



General palaeontology, systematics and evolution (Vertebrate palaeontology)

## First record of Megaraptora (Theropoda, Neovenatoridae) from Brazil

### *Premier enregistrement de Megaraptora (Theropoda, Neovenatoridae) au Brésil*

Ariel H. Méndez<sup>a,\*</sup>, Fernando E. Novas<sup>b</sup>, Fabiano V. Iori<sup>c</sup>

<sup>a</sup> CONICET–INIBIOMA (Instituto de Investigaciones en Biodiversidad y Medioambiente), MPB (Museo Paleontológico Bariloche), Bariloche, Argentina

<sup>b</sup> CONICET–MACN (Museo Argentino de Ciencias Naturales, Laboratorio de Anatomía Comparada y Evolución de los Vertebrados), Buenos Aires, Argentina

<sup>c</sup> Universidade Federal do Rio de Janeiro, Instituto de Geociências, Departamento de Geologia, Rio de Janeiro, Brazil

#### ARTICLE INFO

##### Article history:

Received 27 October 2011

Accepted after revision 26 December 2011

Available online 5 April 2012

Presented by Philippe Taquet

##### Keywords:

Megaraptora

Neovenatoridae

Theropoda

Late Cretaceous

São José do Rio Preto Formation

Brazil

##### Mots clés :

Megaraptora

Neovenatoridae

Theropoda

Crétacé supérieur

Formation São José do Rio Preto

Brésil

#### ABSTRACT

An isolated caudal vertebral centrum of a theropod dinosaur was discovered in the Bauru Basin (Late Cretaceous) of Brazil, in the Maastrichtian São José do Rio Preto Formation. The vertebral centrum has pneumatic features that are similar to those in the megaraptoran theropods *Aerosteon*, *Megaraptor*, and *Orkoraptor*. For example, all these taxa share with the caudal centrum here described the presence of true pleurocoels or pneumatic foramina, immersed within a depression or fossa. Thus, the specimen is considered the first record of Megaraptora in Brazil. The present analysis provides new information on the vertebral caudal anatomy of this clade of bizarre Cretaceous theropods.

© 2012 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

#### R É S U M É

Une vertèbre caudale centrale isolée d'un dinosaure théropode a été découverte dans le bassin Bauru (Crétacé supérieur) du Brésil, dans la Formation maastrichtienne São José do Rio Preto. Le centrum vertébral a des caractéristiques pneumatiques qui sont similaires à celles des théropodes mégaraptorien *Aerosteon*, *Megaraptor* et *Orkoraptor*. Par exemple, tous ces taxa partagent avec le centrum caudal ici décrit la présence de véritables pleurocoèles ou foramens pneumatiques, immergés au sein d'une dépression ou fossette. Ainsi, l'échantillon est considéré comme le premier enregistrement de Megaraptora au Brésil. La présente analyse fournit de nouvelles informations sur l'anatomie vertébrale caudale de ces bizarres théropodes du Crétacé.

© 2012 Académie des sciences. Publié par Elsevier Masson SAS. Tous droits réservés.

## 1. Introduction

The fossil record of Upper Cretaceous theropods from Brazil is currently made up of remains of abelisaurids (Bertini, 1996; Bittencourt and Kellner, 2002; Candeiro et al., 2004, 2006a, b; Kellner and Campos, 2002; Novas et al., 2008), maniraptorans (Machado et al., 2008; Novas

\* Corresponding author.

E-mail address: arielmendez@yahoo.com.ar (A.H. Méndez).

et al., 2005), and isolated teeth of deinonychosaurians (Bertini et al., 1997; Bertini and Franco-Rosas, 2001; Franco-Rosas, 2002), collected from several formations of the Bauru Group (Bittencourt and Langer, 2011). The presence of carcharodontosaurids (Candeiro et al., 2004, 2006b; Silva and Kellner, 1999) on Bauru Group was attributed based on isolated teeth, but these records are considered currently as corresponding to abelisaurids (Canale et al., 2009; Souza et al., 2011). We enlarge this list of Brazilian theropods with the description of an isolated caudal centrum belonging to the clade Megaraptora, constituting the first record of this theropod group from Brazil.

