

INSIGHT ON THE THEROPOD FAUNA FROM THE UBERABA FORMATION (BAURU GROUP), MINAS GERAIS STATE: NEW MEGARAPTORAN SPECIMEN FROM THE LATE CRETACEOUS OF BRAZIL

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Abstract. The first bony theropod record from the Campanian Uberaba Formation (Bauru Group) is described. It consists of an isolated caudal centrum (CPPLIP 1324) found in the city of Uberaba, Minas Gerais State, Brazil. The amphicoelous centrum possesses a length to height ratio of 1.74, deep elliptical lateral pneumatic foramen representing 26% of centrum length with three main sub-circular air chambers, and camellate internal structure. This combination of features is shared with *Aerosteon*, *Megaraptor*, and *Orkoraptor* from the Late Cretaceous of Argentina and with the Megaraptora indet. from the São José do Rio Preto Formation (Bauru Group), São Paulo State, allowing us to refer it to the Megaraptora clade (Tetanurae, Neovenatoridae). As such, the new specimen represents the second megaraptoran from the Late Cretaceous of Brazil and provides new information on tail anatomy on this bizarre group.

Riassunto. Viene qui descritto il primo ritrovamento di ossa di teropode dalla Formazione Uberaba (Gruppo Bauru) di età Campaniana. Si tratta di un corpo vertebrale caudale isolato (CPPLIP 1324) trovato nella città di Uberaba, Stato di Minas Gerais, Brasile. Il corpo vertebrale anficelo ha rapporto lunghezza/altezza di 1.74, un profondo foramen pneumatico laterale ellittico che rappresenta il 26% della lunghezza del corpo con tre cavità pneumatiche principali di forma sub-circolare, e struttura interna a nido d'ape. Questa combinazione di caratteri è condivisa con *Aerosteon*, *Megaraptor* e *Orkoraptor* del Cretaceo superiore dell'Argentina e con il Megaraptora indet. dalla Formazione di São José do Rio Preto (Gruppo Bauru), dello Stato di San Paolo, consentendo di riferire il reperto al clade Megaraptora (Tetanurae, Neovenatoridae). In quanto tale, il nuovo esemplare rappresenta il secondo Megaraptora dal Cretaceo Superiore del Brasile e fornisce

ulteriori informazioni sull'anatomia della coda di questo bizzarro gruppo.

Introduction

The Late Cretaceous continental vertebrate assemblages from Brazil have been focus of systematic researches in the last decades, considerably increasing their fossiliferous content (e.g., Kellner & Campos 2000; Bittencourt & Langer 2011). Particularly, rocks from the Bauru Group outcropping in southeastern Brazil have provided the most abundant and taxonomically varied dinosaur fauna from the Upper Cretaceous of this country (Bittencourt & Langer 2011). Titanosaur sauropods are known to occur in most of all the recognized formations of the Bauru Group (e.g., Santucci & Bertini 2001; Kellner et al. 2006; Santucci 2008; Salgado & Carvalho 2008), commonly including associated partial remains. In contrast, the theropod record is far less abundant by means of isolated occurrence (teeth and partial bones) in several localities of the Bauru Group (e.g., Kellner & Campos 2002; Novas et al. 2005, 2008; Bittencourt & Langer 2011).

Theropod dinosaurs from the Cretaceous of Brazil are still inadequate known; nonetheless, their diversity has been increased considerably in the last decades (see below). Pre-Santonian non-avian theropods in-

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clude: a) teeth of noosaurids (Lindoso et al. 2012); b) teeth and few vertebral elements of carcharodontosaurids (Vilas Bôas et al. 1999; Medeiros & Schultz 2002; Medeiros et al. 2007); c) the spinosaurids *Irritator challengeri* (Martill et al. 1996), *Angaturama limai* (Kellner & Campos 1996; it is considered by some authors as a junior synonym of *I. challenger*; e.g., Sereno et al. 1998; Sues et al. 2002), *Oxalaia quilombesis* (Kellner et al. 2011), and isolated spinosaurid teeth and bones (Campos & Kellner 1991; Kellner & Campos 1999; Medeiros & Schultz 2002; Bittencourt & Kellner 2004; Machado & Kellner 2005, 2007; Medeiros 2006); d) the basal coelurosaurian *Santanaraptor placidus* (Kellner 1999; Novas et al. 2012b); and e) the compsognathid *Mirischia asymmetrica* (Naish et al. 2004). On the other hand, post-Santonian theropod record includes abelisaurids (e.g., Bertini 1996; Kellner & Campos 2002; Novas et al. 2008; Candeiro et al. 2012a), megaraptorans (Méndez et al. 2012), and maniraptorans (Bertini et al. 1997; Bertini & Franco-Rosas 2001; Novas et al. 2005; Machado et al. 2008; Candeiro et al. 2012b). Scanty post-Santonian carcharodontosaurid remains were also reported from a few localities of Minas Gerais and São Paulo in rocks from the Bauru Group (e.g., Candeiro et al. 2006, 2012a; Azevedo et al. 2013); nonetheless, most records are likely dubious, pending further studies (see Canale et al. 2009; Brusatte et al. 2007; Souza et al. 2011, among others). The only formally named theropod and hitherto one of the most complete from post-Santonian times of Brazil is the abelisaurid *Pycnonemosaurus nevesi*, from the Parecis Group of Mato Grosso State (Kellner & Campos 2002). All other theropod records are recognized on the basis of isolated elements.

In this contribution, a partial caudal vertebra (CPPLIP 1324) referred to the theropod clade Megaraptora is described and compared. It constitutes the second megaraptoran record from the Upper Cretaceous of Brazil and the first theropod bone from the Uberaba Formation. Until now, the sparse fossil record of the Uberaba Formation (Bauru Group) was limited to titanosaur sauropods (Santucci 2008) and three associated eggs, briefly described, referred to Theropoda (Kellner et al. 1998; Kellner & Campos 2000).

Geological Settings

The specimen here reported was found in 2011 during the construction of the Uberaba Regional Hospital building ("*Hospital Regional de Uberaba*") located in front of the São João Batista Cemetery, Uberaba city (Minas Gerais State, Brazil), without possibility of access to the outcrop. Based on the rock surrounding the bone before preparation and the location, it certainly comes from the Uberaba Formation. Although

a precise level is unknown, the green fine sandstone that covered the bone would likely correspond to the layers of the upper portion of the unit. A great portion of the Uberaba city was constructed over this unit which is restricted to this portion of the Triângulo Mineiro region (Hasui 1968; Fernandes & Coimbra 2000; Batezelli et al. 2007). Relatively small outcrops can be seen along the city, in road and train rail cuts, in parks or abandoned quarries. The Uberaba Formation is laying in discordance with the basaltic rocks of the Serra Geral Formation, and at the top, only observed in a few places, it is covered by the Marília Formation (Fernandes & Coimbra 2000). To the northwest, the Uberaba Formation has a roughly lateral contact with the Adamantina Formation (Goldberg & Garcia 1995), and most stratigraphic columns of the Bauru Basin placed Uberaba and Adamantina (Vale do Rio do Peixe Formation in Fernandes & Coimbra 2000) as laterally correlated formations (e.g., Fernandes & Coimbra 2000; Batezelli et al. 2007).

