resembles the caudal vertebrae found among basal carcharodontosaurians species and is the first record of the group in Brazil (Figure 7) before the vicariant event. Such record suggests the presence of these animals in South America since the Jurassic, which corroborates the wide distribution of the group through Gondwana before the Early Cretaceous.



Figure 7. Paleoartistic reconstruction of the specimen MCT 2670-LE in the environment of the Sergi Formation. The first plan shows a medium-sized carcharodontosaurian walking in a dry area, close to a *Lepidotes* carcass. The background shows aeolian and shallow lacustrine/fluvial depositional systems, with the occurrence of gymnosperm forests, based on Pierini et al. (2010). Reconstruction scheme by Arthur S. Brum.

Comments on diversification and decline of Carcharodontosauria

The length of the caudal centrum MCT 2670-LE is 44 mm. Comparing with other carcharodontosaurians, *Neovenator* exhibits middle-posterior caudal around 103-106 mm, with body length estimates of 8 m, while in *Acrocantosaurus*, 160 mm and 11.5 m, and *Veterupristisaurus*, 123 mm and 8.5-10 m of body length (Figure 5; Currie & Carpenter 2000, Brusatte et al. 2008, Rauhut 2011). Based on these measurements, we estimate that MCT 2670-LE could represent a 3-4 m body length individual (Figure 7). Although it shows a smaller size in comparison to the pattern observed in Carcharodontosauria (5-12 m in body length), the unfused neurocentral synchondrosis indicates that the individual could be at least a juvenile (for discussion about neurocentral synchondrosis as maturity criteria see Souza 2018) or subadult

carcharodontosaurian. Therefore, MCT 2670-LE could grow more than 4 m (Figure 7). The recovery of MCT 2670-LE in the Upper Jurassic of South America indicates that carcharodontosaurians were already widely distributed at this time (e.g., *Concavenator*, *Lajasvenator* and *Lusovenator*). The specimen MCT 2670-LE also supports the medium-sized pattern found among basal carcharodontosaurians. Such medium size in the Jurassic corroborates the pattern of increase in the body length, with the largest derived forms recovered from mid-Cretaceous outcrops (e.g., Currie & Carpenter 2000, Canale et al. 2015, Coria et al. 2020). Although the occurrence of an indeterminate carcharodontosaurian from the Tithonian of Portugal suggests a medium to a large-sized individual (Malafaia et al. 2019, 2020), which could weaken such hypothesis, the phylogenies still mark the trend in the increase in body length among derived forms (e.g.,

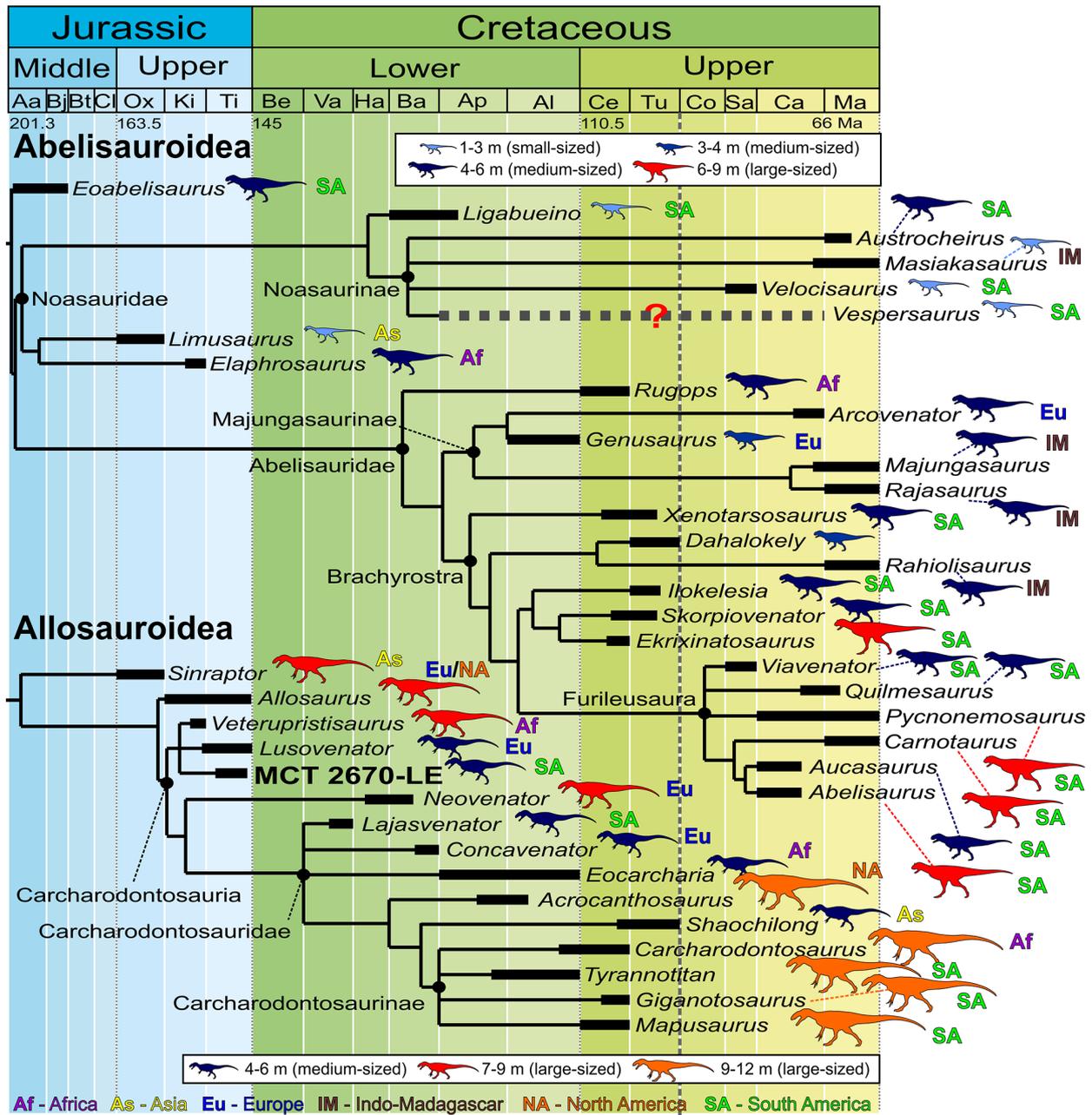


Figure 8. Hypothetical cladogram of abelisauroids and allosauroids (with the assignment of MCT 2670-LE), showing estimated body lengths and distribution from Middle Jurassic to Upper Cretaceous. Body lengths to abelisauroids based on Grillo & Delcourt (2018). Cladogram based on the phylogenies of Langer et al. (2019) to Noosauridae, Filippi et al. (2016) to Abelisauridae, Malafaia et al. (2020) to basal Allosauroidae, Canale et al. (2015) and our phylogenetic results to Carcharodontosauridae. Silhouettes from PhyloPic, by Ian Reid and Scott Hartman.

Carrano et al. 2012, Novas et al. 2013, Canale et al. 2015, Malafaia et al. 2020). The fossil record of Carcharodontosauria is fragmentary and sparse, reaching its diversity with large forms

along the Early-middle Cretaceous (e.g., Coria & Currie 2006, Novas et al. 2013, Canale et al. 2015), which is encompassed by the rarefaction of the group in post-Turonian. At the same time,

the Abelisauridae diversified and increased in body size after the Cenomanian with the group Brachyrostra (Grillo & Delcourt 2018).