Megaraptoran theropods were originally known solely on the basis of *Megaraptor namunhuaiquii*, from Turonian beds of NW Patagonia (Novas, 1998). More recently new discoveries considerably improved the knowledge of the anatomy and taxonomic diversity of this group of bizarre theropods (Calvo et al., 2004; Hocknull et al., 2009; Novas, 2009; Novas et al., 2008; Sereno et al., 2008). In addition, Benson et al. (2010) coined the name Megaraptora for a new theropod clade composed of taxa found in Argentina (*Aerosteon*, *Megaraptor*, and *Orkoraptor*), Australia (*Australovenator*), and Japan (*Fukuiraptor*). Megaraptorans are characterized, among other features, by the presence of pneumatic caudal vertebrae (Benson et al., 2010; Calvo et al., 2004; Novas et al., 2008; Sereno et al., 2008).

We offer here new information about the caudal morphology of megaraptorans, through the description and comparisons of this new remain from the São José do Rio Preto Formation, Bauru Group, Brazil.

## 2. Systematic paleontology

Theropoda Marsh, 1881  
 Tetanurae Gauthier, 1986  
 Neovenatoridae Benson et al., 2010  
 Megaraptora Benson et al., 2010  
 Megaraptora gen. et sp. indet.

*Material:* MPMA 08-003-94, vertebral centrum, Museu de Paleontologia de Monte Alto (MPMA).

*Locality, horizon and age:* Municipality of Ibirá, São Paulo State, Brazil; São José do Rio Preto Formation, Maastichtian, Upper Cretaceous (Bertini and Menegazzo, 2009).

## 3. Description

The theropod vertebral centrum (MPMA 08-003-94) was discovered at the Municipality of Ibirá, São Paulo State, Brazil (Fig. 1), from beds belonging to the São José do Rio Preto Formation (Maastichtian; Bertini and Menegazzo, 2009).

The vertebra only preserves the centrum (Fig. 2). This is almost complete, except for the extreme right dorsal of the anterior articular surface, which is broken. It is long (11,8 cm), low (6,3 cm), and wide (8,5 cm), with a length to height ratio of nearly 1.9. This ratio is similar to that found in caudal vertebra 22 and more posterior vertebrae of *Allosaurus* (Madsen, 1976) and *Tyrannosaurus* (Brochu, 2003). Mid-caudals of *Aerosteon* (Sereno et al., 2008) and

*Orkoraptor* (Novas et al., 2008) exhibit a ratio of 1.2 and 1.3, respectively, similar to the ratio found in caudal vertebrae 14 to 18 of *Allosaurus* and *Tyrannosaurus*. Based on these ratios, the centrum here described probably corresponds to a caudal vertebra from the distal half of the tail.

The centrum is amphicoelous, with subcircular articular surfaces, slightly broader than tall. Centrum margins close to the cranial and caudal articular facets are strongly decorated by longitudinal striations (Fig. 2B, D). The ventral surface of the centrum is almost flat, but bear two slight collateral ridges that separate the ventral surface from the lateral ones (Fig. 2B). The centrum is devoid of facets for articulation with the haemal arches.