The Uberaba Formation comprises a continental sequence of reddish siltstones interbedded with greenish massive sandstones, with conglomeratic lenses, especially at the base (Fernandes & Coimbra 2000), developed in a braided fluvial system (Ferreira Júnior & Guerra 1995; Fernandes & Coimbra 2000). The age of this formation is still out of consensus due to its scanty fossil record and indirect inferences (see Santucci 2008).

Gobbo-Rodrigues et al. (1999) proposed a Campanian-Maastrichtian age for the Adamantina Formation based on ostracods from the São Paulo State. Considering the lateral correlation, a similar age for the Uberaba Formation at Minas Gerais State has been assumed (Santucci 2008). Magnetostratigraphic studies of the Uberaba and Marília Formations (Tamrat et al. 2002) indicate that the deposition of Uberaba could not be older than Campanian; therefore, this data corroborated a post-Santonian age. In contrast, Dias-Brito et al. (2001), also based on ostracods, considered a Santonian age for the top of the Adamantina Formation, and by inference it was used for the Uberaba Formation. Moreover, these authors noted a depositional hiatus of 11 Ma between Adamantina and Marília Formations (Dias-Brito et al. 2001). Recently, Montefeltro et al. (2011) discussed the age of the outcrops of the Adamantina Formation (= Vale do Rio do Peixe Formation) at west Triângulo Mineiro and based upon baurusuchid crocodyliforms suggested biostratigraphic differences between the outcrops from São Paulo and Minas Gerais states. *Pissarrachampsia sera* from west Triângulo Mineiro, and also *Campinasuchus dinizi* from the same unit and found in a near locality (Carvalho et al. 2011), are closer relatives to *Wargosuchus australis* from the Santonian Bajo de la Carpa Formation (Neuquén Group, Argentina) rather than to baurusuchines, which are re-

stricted to the Adamantina Formation outcropping at São Paulo State (Montefeltro et al. 2011). Therefore, the data based on baurusuchids is not conclusive (Montefeltro et al. 2011) but highlights the difficult to correlate units based on tetrapod record for age interpretations. Because the correlation of the outcrops of the Adamantina Formation of Minas Gerais and São Paulo has not been fully explored (e.g., Montefeltro et al. 2011) and due to the broad distribution of this unit, differences in age and lithofacies are expected.

The proposal of a Campanian-Maastrichtian age for the Uberaba Formation is problematic because the supposed coetaneity of Adamantina/Uberaba formations, at least in part, and the partial coetaneity with the youngest and overlaying Marília Formation (Maastrichtian). A pre-Campanian age for the Uberaba Formation contradicts magnetostratigraphic studies (Tamarat et al. 2002); therefore, (a) the Uberaba Formation has not a total lateral correlation with the Adamantina Formation or (b) the age based on ostracodes from the Adamantina Formation is not conclusive for inferring the age of the Uberaba Formation.

Considering the faunal record of the younger Maastrichtian Marília Formation at Triângulo Mineiro region (e.g., Bertini et al. 1993; Santucci & Bertini 2001; Salgado & Carvalho 2008), the above mentioned issues (e.g., magnetostratigraphy), and due to the large span of the interval Campanian-Maastrichtian proposed for the Uberaba Formation, we prefer to use a restricted Campanian age for the Uberaba Formation, a matter which should be accurately addressed in future contributions.

Systematic paleontology

Theropoda Marsh, 1881

Tetanurae Gauthier, 1986

Neovenatoridae Benson et al., 2010

Megaraptora Benson et al., 2010

Gen. et sp. indet., fig.1-2

Referred Material: CPPLIP 1324, middle caudal vertebral centrum (Fig. 1, 2).

Locality, horizon and age: CPPLIP 1324 was found during the construction of the building of the Uberaba Regional Hospital located in front of the Uberaba Cemetery (GPS: 19°44'29.41"S/47°57'34.96"W), Uberaba city, Uberaba County, Minas Gerais State, Brazil; Uberaba Formation, Bauru Group, Campanian, Upper Cretaceous (see Geological Settings).

Description. CPPLIP 1324 consists of an isolated middle caudal vertebral centrum (Fig. 1) of a medium-sized theropod dinosaur. The centrum is almost complete with the outline of the articular surfaces eroded, being the posterior edge more damaged. A remnant of transverse process is partially preserved on the right side (Fig. 1). The centrum measurements are 8 cm maximum long, 4.6 cm maximum tall and 6.1 cm maximum width. Its general aspect is anteroposteriorly long and dorsoventrally short. The length to height (L/h) ratio is 1.74. CPPLIP 1324 is interpreted as a middle caudal centrum because it is anteroposteriorly elongated, and transversely wider than high. In *Neovenator* anterior vertebral caudal bodies are higher dorsoventrally than wide transversely (Brusatte et al. 2008). In more posterior elements, starting at the ?fourteenth caudal (caudal G),