Along the Early Cretaceous, the Aptian-Turonian interval is marked by some horizons exhibiting the co-occurrence of a diverse medium-large sized theropod fauna, with abelisauroids, spinosaurids and carcharodontosaurians, such as in North Africa (Novas et al. 2005, 2013, Rauhut 2011), and ceratosaurians, allosauroids and megalosauroids in North America and Iberian Peninsula (Mateus 2006, Mateus et al. 2006, Malafaia et al. 2020). The inferred semi-aquatic habits of spinosaurids (e.g., Ibrahim et al. 2020) exclude this group from a niche overlap or competition with other medium-large sized predatory theropods in such environments. Regarding the ecological relationship between abelisauroids and carcharodontosaurids in such habitats, Gillo & Delcourt (2017) pointed out a competition between abelisauroids and carcharodontosaurians, which could be observed by similar cranial biomechanical advantages (Sakamoto 2010) and the teeth morphology (Canale et al. 2009), with the post-Turonian replacement of the huge derived carcharodontosaurids by abelisauroids. Recently, Candeiro et al. (2018) discussed niche partitioning and competition attributed to the cohabitation of spinosaurids, abelisauroids and carcharodontosaurians in the Early-middle Cretaceous. They supported the niche partitioning, based on the theropod fauna observed in North Africa (see Rauhut 2011). Such co-existing between different taxa of medium-large body sizes is also well-known in the Morrison Formation and outcrops from the Iberian Peninsula (Mateus 2006, Mateus et al. 2006, Malafaia et al. 2020). In the case of the Morrison Formation, the fossil record and the distinct body sizes between theropods reveals a niche partitioning, mainly based on factors that

include the influence of facultative scavenging, the potential foraging area and energy demand by the body mass among different theropod size classes (Kane et al. 2016).

As many dinosaur taxa, basal theropods also show some pattern in the development of body size dimensions that encompass the Cope's rule (Hone et al. 2005), in which the diversification of a group is also followed by the increase of body mass and niche specificity. Among basal theropod lineages, we observed such a trend in both abelisauroids and allosauroids, but in distinct times of diversification. The earlier diversification and decline process of the lineage is evidenced by the change from the occurrence of medium-sized Jurassic forms, with a wide distribution, to large carcharodontosaurians through the Early Cretaceous and the endemism in this period, as observed in Giganotosaurini (Canale et al. 2015). Regarding abelisauroids, especially abelisauroids, they show an advantage in cursorial potential (Person IV & Currie 2011) over carcharodontosaurians, as indicated by Grillo & Delcourt (2018). The rarefaction of the derived large carcharodontosaurids in the Turonian would enable the abelisauroids diversification, with the increase of their body sizes and occupation of a niche once occupied by carcharodontosaurids. Such occupation may reflect convergent features, as the cranial biomechanics and teeth (Sakamoto 2010, Canale et al. 2009, Delcourt et al. 2020). However, both competition and niche partitioning scenarios should be better delimited with more fossil material of these groups, especially during the Jurassic-Early Cretaceous (Figure 8), which is marked by a gap in both carcharodontosaurian and abelisauroid lineages. Therefore, we provided an alternative scenario, and we could not discard the competition hypothesis.

Comments on the phylogenetic relationships of MCT 2670-LE

An interesting result of our phylogenetic inference is the recovery of a small clade at the base of the Carcharodontosauria, comprehending the earliest records of the group – the Late Jurassic OTUs *Lusovenator*, *Veterupristisaurus*, and MCT 2670-LE. This clade further includes the Early Cretaceous *Siamraptor* and the Albian-Cenomanian UFRJ DG 524-R. All these five taxa share a single synapomorphy: character 359(1): mid and posterior caudals, centrum, mid-width: half or less of articular facets width. This small clade was recovered in a polytomy involving *Siats* as well as (Neovenatoridae + Carcharodontosauridae) and is thus comprised within the Carcharodontosauria, since it is defined as a branch-based clade containing *Carcharodontosaurus* and *Neovenator* but not *Allosaurus* or *Sinraptor* (Benson et al. 2010).

The carcharodontosaurian nature of each of these OTUs is well supported (e.g., see Rauhut 2011, Chokchaloemwong et al. 2019, Malafaia et al. 2020). In fact, we replicate the results of Malafaia et al. (2020) regarding the phylogenetic position of *Lusovenator* as a carcharodontosaurian; we simply add to its branch the OTUs *Veterupristisaurus*, *Siamraptor*, MCT 2670-LE and UFRJ DG 524-R based on the synapomorphy mentioned above, character 359(1). The position of *Lusovenator* itself is supported by three carcharodontosaurian synapomorphies (characters 160(2), 273(2) and 294(1); see the Supplementary Material). However, the monophyly of this possible new clade is still questionable and must be viewed with caution, since it is based on a single synapomorphy and very fragmentary specimens. Future discoveries are needed to shed light on this possible clade.

The new character proposed on this study, 360(2): mid and posterior caudals, centrum, ventral surface with a thin and

deep sulcus, is recovered as a synapomorphy of the Allosauroidea, corroborating the allosauroid nature of MCT 2670-LE. This character state is reversed in *Shaochilong* + Carcharodontosaurinae (see Coria & Currie 2006 for *Mapusaurus*, and Benson et al. 2010 for *Shaochilong*). The presence of this feature indicates that MCT 2670-LE could be a basal carcharodontosaurian, or at least an allosauroid taxon closely related to the Carcharodontosauria clade.

Therefore, despite the fragmentary status of the newly described specimen, our phylogenetic results demonstrate the presence of a combined set of features that undoubtedly resolves MCT 2670-LE as a carcharodontosaurian. Therefore, our results are in agreement with previous work that demonstrates that, despite fragmentary, some fossil specimens have enough combination of features that enable a precise recognition of their evolutionary affinities (e.g., Kearney 2002, Wiens 2003a, b, Kearney & Clark 2003).

CONCLUSIONS

The Sergi Formation has a yet unexplored potential for understanding the relationships of Mesozoic fossil vertebrates. The faunistic content discussed here provides a significant contribution to South American paleontology, especially the knowledge of the Upper Jurassic in Brazil. MCT 2670-LE is the first confirmed dinosaur record for the Jurassic of Brazil and it is assigned to the Allosauroidea, with affinities to the Carcharodontosauria, due to the hour-glass shaped centrum and the ventral surface showing a narrow longitudinal groove, bounded by ventral keels. Within Carcharodontosauria, the specimen is quite similar to *Lusovenator santosi*, *Lajasvenator ascheriae* and *Veterupristisaurus milneri*. Based

on this, the material could represent one of the oldest carcharodontosaurian remains known. Further studies are needed to promote the stratigraphic and temporal refinement of the formation, which in the future may bring more data on a putative Gondwanan origin of the carcharodontosaurians.

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REFERENCES

ADEGAS F, SCHERER CMS & BORN C. 2012. Arcabouço estratigráfico da Formação Sergi (Jurássico Superior) na Bacia de Almada, Bahia. *Rev Bras Geoci* volume 42(Suppl 1): 1-18.

