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New dinosaur remains and the tetrapod fauna from the Upper Cretaceous of Mato Grosso State, central Brazil

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ABSTRACT

Mato Grosso State is the main area of paleontological investigations in central Brazil, especially regarding Upper Cretaceous beds. Fossil collection in the surroundings of the Morro do Cambambe started as early as late nineteenth century, but prospections and studies are still ongoing. This contribution presents new dinosaur specimens recovered from Upper Cretaceous outcrops of the southeastern portion of Mato Grosso State. These remains enabled the first report of a megaraptoran theropod based on a vertebral centrum and the description of abelisaurid (a fragmentary tooth) and titanosaur remains (a tooth and a fragment of a dorsal vertebra). Based on the amount of compiled reports of tetrapod remains from Mato Grosso, mainly from meeting abstracts and technical reports, the evidence at hand indicates a diverse Upper Cretaceous tetrapod assemblage still poorly explored in comparison to other Upper Cretaceous units of Brazil and Gondwana, in general.

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Introduction

Upper Cretaceous Gondwanan faunas are mainly known from Argentinean, Malagasy and Indian fossil sites, among which the former are likely the ones with the most extensive and diverse fossil record (e.g. Tandon et al. 1995; Bonaparte 1996; Rogers et al. 2007; Novas 2009; Novas et al. 2013). However, the post-Cenomanian continental vertebrate assemblages from Brazil have been the focus of systematic researches in the last decades, considerably increasing their known fossil record (Kellner 1996; Kellner & Campos 2000b; Bittencourt & Langer 2011). Particularly, outcrops in São Paulo and Minas Gerais states have been the most studied areas, bringing to light taxonomically diverse vertebrate associations from the Bauru Group of the Paraná Basin. Regarding the tetrapods, these assemblages include anurans, lizards, turtles, mesoeucrocodylians, non-avian dinosaurs and birds (e.g. Campos et al. 2005; França & Langer 2005; Kellner et al. 2005; 2006; Novas et al. 2005; 2008; Salgado & Carvalho 2008; Santucci 2008; Carvalho et al. 2011; Martinelli et al. 2011; 2013; Montefeltro et al. 2011; Báez et al. 2012; Martinelli & Teixeira 2015). In addition to the relatively well-known Bauru Group, other more recent and important records from Brazil include the tapejarid pterosaur *Caiuajara dobruskii* and the acrodontan lizard *Gueragama sulamericana* from the Caiuá Group of the same basin (Manzig et al. 2014; Simões et al. 2015). However, their Upper Cretaceous age is still disputable (e.g. Batezelli & Ladeira 2016).

Nevertheless, other Upper Cretaceous beds from Brazil seem to have been somehow overlooked, like those in the northwestern and central portions of the country. For instance, the Upper Cretaceous vertebrate record from Mato Grosso State is still poorly known and there is no consensus with respect to the geology of the vertebrate-bearing units at this region (see Geological settings). This scenario contrasts with both the vast area where Upper Cretaceous rocks crop out in that state and the history of local paleontological discoveries, which is trackable at least until the end of the nineteenth century (see Table 1 for references). It is also noteworthy that the only named post-Santonian theropod from Brazil, the abelisaurid theropod *Pycnonemosaurus nevesi* Kellner and Campos 2002, is from Mato Grosso (Kellner & Campos 2002).

Despite this and in order to enlarge the knowledge on Upper Cretaceous tetrapod assemblages from Gondwana, we describe new dinosaur specimens from outcrops north to the Chapada dos Guimarães (=Guimarães Plateau), in southeastern Mato Grosso State, central Brazil (Figure 1), including the first remain of a megaraptoran theropod from there. They allow further comparisons with better-known units (e.g. Bauru Group, São Paulo and Minas Gerais states, Brazil, and Neuquén Group, Patagonia, Argentina). In addition, we summarise the historical records of the known Upper Cretaceous Mato Grosso tetrapods and the geological problems, still unresolved, of the continental beds from the southeastern portion of the state. This is followed by taxonomic comments on some punctual published records.

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Table 1. Compilation of references with considerations on the vertebrate paleontological record from Cretaceous beds of Mato Grosso State, central Brazil. Information is presented as it was originally stated in the references. Similar superscript numbers refer to the same vertebrate fossil record.

Reference	Record	Locality	Stratigraphic Attribution
Articles			
Derby (1890)	Mention of vertebrate remains, including a fragment of a turtle shell and a vertebra of a reptile[1]	Near the little village of Chapada (=Morro do Cambambe after Weska 2006)	Secondary age?
Evans (1894)	Mention of vertebrate remains, including a turtle's carapace and a vertebra of another reptile[1]	Chapada	Sandstones of the Tabuleiros
Leme 1924 in du Toit (1952)	Mention of a dinosaur aff. *Scaphonyx*[2]	Cambembe	Not informed
Huene 1930 in Huene (1931)	Mention of titanosaur remains	Pedra	Upper Senonian
Roxo (1937)	Mention of dinosaur and chelonian bones[1,2?]	Morro do Cambambe	Upper Cretaceous
	Mention of reptile vertebrae, ribs and fragments of long bones and two or three small chelonian bones	Morro do Cambambe	Upper Cretaceous
	Mention of bones	Morro Grande	Upper Cretaceous
Mendes (1953)	Mention of fossil reptile bones[3]	Rio Roncador	Cretaceous (Baurú series)
Price (1956)	Mention of fossils, including cervical vertebrae of sauropods[4]	Between the Upper Rio Manso and Serra Azul	Cretaceous
	Mention of dinosaur bone fragments collected by Cicero de Campos[2]	Pedra (=Pedra Grande)	Not informed
	Mention of dinosaur material recorded by Mendes 1953; [3]	Valley of Rio Roncador	Cretaceous
	Mention of dinosaur fossils	Morro do Cambambe	Upper Cretaceous
Kellner and Campos (2000b)	Mention of a basal tetanuran tooth with transverse wrinkles[5]	Morro do Cambambe	Cretaceous strata of Mato Grosso
	Mention of isolated bones and sauropod and theropod teeth[5]	Morro do Cambambe	Cretaceous strata of Mato Grosso
	Mention of isolated sauropod bones, including Titanosauridae[6]	Fazenda Confusão	Cretaceous strata of Mato Grosso
	Mention of an incomplete theropod skeleton[7] found associated to titanosaur remains[8]	Fazenda Roncador	Cretaceous strata of Mato Grosso
Bittencourt and Kellner (2002)	Description of nine abelisaurid teeth[7]	Not informed	Continental Cretaceous of Mato Grosso
Kellner and Campos (2002)	Description of *Pycnonemosaurus nevesi*[7]	Fazenda Roncador	Bauru Group
	Several isolated sauropod bones, including titanosaur caudal vertebrae[8]	Fazenda Roncador	Bauru Group
Franco-Rosas et al. (2004)	Description of vertebrae and a tíbia assigned to *Gondwanatitan* sp.[9]	Morro do Cambambe	Cambambe Formation
Bittencourt and Langer (2011)	Mention of *Gondwanatitan* sp.[9]	Not informed	Parecis Group
	Mention of isolated teeth attributed to Abelisauridae[7]	Not informed	Parecis Group
	Mention of isolated teeth attributed to Deinonychosauria[10]	Not informed	Parecis Group
	Mention of *P. nevesi*[7]	Not informed	Parecis Group
	Mention of Theropoda indet.[5, 11]	Not informed	Parecis Group
	Mention of a partial postcranium attributed to Titanosauria indet.[6,12]	Not informed	Parecis Group
	Mention of isolated attributed to Titanosauria indet.[5]	Not informed	Parecis Group
Faria et al. (2012)	Mention of *Gondwanatitan* sp.[9]	Serra do Cambambe	Bauru Group
	Mention of *Pycnonemosaurus*[7]	Fazenda Roncador	Bauru Group
	Mention of teeth attributed to Abelisauridae indet.[7]	Fazenda Roncador	Bauru Group
	Mention of titanosaurid vertebrae and fragments[8]	Fazenda Roncador	Bauru Group
	Mention of teeth attributed to Sauropoda indet.[5]	Morro do Cambambe	Bauru Group
	Mention of teeth attributed to Theropoda indet.[10]	Morro do Cambambe	Bauru Group
Souto and Fernandes (2015)	Brief description of a coprolite from a herbivore	Morro do Cambambe	Cambambe Formation (Bauru Basin)
Books and chapters			
Savage-Landor (1913)	Brief description of reptile vertebrae and skulls[4] and two mammal skulls	Rio Pedra Grande	Not informed
	Mention of fossils and fragments, including a pelvis and a petrified foot of an enormous animal	Rio Pedra Grande	Not informed
	Mention of fossil bones of a gigantic animal found by a Brazilian expedition	200 km south to Riacho Pedra Grande	Not informed
	Mention of remains of a giant animal found by a Brazilian expedition	Rio Paranatinga	Not informed
Oliveira and Leonardos (1943)	Mention of dinosaurs and chelonians[1,2]	Morro do Cambambe	Baurú Formation
Du Toit (1952)	Mention of dinosaurs and chelonians[1]	Morro do Cambambe	Bauru Formation
Campos and Campos (1975)	Titanosaurid caudal vertebra, pubis fragments and ribs, collected by L. I. Price and C. O. Berbert in 1971[13]	Fazenda Confusão	Bauru Formation
Souza et al. (2011)	Brief description of a caudal centrum and a radius of Sauropoda and a theropod caudal vertebra	Jangada Roncador	Cachoeira do Bom Jardim Formation
	Brief description of a theropod (Abelisauridae) tooth	Morro do Cambambe	Cambambe Formation