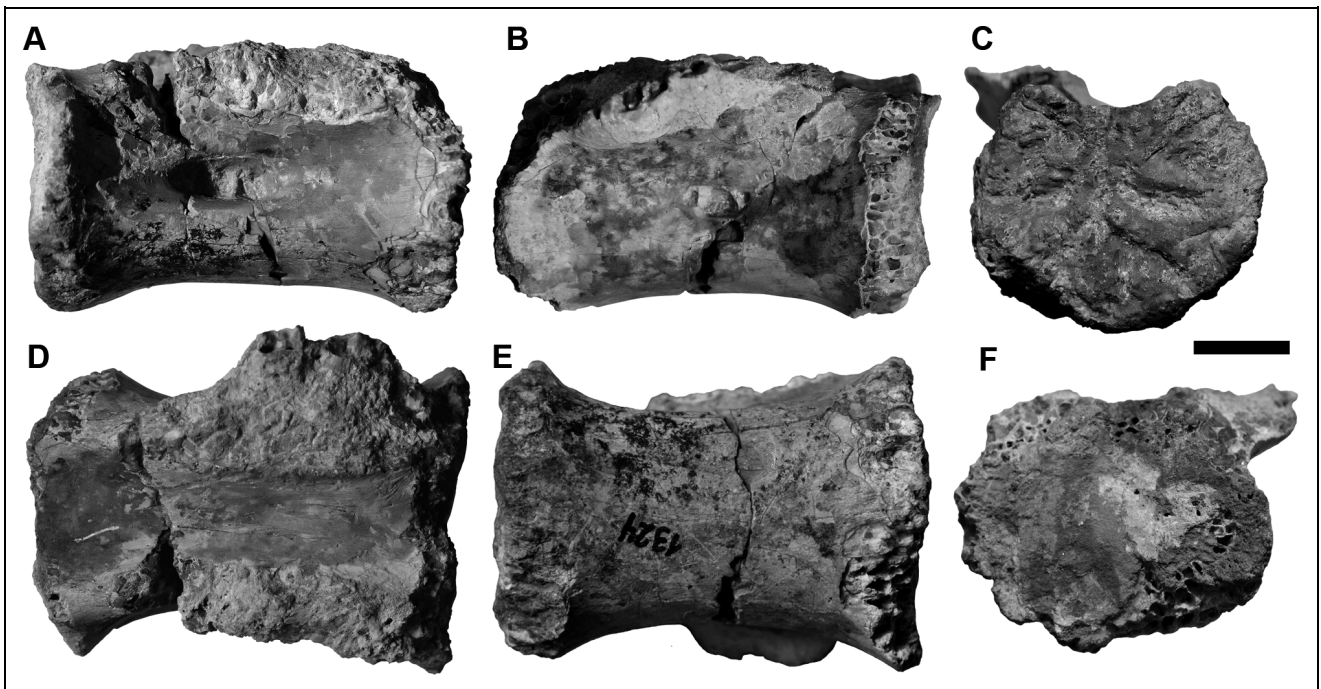


Fig. 1 - Megaraptora indet. from the Uberaba Formation (Bauru Group), Uberaba, Minas Gerais State, Brazil. CPPLIP 1324, posterior caudal centrum in: A) left lateral, B) right lateral, C) anterior, D) dorsal, E) ventral, and F) posterior views. Scale bar equals 20 mm.

the articular surfaces are wider than high (Brusatte et al. 2008). The transverse process is also high in anterior caudals and in the ?fourteenth caudal (caudal G) it is placed in a lower position (Brusatte et al. 2008). Based upon these features, we likely positioned the specimen CPPLIP 1324 as a middle caudal body, posterior to the caudal G of *Neovenator* (Brusatte et al. 2008).

The centrum is amphicoelous with the articular surfaces sub-circular in outline, except for the dorsal margin that forms the floor of the neural canal, which is concave. The articular surfaces have broad sulci indicating attachment for cartilaginous tissues. The edges of the articular surfaces are broken, showing a strongly camellate internal tissue (Fig. 2). The camellate structure is constituted of chambers that are subrectangular in cross-section, separated one to each other by thin laminae of bone. The chambers exhibit a regular placement along the articular edge and are larger at the ventral margin of the articular surfaces and at the conjunction with the neural arch. In lateral view, each side of the

centrum is dominated by a deep elliptical shaped pneumatic foramen that represents 26% of the centrum length (Fig. 1, 2). It is located at middle height and length. On the right side, the pneumatic foramen is shallower, with three main sub-circular air chambers separated by thin bone laminae. The anterior and posterior chambers are similar in size, about three times smaller than the central one. Near the anterior edge of the pneumatic foramen, there are very small foramina, possibly nutritious ones. On the left side, the pneumatic foramen is deeper, with at least one thin lamina of bone separating two main air chambers. The anterior one is the largest but probably it constitutes two collapsed chambers, with the separating wall broken off.

Tomography of CPPLIP 1324 reveals the changes in size of the internal chambers and the connections of the chambers of the pneumatic foramina in the center of the vertebral body (Fig. 2). At the $\frac{1}{4}$ anterior and posterior portions of the centrum, the internal chambers are larger near the edge of the bone forming a periphery

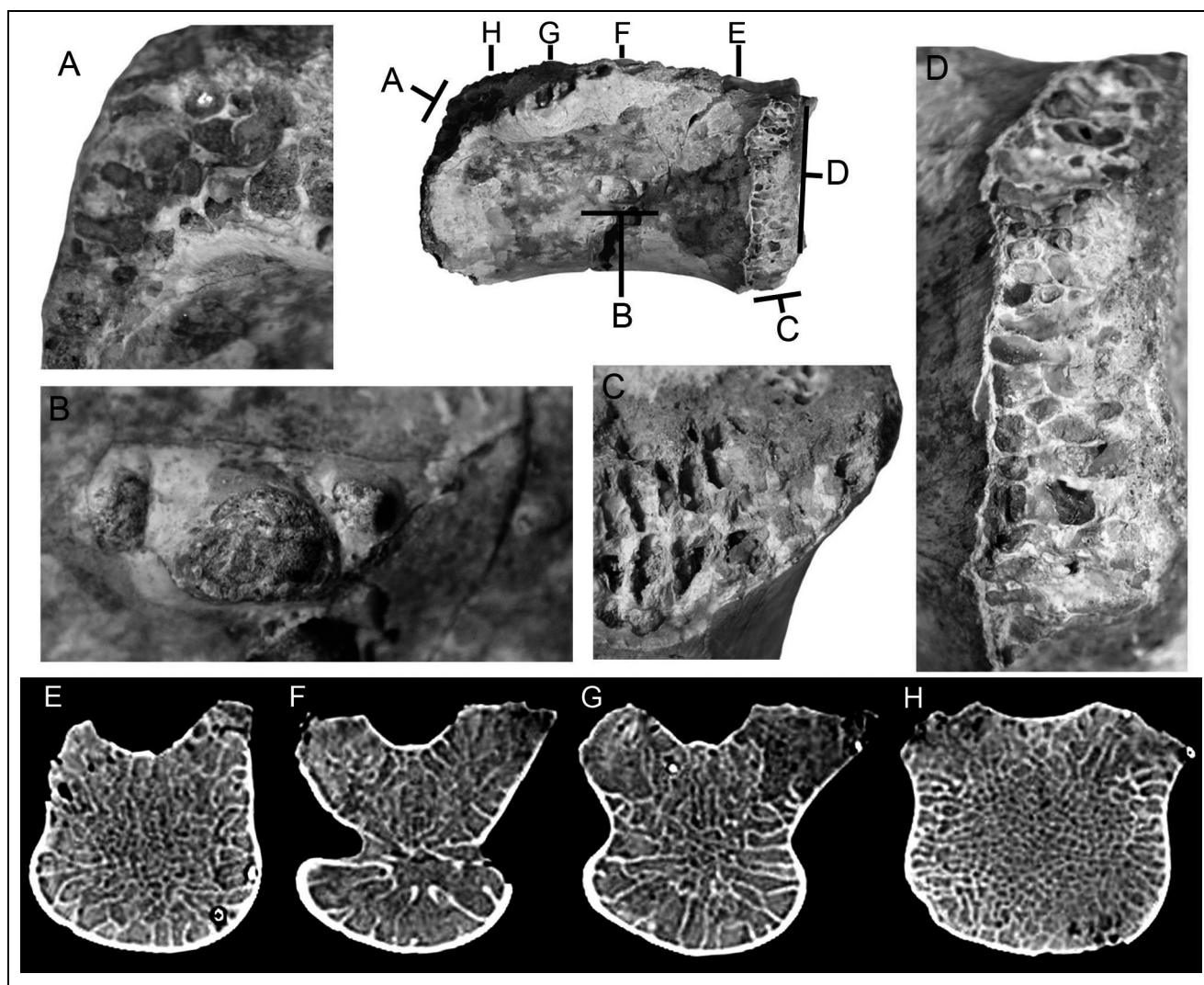


Fig. 2 - Details of the pneumatic foramen and camellate internal structure of *Megaraptora* indet. CPPLIP 1324. Caudal centrum in right lateral.

band, and become smaller to the inner side. Moving to the longitudinal center, the peripheral chambers become even larger. At the portion of the pneumatic foramen, chambers are notably great with slightly broader bone laminae. It can be seen that the chambers of the pneumatic foramina open internally and contact one to each other (Fig. 2).