ALMEIDA FFM. 1967. Origem e evolução da plataforma brasileira. In: *Boletim do Departamento Nacional da Produção Mineral/Divisão de Geologia e Mineralogia*, Rio de Janeiro, 241, p. 1-39.

ALMEIDA FD, HASUI Y, BRITO NEVES BD & FUCK RA. 1977. Províncias estruturais brasileiras. *Simpósio de Geologia do Nordeste* 8(1977): 363-391

APESTEGUÍA S. 2002. Successional structure in continental tetrapod faunas from Argentina along the Cretaceous. In: *Boletim Do II Simpósio Del Cretácio de América Del Sur*. São Pedro, Brazil, p. 135-141.

ASSINE ML. 1992. Análise Estratigráfica da Bacia do Araripe, Nordeste do Brasil. *Rev Bras Geoci* 22(3): 289-300.

ASSINE ML. 2007. A Bacia do Araripe. *Boletim de Geociências PETROBRAS*, Rio de Janeiro 15(2): 371-389.

AZAMBUJA FILHO NC. 1998. Guidebook to the Rift-Drift Sergipe-Alagoas Basin. Prepared during the 1998 AAPG International Conference & Exhibition. doi: 10.13140/RG.2.2.17330.22729.

AZEVEDO RPF, SIMBRAS FM, FURTADO MR, CANDEIRO CRA & BERGQVIST LP. 2013. First Brazilian carcharodontosaurid and other new theropod dinosaur fossils from the Campanian-Maastrichtian Presidente Prudente Formation, São Paulo State, southeastern Brazil. *Cretac Res* 40: 131-142. <https://doi.org/10.1016/j.cretres.2012.06.004>.

BACIA DE CAMAMU-ALMADA: Sumário Geológico e Setores em Oferta. 2015. Décima Terceira rodada de licitações, Agência Nacional do Petróleo, Gás Natural e Biocombustíveis, Superintendência de Definição de Blocos - SDB. Retrieved from: http://rodadas.anp.gov.br/arquivos/Round_13/areas_oferecidas_r13/Sumarios_Geologicos/Sumario_Geologico_Bacia_Camamu-Almada_R13.pdf.

BAHIA RBC. 2007. Evolução Tectonossedimentar da Bacia dos Parecis - Amazônia. Phd Thesis of Universidade Federal de Ouro Preto, Minas Gerais, 150 p.

BANDEIRA KLN, BRUM AS, PÊGAS RV, CIDADE GM, HOLGADO B, CIDADE A & SOUZA RG. 2018. The Baurusuchidae vs Theropoda record in the Bauru Group (Upper Cretaceous, Brazil): a taphonomic perspective. *J Iber Geol* 44: 25-54. <https://doi.org/10.1007/s41513-018-0048-4>.

BANDEIRA KLN, MACHADO EB, CAMPOS DA & KELLNER AWA. 2019. New titanosaur (Sauropoda, Dinosauria) records from the Morro do Cambambe unit (upper cretaceous), Mato Grosso state, Brazil. *Cret Res* 103: 04155. <https://doi.org/10.1016/j.cretres.2019.06.001>.

BENSON RBJ. 2010. A description of *Megalosaurus bucklandii* (Dinosauria: Theropoda) from the Bathonian of the UK and the relationships of Middle Jurassic theropods. *Zoological Zoo J Linn Soc* 158: 882-935. <https://doi.org/10.1111/j.1096-3642.2009.00569.x>.

- BENSON RBJ, CARRANO MT & BRUSATTE SL. 2010. A new clade of archaic large-bodied predatory dinosaurs (Theropoda: Allosauroidea) that survived to the latest Mesozoic. *Naturwissenschaften* 97: 71-78.
- BELLIENI G ET AL. 1992. Evidence of magmatic activity related to Middle Jurassic and Lower Cretaceous rifting from northeastern Brazil (Cearfi-Mirim): K/Ar age, palaeomagnetism, petrology and Sr-Nd isotope characteristics. *Chem Geol* 97: 9-32.
- BITTENCOURT JS & LANGER MC. 2011. Mesozoic dinosaurs from Brazil and their biogeographic implications. *An Acad Bras Cienc* 83: 23-60.
- BONGIOLO DE & SCHERER CMS. 2010. Facies architecture and heterogeneity of the fluvial and aeolian reservoirs of the Sergi formation (Upper Jurassic), Recôncavo Basin, NE Brazil. *Marine Petrol Geol* 27: 1885-1897.
- BORBA C, PAIM PSG & GARCIA AJV. 2011. Estratigrafia dos depósitos iniciais do rifte no Campo de Furado, região de São Miguel dos Campos, Bacia de Sergipe-Alagoas. *Rev Bras Geoci* 41(1): 18.
- BRASIL. 1975. Projeto RADAMBRASIL: Levantamento dos Recursos Naturais. Folha NA 20 Boa Vista e parte das Folhas NA 21 Tumucumaque, NB 20 Roraima e NB 2, vol.8. IBGE: 428 p.
- BRAUN OPG. 1966. Estratigrafia dos sedimentos da parte interior da região nordeste do Brasil (Bacias de Tucano-Jatobá, Mirandiba e Araripe). Bol Departamento Nacional da Produção Mineral/Divisão de Geologia e Mineralogia, Rio de Janeiro, 236: 1-76.
- BRITT BB. 1991. Theropods of Dry Mesa Quarry (Morrison Formation, Late Jurassic), Colorado, with emphasis on the osteology of *Torvosaurus tanneri*. *Brigham Young Univ Geol Stud* 37: 1-72.
- BRITO IM. 1987. As Unidades Litoestratigráficas da passagem Jurássico-Cretáceo no Nordeste do Brasil. *Rev Bras Geoci* 17(2): 81-85.
- BRITO PM, BERTINI RJ, MARTILL DM & SALLES LO. 1994. Vertebrate fauna from the Missão Velha Formation (Lower Cretaceous, N.E. Brazil): 139-140. *Boletim do 3º sobre o Cretáceo do Brasil, Campus de Rio Claro/SP, UNESP*.
- BROWN DS. 1981. The English Upper Jurassic Plesiosauroidea (Reptilia) and a review of the phylogeny and classification of the Plesiosauroidea. *Bull Br Museum Nat Hist Geol* 35: 253-347.
- BRUSATTE SL, BENSON RBJ & HUTT S. 2008. The osteology of *Neovenator salerii* (Dinosauria: Theropoda) from the Wealden Group (Barremian) of the Isle of Wight. *Monogr Palaeontogr Soc*: 1-75.
- BRUSATTE SL, BENSON RBJ, CHURE D, XU X, SULLIVAN C & HONE D. 2009. The first definitive carcharodontosaurid (Dinosauria: Theropoda) from Asia and the delayed ascent of tyrannosaurids. *Naturwissenschaften* 96(9): 1051-1058. doi:10.1007/s00114-009-0565-2.
- BRUSATTE SL, CANDEIRO CRA & SIMBRAS FM. 2017. The last dinosaurs of Brazil: The Bauru Group and its implication for the end-Cretaceous mass extinction. *An Acad Bras Cienc* 89: 1465-1485. <https://doi.org/10.1590/0001-3765201720160918>.
- BRUSATTE SL & SERENO PC. 2008. Phylogeny of Allosauroidea (Dinosauria: Theropoda): Comparative analysis and resolution. *J Syst Palaeontol* 6: 155-182. <https://doi.org/10.1017/S1477201907002404>.
- CALVO JO & CORIA R. 1998. New specimen of *Giganotosaurus carolini* Coria & Salgado, 1995, supports it as the largest theropod ever found. *Gaia* 15: 117-122.
- CANALE JI, NOVAS FE & POL D. 2015. Osteology and phylogenetic relationships of *Tyrannotitan chubutensis* Novas, de Valais, Vickers-Rich and Rich, 2005 (Theropoda: Carcharodontosauridae) from the Lower Cretaceous of Patagonia, Argentina. *Hist Biol* 27: 1-32. <https://doi.org/10.1080/08912963.2013.861830>.
- CANALE JI, SCANFERLA CA, AGNOLIN FL & NOVAS FE. 2009. New carnivorous dinosaur from the Late Cretaceous of NW Patagonia and the evolution of abelisaurid theropods. *Naturwissenschaften* 96: 409-414. <https://doi.org/10.1007/s00114-008-0487-4>.
- CANDEIRO CRA, ABRANTES CT, ABRANTES EA, AVILLA LS, MARTINS VC, MOREIRA AL, TORRES SR & BERGQVIST LP. 2004. Dinosaurs remains from western São Paulo state, Brazil (Bauru Basin, Adamantina Formation, Upper Cretaceous). *J South Am Earth Sci* 18: 1-10. <https://doi.org/10.1016/j.jsames.2004.08.004>.
- CANDEIRO CRA, MARTINELLI AG, AVILLA LS & RICH TH. 2006. Tetrapods from the Upper Cretaceous (Turonian-Maastrichtian) Bauru Group of Brazil: a reappraisal. *Cretac Res* 27: 923-946. <https://doi.org/10.1016/j.cretres.2006.05.002>.
- CANDEIRO CRA, CURRIE PJ & BERGQVIST LP. 2012. Theropod teeth from the Marília Formation (late Maastrichtian) at the paleontological site of Peirópolis in Minas Gerais State, Brazil. *Rev Bras Geoci* 42: 323-330. <https://doi.org/10.5327/Z0375-75362012000200008>.
- CANDEIRO CRA, BRUSATTE SL, VIDAL L & PEREIRA PVLGC. 2018. Paleobiogeographic evolution and distribution of