Bittencourt and Langer (2012)	Mention of *Gondwanatitan* sp.[9]	Not informed	'Cambambe Formation' of the Parecis Group
	Mention of *P. nevesi*[7]	Not informed	Parecis Group
	Mention of teeth attributed to Abelisauridae[7]	Not informed	Parecis Group
	Mention of teeth attributed to Deinonychosauria[10]	Not informed	Parecis Group
Abstracts			
Price (1961)	Mention of dinosaur bones	Morro do Cambambe and northeast to Cuiabá	Not informed
Azevedo et al. (1995)	Mention of theropod and sauropod teeth[5] and indeterminate bone fragments	Morro do Cambambe	Cambambe Formation
	Mention of a sauropod femur along with rib fragments and isolated bones exhibited at the Museu Ramis Bucair, Cuiabá Municipality, Mato Grosso State, Brazil	Morro do Cambambe?	Cambambe Formation
Kellner et al. (1995a)	Mention of dinosaur bones[13]	Córrego Confusão	Correlated to the Bauru Group
	Mention of sauropod vertebrae and ribs, likely Titanosauridae[6], and indeterminate bone fragments	Ribeirão Confusão	Correlated to the Bauru Group
	Mention of a sauropod femur housed at the Colégio Comercial de Contabilidade Luiz Orione, Guiratinga Municipality, Mato Grosso State, Brazil[6]	Córrego Confusão	Correlated to the Bauru Group
Kellner et al. (1995b)	Mention of sauropod bones and unidentified fragments[6]	Confusão Farm	Similar to the layers of the Bauru Group
	Mention of theropod and titanosaurid teeth[5]	Cambambe Hill	Bauru Group
Silva and Kellner (1998)	Brief description of a theropod tooth[5]	Morro do Cambambe	Upper portion of the Bauru Group
Kellner and Campos (2000a)	Brief description of a partial post-cranial skeleton and teeth of a theropod[7]	Fazenda Roncador	Continental Cretaceous strata of Mato Grosso
	Mention of titanosaurid[8] and turtle remains	Fazenda Roncador	Continental Cretaceous strata of Mato Grosso
Marconato et al. (2001)	Mention of vertebrate ribs, epiphyses, and weathered fragments, including a turtle carapace fragment	Morro do Cambambe	Not informed
	Brief description of a dinosaur chevron and theropod[10] and sauropod teeth	Morro do Cambambe	Not informed
Franco-Rosas (2001)	Mention of fossil elements and fragments attributed to theropods, sauropods, crocodiles and turtles	Not informed	Cambambe Formation
	Brief description of teeth attributed to Velociraptoridae and a small theropod[10]	Morro do Cambambe	Cambambe Formation
Franco-Rosas et al. (2001)	Mention of bone fragments typical of fishes and reptiles, including two theropod teeth	Near Rio Roncador	Not informed
	Brief description of three fish? coprolites	Near Rio Roncador	Not informed
Marconato et al. (2003)	Brief description of a coprolite attributed to a large herbivorous animal	Paranatinga	Parecis Group
Kellner et al. (2004)	Several fragmentary bones and teeth[11]	Near Confusão Creek	Correlated with the lithostratigraphic units of the Bauru Group
	Mention of a sequence of titanosaur dorsal and caudal vertebrae, found associated with long bones[12]	Near Confusão Creek	Correlated with the lithostratigraphic units of the Bauru Group
Marconato et al. (2004)	Brief description of two partial skeletons attributed to two new taxa of 'notosuchian' crocodiles[14]	Nordeste do Mato Grosso	Parecis Group
Alves et al. (2006)	Mention of twenty-two theropod teeth	Confusão	Bauru Group
Ghilardi et al. (2011)	Review of previous records[7,9,11,12,14]	Morro do Cambambe, Roncador Farm, Confusão Creek, and Araguaia River	Marília Formation of the Bauru Group and Salto das Nuvens Formation of the Parecis Group
	Mention of a distal portion of a humerus and a middle portion of a tibia attributed to sauropods	Araguaia River, near the city of Araguaiana	Marília Formation
	Mention of photographic records of bone fragments	Araguaia River, near the city of Araguaiana	Marília Formation
Bandeira et al. (2016)	Brief description of titanosaur remains	Morro do Cambambe	Cambambe Formation
Theses			
Marconato (2006)	Description of 'Crocodiles 1 and 2'[14]	Baixo Araguaia	'Tapirapé Sequence' of the Parecis Group

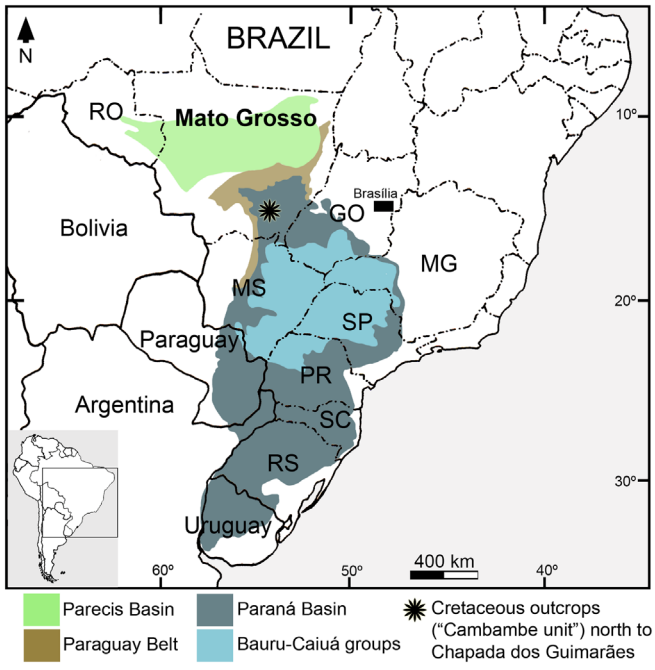

Figure 1. Location map of the area with Upper Cretaceous fossiliferous outcrops in southeastearn Mato Grosso State, central Brazil. Abbreviations: GO, Goiás State; PR, Paraná State; RO, Rondônia State; RS, Rio Grande do Sul State; SC, Santa Catarina State; SP, São Paulo State. Modified from Menegazzo et al. (2016).

Although our study is based upon fragmentary and isolated specimens, the Upper Cretaceous beds of Mato Grosso are promissory to expand the paleontological studies in central Brazil.

Geological settings

The first discoveries of Cretaceous tetrapods in Mato Grosso were made in the late nineteenth century in the southeastern portion of the state (Derby 1890; Evans 1894; Price 1961). Particularly, there are two areas in this region of Mato Grosso where the most fossiliferous outcrops are located (Table 1). One of them corresponds to the Chapada dos Guimarães where the Morro do Cambambe and Fazenda Roncador are located, north to Cuiabá Municipality. The other includes the Graben do Tesouro and Fazenda Confusão, located southeast to the former region. Those two fossiliferous areas are about 250 km distant from each other.

In the last years, a few Cretaceous records were also recovered from the northern portion of the state, in rocks of the Parecis Basin (sensu Barros et al. 1982), but these findings remain formally unpublished (Marconato et al. 2003; 2004; Marconato 2006). Since the initial discoveries of Cretaceous tetrapods in Mato Grosso, only few contributions have been made in order to address this fauna and their geological settings (Table 1). Furthermore, most data are still available only as preliminary notes and technical reports of the Serviço Geológico e Mineralógico do Brasil (e.g. Smith 1921 in Oliveira & Leonardos 1943; Roxo 1937) and Petrobras (Bauer & Largher 1958), scientific meeting abstracts (e.g. Franco-Rosas 2001; Rubert et al. 2004; Ghilardi et al. 2011) or unpublished thesis (Weska 1987, 1996; Marconato 2006).