In dorsal view, the centrum has a relatively broad, transversely concave floor of the neural canal, bearing a pair of small, elliptic foramina just posterior to the transversal middle line of the centrum (Fig. 1). The region for the attachment of the neural arch occupies most of the centrum length, leaving only a small portion free at the front. On the right side, there is a small portion of transverse process without well defined edges. The transverse process is in a low position and it is highly pneumatic as the centrum. It is tightly attached to the body without any evidence of suture, indicating that this element belongs to a mature individual. Moreover, the surface at the left side where the base of the neural arch should be placed was covered by rock suggesting that it was broken before burial.

The ventral surface is almost flat with concave lateral outlines when observed in ventral view. On the axial line, there is a very shallow elevation that does not reach to constitute a real crest. Because ventral edges of the articular surfaces are eroded, there is no clear evidence of facets for haemal arch (Fig. 1). Possibly, these facets are not evident because they usually are less visible in middle and posterior caudals, due to the reduction of the haemal arches.

Discussion

Taxonomical assignment of CPPLIP 1324. Among the theropod record from Brazil, CPPLIP 1324 exhibits close resemblances with the recently described Megaraptora gen. et sp. indet. (MPMA 08-003-94) from the São José do Rio Preto Formation (Méndez et al. 2012), found at Ibirá, São Paulo State, Brazil (Fig. 3C). As in MPMA 08-003-94, the caudal centrum from Uberaba has notorious pneumaticity evidenced by a large lateral pneumatic foramen and camellate internal structure (see Fig. 2).

Among theropods, the caudal vertebral pneumaticity occurred independently among distinctive clades such as ceratosaurs, megaraptorans, carcharodontosaurids, and some coelurosaurians (e.g., oviraptorosaurians and therizinosaurians) (Stromer 1931; Britt 1993; Sues 1997; Xu et al. 2002; O'Connor & Claessens 2005; O'Connor 2006; Barsbold et al. 2000; Brusatte et al. 2008; Novas et al. 2008; Sereno et al. 2008; Zanno et al. 2009; Benson et al. 2010, 2012). Particularly, *Aerosteon*, *Megaraptor*, and *Orkoraptor* (Sereno et al. 2008;

Novas et al. 2008; Calvo et al. 2004) from the Late Cretaceous of Argentina are the only South American named theropods with pneumatic foramen on caudal centra. They were recently nested into the Megaraptora clade, within a large group, called Carcharodontosauria (see Benson et al. 2010 and Carrano et al. 2012; although coelurosaurian affinities were proposed recently, see Novas et al. 2012). The size and depth of pneumatic foramen of CPPLIP 1324 are more similar to *Aerosteon* (Fig. 3) than to other megaraptorans. In *Aerosteon*, the middle centrum is proportionally shorter anteroposteriorly than in CPPLIP 1324, possibly because the Brazilian specimen occupies a slightly posterior position in the tail. Despite the fragmentary nature of CPPLIP 1324, we refer it to the neovenatorid clade Megaraptora due to the large pneumatic foramen and the camellate internal structure.

According to Brusatte et al. (2008), the pneumatic foramina are prominent in anterior caudals of the basal neovenatorid *Neovenator* but posteriorly they are shallower and poorly expressed, being absent up to the twenty first element (caudal J). According to the proportions of the centrum, the position of the base of the transverse process, and the almost flat ventral surface, the presence of such a large pneumatic foramen in the lateral surface of CPPLIP 1324, in that portion of the tail, is likely a difference with *Neovenator* (Fig. 3A). Although preliminary, it can be indicating that megaraptorans have a more advance pneumatic condition than in the basal *Neovenator*. Furthermore, the Brazilian specimen differs from *Neovenator* (Brusatte et al. 2008; Fig. 3A) because the base of the transverse process is located slightly posterior in comparison to the British theropod.

CPPLIP 1324 can be excluded from carcharodontosaurids, particularly those coming from Patagonia (e.g., *Mapusaurus*, *Giganotosaurus*), because in the latter the caudals lack real pneumatic foramen (e.g., Coria & Currie 2006). An anterior caudal assigned to *Carcharodontosaurus* by Stromer (1931), from the early Late Cretaceous of Africa, has a pneumatic foramen, different to the condition of South American carcharodontosaurids. Direct comparison with CPPLIP 1324 cannot be done because they have different position on the tail. Nonetheless, the resemblance of CPPLIP 1324 with other megaraptorans (e.g., *Aerosteon*) than with most carcharodontosaurids is notorious.

Due to the pneumatic condition of CPPLIP 1324, comparison with therizinosauroids and oviraptorosaurs are pertinent. Nonetheless, material of the first group has not been documented so far in South America and the occurrence of oviraptorosaurs in South America was dismissed (see Agnolin & Martinelli 2007). As in the Brazilian specimen, oviraptorosaurs and most therizinosauroids have caudal centra with a pneumatic foramen