- Carcharodontosauridae (Dinosauria, Theropoda) during the middle Cretaceous of North Africa. *Pap Avulsos Zool* 58: 0-4. <https://doi.org/10.11606/1807-0205/2018.58.29>.
- CARRANO MT, BENSON RBJ & SAMPSON SD. 2012. The phylogeny of Tetanurae. *J Syst Paleontol* 10: 211-300.
- CARVALHO IS. 1993. Os conchostráceos fósseis das bacias interiores do Nordeste do Brasil. Programa de Pós-Graduação em Geologia, Universidade Federal do Rio de Janeiro. Tese (Doutorado), Rio de Janeiro: 319pp.
- CARVALHO ARA, OLIVEIRA GR & BARRETO AMF. 2021. New Crocodylomorpha remains from the Late Jurassic Aliança Formation (Dom João stage), Jatobá Basin. *J South Am Earth Sci* 109: 103256. <https://doi.org/10.1016/j.jsames.2021.103256>
- CARVALHO IS, NOVAS FE, AGNOLÍN FL, ISASI MP, FREITAS FI & ANDRADE JA. 2015. A new genus and species of enantiornithine bird from the Early Cretaceous of Brazil. *Braz J Geol* 45(2): 161-171.
- CARVALHO IS & FERNANDES ACS. 1993. Icnologia da Bacia de Mangabeira, Cretáceo do Ceará. *Anais da Academia Brasileira de Ciências*, 65(3): 253-264
- CHARIG AJ & MILNER AC. 1986. *Baryonyx*, a remarkable new theropod dinosaur. *Nature* 324: 359-361. <https://doi.org/10.1038/324359a0>.
- CHOKCHALOEMWONG D, HATTORI S, CUESTA E, JINTASAKUL P, SHIBATA M & AZUMA Y. 2019. A new carcharodontosaurian theropod (Dinosauria: Saurischia) from the Lower Cretaceous of Thailand. *PLoS ONE* 14 (10): e0222489.
- CHURE DJ. 2000. A new species of *Allosaurus* from the Morrison Formation of Dinosaur National Monument (UT-CO) and a revision of the theropod family Allosauridae. Columbia University.
- CORIA RA & CURRIE PJ. 2006. A new carcharodontosaurid (Dinosauria, Theropoda) from the Upper Cretaceous of Argentina. *Geodiversitas* 28: 71-118.
- CORIA RA & CURRIE PJ. 2016. A New Megaraptoran Dinosaur (Dinosauria, Theropoda, Megaraptoridae) from the Late Cretaceous of Patagonia. *PLoS ONE* 11(7): e0157973. <https://doi.org/10.1371/journal.pone.0157973>.
- CORIA RA & SALGADO L. 2005. Mid-Cretaceous turnover of saurischian dinosaur communities: evidence from the Neuquen Basin. Geological Society, London, Special Publications 252: 317-327. <https://doi.org/10.1144/GSL.SP.2005.252.01.16>.
- CORIA RA & SALGADO L. 1995. A new giant carnivorous dinosaur from the Cretaceous of Patagonia. *Nature* 377: 224-226.
- CORIA RA, CURRIE PJ, ORTEGA F & BAIANO MA. 2020. An Early Cretaceous, medium-sized carcharodontosaurid theropod (Dinosauria, Saurischia) from the Mulichinco Formation (upper Valanginian), Neuquén Province, Patagonia, Argentina. *Cretac Res* 111: 104319. <https://doi.org/10.1016/j.cretres.2019.104319>.
- COSTA IP, BUENO GV, MILHOMEM PS, SILVA HSLE & KOSIN MD. 2007. Sub-bacia de Tucano Norte e Bacia de Jatobá. *Boletim de Geociências Petrobras* 15(2): 445-453.
- CSIKI-SAVA Z, BRUSATTE SL & VASILE S. 2016. "*Megalosaurus* cf. *superbus*" from southeastern Romania: The oldest known Cretaceous carcharodontosaurid (Dinosauria: Theropoda) and its implications for earliest Cretaceous Europe-Gondwana connections. *Cretac Res* 60: 221-238. <https://doi.org/10.1016/j.cretres.2015.12.004>.
- CRAWFORD FD, SZELEWSKI CE & ALVEY GD. 1984. Geology and exploration in the Takutu Graben of Guyana. *Oil & Gas J* 82(10): 122-139.
- CUESTA E, ORTEGA F & SANZ JL. 2018. Appendicular osteology of *Concavenator corcovatus* (Theropoda: Carcharodontosauridae) from the Lower Cretaceous of Spain. *J Vertebr Paleontol* 38 (4): e148515. <https://doi.org/10.1080/02724634.2018.1485153>.
- CUESTA E, ORTEGA F & SANZ JL. 2019. Axial osteology of *Concavenator corcovatus* (Theropoda; Carcharodontosauria) from the Lower Cretaceous of Spain. *Cretac Res* 95: 106-120.
- CURRIE PJ & CARPENTER K. 2000. A new specimen of *Acrocanthosaurus atokensis* (Theropoda, Dinosauria) from the lower Cretaceous Antlers formation (Lower Cretaceous, Aptian) of Oklahoma, USA. *Geodiversitas* 22: 207-246.
- DELCOURT R, BRILHANTE NS, GRILLO ON, GHILARDI AM, AUGUSTA BG & RICARDI-BRANCO F. 2020. Carcharodontosauridae theropod tooth crowns from the Upper Cretaceous (Bauru Basin) of Brazil: A reassessment of isolated elements and its implications to palaeobiogeography of the group. *Palaeogeogr Palaeoclimatol Palaeoecol* 556: 109870. <https://doi.org/10.1016/j.palaeo.2020.109870>.
- DELCOURT R & GRILLO ON. 2018. Reassessment of a fragmentary maxilla attributed to Carcharodontosauridae from Presidente Prudente Formation, Brazil. *Cretac Res* 84: 515-524. <https://doi.org/10.1016/j.cretres.2017.09.008>.
- DERBY OA. 1879. Contribuições para o estudo da geologia do Valle do rio São Francisco. *Arq Mus Nac* 4: 87-119.
- EIRAS JF & KINOSHITA K. 2006. Bacias sedimentares brasileiras: Bacia do Tacutu. *Phoenix* 87: 1-6.