The localities with fossils mentioned in this contribution are settled in the southeastern portion of the state, south to the Neoproterozoic Paraguay Belt (Figure 1), and the interpretations of the stratigraphy of the fossil-yielding beds have fluctuated radically over the years (see below). North to the Paraguay Belt, the Parecis Basin is developed and well defined geographically (Bahia et al. 2006; 2007; Menegazzo et al. 2016) and the Parecis Group is restricted to units deposited during the Upper Cretaceous (Bahia et al. 2006; 2007). The recognised formations of the Parecis Group are the Salto das Nuvens (below) and the Utiariti (above) formations (Bahia et al. 2006; 2007; Batezelli & Ladeira 2016; Menegazzo et al. 2016).

On the other hand, the stratigraphic referral of the Cretaceous rocks cropping out south to the Paraguay Belt is still controversial. They were ambiguously included as part of either the Parecis Basin (Weska 2006) or the Bauru Group (Weska 1987, 1996; Weska et al. 1993; 1996; Gibson et al. 1997; Kellner & Campos 2002). Such a problematic issue is commented below.

Some of the first correlations between rocks from southeastern Mato Grosso and the Bauru Group include those of Bauer and Largher (1958), Oliveira and Mülhmann (1965) and Gonçalves and Schneider (1970). Later, Weska (1987), in his dissertation, and Weska et al. (1996), in a scientific meeting abstract, informally defined four formations cropping out in the southeastern portion of the state and included them as part of the Bauru Group, laterally chrono-correlated with the Bauru Group formations (i.e. Adamantina and Marilia formations) cropping out along Goiás, Minas Gerais and São Paulo states. The formations proposed by Weska (1987; Weska et al. 1996) are (from the bottom to the top): Paredão Grande, Quilombinho, Cachoeira do Bom Jardim and Cambambe. In a subsequent paper, Weska (2006) summarised all his preliminary contributions and, contrarily, claimed that most formations recognised by him in the southeastern portion of Mato Grosso were actually similar to the formations of the Parecis Group rather than to the Bauru Group. Consequently, Weska (2006) proposed a sequence of the following formations (from the bottom to the top): Paredão Grande, Salto das Nuvens, Cachoeira do Bom Jardim and Utiariti, corresponding to the Upper Cretaceous of Mato Grosso. The Salto das Nuvens and Utiariti formations were originally described from the Parecis Group in the north of the state (Bahia et al. 2006; 2007). In the proposed scheme of Weska (2006), the Quilombinho and Cambambe formations (after Weska 1987) were synonymised and replaced with the Salto das Nuvens and Utiariti formations of the Parecis Group, respectively (see Bahia et al. 2006). Also, Weska (2006) maintained the Cachoeira do Bom Jardim Formation (originally proposed in his dissertation), positioned in between the known formations of the Parecis Group.

The radical changes between Weska (1987; see also Weska et al. 1996) and Weska (2006) is not clearly justified. Furthermore, the suppression of the Bauru Group in the southeastern portion of the state, considering the structural significance of the limits of the Parecis and Paraná basins (e.g. Bahia et al. 2006; Menegazzo et al. 2016), is not addressed at all. In addition, the inclusion of the Cachoeira do Bom Jardim Formation, proposed by Weska (1987) for the Bauru Group, by Weska (2006) in between the Salto das Nuvens (below) and Utiariti (above) formations of the Parecis Group has no basis.

Another problem to note is that the formations proposed in unpublished theses and scientific meeting abstracts are invalid according to the Article B19 of the Brazilian Stratigraphic Code

and Guide to Stratigraphic Classification (Comissão Especial de Nomenclatura Estratigráfica 1986). Consequently, these proposals (Weska 1987, 2006; Weska et al. 1996), in which the Cachoeira do Bom Jardim and Paredão Grande formations are maintained within the Parecis Group, should not be considered valid. Currently, they are not used in recent geological contributions (Gibson et al. 1997; Bahia et al. 2006; 2007; Batezelli & Ladeira 2016; Menegazzo et al. 2016).

Paleontological studies have followed the same incongruities over the years, still without a clear panorama. Kellner and Campos (2002) mentioned that *Pycnonemosaurus nevesi*, from the Fazenda Roncador, came from the Bauru Group, without specifying a formation. Franco-Rosas et al. (2004) and Ghilardi et al. (2011), among others, considered that the studied fossils were from the Cambambe Formation of the Bauru Group. On the other hand, Bittencourt and Langer (2011) mentioned that *P. nevesi* and the titanosaurs described by Franco-Rosas et al. (2004) belonged to the Parecis Group, without specifying a formation either. Recently, Souza et al. (2011) described more dinosaur remains from the Jangada Roncador locality and ascribed them to the Cachoeira do Bom Jardim Formation, following the stratigraphic scheme of Weska (2006).

Recent geological contributions on the Parecis (e.g. Bahia et al. 2006; 2007) and Bauru groups (e.g. Gibson et al. 1997; Batezelli & Ladeira 2016; Menegazzo et al. 2016) did not recognise the proposal of Weska (2006). In addition, the geological map of Mato Grosso State (scale 1:1.000.000; Lacerda et al. 2004) settles the Cretaceous fossiliferous localities of the southeastern part of the state within the Paraná Basin and the rocks are considered as 'Undifferentiated Bauru Group'.

Thus, the geological and paleontological realm of the southeastern portion of the Mato Grosso State, between the Parecis and Bauru groups, remains undefined and the problem might only be solved with integrated fieldworks along the Mato Grosso State.

The fossil remains herein described fall in this problematic issue and currently little contribute to clarify this stratigraphic controversy, since their main impact lies on taxonomic issues. Because of the aforementioned geological problems and the fossils come from the Morro do Cambambe region, whose most fossil-yielding beds were previously included in the Cambambe Formation, we opted to use in this contribution the informal name 'Cambambe Unit', between single quotation marks, included within the boundaries of the Paraná Basin.

Despite the stratigraphic uncertainties, the age of the basalt upon which the sedimentary units are laying (Gibson et al. 1997) and their fossil content indicate that the tetrapod associations have an Upper Cretaceous age (no older than Santonian), sharing similarities at some taxonomic levels with units from the Bauru Group in southeastern Brazil and the Neuquén Group in Patagonia, Argentina (see below).

Palaeontological background

The presence of Cretaceous vertebrate fossils in Mato Grosso was firstly reported by Derby (1890) and Evans (1894), the former mentioning some remains from beds of 'secondary age' (p. 63), including fragments of a turtle shell and a reptilian vertebra. The provenance of these findings seems to be the Morro do Cambambe region according to Weska (2006). Later, Leme (1911 in Oliveira & Leonardos 1943) was the first to identify dinosaur remains from that area.

During the 1940s and1950s, paleontologist Llewellyn Ivor Price and his crew performed fieldworks in the Morro do Cambambe and Fazenda Roncador localities and were able to collect bone remains and teeth, which are now housed at the Museu de Ciências da Terra, Rio de Janeiro Municipality, Brazil (Bastos 1946; Roxo 1956; Lamego 1957, 1958, 1959; Kellner & Campos 2002). Among them, some teeth, parts of seven caudal vertebrae, fragments of ribs and incomplete right tibia and fibula were later described as the holotype of *Pycnonemosaurus nevesi* by Kellner and Campos (2002). Then, Franco-Rosas et al. (2004) described five isolated bones (four partial vertebrae and a portion of tibia) from the Morro do Cambambe as belonging to the aeolosaurine titanosaur *Gondwanatitan* sp., a sauropod taxon firstly recorded from the Upper Cretaceous of the Bauru Group (Kellner & Azevedo 1999). More recently, Souza et al. (2011) briefly described a vertebral centrum and a radius attributed to Sauropoda and a vertebral centrum and a tooth, the latter regarded as Abelisauridae, all from the Jangada Roncador locality, but without justifying their assignments.

Other mentions of dinosaurs include fragmentary and/or undescribed bones and teeth of both sauropods and theropods from the Morro do Cambambe, Fazenda Confusão and Rio Araguaia, including possible deinonychosaurian teeth (Price 1961; Campos & Campos 1975; Azevedo et al. 1995; Kellner et al. 1995a, 1995b, 2004; Marconato et al. 2001; Franco-Rosas 2001; Ghilardi et al. 2011). These records have been reviewed by Kellner and Campos (2000b), Bittencourt and Langer (2011, 2012) and Faria et al. (2012). Finally, the Cretaceous vertebrate fossil record from Mato Grosso also comprises coprolites and partial skeletons of crocodylomorphs, the latter from the northeastern part of the state (Franco-Rosas et al. 2001; Marconato et al. 2003; 2004; Marconato 2006; Souto & Fernandes 2015). Particularly, the crocodylomorphs represent two new notosuchian taxa and are yet to be formally described. A more comprehensive overview of the literature that mentions Upper Cretaceous vertebrate body and trace fossils from Mato Grosso is presented in Table 1.

Material and methods

The specimens described here were collected by paleontologist Dharani Sundaram during the 1990s and donated to the vertebrate paleontological collection of the Departamento de Paleontologia e Estratigrafia of the Universidade Federal do Rio Grande do Sul (UFRGS), Porto Alegre Municipality, Brazil. All specimens were recovered from Cretaceous outcrops in the Morro do Cambambe area (see Geological settings).