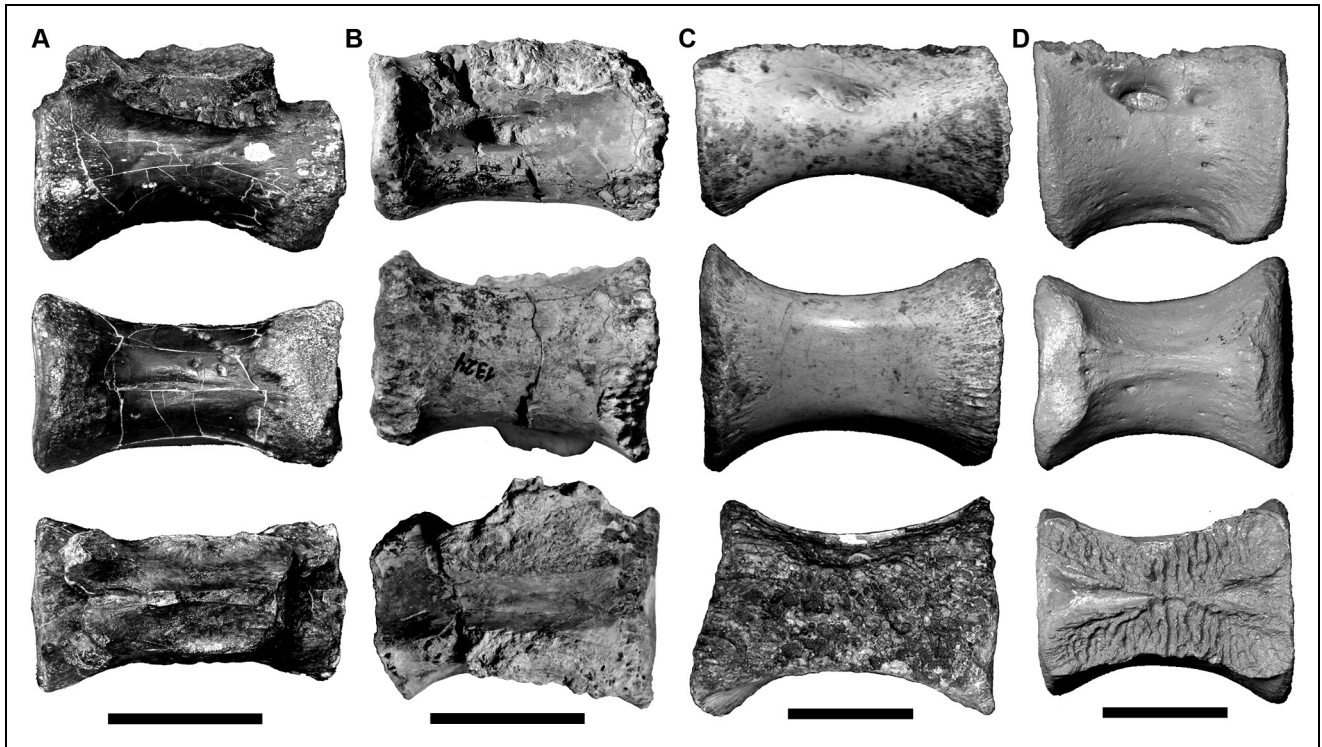


Fig. 3 - Comparison of caudal vertebrae among Neovenatoridae in left lateral, ventral and dorsal views. A) *Neovenator salerii*, caudal vertebra "I" (modified from Brusatte et al. 2008: Plate 19); B) *Megaraptora* indet. CPPLIP 1324; C) *Megaraptora* indet. MPMA 08-003-94 (lateral and ventral views modified from Méndez et al. 2012); D) *Aerosteon riocoloradensis*, middle caudal centrum (modified from Sereno et al. 2008 and Méndez et al. 2012). Scale bar equals 50 mm.

that is inter- and intra-specifically variable (e.g., Sues 1997; Barsbold et al. 2000; Zhang et al. 2001; Osmólska et al. 2004; Xu et al. 2002, 2007; Zanno et al. 2009). Differing from CPPLIP 1324, the pneumatic foramen in these groups is positioned very close to the transverse process (e.g., Sues 1997; Xu et al. 2007) and it is proportionally smaller than in CPPLIP 1324. Furthermore, oviraptorosaurs usually have caudals with a medial groove (shallow or deep) on the ventral surface of the centrum, delimited by longitudinal ridges (e.g., Sues 1997; Xu et al. 2007), differing from the condition of CPPLIP 1324. Although the comparison is significantly limited, the absent of these coelurosaurians in the South American fossil record alert us on the referral of the Brazilian specimen to these groups, also taking into consideration the isolated and fragmentary nature of CPPLIP 1324.

Comparisons with the other Brazilian megaraptoran. In general aspect, CPPLIP 1324 and MPMA 08-003-94 (Méndez et al. 2012) are quite similar. The main differences are that the pneumatic foramen of CPPLIP 1324 is deeper, located at mid height and length of the body of the centrum, and with discrete edges. In MPMA 08-003-94 the pneumatic foramen, located in a slightly higher position, slopes gradually the lateral surface, and the internal divisions are not symmetrical (Fig. 3C). In CPPLIP 1324 the L/h ratio is slightly lower than in MPMA 08-003-94 (1.7 vs. 1.9,

respectively). A very subtle median elevation on the ventral surface of CPPLIP 1324 is observed, being totally absent in the Ibirá specimen. These differences would correspond to different position in the tail, being CPPLIP 1324 anteriorly positioned on the tail than MPMA 08-003-94. Although the difference in the tail position, it is noteworthy that MPMA 08-003-94 is approximately 30% larger than CPPLIP 1324 indicating a larger individual/species in the Maastrichtian of São Paulo. Despite specimens are isolated they share close resemblances supporting their phylogenetic proximity. Both individuals come from different units from the Bauru Group. CPPLIP 1324 is considered to be Campanian in age (see Geological Settings), from the Uberaba Formation, and MPMA 08-003-94 to be Maastrichtian, coming from the São José do Rio Preto Formation (Bertini & Menegazzo 2009; Méndez et al. 2012). They clearly show the occurrence of still poorly known theropod lineages in Brazil, and MPMA 08-003-94 represents the youngest record of this clade, together with *Orkoraptor* from the Maastrichtian Pari Aike Formation of Patagonia, Argentina (Novas et al. 2008).

Conclusion

CPPLIP 1324 represents the second Megaraptoran record from Brazil, being both occurrences confined

to the Late Cretaceous of the Bauru Group. With the exception of *Pycnonemosaurus nevesi*, from the Parecis Group of Mato Grosso State (Kellner & Campos 2002), the theropod record from Bauru Group is still poorly represented, based upon fragmentary and isolated material (teeth, vertebrae, claw, furcula, etc.) that allow limited taxonomic analyses, and some records must be carefully evaluated. The new specimen also represents the first theropod bone from the Uberaba Formation, which until now only yielded titanosaur remains (Santucci 2008) and theropod eggs (Kellner et al. 1998).

The recent findings of Megaraptorans in the São José do Rio Preto Formation (Méndez et al. 2012) and now in the Uberaba Formation (this paper) enrich the still poorly understood theropod fossil record in central South America by the Upper Cretaceous. Although it was briefly suggested that mesoeucrocodylians, such as baurusuchids, occupied the ecological niches of theropods due to their abundant fossil record and several

terrestrial and hyper-carnivorous adaptations (e.g., Gasparini et al. 1993; Candeiro & Martinelli 2006; Riff & Kellner 2011), we believe that pertinent morph-spatial and morph-ecological comparisons in detail are still poorly explored. In contrast, the theropod record is growing both taxonomically and in number of available specimens. As such, the inferences on the supposed taxa that occupied the terrestrial carnivorous niches are likely preliminary and still unrealistic.