- EZCURRA MD & MÉNDEZ AH. 2009. First report of a derived abelisauroid theropod from the Bajo de la Carpa Formation (Late Cretaceous), Patagonia, Argentina Bull Geosci 84: 547-554. <https://doi.org/10.3140/bull.geosci.1106>.
- FAMBRINI GL, TESSER JR S, NEUMANN VHML, SOUZA BYC & FILHO WFS. 2009. Fácies e Sistemas Depositionais na área-tipo da Formação Missão Velha, Bacia do Araripe, Nordeste do Brasil. Estudos Geológicos 19(1): 161-190.
- FERNANDES MA, FERNANDES LBR & SOUTO PRF. 2004. Occurrence of Urolites related to Dinosaurs in the Lower Cretaceous of the Botucatu Formation, Paraná Basin, São Paulo State, Brazil. Revista Brasileira de Paleontologia: 7(2): 263-268.
- FERREIRA TS, CAIXETA JM & LIMA FD. 2009. Controle do embasamento do rifteamento das bacias de Camamu e Almada. Boletim de Geociências da Petrobrás, Rio de Janeiro 17(1): 724: 69-88.
- FILIPPI LS, MÉNDEZ AH, VALIERI RDJ & GARRIDO AC. 2016. A new brachyrostran with hypertrophied axial structures reveals an unexpected radiation of the latest Cretaceous abelisauroids. Cretac Res 61: 209-219. <https://doi.org/10.1016/j.cretres.2015.12.018>.
- FRANCISCHINI H, SALES MAF, DENTZIEN-DIAS P & SCHULTZ CL. 2017. The Presence of Ankylosaur Tracks in the Guarã Formation (Brazil) and Remarks on the Spatial and Temporal Distribution of Late Jurassic Dinosaurs. Ichnos. <https://doi.org/10.1080/10420940.2017.1337573>.
- FRANCO LS. 2018. Interpretação paleoambiental de um afloramento da Formação Serraria da Sub-bacia de Alagoas e caracterização petrográfica do nível estratigráfico correlato. Scientific initiation monograph of Universidade Federal de Sergipe, Sergipe, Brazil: 74 p.
- FREITAS FI, HESSEL MH & NETO JAN. 2008. Troncos fósseis da Formação Missão Velha na porção leste da Bacia do Araripe, Ceará. Rev Geol 21(2): 193-206.
- FREITAS VA & SILVEIRA RL. 2017. Bacia de Sergipe-Alagoas - Terra: Sumário Geológico e Setores em Oferta. 2015. Décima Quarta rodada de licitações, Agência Nacional do Petróleo, Gás Natural e Biocombustíveis, Superintendência de Definição de Blocos - SDB. Retrieved from: http://rodadas.anp.gov.br/arquivos/Round14/Mapas/sumarios/Sumario_Geologico_R14_SEL_Terra.pdf.
- GALLO V. 2005. Redescription of *Lepidotes piauhyensis* Roxo and Löfgren, 1936 (Neopterygii, Semionotiformes, Semionotidae) from the Late Jurassic-Early Cretaceous of Brazil. J Vertebr Paleontol 25: 757-769.
- GALLO V & BRITTO PM. 2004. An overview of Brazilian semionotids. In: G. Arratia and A. Tintori (eds.), Mesozoic Fishes 3—Systematics, Paleoenvironments and Biodiversity. Verlag Dr. Friedrich Pfeil, München, p. 253-264.
- GOLOBOFF PA & CATALANO SA. 2016. TNT version 1.5, including a full implementation of phylogenetic morphometrics. Cladistics 32: 221-238.
- GRILLO ON & DELCOURT R. 2017. Allometry and body length of abelisauroid theropods: *Pycnonemosaurus nevesi* is the new king. Cretac Res 69: 71-89. <https://doi.org/10.1016/j.cretres.2016.09.001>.
- GUZMÁN J, FAMBRINI G, OLIVEIRA E & USMA-CUERVO C. 2015. Estratigrafia da Bacia de Jatobá: estado da arte. Estudos Geológicos 25: 53-76.
- GUZMÁN-GONZÁLEZ J, PIOVESAN EK, FAMBRINI GL & OLIVEIRA E. 2016. Non-marine ostracoda from the Aliança Formation in the north-central portion of the Jatobá Basin, northeastern Brazil. Rev Bras Paleontol 19: 15-24.
- HAMMER Ø, HARPER DAT & RYAN PD. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. Palaeontol Electron 4: 9.
- HANSON M & MAKOVICKY PJ. 2014. A new specimen of *Torvosaurus tanneri* originally collected by Elmer Riggs, Historical Biology 26(6): 775-784. [10.1080/08912963.2013.853056](https://doi.org/10.1080/08912963.2013.853056).
- HARRIS JD. 1998. A reanalysis of *Acrocanthosaurus atokensis*, its phylogenetic status, and paleobiogeographic implications, based on a new specimen from Texas. Bull New Mex Museum Nat Hist Sci 13: 1-75.
- HESSEL MH. 2014. Bacias interiores do nordeste brasileiro e seus fósseis de invertebrados. In: Ghilardi RP & Scheffler SM (Eds), Paleontologia de Invertebrados, o legado brasileiro. Porto Alegre, Sociedade Brasileira de Paleontologia: 55-74.
- HONE DWE, KEESEY TM, PISANI D & PURVIS A. 2005. Macroevolutionary trends in the Dinosauria: Cope's rule. J Evol Biol 18: 587-595. <https://doi.org/10.1111/j.1420-9101.2004.00870.x>.
- HUTT S, MARTILL DM & BARKER MJ. 1996. The first European allosaurid dinosaur (Lower Cretaceous, Wealden Group, England). Neues Jahrb Geol Palaontol Monatsheft: 635-644.
- IBRAHIM N, MAGANUCO S, DAL SASSO C, FABBRI M, AUDITORE M, BINDELLINI G & WIEMANN J. 2020. Tail-propelled aquatic locomotion in a theropod dinosaur. Nature 581(7806) 67-70. <https://doi.org/10.1038/s41586-020-2190-3>.