For the description of the vertebral features, the terminology of Wilson (1999) and Wilson et al. (2011) is followed wherever possible, whereas for isolated tooth crowns we adopted that proposed by Hendrickx et al. (2015). Due to the fragmentary nature of most remains, high-level taxonomic assignments were possible mainly by comparisons with the literature cited in the respective sections. However, specifically for the taxonomic assignment of the isolated and fragmentary theropod tooth crown UFRGS-PV-038-K, it was used a cladistic approach following

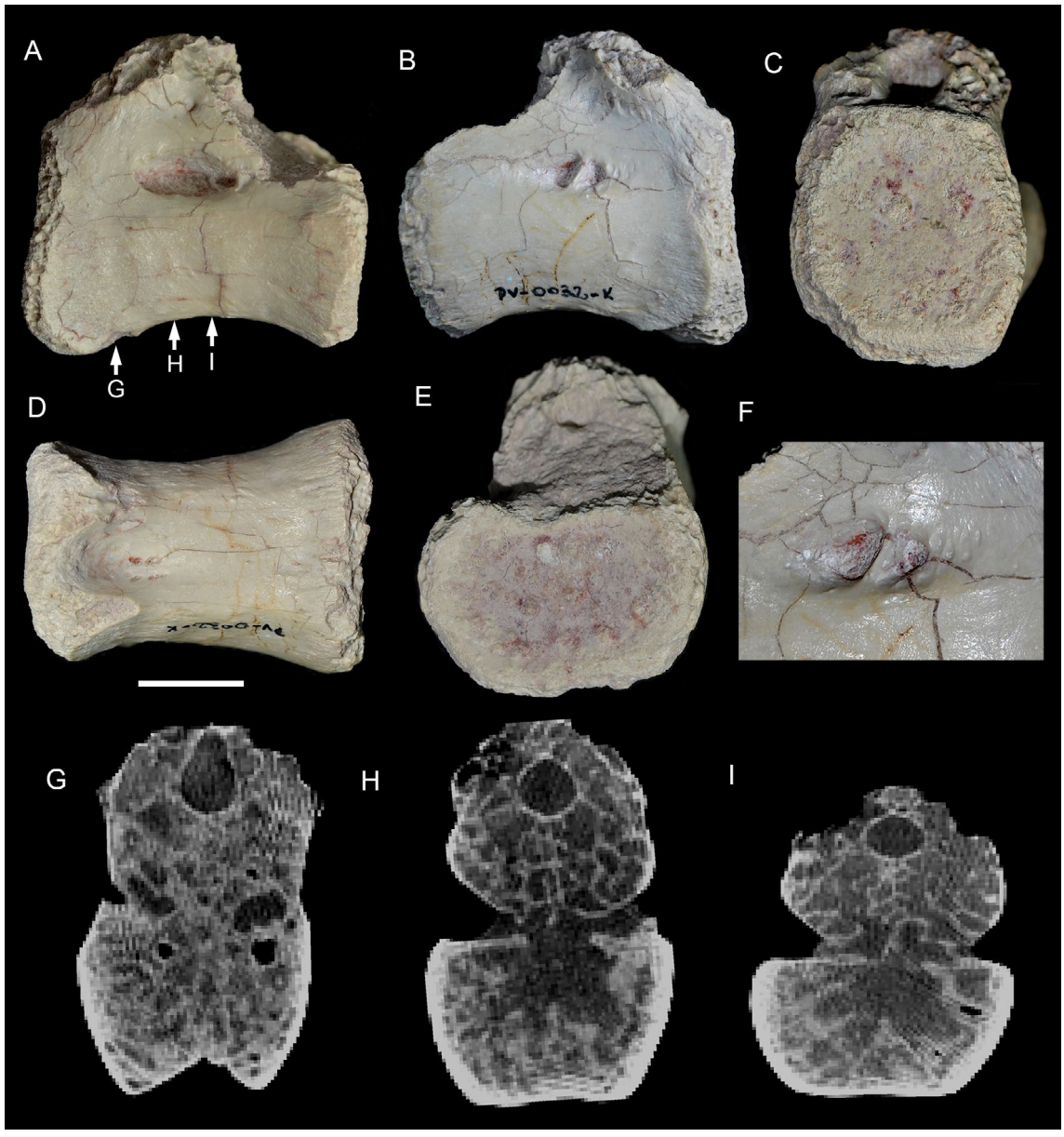

Figure 2. Megaraptora indet. from the Upper Cretaceous of Mato Grosso State, central Brazil. Specimen UFRGS-PV-032-K, middle caudal vertebral centrum in left lateral (A), right lateral (B), anterior (C), ventral (D) and posterior (E) views. Detail of the right lateral pleurocoel with chambers (F) and computed tomography slices (G-I) exhibiting the camellate internal tissue and the medial contact between right and left chambers. Scale bar equals 20 mm.

Hendrickx and Mateus (2014) by coding and including this specimen in their theropod data matrix of dentition-based characters (Appendix A). We also adopted the search parameters and options set by them in the software TNT v1.1 (Goloboff et al. 2008). Nevertheless, in order to diminish the influence of missing data, we removed from the matrix the isolated tooth crowns from the Lourinhã Formation (Upper Jurassic, Portugal) described by those authors. Once assigned to a particular taxon, each specimen was then compared mainly to those records to which it was more temporally and geographically close.

Finally, a computed tomography (CT) scanning of the vertebral element UFRGS-PV-032-K referred to Megaraptora was performed at the Serpal Clínica de Diagnóstico, Porto Alegre Municipality, Brazil, under a medical GE Light Speed Machine. It yielded 105 slices in coronal slice plan with dimensions of 512 × 512 pixels, each pixel measuring 0.488 mm. The other CT scan parameters are: slice thickness of 1 mm, slice increment (interslice spacing) of 0.6 mm, field of view of 250 mm, 120 kV and 150 mA. The obtained data was output from the scanner in DICOM format and then imported into InVesalius 3.0 – Beta 2 (Centro de Tecnologia da Informação Renato Archer – CTI, Brazil) for analyzing the internal structure of that vertebra.

Systematic palaeontology

DINOSAURIA Owen 1842
SAURISCHIA Seeley 1888
THEROPODA Marsh 1881
TETANURAE Gauthier 1986
MEGARAPTORA Benson et al. 2010
Gen. et sp. indet.

Referred material – UFRGS-PV-032-K, a middle caudal vertebral centrum (Figures 2 and 3).

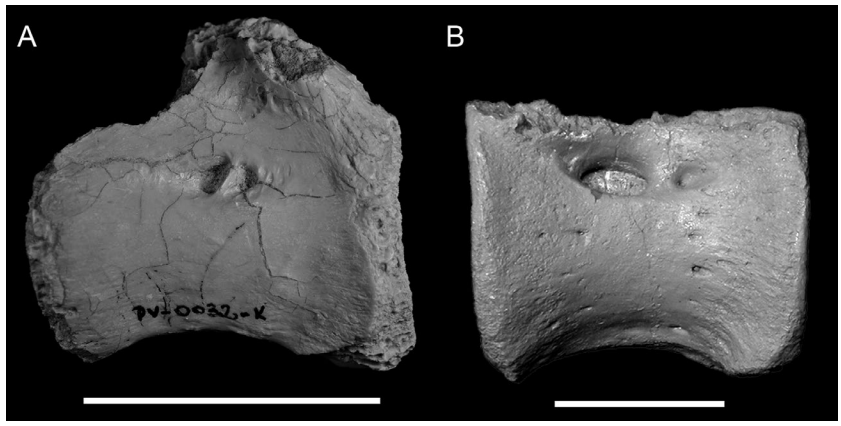

Figure 3. Caudal vertebrae of two megaraptorans. Specimen UFRGS-PV-032-K, Megaraptora indet., from the Upper Cretaceous of Mato Grosso State, central Brazil, in right lateral view (A) and middle caudal centrum of *Aerosteon riocoloradensis* from the Upper Cretaceous of Argentina (modified from Sereno et al. 2008) in left lateral view (B). Scale bar equals 50 mm.