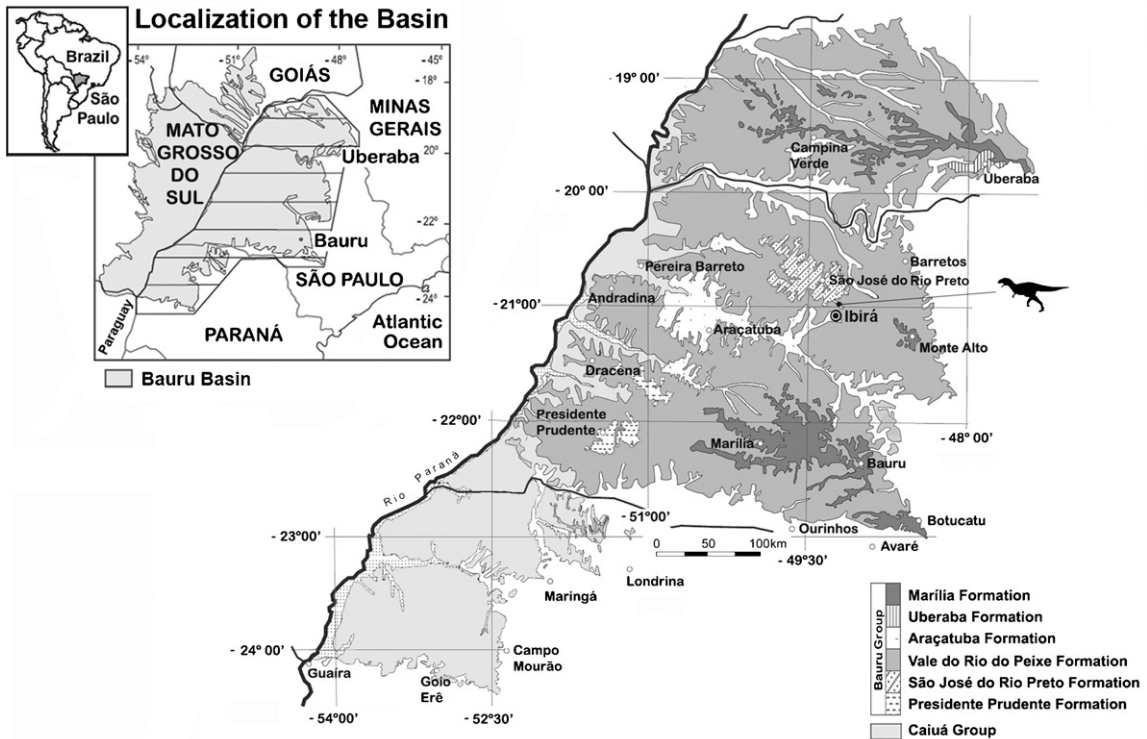
On both lateral sides, the centrum exhibits on its upper half a large and elliptical depression, which occupies two quarters of the vertebral body length, containing two air chambers or pneumatic foramina and a shallow hollow in the most posterior part of the depression (Fig. 2A). These chambers are separated by thin septa (Fig. 2C). Furthermore, posterior to the pneumatic depression, the lateral surface of the vertebral body exhibits some kind of small pneumatopores.

## 4. Comparison of MPMA 08-003-94

Caudal pneumaticity is rare condition in theropod dinosaurs documented only in a few clades (i.e., Megaraptora, Oviraptorosauria, Therizinosauria, and Carcharodontosauridae; Benson et al., 2011). So far, the presence of remains of therizosaurs in South America has not been documented and the oviraptorosaurs is at least doubtful (Agnolín and Martinelli, 2007). Also noteworthy is that the distal caudal vertebrae of oviraptorosaurs not bear pleurocoels, while they are present in the Brazilian centrum and *Aerosteon*. Stromer (1931), described an anterior caudal vertebra assigned to *Carcharodontosaurus*, which has pneumatic features. However, the general morphology and proportions (length to height ratio is 1,1 in *Carcharodontosaurus*) of the vertebrae of this African theropod specimen does not coincide with those observed in MPMA 08-003-94, as well as those of other members of Megaraptora (*Orkoraptor*, *Aerosteon*, *Megaraptor*).

Among theropod groups known from the Cretaceous of South America (i.e., abelisauroids, megaraptorans, maniraptorans, carcharodontosaurids, spinosaurids), only megaraptorans (e.g., *Aerosteon*, *Megaraptor*, *Orkoraptor*), exhibit pneumatic foramina on their caudal vertebrae. South American carcharodontosaurids (e.g. *Tyrannotitan*, *Giganotosaurus*) show a broad, shallow depression on the lateral surfaces of caudal vertebrae but not a pneumatic foramen as is present in megaraptorans and the Brazilian specimen. Pneumatic features present in MPMA 08-003-94 resemble the mid and posterior caudals of *Aerosteon riocolaradensis* (Sereno et al., 2008; Fig. 9B), in which the sides of the centrum bear pleurocoels (Fig. 3E) that enter the vertebral body, as well as the presence of small pneumatopores on the lateral surface of the centrum. A similar situation is also recorded in isolated caudal vertebrae of *Megaraptor namunhuaiquii* (J.D. Porfiri, pers. comm.).