- KANE A, HEALY K, RUXTON GD & JACKSON AL. 2016. Body size as a driver of scavenging in theropod dinosaurs. *Am Nat* 187: 706-716. <https://doi.org/10.1086/686094>.
- KEARNEY M. 2002. Fragmentary taxa, missing data, and ambiguity: Mistaken assumptions and conclusions. *Syst Biol* 51: 369-381. <https://doi.org/10.1080/10635150252899824>.
- KEARNEY M & CLARK JM. 2003. Problems due to missing data in phylogenetic analyses including fossils: a critical review. *J Vertebr Paleontol* 23(2): 263-274. [https://doi.org/10.1671/0272-4634\(2003\)023\[0263:PDTMDI\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2003)023[0263:PDTMDI]2.0.CO;2).
- KUCHLE J, SCHERER CMS, BORN CC, ALVARENGA RS & ADEGAS F. 2011. A contribution to regional stratigraphic correlations of the Afro-Brazilian depression e The Dom João Stage (Brotas Group and equivalent units e Late Jurassic) in Northeastern Brazilian sedimentary basins. *J S Am Earth Sci* 31: 358-371.
- LANGER MC ET AL. 2019. A new desert-dwelling dinosaur (Theropoda, Noasaurinae) from the Cretaceous of south Brazil. *Sci Rep* 9: 9379. <https://doi.org/10.1038/s41598-019-45306-9>.
- LEITE JF, PIRES STM & ROCHA EGAD. 2001. Estudo Hidrogeológico da Bacia do Jatobá/PE. *Série Hidrogeologia. Estudos e Projetos* (7): 55.
- LEONARDI G, CARVALHO IS & FERNANDES MA. 2007. The desert ichnofauna from Botucatu Formation (Upper Jurassic - Lower Cretaceous), Brazil. In: Carvalho IS, Cassab RCT, Schwanke C, Carvalho MA, Fernandes ACS, Rodrigues MAC, Carvalho MSS, Arai M & Oliveira MEQ (Eds), *Paleontologia: Cenários da Vida*, vol. 1. Interciência: 379-391. doi: 10.13140/RG.2.2.18583.78240.
- MANTELL GA. 1827. Illustrations of the geology of Sussex. *Fellow R Coll Surg*, 92 p.
- MADSEN JH. 1976. *Allosaurus fragilis*: a revised osteology. *Utah Geol Surv Bull* 109: 1-163.
- MAGNAVITA LP & CUPERTINO JA. 1988. Conceção atual sobre as bacias de Tucano e Jatobá, Nordeste do Brasil. *Bol Geocie Petrobras* 1(2): 119-134.
- MAGNAVITA LP, SZATMARI P, CUPERTINO JA & DESTRO NDGR. 2012. The Recôncavo Basin. In: Roberts DG & Bally AW (Eds), *Regional Geology and Tectonics: Phanerozoic Rift Systems and Sedimentary Basins*. Amsterdam: Elsevier Science, p. 383-420.
- MALAFIA E, MOCHO P, ESCASO F & ORTEGA F. 2020. A new carcharodontosaurian theropod from the Lusitanian Basin: evidence of allosauroid sympatry in the European Late Jurassic. *J Vertebr Paleontol*: e1768106. <https://doi.org/10.1080/02724634.2020.1768106>.
- MALAFIA E, MOCHO P, ESCASO F & ORTEGA F. 2017. New data on the anatomy of *Torvosaurus* and other remains of megalosauroid (Dinosauria, Theropoda) from the Upper Jurassic of Portugal. *J Iber Geol* 43: 33-59. <https://doi.org/10.1007/s41513-017-0003-9>.
- MALAFIA E, MOCHO P, ESCASO F, DANTAS P & ORTEGA F. 2019. Carcharodontosaurian remains (Dinosauria, Theropoda) from the Upper Jurassic of Portugal. *J Paleontol* 93: 157-172.
- MARTINELLI AG, RIBEIRO LCB, MÉNDEZ AH, NETO FM, CAVELLANI CL, FELIX E, FERRAZ MLF & TEIXEIRA VPA. 2013. Insight on the theropod fauna from the Uberaba Formation (Bauru Group), Minas Gerais state: New megaraptoran specimen from the Late Cretaceous of Brazil. *Riv Ital Paleontol Stratigr* 119: 205-214.
- MARZOLI A, RENNE PR, PICCIRILLO EM, ERNESTO M, BELLINI G & MIN A. 1999. Extensive 200-Million-Year-Old continental flood basalts of the Central Atlantic Magmatic Province. *Science* 284: 616-618. doi: 10.1126/science.284.5414.616.
- MATEUS O. 2006. Late Jurassic dinosaurs from the Morrison Formation (USA), the Lourinhã and Alcobaça Formations (Portugal), and the Tendaguru beds (Tanzania): a comparison. *New Mex Museum Nat Hist Sci Bull* 36: 223-231.
- MATEUS O, ARAÚJO R, NATÁRIO C & CASTANHINHA R. 2011. A new specimen of the theropod dinosaur *Baryonyx* from the early Cretaceous of Portugal and taxonomic validity of *Suchosaurus*. *Zootaxa* 2827: 54-68. <https://doi.org/10.11646/zootaxa.2827.1.3>.
- MATEUS O, WALLEN A & ANTUNES MT. 2006. The large theropod fauna of the Lourinha Formation (Portugal) and its similarity to the Morrison Formation, with a description of a new species of *Allosaurus*. *New Mex Museum Nat Hist Sci Bull* 36: 123-129.
- MEDEIROS MA, LINDOSO RM, MENDES ID, CARVALHO IS. 2014. The Cretaceous (Cenomanian) continental record of the Laje do Coringa flagstone (Alcântara formation), northeastern South America. *J South Am Earth Sci* 53: 50-58.
- MEDEIROS MA & SCHULTZ CL. 2002. A fauna dinossauriana da "Laje do Coringa", Cretáceo Médio do nordeste do Brasil. *Arq Mus Nac* 60: 155-162.
- MELO BGV & CARVALHO IS. 2017. A Fauna da Formação Brejo Santo, Neojurássico da Bacia do Araripe, Brasil: Interpretações Paleoambientais. *An Instituto de Geociências UFRJ* 40(3/2017): 62-74.
- MELTON B. 2008. A geological and Geophysical study of the Sergipe-Alagoras Basin. MSc thesis from Texas A&M University: 60 p. (Unpublished).
- MÉNDEZ AH, NOVAS FE & IORI FV. 2012. First record of Megaraptora (Theropoda, Neovenatoridae) from