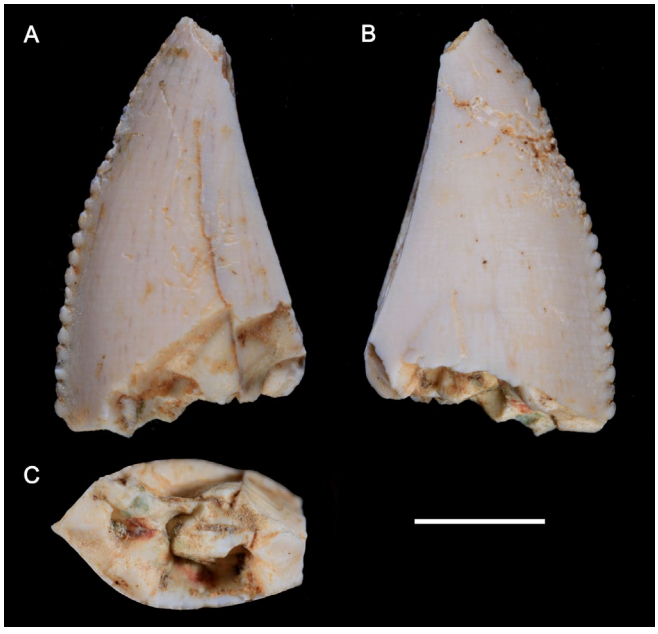

Figure 4. Abelisauria indet. from the Upper Cretaceous of Mato Grosso State, central Brazil. Specimen UFRGS-PV-038-K, fragment of an isolated tooth crown in lingual (?) (A), labial (?) (B) and basal (C) views. Scale bar equals 3 mm.

Locality and horizon – Morro do Cambambe, Chapada dos Guimarães Municipality, southeastern Mato Grosso State; 'Cambambe Unit', Paraná Basin.

Description – Most of the centrum is preserved, lacking only its anterodorsal border, with a small portion of the neural arch. The centrum measurements are 6.1 cm maximum length, 4.5 cm maximum height and 5.1 cm maximum width. The length to height (L/H) ratio is 1.35. The centrum is amphicoelous with the articular surfaces sub-circular in outline. The anterior surface (Figure 2(C)) is more rounded than the posterior one (Figure 2(E)), being slightly taller than wide, whereas the latter is the contrary, being slightly heart-shaped. Both articular surfaces have conspicuous rugose texture indicating attachment for cartilaginous tissues (Figure 2(A)–(E)). The broken portions of the centrum and the neural arch exhibit a strongly camellate internal tissue, which is also corroborated by the CT images (Figure 2(A)–(C), (E), (G)–(I)). It has ovoid to subrectangular chambers, bordered by thin laminae of bone. The chambers seem to be larger at the neural arch and the place where the haemal arch articulates. One of the most conspicuous features of this element is the presence of a large and deep elliptical pneumatic foramen on each lateral side of the centrum (Figure 2(A), (B), (F)). It is located at the middle length, closer to the contact with the neural arch than to the ventral edge. The right foramen has well-defined edges and is deeper than the left one. It is internally divided in at least two chambers by a thin lamina (Figure 2(A)). The smaller chamber is restricted to the anteriormost portion of the foramen whereas the posterior one represents nearly most of this pneumatic cavity.

On the left side, the edge of the foramen slopes the bone gradually and this opening is also divided in two chambers, but it is quite different from the right one in overall shape (Figure 2(B)). The crest is thicker and anterolaterally projected. The anterior chamber is larger than the posterior one and small foramina open through the anterior wall of the pneumatic cavity. Above the right pneumatic foramen there is also a small foramen perforating the neural arch. The CT images exhibit the medial connection of both chambers and its relationship with the internal camellate tissue, corroborating their pneumatic function.

The ventral surface is slightly concave at the anterior half and conspicuously concave at the posterior one, which is laterally bordered by prominent crests that extend until the haemal articular processes. The concave surface has several foramina piercing the bone (Figure 2(D)).

The neural canal is circular, quite small, a condition observed in posterior vertebral elements. There is no evidence of neurocentral suture between the neural arch and the centrum, probably indicating that the animal was not a juvenile at the time of its death (Brochu 1996).

Comments – UFRGS-PV-032-K closely resembles the morphology of indeterminate Upper Cretaceous megaraptorans from the São José do Rio Preto (MPMA 08–003-94; Méndez et al. 2012) and Uberaba (CPPLIP 1324; Martinelli et al. 2013) formations. All these specimens, comprising isolated caudal centra, have conspicuous pneumatic foramina and camellate internal structure. Recently, Motta et al. (2016) commented on the published isolated material of Megaraptora from the Cretaceous of

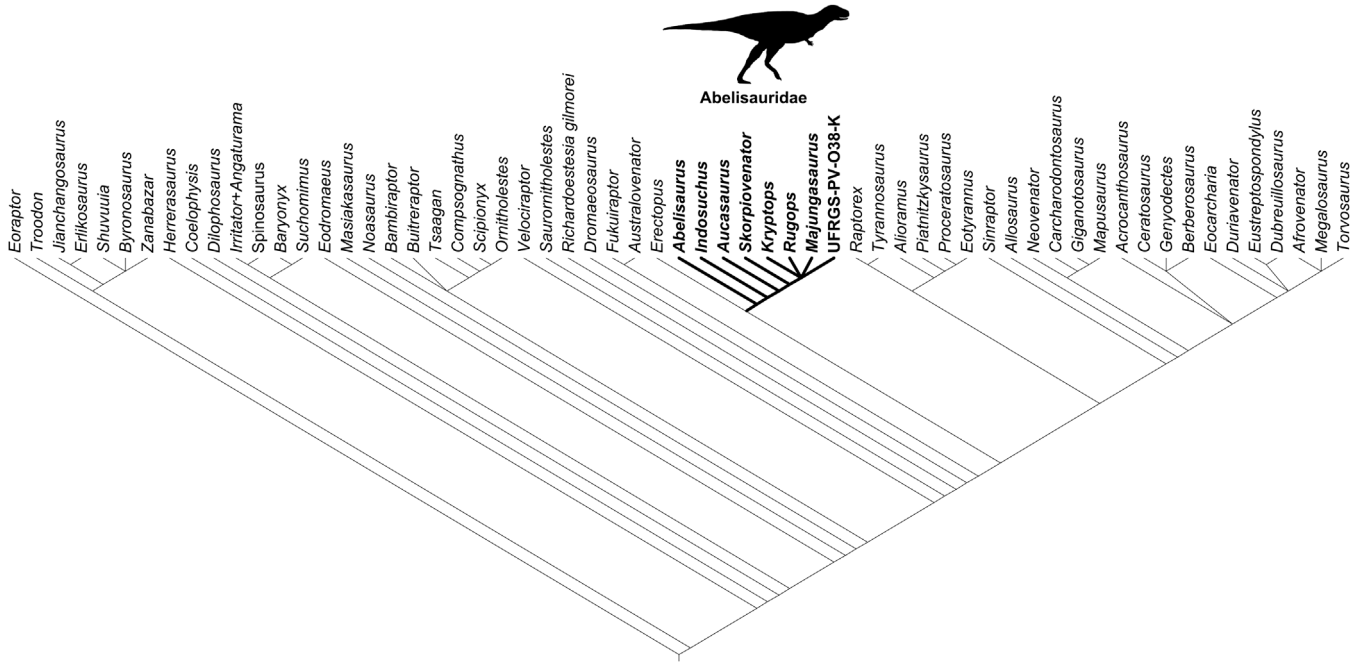

Figure 5. Strict consensus tree (length = 688 steps; CI = 0.29; RI = 0.55) of the five most parsimonious trees obtained by the present cladistic analysis. Abelisaurid taxa are highlighted in bold. The abelisaurid silhouette is from Sales et al. (2016).

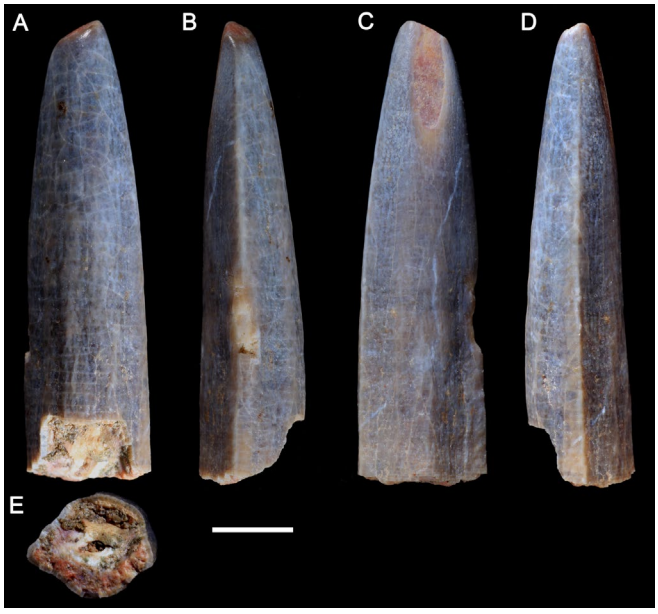

Figure 6. Titanosauria indet. from the Upper Cretaceous of Mato Grosso State, central Brazil. Specimen UFRGS-PV-037-K, fragment of an isolated tooth crown in labial (A), distal (?) (B), lingual (C), mesial (?) (D) and basal (E) views. Scale bar equals 3 mm.