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REFERENCES

- Agnolin F.L. & Martinelli A.G. (2007) - Did oviraptorosaurs (Dinosauria; Theropoda) inhabit Argentina? - *Cretaceous Res.*, 28: 785-790.
- Azevedo R.P., Simbras F.M., Furtado M.R., Candeiro C.R.A. & Bergqvist L.P. (2013) - First Brazilian carcharodontosaurid bone remain and the theropod record from the Campanian-Maastrichtian Presidente Prudente Formation, São Paulo State, Southeastern Brazil. *Cretaceous Res.*, 40: 131-142.
- Barsbold R., Osmólska H., Watabe M., Currie P.J. & Tsogtbataar K. (2000) - A new oviraptorosaur (Dinosauria, Theropoda) from Mongolia: the first dinosaur with a pygostyle. *Acta Palaeontol. Polonica*, 45: 97-106.
- Batezelli A., Saad A.R. & Basile G. (2007) - Arquitetura deposicional e evolução da seqüência aluvial neocretácea da porção setentrional da Bacia Bauru, no sudeste brasileiro. *Rev. Bras. Geociências*, 37(1): 163-181.
- Benson R.B.J., Carrano M.T. & Brusatte S.L. (2010) - A new clade of archaic large bodied predatory dinosaurs (Theropoda: Allosauroidea) that survived to the Latest Mesozoic. *Naturwissenschaften*, 97: 71-78.
- Benson R.B.J., Butler R.J. & Carrano M.T. (2012) - Air-filled postcranial bones in theropod dinosaurs: physiological implications and the 'reptile'-bird transition. *Biol. Rev.*, 87: 168-193.
- Bertini R.J. (1996) - Evidências de Abelisauridae (Carnosauria: Saurischia) do Neo-Cretáceo da Bacia do Paraná. *Bol. IV Simp. Cret. Brasil, Águas de São Pedro*, 267-271.
- Bertini R.J. & Franco-Rosas A.C. (2001) - Scanning electronic microscopic analysis on Maniraptoriformes teeth from the Upper Cretaceous of Southeastern Brazil. *J. Vert. Paleontol.*, 21(Suppl 3): 33A.
- Bertini R.J. & Menegazzo M.C. (2009) - Reflections about geology and biochronology of the "Bauru Basin" deposits. *Anais XI Simp. Geol. Sudeste*, São Pedro, 71.
- Bertini R.J., Franco A.C., Toledo C.E.V. & Campos A.C.A. (1997) - Theropod teeth from the Adamantina Formation, Upper Cretaceous of São Paulo State. Analysis of dental morphology. *Bol. Resumos, XV Cong. Bras. Paleontol.*, São Pedro: 103.
- Bertini R.J., Marshall L.G., Gayet M. & Brito P.M. (1993) - Vertebrate faunas from the Adamantina and Marília formations (Upper Bauru Group, Late Cretaceous, Brazil) in their stratigraphic and paleobiogeographic context. *N. Jahrb. Geol. Pal., Abh.*, 188: 71-101.
- Bittencourt J.S. & Kellner A.W.A. (2004) - On a sequence of sacrocaudal theropod dinosaur vertebrae from the Lower Cretaceous Santana Formation, northeastern Brazil. *Arq. Mus. Nac.*, 62: 309-320.
- Bittencourt J.S. & Langer M.C. (2011) - Mesozoic dinosaurs from Brazil and their biogeographic implications. *Anais Acad. Bras. Ciênc.*, 73: 23-60.
- Britt B.B. (1993) - Pneumatic postcranial bones in dinosaurs and other archosaurs. PhD thesis, University of Calgary, Alberta, Canada, 383 pp.
- Brusatte S.L., Benson R.B.J. & Hutt S. (2008) - The osteology of *Neovenator salerii* (Dinosauria: Theropoda) from the Wealden Group (Barremian) of the Isle of Wight. *Palaeont. Soc. Mon.*, 162(631): 1-75.
- Brusatte S.L., Benson R.B.J., Carr T.D., Williamson T.E. & Sereno P.C. (2007) - The systematic utility of thero-