Notably, a caudal vertebra with the same kind of pneumatic features was originally described by von Huene

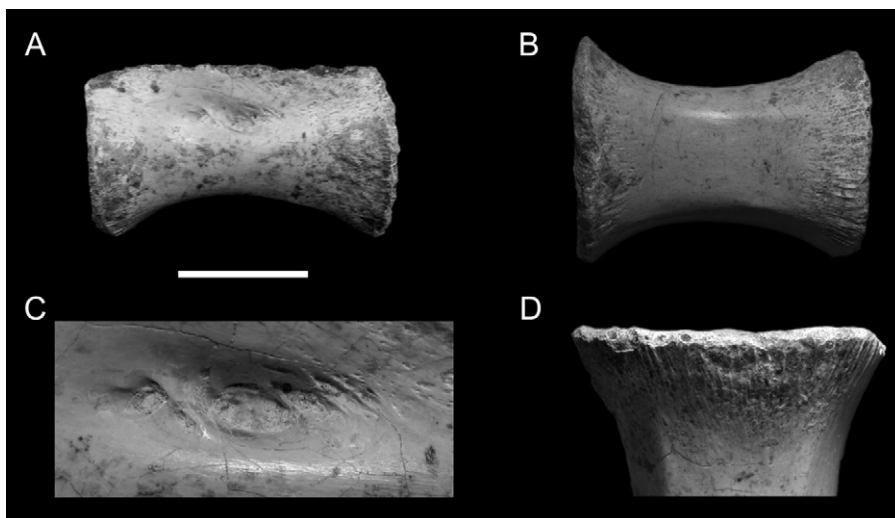


**Fig. 1.** Map showing the Ibirá locality, São Paulo State (São José do Rio Preto Formation) where the specimen MPMA 08-003-94 was found. Modified from Fernandes and Coimbra, 2000.

**Fig. 1.** Carte montrant la localité d'Ibirá, État de São Paulo (Formation São José do Rio Preto) où le spécimen MPMA 08-0003-94 a été trouvé (modifié par Fernandés et Coimbra, 2000).

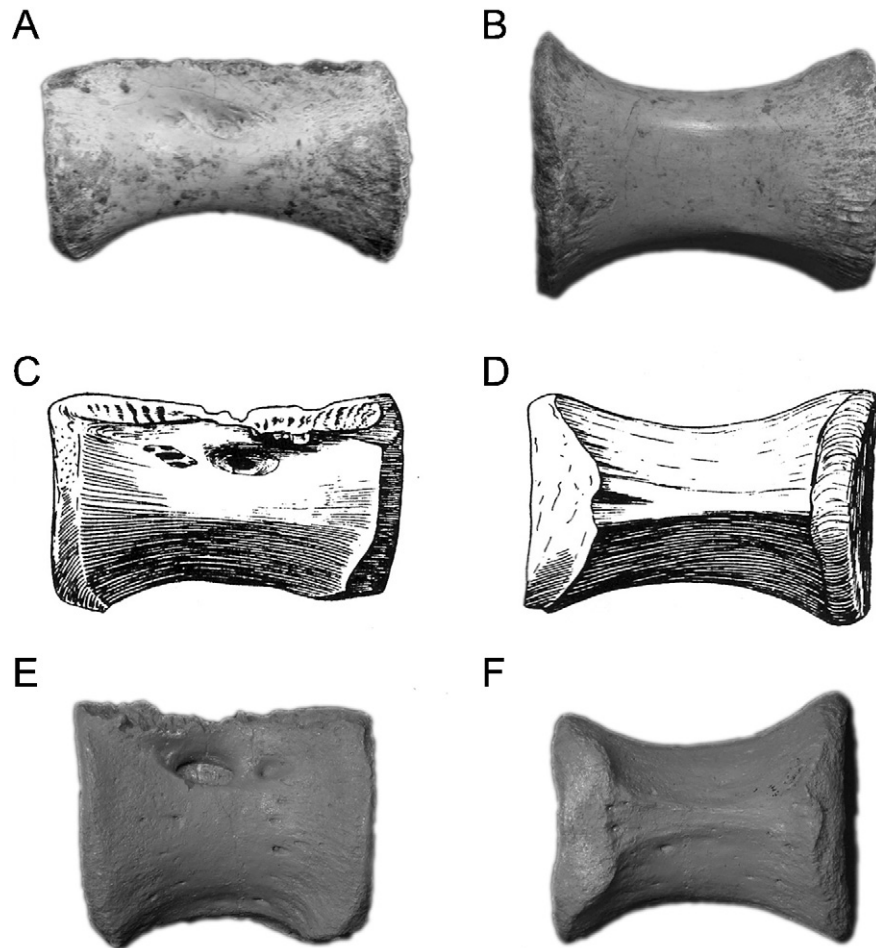
(1929) (Plate 41, 6b) as an isolated caudal of an indeterminate carnosaur. This material was collected along the south bank of the Senguer River (south of Chubut Province, Patagonia, Argentina) by Carlos Ameghino, by the end of the

19th century, from beds that may belong to Cenomanian-Turonian Lower Member of the Bajo Barreal Formation (Novas, 2009). The morphology of the caudal centrum described by von Huene is very similar to that from Brazil



**Fig. 2.** Megaraptora indet. caudal centrum (MPMA 08-003-94) in lateral (A) and ventral (B) views. Detail of pneumatic cavity (C) and ventral rugosity (D). Scale 5 cm.