Brazil. Based on the material of *Aoniraptor libertatem*, they suggested that the caudal vertebrae from Brazil (Méndez et al. 2012; Martinelli et al. 2013) could be, instead, sacral centra. In addition, Motta et al. (2016) observed that these elements resembled more *Aoniraptor* than *Megaraptor*, which has stouter elements in the sacrum. They considered that the centra from Brazil are sacral elements because of the absence of a middle longitudinal keel on the ventral surface, an anteroposteriorly elongated centrum and rugose anterior articular surface. However, the specimen here reported, which is likely a caudal vertebra due to the presence of haemal processes, has rugose anterior articular surface and a similar morphology, at least, to that from the Uberaba Formation (Martinelli et al. 2013). Only new material can elucidate this issue and these findings clearly prove that the diversity and morphology of megaraptorans are still poorly understood, especially those from Brazil.

Relatively well-documented South American theropods with conspicuous pneumatic foramina in caudal vertebrae are *Aerosteon* (Sereno et al. 2008), *Megaraptor* (Calvo et al. 2004; Porfiri et al. 2014) and *Orkoraptor* (Novas et al. 2008) from the Upper Cretaceous of Argentina. Besides, caudal vertebral pneumaticity has been documented in different theropod clades, acquired independently by megaraptorans, carcharodontosaurids and some coelurosaurs (e.g. oviraptorosaurians and therizinosaurians) (Sues 1997; O'Connor 2006; Brusatte et al. 2008; Sereno et al. 2008; Benson et al. 2010; 2012).

Particularly, the morphology of the centrum, including the pneumatic foramina, of UFRGS-PV-032-K closely resembles that of *Aerosteon* (Sereno et al. 2008) instead of other megaraptorans (Figure 3). Although based on sparse evidence, UFRGS-PV-032-K likely represents a megaraptoran taxon in the Upper Cretaceous of central Brazil due to the presence of large pneumatic foramen in the caudal vertebrae and its camellate internal structure. Recently, findings of this group in South America (Calvo et al. 2004; Coria & Currie 2006; Sereno et al. 2008; Novas et al. 2008; Porfiri et al. 2014; Motta et al. 2016) have increased in number, but the records from Brazil are still limited and punctual, based on isolated specimens.

Souza et al. (2011) mentioned an isolated vertebral centrum (CD-CRP-127; figure 4, p. 660) attributed to Theropoda from the Cachoeira do Bom Jardim Formation (but see Geological settings), found at the Jangada Roncador locality. They did not refer the centrum to a specific location in the vertebral series.

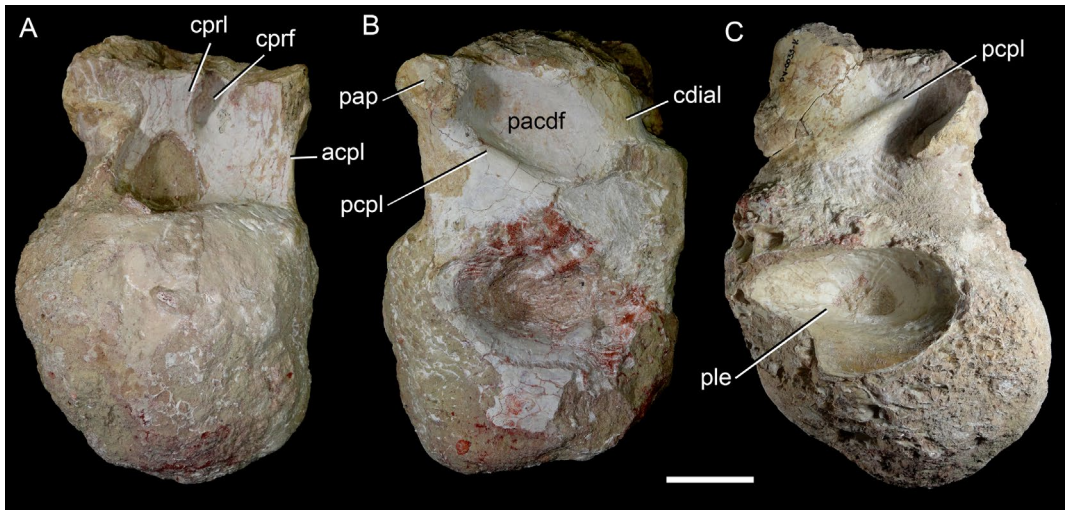

Figure 7. Titanosauria indet. from the Upper Cretaceous of Mato Grosso State, central Brazil. Specimen UFRGS-PV-033-K, partial dorsal vertebra in anterior (A), left lateral (B) and right lateral (C) views. Scale bar equals 50 mm. Abbreviations: acpl, anterior centroparapophyseal lamina; cdial, centrodiapophyseal lamina; cprf, centroprezygapophyseal fossa; cprl, centroprezygapophyseal lamina; pacdf, paraphophyseal centrodiapophyseal fossa; pap, parapophysis; pcpl, posterior centroparapophyseal lamina; ple, pleurocoel.

Considering the anteroposteriorly short centrum, the lack of ventral processes for the haemal arch and the presence of a large foramen near the dorsal edge of the centrum, this element likely corresponds to a dorsal vertebra. Based on the published photographs, the external surface of the bone is eroded, exhibiting its internal structure. To note, it has a strongly camellate internal tissue with ovoid to subrectangular chambers, bordered by thin laminae of bone. Along the lateral articular borders, the chambers seem to be regular and subrectangular, similar to the condition present in UFRGS-PV-032-K, referred to Megaraptora indet. This camellate structure is similar to that observed in *Aerosteon* (Sereno et al. 2008) and, considering the evidence at hand, we are confident that the specimen described by Souza et al. (2011) as a theropod constitutes, in fact, one more record of Megaraptora from Brazil.

CERATOSAURIA Marsh 1884
ABELISAUROIDEA Bonaparte 1991
ABELISAURIDAE Bonaparte & Novas 1985
Gen. et sp. indet.

Referred material – UFRGS-PV-038-K, an isolated partial tooth crown (Figure 4).

Locality and horizon – Morro do Cambambe, Chapada dos Guimarães Municipality, southeastern Mato Grosso State; 'Cambambe Unit', Paraná Basin.

Description – The specimen UFRGS-PV-038-K is a partial crown, lacking both its basal-most and apical-most portions and its distal margin (Figure 4), but no post-mortem distortion or compression appears to have occurred. It measures 8.9 mm in apico-basal length at its greatest depth and 5.8 mm in mesio-distal length, from the base of the anterior carina to the basal end of its preserved distal portion. The enamel presents breaks and scratches and seems to have been weathered in some parts, but it does not bear any sort of flute, ridge, striation, undulation, groove or depression. Due to the position of the anterior carina and the fact that one side is less convex than the other, we infer that the former corresponds to the lingual one. Although it is not possible to check perfectly the basal cross-section of the crown, as far as it is possible to verify, UFRGS-PV-038-K is labiolingually compressed (Figure 4(C)), which, along with the presence of the anterior carina, is enough to place it in the ziphodont category of Hendrickx et al. (2015). Also, the basal cross-section must have been intermediary between the lanceolate and lenticulate conditions.

The anterior margin of UFRGS-PV-038-K is curved distally, presenting a convex profile in lateral view, with its carina being serrated and not twisted. Considering the degree of curvature, it is likely that the apical-most preserved portion of the anterior carina was quite close to the crown apex (Figure 4(A), (B)). However, nothing can be said on the distal margin with certainty, yet it might have been relatively straight and perpendicular to the crown cervix. The denticles, only preserved in the lower two-thirds of the carina, vary in shape, especially regarding their external margin. This is possibly due to the different degrees of both wearing and/or weathering experienced by each of them. However, in general, they are apically inclined and the best-preserved ones have their external margins weakly apically hooked or convex. In addition, the denticles are relatively large and sub-equal in size. Interdenticular spaces can be seen between some denticles, and, wherever observable, they end as subtriangular interdenticular slits.

Comments – The ziphodont condition, the degree of both labiolingual compression and mesiodistal curvature and the serrated carina placed on the same plane of (mesio-distal) curvature enable the identification of UFRGS-PV-038-K as a lateral tooth crown attributable to the dinosaurian clade Theropoda (Buffetaut et al. 2008; Buffetaut 2010; Hone et al. 2010; Hendrickx et al. 2015). In addition, the strict consensus tree (length = 688 steps, CI = 0.29, RI = 0.55) of the five most parsimonious trees obtained by this cladistic analysis indicates abelisaurid affinities for this tooth crown (Figure 5). The consensus topology was almost identical to that obtained by Hendrickx and Mateus (2014). Although, due to missing data, it is not possible to verify if UFRGS-PV-038-K possessed all abelisaurid synapomorphies

recovered by this analysis and Hendrickx and Mateus (2014), like hooked and apically inclined distal denticles in lateral teeth, its placement within Abelisauridae is supported by a unique combination of features, including: (1) a lanceolate to lenticulate basal cross-section; (2) vertical-subrectangular denticles on mesial carina; (3) lack of biconvex denticles on mesial carina; and, (4) absence of large transverse undulations on the crown. Furthermore, Hendrickx and Mateus (2014) called attention for the potential of such an analysis to recover individual clades at approximately family level. Despite the large number of convergence in theropod dentition and its impedance on recovering 'accurate' phylogenetic relationships when considered alone in cladistics, UFRGS-PV-038-K is part of a polytomy along with African and Malagasy abelisaurid taxa. Argentinean and Indian genera represent successive outgroups to that node. This result may (or not) have some phylogenetic significance at infra-familiar levels.