- pod enamel wrinkles. *J. Vert. Paleontol.*, 27(4): 1052-1056.
- Calvo J.O., Porfiri J.D., Veralli C., Novas F.E. & Pobleto F. (2004) - Phylogenetic status of *Megaraptor namunbhuiquii* Novas based on a new specimen from Neuquén, Patagonia, Argentina. *Ameghiniana*, 41: 565-575.
- Campos D.A. & Kellner A.W.A. (1991) - Dinosaurs of the Santana Formation with comments on other Brazilian occurrences. In: Maisey J.G. (Ed.) - Santana fossils: an illustrated atlas. p. 372-375. Neptune: T.F.H.
- Canale J., Scanferla C., Agnolin F. & Novas F. (2009) - New carnivorous dinosaur from the Late Cretaceous of NW Patagonia and the evolution of abelisaurid theropods. *Naturwissenschaften*, 96: 409-414.
- Candeiro C.R.A. & Martinelli A.G. (2006) - Paleogeographical and chronostratigraphical distribution of mesoeucrocylian species from the Upper Cretaceous beds from Bauru (Brazil) and Neuquén (Argentina) Groups, Southern South America. *J. S. Amer. Earth Sc.*, 22: 116-129.
- Candeiro C.R.A., Currie P.J. & Bergpvist L.P. (2012a) - Theropod teeth from Marília Formation (late Maastichtian) at the Paleontological Site of Peirópolis in Minas Gerais State, Brazil. *Rev. Bras. Geociênc.*, 42: 323-330.
- Candeiro C.R.A., Fanti F., Cau A., Nava W.R. & Novas F.E. (2012b) - First evidence of an unenlagiid (Dinosauria, Theropoda, Maniraptora) from the Bauru Group, Brazil. *Cretaceous Res.*, 32: 223-226.
- Candeiro C.R.A., Santos A.R., Rich T.H., Marinho T.S. & Oliveira E.C. (2006) - Vertebrate fossils from the Adamantina Formation (Late Cretaceous), Prata paleontological district, Minas Gerais State, Brazil. *Geobios*, 39: 319-327.
- Carrano M.T., Benson R.B.J. & Sampson S.D. (2012) - The phylogeny of Tetanurae (Dinosauria: Theropoda). *J. Syst. Paleontol.*, 10(2): 211-300.
- Carvalho I.S., Teixeira V.P.A., Ferraz M.L.F., Ribeiro L.C.B., Martinelli A. G., Neto F.M., Sertich J.J., Cunha G.C., Cunha I.C. & Ferraz P.F. (2011) - *Campinasuchus dinizi* gen. et sp. nov., a new Late Cretaceous baurusuchid (Crocodyliformes) from the Bauru Basin, Brazil. *Zootaxa*, 2871: 19-42.
- Coria R.A. & Currie P.J. (2006) - A new carcharodontosaurid (Dinosauria, Theropoda) from the Upper Cretaceous of Argentina. *Geodiversitas*, 28(1): 71-118.
- Dias-Brito D., Musacchio E.A., Castro J.C., Maranhão M.S.A.S., Suarez J.M. & Rodrigues R. (2001) - Grupo Bauru: uma unidade continental do Cretáceo no Brasil - concepções baseadas em dados micropaleontológicos, isotópicos e estratigráficos. *Rev. Paleobiol.*, 20(1): 245-304.
- Fernandes L.A. & Coimbra A.M. (2000) - Revisão estratigráfica da parte oriental da Bacia Bauru (Neocretáceo). *Rev. Bras. Geociênc.*, 30(4): 717-728.
- Ferreira Júnior P.D. & Guerra W.J. (1995) - Análise de elementos arquiteturais na caracterização do sistema fluvial da Formação Uberaba, Cretáceo Superior da Bacia do Paraná, no Triângulo Mineiro. *Anais VIII Simp. Geol. Minas Gerais, Minas Gerais*: 104-106.
- Gasparini Z., Fernandez M. & Powell J. (1993) - New tertiary sebecosuchians (Crocodylomorpha) from South America: phylogenetic implications. *Hist. Biol.*, 7: 1-19.
- Gobbo-Rodrigues S.R., Petri S. & Bertini R.J. (1999) - Ocorrências de ostrácodes na Formação Adamantina do Grupo Bauru, Cretáceo Superior da Bacia do Paraná e possibilidades de correlação com depósitos isócronos argentinos. Parte I - Família Ilyocyprididae. *Acta Geol. Leopold.*, 23(49): 3-13.
- Goldberg K. & Garcia A.J.V. (1995) - Faciologia dos calcários do Grupo Bauru na região de Uberaba, MG. *Geociências*, 14(2): 121-131.
- Hasui Y. (1968) - A Formação Uberaba. *Anais XXII Cong. Bras. Geol., Belo Horizonte*: 167-179.
- Kellner A.W.A. (1999) - Short note on a new dinosaur (Theropoda, Coelurosauria) from the Santana Formation (Romualdo Member, Albion), northeastern Brazil. *Bol. Mus. Nac.*, n.s., Geol., 49: 1-8.
- Kellner A.W.A. & Campos D.A. (1996) - First Early Cretaceous theropod dinosaur from Brazil with comments on Spinosauridae. *N. Jahrb. Geol. Pal., Abh.*, 199: 151-166.
- Kellner A.W.A. & Campos D.A. (1999) - Vertebrate Paleontology in Brazil: a review. *Episodes*, 22: 238-251.
- Kellner A.W.A. & Campos D.A. (2000) - Brief review of dinosaur studies and perspectives in Brazil. *Anais Acad. Bras. Ciênc.*, 72: 509-538.
- Kellner A.W.A. & Campos D.A. (2002) - On a theropod dinosaur (Abelisauria) from the continental Cretaceous of Brazil. *Arq. Mus. Nac.*, 60: 163-170.
- Kellner A.W.A., Campos D.A., Azevedo S.A.K. & Carvalho L.B. (1998) - Theropod dinosaur eggs from the continental Upper Cretaceous of Minas Gerais. *J. Vert. Paleontol.*, 18(Suppl.): 55A.
- Kellner A.W.A., Campos D.A., Azevedo S.A.K., Trotta M.N.F., Henriques D.D.R., Craik M.M.T. & Silva H.P. (2006) - On a new titanosaur sauropod from the Bauru Group, Late Cretaceous of Brazil. *Bol. Mus. Nac.*, 74: 1-32.
- Kellner A.W.A., Azevedo S.A., Machado E.B., Carvalho L.B. & Henriques D.R. (2011) - A new dinosaur (Theropoda, Spinosauridae) from the Cretaceous (Cenomanian) Alcântara Formation, Cajual Island, Brazil. *Anais Acad. Bras. Ciênc.*, 83: 99-108.
- Lindoso R.M., Medeiros M.A., Carvalho I.S. & Marinho T.S. (2012) - *Masiakasaurus*-like theropod teeth from the Alcântara Formation, São Luís Basin (Cenomanian), northeastern Brazil. *Cretaceous Res.*, 36: 119-124.
- Machado E.B. & Kellner A.W.A. (2005) - Notas sobre Spinosauridae (Theropoda, Dinosauria). *An. Inst. Geociênc.*, 28: 158-173.
- Machado E.B. & Kellner A.W.A. (2007) - On a supposed ornithischian dinosaur from the Santana Formation, Araripe Basin, Brazil. In: Carvalho I.S., Cassab R.C.T., Schwanke C., Carvalho M.A., Fernandes A.C.S., Rodrigues M.A.C., Carvalho M.S.S., Arai M.