- Brazil. *Comptes Rendus Palevol* 11: 251-256. <https://doi.org/10.1016/j.crpv.2011.12.007>.
- MÉNDEZ AH. 2014. The caudal vertebral series in abelisaurid dinosaurs. *Acta Palaeontol Pol* 59(1): 99-107.
- MILANI EJ. 2007. Cartas Estratigráficas. *Boletim de Geociências da Petrobras* 15(2): 573.
- MONTEFELTRO FC, LARSSON HCE, FRANÇA MAG & LANGER MC. 2013. A new neosuchian with Asian affinities from the Jurassic of northeastern Brazil. *Naturwissenschaften* 100(9): 835-841. doi:10.1007/s00114-013-1083-9.
- MOTTA MJ, ROLANDO AMA, ROZADILLA S, AGNOLÍN FE, CHIMENTO NR, EGLI FB & NOVAS FE. 2016. New Theropod Fauna From the Upper Cretaceous (Huincul Formation) of Northwestern Patagonia , Argentina. *New Mex. Museum Nat Hist Sci Bull* 71: 231-253.
- MUSSA D & MUNIZ GCB. 1985. Tronco silicificado da Formação Sergi, Estado de Pernambuco, Brasil. *Congresso Brasileiro de Geologia*, 9. Fortaleza: Anais, p. 58.
- NETTO AST & OLIVEIRA JJ. 1985. O preenchimento da Rift-Valley na Bacia do Recôncavo. *Rev Bras Geoci* 15(2): 97-102.
- NOVAS FE, AGNOLÍN FL, EZCURRA MD, PORFIRI J & CANALE JL. 2013. Evolution of the carnivorous dinosaurs during the Cretaceous: The evidence from Patagonia. *Cretac Res* 45: 174-215. <https://doi.org/10.1016/j.cretres.2013.04.001>.
- NOVAS FE, VALAIS S, VICKERS-RICH P & RICH T. 2005. A large Cretaceous theropod from Patagonia, Argentina, and the evolution of carcharodontosaurids. *Naturwissenschaften* 92: 226-230. <https://doi.org/10.1007/s00114-005-0623-3>.
- O'CONNOR PM. 2007. The postcranial axial skeleton of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. *J Vertebr Paleontol* 27: 127-163. [https://doi.org/10.1671/0272-4634\(2007\)27](https://doi.org/10.1671/0272-4634(2007)27).
- ORTEGA F, ESCASO F & SANZ JL. 2010. A bizarre, humped Carcharodontosauria (Theropoda) from the lower cretaceous of Spain. *Nature* 467: 203-206. <https://doi.org/10.1038/nature09181>.
- PADIAN K, HUTCHINSON JR & HOLTZ TR. 1999. Phylogenetic definitions and nomenclature of the major taxonomic categories of the carnivorous Dinosauria (Theropoda). *J Vertebr Paleontol* 19(1): 69-80.
- PEDREIRA AJ. 2000. Sergi River Canyon, Brazil. In: Schobbenhaus C, Campos DA, Queiroz ET, Winge M & Berbert-Born M (Eds), *Sítios Geológicos e Paleontológicos do Brasil*, SIGEP. <http://sigep.cprm.gov.br/sitio095/sitio095english.html>.
- PEDREIRA AJ & BAHIA RBC. 2000. Sedimentary Basins of Rondônia State, Brazil: Response to the Geotectonic Evolution of the Amazonian Craton. *Rev Bras Geoci* 30(3): 477-480.
- PEDREIRA AJ & BAHIA RBC. 2004. Estratigrafia e Evolução da Bacia dos Parecis Região Amazônica, Brasil. *CPRM - Serviço Geológico do Brasil*: 40 p.
- PEREIRA PVLGC, VEIGA IM, RIBEIRO TB, CARDOZO RH, CANDEIRO CRA, BERGQVIST LP. 2020a. The Path of Giants: A New Occurrence of Rebbachisauridae (Dinosauria, Diplodocoidea) in the Açu Formation, NE Brazil, and its Paleobiogeographic Implications. *J South Am Earth Sci* 3:102515.
- PEREIRA PVLGC, RIBEIRO TB, BRUSATTE SL, CANDEIRO CRA, MARINHO TS & BERGQVIST LP. 2020b. Theropod (Dinosauria) diversity from the Açu Formation (mid-Cretaceous), Potiguar Basin, Northeast Brazil. *Cretac Res* 114: 104517. <https://doi.org/10.1016/j.cretres.2020.104517>.
- PERSONS IVWS & CURRIE PJ. 2011. Dinosaur speed demon: The caudal musculature of *Carnotaurus sastrei* and implications for the evolution of South American abelisaurids. *PLoS One* 6: e25763. <https://doi.org/10.1371/journal.pone.0025763>.
- PIERINI C, MIZUSAKI AM, PIMENTEL FACCINI UF & SCHERER CMS. 2010. Paleoweathering features in the Sergi Formation (Jurassic-Cretaceous), northeastern Brazil, and implications for hydrocarbon exploration. *J South Am Earth Sci* 29: 412-426. <https://doi.org/10.1016/j.jsames.2009.04.002>.
- PINHEIRO AEP, PEREIRA PVGC, SOUZA LG, BRUM AS, LOPES RT, MACHADO AS, BERGQVIST LP & SIMBRAS FM. 2018. Reassessment of the enigmatic crocodyliform "*Goniopholis paulistanus* Roxo, 1936: Historical approach, systematic, and description by new materials. *PLoS ONE* 13(8): e0199984.
- RAUHUT OWM. 1999. A dinosaur fauna from the Late Cretaceous (Cenomanian) of northern Sudan. *Palaeontol Afr* 35: 61-84.
- RAUHUT OWM. 2011. Theropod dinosaurs from the Late Jurassic of Tendaguru (Tanzania). *Spec Pap Palaeontol*: 195-239.
- RAUHUT OWM, HÜBNER TR & LANSER K-PL. 2016. A new megalosaurid theropod dinosaur from the late Middle Jurassic (Callovia) of north-western Germany: Implications for theropod evolution and faunal turnover in the Jurassic. *Palaeontol Electronica* 19: 1-65.
- RICARDI-BRANCO F. 2004. Jazigos Paleobotânicos do Brasil. In: Carvalho IS (Ed), *Paleontologia*, vol 2. Editora Interciência, RJ, p. 85-96.
- ROCHA DEGA. 2011. Caracterização do intervalo carbonático aptiano da Bacia do Jatobá, NE do Brasil. Tese de Doutorado em Geociências - Centro de Tecnologia e Geociências, UFPE, 124 p.
- ROCHA DEGA, AMARAL CA & MEDEIROS VC. 2008. Bacias Sedimentares e Magmatismo Juro-Cretáceo. In: Medeiros VC (Ed), *Geologia e Recursos Minerais da Folha Souza*,