On the other hand, comparisons between this new crown and those from the other abelisaurid from Mato Grosso, i.e. isolated teeth associated with the holotype of *Pycnonemosaurus nevesi*, are partially hampered by the fact that the latter was not included in the original data matrix of Hendrickx and Mateus (2014). Also, once we could not examine personally *P. nevesi*, we must rely for that purpose on the data provided by Bittencourt and Kellner (2002). Considering the description and figures presented by these authors, the Morro do Cambambe crown and the (much larger) best-preserved tooth associated with *P. nevesi* seem to share comparable degrees of both mesio-distal curvature and labio-lingual compression. Also, one may consider that the number of denticles per millimeter does not differ significantly between them (nearly 2.8 in UFRGS-PV-038-K versus 2 in *P. nevesi*), whereas the absence of apically hooked mesial denticles in *P. nevesi* may be due to wearing or weathering of their mesial margins. However, more remarkable, UFRGS-PV-038-K differs from the formal species both in having vertically subrectangular denticles instead of subquadrangular ones and not presenting interdenticular sulci (if it presents any) as marked as those figured by Bittencourt and Kellner (2002). Actually, the features seen in *P. nevesi* in combination are enough to distinguish it from any other abelisaurid species included in the data matrix of Hendrickx and Mateus (2014). So far, it seems unlikely that a single species could comprise within its intraspecific variation all the differences between *P. nevesi* and the Morro do Cambambe crown. Thus, it is possible that two abelisaurid taxa inhabited Mato Grosso during the Upper Cretaceous.

Finally, the shed crown presented by Souza et al. (2011) and attributed to Abelisauridae cannot be ideally compared with either the partial crown here described or *P. nevesi*. Although its outline resembles the ones observed in abelisaurid tooth crowns, this feature is widespread among theropods and the description and figure presented by the authors do not allow a re-evaluation of the taxonomic identity of the specimen reported by them.

SAUROPODA Marsh 1878
NEOSAUROPODA Bonaparte 1986
MACRONARIA Wilson & Sereno 1998
TITANOSAURIFORMES Salgado et al. 1997
TITANOSAURIA Bonaparte & Coria 1993
Gen. et sp. indet.

Referred material – UFRGS-PV-037-K, a partial tooth crown (Figure 6).

Locality and horizon – Morro do Cambambe, Chapada dos Guimarães Municipality, southeastern Mato Grosso State; 'Cambambe Unit', Paraná Basin.

Description – UFRGS-PV-037-K comprises only the crown, so no inference on its root is possible. Despite that, it is relatively well preserved, presenting only two major breaks, one on the basal-most part of the labial side (Figure 6(A)) and the other on the distal(?) carina (Figure 6(B)), but with no indication of post-mortem distortion (Figure 6). It measures 9.7 mm in maximum crown base length, 3.9 mm in maximum crown base width and 16.7 mm in maximum crown height. Regarding its general morphology, the crown is straight and fairly cylindrical and presents slenderness (Upchurch 1998) and compression (Díez Díaz et al. 2013) indexes of 1.72 and 0.93, respectively. Both sides are well mesio-distally convex, but one of them is much more convex than the other and hence is here regarded as the labial one. Actually, the convexity of the lingual side is restricted to its central part, while its mesial and distal margins are flat. Thus, both sides along with the carinae result in a 'lemon-shaped' basal cross-section, reminiscent of the 'salinon-shaped' morphology described by Hendrickx et al. (2015). Both carinae are well marked and relatively straight, but one of them is shorter than the other because of the differential wearing of the crown apex. No sort of serration is observed, but few faint and spaced marginal undulations can be seen in the basal part of the shortest carina, on the lingual side, starting just below the break. Besides marginal undulations, no other significant ornamentation, such as flutes, ridges, grooves and striations, is found. The enamel is almost smooth, especially in the central part of the labial and lingual sides. However, its surface is irregular close to the carinae, but the presence of many cracks and scratches throughout the entire crown, possibly due to taphonomic causes, cast doubt on if the irregularities represent the original condition of the enamel. Other relevant attributes of the crown surface are the oval-shaped and almost vertical apical wear facet in the lingual side, exposing the dentine, and the spalled surface (*sensu* Hendrickx et al. 2015), also in the apex but mainly visible in the labial side (Figure 6(A)).

Comments – The tooth crown UFRGS-PV-037-K is clearly attributable to the 'chisel-like' morphological class of Calvo (1994). Cylindrical and slender crowns are also found among diplodocoids (Upchurch 1998; Apesteguía 2007; Chure et al. 2010; Díez Díaz et al. 2012). However, the almost right angle of the wear facet, with respect to the labiolingual axis, measures much more than that seen in that taxon, but within the range of titanosaurs (Díez Díaz et al. 2012). In fact, chisel-like teeth are considered by Calvo (1994) as typical of titanosaurids and, hence, UFRGS-PV-037-K can be assigned to Titanosauria, which is in accordance with the fact of this taxon comprising the only Campanian–Maastrichtian sauropods with slender crowns (Chure et al. 2010). Furthermore, the presence of a wear facet exposing the dentine in the lingual side indicates that this was a fully functional upper crown (Díez Díaz et al. 2012). Its maximum width and compression index fall within the range of adult *Lirainosaurus* teeth (Díez Díaz et al. 2012, 2013). On the other hand, the height and slenderness index of UFRGS-PV-037-K measure less than those of adult *Lirainosaurus* teeth, which may indicate that the Cambambe crown also misses its

basal-most part, besides the root. Actually, the slenderness index is not enough for assigning a tooth to derived titanosaurs and, in this regard, the compression index is more useful (Díez Díaz et al. 2013). Except for the presence of some marginal undulations, it lacks other ornamentations seen in some titanosaurids, like the flutes of *Alamosaurus* teeth (Kues et al. 1980), but approaches the condition seen in other specimens, including some from Brazil (e.g. Kellner 1996: figure 7; Zaher et al. 2011: figure 2). This sort of difference might have taxonomic implications as proposed by Díez Díaz et al. (2013), but it is not possible to attribute it safely to any Upper Cretaceous taxa, as most of them, especially those from Brazil, were found without associated teeth or any jaw element with articulated teeth (e.g. Kellner & Azevedo 1999; Campos et al. 2005; Salgado & Carvalho 2008; Santucci & Arruda-Campos 2011). Although sauropod teeth from the Upper Cretaceous Mato Grosso beds were already reported, including some assigned to Titanosauria (see Table 1), UFRGS-PV-037-K is the first titanosaur crown from the 'Cambambe Unit' to be described in detail.

LITHOSTROTIA Upchurch et al. 2004

Gen. et sp. indet.

Referred material – UFRGS-PV-033-K, a partial dorsal vertebra (Figure 7).

Locality and horizon – Morro do Cambambe, Chapada dos Guimarães Municipality, southeastern Mato Grosso State; 'Cambambe Unit', Paraná Basin.

Description – UFRGS-PV-033-K consists of most of the centrum and part of the base of the neural arch of a dorsal vertebra (Figure 7). It is a large element, measuring ~16 cm in anteroposterior preserved length and 15.5 cm in maximum transverse width at the centrum. The centrum is opisthocoelous and the anterior articular surface is slightly broader than tall (Figure 7(A)). A large drop-shaped pleurocoel occupies most of each lateral surface of the centrum (Figure 7(B), (C)). It is very deep in its anterior portion and has small foramina. The pleurocoels are proportionally larger than in *Uberabatitan* (Salgado & Carvalho 2008), *Trigonosaurus* (Campos et al. 2005) and *Tapuiasaurus* (Zaher et al. 2011). There is no evidence of neurocentral suture between the centrum and neural arch. Most of the neural arch is missed; only part of the neural canal and both pedicel below the parapophysis are preserved. The parapophysis is observed only on the left side and the relationship with the diapophysis is unknown (Figure 7(B)). The parapophysis has two laminae. The anterior centroparapophyseal lamina descends vertically to the centrum and the blunt posterior centroparapophyseal lamina descends to the posterior portion of the centrum. The development of the posterior centroparapophyseal is conspicuous in comparison to the small lamina observed in *Trigonosaurus* (Campos et al. 2005). Both laminae delimit a large triangular but shallow fossa. In the posterior portion of the left base arch, only part of the centrodiapophyseal lamina is preserved. Between this lamina and the posterior centroparapophyseal lamina is delimited a shallow depression with a deep concavity (i.e. paraphophyseal centrodiapophyseal fossa) placed just posterior to the parapophysis. In anterior view, the centroprezygapophyseal lamina is preserved. It has a transversely wide and flat surface (Figure 7(A)). There is a deep fossa, the centroprezygapophyseal fossa, between the centroprezygapophyseal and the anterior centroparapophyseal laminae.