- & Oliveira M.E.Q. (Eds) - Paleontologia: Cenários de Vida, Interciência 1: 291-299, Rio de Janeiro.
- Machado E.B., Campos D.A. & Kellner A.W.A. (2008) - On a theropod scapula (Upper Cretaceous) from the Marília Formation, Bauru Group, Brazil. *Paläontol. Z.*, 82(3): 308-313.
- Martill D.M., Cruickshank A.R.I., Frey E., Small P.G. & Clarke M. (1996) - A new crested maniraptoran dinosaur from the Santana Formation (Lower Cretaceous) of Brazil. *J. Geol. Soc.*, 153: 5-8.
- Medeiros M.A. (2006) - Large theropod teeth from the Eocenomanian of northeastern Brazil and the occurrence of Spinosauridae. *Rev. Bras. Paleontol.*, 9, 333-338.
- Medeiros M.A. & Schultz C.L. (2002) - A fauna dinossauriana da "Laje do Coringa", Cretáceo médio do Nordeste do Brasil. *Arg. Mus. Nac.*, 60: 155-162.
- Medeiro M.A., Freire P.C., Pereira A.A., Santos R.A., Lindoso R.M., Coêlho A.F., Passos E.B. & Sousa E. (2007) - Another African dinosaur recorded in the Eocenomanian of Brazil and a revision on the paleofauna of the Laje do Coringa site. In: Carvalho I.S., Cassab R.C.T., Schwanke C., Carvalho M.A., Fernandes A.C.S., Rodrigues M.A.C., Carvalho M.S.S., Arai M. & Oliveira M.E.Q. (Eds) - Paleontologia: Cenários de Vida, Interciência 1: 413-423, Rio de Janeiro.
- Méndez A.H., Novas F. & Iori F. (2012) - First record of Megaraptora (Theropoda, Neovenatoridae) from Brazil. *C. Rend. Palevol*, 11: 251-256.
- Montefeltro F.C., Larsson H.C.E. & Langer M.C. (2011) - A new baurusuchid (Crocodyliformes, Mesoeucrocodylia) from the Late Cretaceous of Brazil and the phylogeny of Baurusuchidae. *PLoS ONE*, 6 (7): e21916.
- Naish D., Martill D.M. & Frey E. (2004) - Ecology, systematics and biogeographical relationships of dinosaurs, including a new theropod, from the Santana Formation (?Albian, Early Cretaceous) of Brazil. *Hist. Biol.*, 16: 57-70.
- Novas F.E., Ribeiro L.C.B. & Carvalho I.S. (2005) - Maniraptoran theropod ungual from the Marília Formation (Upper Cretaceous), Brazil. *Rev. Mus. Arg. Cs. Nat.*, n.s., 7: 31-35.
- Novas F.E., Ezcurra M.D. & Lecuona A. (2008) - *Orkoraptor burkei* nov. gen. et sp., a large theropod from the Maastrichtian Pari Aike Formation, Southern Patagonia, Argentina. *Cretaceous Res.*, 29: 468-480.
- Novas F.E., Agnolin F.L., Ezcurra M.D., Canale J.I. & Porfiri J.D. (2012a) - Megaraptorans as members of an unexpected evolutionary radiation of tyrant-reptiles in Gondwana. XXVI Jorn. Argentinas Paleont. Vert., Universidad Maimônides, May 21- 23, 2012, Buenos Aires.
- Novas F.E., Ezcurra M.D., Agnolin F.L., Pol D. & Ortíz R. (2012b) - New Patagonian Cretaceous theropod sheds light about the early radiation of Coelurosauria. *Rev. Mus. Arg. Cs Nat.*, n.s., 14: 57-81.
- O'Connor P.M. (2006) - Postcranial pneumaticity: an evaluation of soft-tissue influences on the postcranial skeleton and the reconstruction of pulmonary anatomy in archosaurs. *J. Morphol.*, 267: 1199-1226.
- O'Connor P.M. & Claessens L.P.A. (2005) - Basic avian pulmonary design and flow through ventilation in non-avian theropod dinosaurs. *Nature*, 436: 253-256.
- Osmólska H., Currie P.J. & Barsbold R. (2004) - Oviraptorosauria. In: Weishampel D.B., Dodson P. & Osmólska H. (Eds.) - The Dinosauria. University of California Press, Berkeley, California: 165-183.
- Riff D. & Kellner A.W.A. (2011) - Baurusuchid crocodyliforms as theropod mimics: clues from the skull and appendicular morphology of *Stratiotosuchus maxhechti* (Upper Cretaceous of Brazil). *Zool. J. Linn. Soc.*, 163: 37-56.
- Salgado L. & Carvalho I.S. (2008) - *Uberabatitan ribeiroi*, a new titanosaur from the Marília Formation (Bauru Group, Upper Cretaceous), Minas Gerais, Brazil. *Palaeontology*, 51: 881-901.
- Santucci R.M. (2008) - First titanosaur (Saurischia, Sauropoda) axial remains from the Uberaba Formation, Upper Cretaceous, Bauru Group, Brazil. *Hist. Biol.*, 20(3): 165-173.
- Santucci R.M. & Bertini R.J. (2001) - Distribuição paleogeográfica e biocronológica dos titanossauros (Saurischia, Sauropoda) do Grupo Bauru, Cretáceo Superior do sudeste brasileiro. *Rev. Bras. Geociênc.*, 31(3): 307-314.
- Sereno P.C., Beck A.L., Dutheil D.B., Gado B., Larsson H.C.E., Lyon G.H., Marcot J. D., Rauhut O.W.M., Sadleir R.W., Sidor C.A., Varricchio D., Wilson G.P. & Wilson J. A. (1998) - A long snouted predatory dinosaur from Africa and the evolution of spinosaurids. *Science*, 282: 1298-1302.
- Sereno P.C., Martinez R.N., Wilson J.A., Varricchio D.J., Alcober O.A. & Larsson H.C.E. (2008) - Evidence for avian intrathoracic air sacs in a new predatory dinosaur from Argentina. *PLoS ONE*, 3(9): 1-20.
- Souza R., Cidade G., Matos J.A., Ramiro S., Costa A.C., Riff, D. & Martinelli A.G. (2011) - Revisiting the alleged record of Carcharodontosauridae (Theropoda: Allosauroidae) from the Upper Cretaceous Bauru Group, Brazil. *Ameghiniana*, 48(4): R210-211.
- Stromer E. (1931) - Wirbeltier-Reste der Baharije-Stufe (unterstes Cenoman). 10. Ein Skelett-Rest von *Carcharodontosaurus* nov. gen. *Abh. Königl. bayer. Akad. Wiss.*, 9: 1-23.
- Sues H.-D. (1997) - On *Chirostenotes*, a Late Cretaceous oviraptorosaur (Dinosauria: Theropoda) from western North America. *J. Vert. Paleontol.*, 17: 698-716.
- Sues H.-D., Frey E., Martill D.M. & Scott D.M. (2002) - *Irritator challengerii*, a spinosaurid (Dinosauria: Theropoda) from the Lower Cretaceous of Brazil. *J. Vert. Paleontol.*, 22(3): 535-547.
- Tamrat E., Ernesto M., Fulfaro V.J., Saad A.R., Batezelli A. & Oliveira A.F. (2002) - Magnetoestratigrafia das Formações Uberaba e Marília (Grupo Bauru) no Triângulo Mineiro. *Bol. VI Simp. Cret. Bras.*, II Simp. Cret. Am. Sur, São Pedro: 323-327.
- Vilas Bôas I., Carvalho I.S., Medeiros M.A. & Pontes H. (1999) - Dentes de *Carcharodontosaurus* (Dinosauria, Tyrannosauridae) do Cenomaniano, Bacia de São Luís

- (norte do Brasil). *Anais Acad. Bras. Ciênc.*, 71: 846-847.
- Xu X., Tan Q., Wang J., Zhao X.-J. & Tan L. (2007) - Gigantic bird-like dinosaur from the Late Cretaceous of China. *Nature*, 447: 844-847.
- Xu X., Zhang X.-H., Sereno P., Zhao X.-J., Kuang X.-W., Han J. & Tan L. (2002) - A new therizinosauroid (Dinosauria, Theropoda) from the Upper Cretaceous Iren Dabasu Formation of Nei Mongol. *Vert. Palasiatica*, 40: 228-240.
- Zanno L.E., Gillette D.D., Albright L.B. & Titus A.L. (2009) - A new North American therizinosauroid and the role of herbivory in 'predatory' dinosaur evolution. *Proc. R. Soc. B*, 276: 3505-3511.
- Zhang X.-H., Xu X., Zhao X.-J., Sereno P., Kuang X.-W. & Tan L. (2001) - A long-necked therizinosauroid dinosaur from the Upper Cretaceous Iren Dabasu Formation of Nei Mongol, People's Republic of China. *Vert. Palasiatica*, 39: 282-290.