- SB. 34-Z-A. Estados da Paraíba, Rio Grande do Norte e Ceará. CPRM - Serviço Geológico do Brasil: 49-74.
- SALEM AM, MORAD S, MATO LF & AL-AASM IS. 2000. Diagenesis and Reservoir-Quality Evolution of Fluvial Sandstones During Progressive Burial and Uplift: Evidence from the Upper Jurassic Boipeba Member, Recôncavo Basin, Northeastern Brazil. *AAPG Bulletin* 84(7): 1015-1040.
- SAKAMOTO M. 2010. Jaw biomechanics and the evolution of biting performance in theropod dinosaurs. *Proc R Soc B Biol Sci* 277: 3327-3333. <https://doi.org/10.1098/rspb.2010.0794>.
- SANTOS CF, CUPERTINO JA & BRAGA JAE. 1990. Síntese sobre a geologia das bacias do Recôncavo, Tucano e Jatobá. In: Raja GP & Milani EJ (Eds), *Origem e Evolução de Bacias Sedimentares*. Rio de Janeiro: Petrobras, p. 235-266.
- SANTOS MECM & CARVALHO MSS. 2004. Paleontologia das Bacias do Parnaíba, Grajaú e São Luís: Reconstituições Paleobiológicas. CPRM, Serviço Geológico do Brasil, 211 p.
- SCHERER CMS. 2000. Eolian dunes of the Botucatu Formation (Cretaceous) in Southernmost Brazil: morphology and origin. *Sediment Geol* 137: 63-84.
- SCHERER CMS & LAVINA ELC. 2005. Sedimentary cycles and facies architecture of aeolian-fluvial strata of the Upper Jurassic Guarã Formation, southern Brazil. *Sedimentol* 52: 1323-1341.
- SCHERER CMS & LAVINA ELC. 2006. Stratigraphic evolution of a fluvial - eolian succession: The example of the Upper Jurassic - Lower Cretaceous Guarã and Botucatu formations, Paraná Basin, Southernmost Brazil. *Gondwana Res* 9: 475-484.
- SCHERER CMS, LAVINA ELC, DIAS FILHO DC, OLIVEIRA FM, BONGIOLO DE & AGUIAR ES. 2007. Stratigraphy and facies architecture of the fluvial - aeolian - lacustrine Sergi Formation (Upper Jurassic), Recôncavo Basin, Brazil. *Sediment Geol* 194: 169-193.
- SCHNEIDER CA, RASBAND WS & ELICEIRI KW. 2012. NIH Image to ImageJ: 25 years of image analysis. *Nat. Methods* 9: 671-675. <https://doi.org/10.1038/nmeth.2089>.
- SCHOBHENHAUS C, CAMPOS DA, DERZE GR & ASMUS HE. 1984. *Geologia do Brasil*. Departamento Nacional de Produção Mineral, 500 p.
- SERENO PC, DUTHEIL DB, LAROCHE M, LARSSON HCE, LYON GH, MAGWENE PM, SIDOR CA, VARRICCHIO DJ & WILSON JA. 1996. Predatory dinosaurs from the Sahara and Late Cretaceous faunal differentiation. *Science* 272: 986-991. <https://doi.org/10.1126/science.272.5264.986>.
- SERENO PC, MARTINEZ RN, WILSON JA, VARRICCHIO DJ, ALCOBER AO & LARSON HCE. 2008. Evidence for avian intrathoracic air sacs in a new predatory dinosaur from Argentina. *Plos ONE* 3(9): e3303.
- SILVA AJP, LOPES RC, VASCONCELOS AM & BAHIA RBC. 2003. Bacias Sedimentares Paleozóicas e Meso-Cenozóicas Interiores. In: Bizzi LA, Schobbenhaus C, Vidotti RM & Gonçalves JH (Eds), *Geologia, Tectônica e Recursos Minerais do Brasil*, CPRM - Serviço Geológico do Brasil: 55-85. <https://doi.org/10.1371/journal.pone.0003303>.
- SILVA MC, CARVALHO MSS, BARRETO AMF & CARVALHO ISC. 2011. Paleoiçtíofauna da Formação Aliança (Jurássico Superior), Bacia de Jatobá, Nordeste do Brasil. In: Carvalho IS, Srivasta NK, Strohschoen O & Lana CC (Eds), *Paleontologia: cenários de vida*, vol. 4, Rio de Janeiro: Interciência, p. 595-608.
- SOUZA RG. 2018. Comments on the Serial Homology and Homologues of Vertebral Lateral Projections in Crocodylia (Eusuchia). *Anat. Rec* 301(7): 1203-1215.
- STOVALL JW & LANGSTON W. 1950. *Acrocantiosaurus atokensis*, a new genus and species of Lower Cretaceous Theropoda from Oklahoma. *Am Midl Nat* 1950(43): 696.
- VAZ PT, WANDERLEY FILHO JR & BUENO GV. 2007. A Bacia do Tacutu. *Boletim de Geociências da Petrobras*, Rio de Janeiro, 15(2): 289-297.
- VIANA CF, GAMA JR EG, SIMÕES JA, MOURA JA, FONSECA JR & ALVES RJ. 1971. Revisão estratiigráfica da Bacia Recôncavo/Tucano. *Bol Têc Petrobras*, Rio de Janeiro, 14(3/4): 157-192.
- VILAS BÔAS I, CARVALHO IS, MEDEIROS MA & PONTES H. 1999. Dentes de *Carcharodontosaurus* (Dinosauria, Tyrannosauridae) do Cenomaniano, Bacia de São Luís (norte do Brasil). *An Acad Bras Cienc* 71: 846-847.
- VILAS BOAS DBR, SOUZA PAVD & HOLZ M. 2018. Correlação Sismoestratiigráfica entre as bacias do Recôncavo e de Camamu. *Geociências* 37(3): 467-481.
- VITA LPM & CUPERTINO JA. 1988. A new approach to the geological configuration of the Lower Cretaceous Tucano and Jatobá basins, northeastern Brazil. *Rev Bras Geoci* 18(2): 220-230.
- WELLES SP. 1952. A review of the North American Cretaceous elasmosaurs. *Univ Calif Publ Geol Sci* 29: 47-144.
- WELLES SP. 1984. *Dilophosaurus wetherilli* (Dinosauria, Theropoda). Osteology and comparisons. *Palaeontographica Abt A* 185: 85-180.
- WIENS JJ. 2003a. Incomplete taxa, incomplete characters, and phylogenetic accuracy: Is there a missing data problem? *J Vertebr Paleontol* 23: 297-310. [https://doi.org/10.1671/0272-4634\(2003\)023\[0297:ITICAP\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2003)023[0297:ITICAP]2.0.CO;2).
- WIENS JJ. 2003b. Missing Data, Incomplete Taxa, and Phylogenetic Accuracy. *Syst Biol* 52(4): 528-538. <https://doi.org/10.1080/10635150390218330>.
- WILSON JA. 2006. Anatomical nomenclature of fossil vertebrates: standardized terms or 'lingua

franca? J Vertebr Paleontol 26: 511-518. [https://doi.org/10.1671/0272-4634\(2006\)26](https://doi.org/10.1671/0272-4634(2006)26).

ZANNO LE & MAKOVICKY PJ, 2013. Neovenatorid theropods are apex predators in the Late Cretaceous of North America. Nature Communications, 4.

SUPPLEMENTARY MATERIAL

Supplementary Appendix. Phylogenetic dataset (character list and scorings) and supplementary figures.

Figure S1. Strict consensus tree from our phylogenetic analysis.

Figure S2. Linear regressions of the caudal vertebrae of abelisaurids, megalosauroids, carcharodontosaurians, megaraptorans, MCT 2670-LE and UFRJ-DG 528-R.

Figure S3. Principal component (a) and linear discriminant analyses (b) of abelisaurids, megalosauroids, carcharodontosaurians and megaraptorans.

Table S1. Linear morphometrics dataset.

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Author contributions

The conceptualization of this project was developed by KLN and ASB. The preparation of the studied specimen was made by PVLGCP. Geological analysis of fossil site was carried by KLN, RVP and AEPP. Anatomical description and comparisons were performed by KLN, ASB, RVP and PVLGCP. Scorings of the matrix was performed by RVP and LGS. Phylogenetic analysis was performed by RVP, LGS and AEPP. Figures were prepared by ASB, RVP and LGS. All authors have contributed to the discussion of results, the manuscript input, the English revision, and approved the final version.