Comparison of this element is limited among Brazilian taxa. Based on the available and homologous dorsal vertebrae of *Trigonosaurus*, the specimen UFRGS-PV-033-K corresponds to a larger animal, with larger pleurocoels, more developed posterior centroparapophyseal lamina and apparently less pneumatised neural arch.

Comments – Due to the isolated nature of the specimen here described, its taxonomy and comparisons are limited. However, UFRGS-PV-033-K can be unambiguously referred to lithostrotian titanosaurs (Salgado et al. 1997; Wilson & Sereno 1998; Upchurch et al. 2004), the most abundant dinosaur clade of the Upper Cretaceous of Brazil (e.g. Bittencourt & Langer 2011). This dorsal vertebra possesses a marked development of the posterior centroparapophyseal lamina, not seen in *Trigonosaurus*, perhaps indicating the presence of a different morphotype in the Cretaceous of Mato Grosso.

Several mentions are known concerning sauropod or titanosaur remains from the Upper Cretaceous of Mato Grosso (see Table 1), but only two papers were formally published (Franco-Rosas et al. 2004; Souza et al. 2011).

Franco-Rosas et al. (2004) described a few titanosaur specimens from the Morro do Cambambe area as belonging to *Gondwanatitan* sp., an Aeolosaurini genus previously recognised in western São Paulo State, from the Adamantina Formation of the Bauru Group (Kellner & Azevedo 1999). The specimens from Mato Grosso include an incomplete anterior caudal centrum, incomplete anterior caudal neural arch, partial middle caudal vertebra and partial left tibia. Along their contribution, the authors did not specify if the specimens with different collection numbers were found associated or not. Therefore, we are not confident about the taxonomic referral of each specimen. Particularly, the partial middle caudal vertebra (MP 287) has the neural arch strongly anteriorly inclined, as occurs in aeolosaurine titanosaurs (e.g. Franco-Rosas et al. 2004; Casal et al. 2007; Martinelli et al. 2011).

The dorsal vertebra here described cannot be referred unambiguously to Aeolosaurini, therefore the vertebra described by Franco-Rosas et al. (2004) indicates the presence of another titanosaurid morphotype, i.e. aeolosaurines, in the Cretaceous of Mato Grosso. Nonetheless, the taxonomy of the other specimens described by Franco-Rosas et al. (2004), if they are not associated unambiguously to that vertebra, remains problematic.

Souza et al. (2011) mentioned a sauropod vertebral centrum (CRP-127) from the Jangada Roncador as coming from the Cachoeira do Bom Jardim Formation (but see Geological settings). In the conclusion, they contradictorily stated that it 'possibly' corresponds to Titanosauria but could be referred to the *Aeolosaurus* genus. The procoelus nature of this specimen (CD-CRP-127; Souza et al. 2011: figure 2, p. 658) is unambiguously indicative of lithostrotian titanosaurian affinities, but it lacks any feature to consider it as particularly related to *Aeolosaurus* or even Aeolosaurini. Souza et al. (2011) also mentioned a partial radius as belonging to Sauropoda.

Based on the available data, we are confident that at least two sauropod taxa are represented among the described specimens from Mato Grosso and further studies and discoveries will reveal the real diversity of the group in this Brazilian state.

Figure 8. Reconstruction of a hypothetical landscape of southeastern Mato Grosso State, central Brazil, during the Upper Cretaceous, exhibiting chelonian and crocodyliform reptiles, three titanosaur sauropods and megaraptoran and abelisauroid theropods. Made by Jorge Blanco.

Discussion

Upper Cretaceous beds from Mato Grosso are still poorly known, despite findings of vertebrate fossils since the nineteenth century. This fact is clearly demonstrated in the compiled data of Table 1, in which most records are based on meeting abstracts and brief reports, whereas only few detailed contributions were published. Here, we presented: 1) the first record of Megaraptora; 2) the first formal description of a tooth crown and a partial dorsal vertebra belonging to titanosaur sauropods; and 3) the description of a partial abelisaurid tooth exhibiting a morphotype different from that associated with *Pycnonemosaurus nevesi* (Bittencourt & Kellner 2002).

Regarding the faunal diversity of the 'Cambambe Unit', it is represented so far by turtles, abelisaurid, maniraptoran and megaraptoran theropods and titanosaur sauropods (Figure 8; this work and Derby 1890; Roxo 1937; Kellner & Campos 2000b, 2002; Franco-Rosas 2001; Marconato et al. 2001; Bittencourt & Kellner 2002; Franco-Rosas et al. 2004; Bittencourt & Langer 2011, 2012). The evidence at hand points to at least two different lithostrotian sauropods (i.e. the vertebra here described and the record of *Gondwanatitan* sp.) and two medium to large-sized theropods, namely abelisaurids and megaraptorans, in the tetrapod assemblage of the 'Cambambe Unit'. Actually, even the abelisaurids were possibly represented by two taxa, given the remarkable differences between the teeth associated to *P. nevesi* and the new crown described here. Two or more abelisaurid taxa are found in other Gondwanan deposits, like the Cenomanian Huincul (*Ilokelesia* and *Skorpiovenator*) and the Campanian Anacleto (*Abelisaurus* and *Aucasaurus*) formations, in Argentina, and the Maastrichtian Lameta Formation (e.g. *Indosuchus*, *Rajasaurus* and *Rahiolisaurus*), in India (Bonaparte & Novas 1985; Coria & Salgado 2000; Coria et al. 2002; Wilson et al. 2003; Canale et al. 2009; Carrano & Sampson 2008; Novas et al. 2010; 2013). In these cases, sympatric (=from the same deposits) species are relatively similar in size, with estimated body lengths of 5–8 m. On the other hand, *P. nevesi* is inferred to have measured ~9 m, being the largest abelisauroid taxon (Grillo & Delcourt 2017). Although it is not possible to infer the size of the individual to which UFRGS-PV-038-K belonged, this tooth is indeed much smaller than those associated to *P. nevesi*. However, inferring the presence of two abelisaurid taxa of significantly different sizes in the Upper Cretaceous of central Brazil is still speculative. Finally, the two notosuchians from the northern part of Mato Grosso (from the Parecis Basin) suggest that the diversity of crocodylomorphs was high locally (Marconato et al. 2004; Marconato 2006) and the same might have been the case for the southeastern Upper Cretaceous outcrops.

In general, the faunal composition makes the 'Cambambe Unit' similar to other Upper Cretaceous Gondwanan continental fossil assemblages, like the Bauru and Neuquén groups, in Brazil and Argentina, respectively (Candeiro et al. 2006; Novas 2007; Salgado et al. 2009; Bittencourt & Langer 2011, 2012). This is in accordance with the fact of these deposits being of close ages and part of the same landmass. Actually, even some patterns in the fossil record from Mato Grosso equals those from other formations, like the predominance of sauropods among dinosaur post-cranial remains as a whole and abelisaurids among theropod remains (Kellner 1996; Kellner & Campos 2000b; Candeiro et al. 2006; Novas 2007; Bittencourt & Langer 2011; Tavares et al. 2014).

Nevertheless, more collection and description efforts are mandatory for a more comprehensive appreciation of the Upper Cretaceous Gondwanan faunas, particularly those from central South America. Mato Grosso fossil sites are ideal in this regard

and the potential for new relevant findings are clearly demonstrated by those here reported.

Conclusion

Mato Grosso State is a pivotal location for discussions on faunal diversity of central Brazil and, hence, South America during the Upper Cretaceous. The current evidence indicates that theropods were represented in Mato Grosso fossil record by megaraptorans and abelisaurids, the latter possibly including two taxa. Titanosaur sauropods were also part of this assemblage, but further studies are required to address their real diversity. The preliminary mentions of other tetrapod groups, such as crocodylomorphs and turtles, reflect the understudied condition of this assemblage. In general, the occurrence of megaraptorans, abelisaurs and titanosaurs indicate a similar composition to other Upper Cretaceous South American fossil sites. These data help to fill in only partially the gaps on the knowledge of the Upper Cretaceous faunas from central South America and more efforts are mandatory for a better depiction of them.

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Appendix A. Character coding of UFRGS-PV-038-K based on the character statement list of Hendrickx and Mateus (2014)

??0001000?????1???3?1[012]?0?0?00??2?????????0-0-0---000-????????????????????????