**Fig. 2.** Centre caudal de Megaraptora indet (MPMA 08-003-94) vues latérale (A) et ventrale (B). Détails de la cavité pneumatique (C) et rugosités ventrales (D). Échelle 5 cm.



**Fig. 3.** Megaraptoran caudal vertebrae. (A, B) MPMA 08-003-94; (C, D) Senguer River caudal vertebra (von Huene, 1929), and (E, F) *Aerosteon*, in lateral and ventral views respectively. Not to scale.

**Fig. 3.** Vertèbres caudales de Megaraptor (A, B) MPMA 08-003-94, (C, D) Rivière Senguer, vertèbre caudale (von Huene, 1929), et (E, F) *Aerosteon*, respectivement en vues latérale et ventrale. Pas à l'échelle.

in the shape of the pneumatic opening (Fig. 3C), but differs substantially in the shape of the ventral surface, because the centrum from Senguer River has a well defined median keel (Fig. 3D), similar to that observed in the medial caudal vertebrae of *Aerosteon* (Fig. 3F) and *Megaraptor*. In contrast, the ventral surface is flat in the centrum from Brazil. Such difference reflects the respective position of the centrum along the tail, being more distal the material from Brazil. This is in agreement with the proportions of the centrum that match with those present in the caudal vertebrae down to 20 of basal tetanurans (e.g., *Allosaurus*) or large coelurosaurs (e.g., *Tyrannosaurus*), while in smaller coelurosaurs (e.g., *Deinonychus*) this ratio is present only in the anterior caudals. The absence of a conspicuous contact surface for the haemal arch is morphologically similar to that observed in the vertebrae posterior to caudal 22 of *Allosaurus*, while in *Tyrannosaurus* this ventral shape is present from caudal 29. In sum, the isolated caudal centrum here described from the Late Cretaceous of Brazil is considered as belonging to Megaraptora by having true pneumatic foramina in the mid-caudal vertebra, thus constituting the

first record of this group in Brazil, extending the geographical distribution of this clade in South America.

## 5. Conclusions

For the first time, a megaraptoran remain is reported from the Brazilian Bauru Group. No autapomorphies were identified to diagnose a new genus and species within Megaraptora.

This new finding allows the extension of the record of theropod groups that inhabited Brazil and enlarges the biogeographical distribution of megaraptorans, which until now in South America were only known from Argentina. It also allows detailed knowledge of anatomical features present at least in the South American megaraptorans. These features are still not attributable to other members of Neovenatoridae, not belonging to less inclusive clade Megaraptora, because preserved caudal vertebrae of *Neovenator* (Brusatte et al., 2008) are apneumatic and *Chilantaisaurus* (Benson and Xu, 2008) do not preserve any caudal vertebrae. At the same time, the present study

allows us to clarify the taxonomic allocation of certain old discoveries made at the end of the 19th century, such as a “carnosaurian” caudal centrum from Senguer River, Chubut Province, Argentina (von Huene, 1929).

Interestingly, the fossil record of South American megaraptorans is concentrated in different sedimentary units considered Cenomanian to Maastrichtian in age. This is the case for *Megaraptor namunhuaiquii* (Portezuelo Formation, Turonian-Coniacian; Calvo et al., 2004; Novas, 1998), *Aerosteon riocoloradensis* (Plottier Formation; Novas et al., in press; Sereno et al., 2008), *Orkoraptor burkei* (Pari Aike Formation, Maastrichtian; Novas et al., 2008, in press), the Senguer River specimen (presumably from the Lower Member of the Bajo Barreal Formation, Cenomanian-Turonian; Novas, 2009; von Huene, 1929), and the specimen from Bauru Group (São José do Rio Preto Formation, Fernandes, 1998). This lends support to the interpretation that megaraptorans were relatively diverse in South America during the Late Cretaceous.

This finding from the Ibirá area demonstrates that members of the clade Megaraptora lived alongside with abelisaurids (Kellner and Campos, 2002; Novas et al., 2008), and deinonychosaurian theropods (Bertini et al., 1997; Bertini and Franco-Rosas, 2001; Franco-Rosas, 2001, 2002).

## Acknowledgments

AHM thanks CONICET for financial support and Juan I. Canale for his valuable comments on the material described herein. Geraldine Sagner kindly translated the title, abstract and figure legends of this contribution into French. FVI thanks Professor Antonio Celso de Arruda Campos (Museum of Paleontology, Monte Alto) for access to the collection. FEN thanks Roger Benson for providing photographic material of *Aerosteon*, J.D. Porfiri (Centro Paleontológico Lago Barreales-Proyecto Dino, Universidad Nacional del Comahue) for providing information on Megaraptor specimens under his care. We thank Roger Benson, Steve Brusatte, Agustín Martinelli and two anonymous reviewers for the useful comments they made that improved the quality of this article.

## References

- Agnolín, F.L., Martinelli, A.G., 2007. Did oviraptorosaurs (Dinosauria; Theropoda) inhabit Argentina? Cretaceous Res. 28, 785–790.
- Benson, R.B.J., Xu, X., 2008. The anatomy and systematic position of the theropod dinosaur *Chilantaisaurus tashuikouensis* Hu, 1964 from the Early Cretaceous of Alanshan, People's Republic of China. Geol. Mag. 145 (6), 778–789.
- 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., O'Connor, P.M., 2011. Air-filled postcranial bones in theropod dinosaurs: physiological implications and the “reptile”-bird transition. Biol. Rev., doi:10.1111/j.1469-185X.2011.00190.x.
- Bertini, R.J., 1996. Evidências de Abelisauridae (Carnosauria: Saurischia) do Neo-Cretáceo da Bacia do Paraná. Boletim 4<sup>o</sup> Simpósio sobre o Cretáceo do Brasil, Águas de São Pedro, pp. 267–71.
- Bertini, R.J., Franco-Rosas, A.C., 2001. Scanning electronic microscopic analysis on Maniraptoriformes teeth from the Upper Cretaceous of southeastern Brazil. J. Vert. Paleont. 21 (Suppl. 3), 33A.
- Bertini, R.J., Menegazzo, M.C., 2009. Reflections about geology and biochronology of the “Bauru Basin” deposits. Anais XI Simpósio de Geologia do Sudeste, São Pedro, 71 p.
- 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. In: Congresso Brasileiro de Paleontologia 15, São Pedro, Boletim de Resumos, São Pedro, UNESP, 103 p.
- Bittencourt, J.S., Kellner, A.W.A., 2002. Abelisauria (Theropoda, Dinosauria) teeth from Brazil. Bol. Mus. Nac. Geol., Nova Série, Rio de Janeiro 63, 1–8.
- Bittencourt, J.S., Langer, M.C., 2011. Mesozoic dinosaurs from Brazil and their biogeographic implications. An. Acad. Bras. Ciênc. 73, 23–60.
- Brochu, C.A., 2003. Osteology of *Tyrannosaurus rex*: Insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. J. Vert. Paleont. 22 (Suppl. 4), 1–138.
- 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. Monogr. Palaeontographical Soc. 162 (631), 1–166.
- Calvo, J.O., Porfiri, J.D., Veralli, C., Novas, F.E., Poblete, F., 2004. Phylogenetic status of *Megaraptor namunhuaiquii* Novas based on a new specimen from Neuquén, Patagonia, Argentina. Ameghiniana 41, 565–575.
- Canale, J.I., Scanferla, C.A., Agnolín, F.L., Novas, F.E., 2009. New carnivorous dinosaur from the Late Cretaceous of NW Patagonia and the evolution of abelisaurid theropods. Naturwissenschaften 96 (3), 409–414.
- Candeiro, C.R.A., Abranches, C.T., Abrantes, E.A., Avilla, L.S., Martins, V.C., Moreira, A., Torres, S., Bergqvist, L.P., 2004. Dinosaurs remains from western São Paulo state, Brazil (Bauru Basin, Adamantina Formation, Upper Cretaceous). J. S. Am. Earth. Sci. 18, 1–10.
- Candeiro, C.R.A., Martinelli, A.G., Avilla, L.S., Rich, T.H., 2006a. Tetrapods from the Upper Cretaceous (Turonian-Maastrichtian) Bauru Group of Brazil: a reappraisal. Cretaceous Res. 27, 923–946.
- Candeiro, C.R.A., Santos, A.R., Rich, T.H., Marinho, T.S., Oliveira, E.C., 2006b. Vertebrate fossils from the Adamantina Formation (Late Cretaceous), Prata paleontological district, Minas Gerais State. Brazil. Geobios 39, 3196327.
- Fernandes, L.A., 1998. Estratigrafia e evolução geológica da parte Oriental da Bacia Bauru (KS, Brasil). Ph.D. Thesis Universidade de São Paulo, São Paulo: 216 p.
- Fernandes, L.A., Coimbra, A.M., 2000. Revisão Estratigráfica da Parte Oriental da Bacia Bauru (Neocretáceo). Rev. Bras. Geociênc. 30, 717–728.
- Franco-Rosas, A.C., 2001. Dentes de teropodomorfos da Formação Cambambe, Mato Grosso. In: Congresso Brasileiro de Paleontologia 17, Rio Branco, Boletim de Resumos, Rio Branco, UFAC, 157 p.
- Franco-Rosas, A.C., 2002. Methodological parameters for identification and taxonomic classification of isolated theropodomorph teeth. An. Acad. Bras. Ciênc. 74, 367.
- Gauthier, J.A., 1986. Saurischian monophyly and the origin of birds. Mem. Calif. Acad. Sci. 8, 1–55.
- Hocknull, S.A., White, M.A., Tischler, T.R., Cook, A.G., Calleja, N.D., Sloan, T., Elliott, D.A., 2009. New mid-Cretaceous (Latest Albian) dinosaurs from Winton, Queensland, Australia. PLoS ONE 4 (7), 1–51.
- Kellner, A.W.A., Campos, D.A., 2002. On a theropod dinosaur (Abelisauria) from the continental Cretaceous of Brazil. Arq. Mus. Nac., Rio de Janeiro 60, 163–170.
- 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, 308–313.
- Madsen, J.H., 1976. *Allosaurus fragilis*: a revised osteology. Utah Geol. Surv. Bull. 109, 1–163.
- Marsh, O.C., 1881. Principal characters of American Jurassic dinosaurs. Part V. Am. J. Sci., series 3 21, 417–423.
- Novas, F.E., 1998. *Megaraptor namunhuaiquii*, gen. et sp. nov., a large-clawed, Late Cretaceous theropod from Patagonia. J. Vert. Paleont. 18, 4–9.
- Novas, F.E., Ribeiro, L.C.B., Carvalho, I.S., 2005. Maniraptoran theropod ungual from the Marília Formation (Upper Cretaceous), Brazil. Rev. Mus. Argentino Cienc. Nat. 7:31–36.
- Novas, F.E., 2009. The age of dinosaurs in South America. Indiana University Press, Bloomington, 452p.
- 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., Agnolín, F.L., Ezcurra, M.D., Porfiri, J., Canale, J.I., in press. Evolution of the carnivorous dinosaurs during the Cretaceous: the evidence from the Patagonia. Cretaceous Res.
- 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.

- Silva, H.P., Kellner, A.W.A., 1999. Novos dentes de theropoda do Cretáceo continental do Brasil. *Paleontol. em Destaque* 26, 66.
- Souza, R., Cidade, G., Matos, J.A., Pereira, S.R., Costa, A.C., Riff, D., Martinelli, A.G., 2011. Revisiting the alleged record of *Carcharodontosauridae* (Theropoda: Allosauroidea) from the Upper Cretaceous Bauru Group, Brazil. In: *IV Congreso Latinoamericano de Paleontología de Vertebrados*, San Juan, Resúmenes: 341.
- Stromer, E., 1931. Ergebnisse der Forschungsreisen Prof. E. Stromer in den Wüsten Ägyptens. II. Wilbeltierreste der Baharije-Stufe (unterstes Cenoman). 10. Ein Skelett-Rest von *Carcharodontosaurus* nov. gen. *Abh Bayerischen Akad. Wiss. Math-Nat. Abt., Neue Folge* 9, 1–23.
- von Huene, F.F., 1929. Los Saurisquios y Ornitisquios del Cretáceo Argentino. *An. Mus. La Plata (Serie 2)* 3, 1–194.