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First evidence of an unenlagiid (Dinosauria, Theropoda, Maniraptora) from the Bauru Group, Brazil

Carlos Roberto A. Candeiro [a,*], Andrea Cau [b], Federico Fanti [c], Willian R. Nava [d], Fernando E. Novas [e]

[a] Laboratório de Geologia, Curso de Geografia, Campus Pontal, Universidade Federal de Uberlândia, Avenida 20, 1.600 Bairro Tupã, CEP 38304-402, Ituiutaba, Minas Gerais, Brazil
[b] Museo Geologico Giovanni Capellini, Via Zamboni 63, I–40127 Bologna, Italy
[c] Dipartimento di Scienze della Terra e Geologico-Ambientali, Alma Mater Studiorum, Università di Bologna, Via Zamboni 67, I–40127 Bologna, Italy
[d] Museu de Paleontologia de Marília, Secretaria Municipal da Cultura e Turismo Prefeitura de Marília, Av. Sampaio Vidal, 245, Centro, 17500–020 Marília, São Paulo, Brazil
[e] Laboratorio de Anatomia Comparada y Evolucion de los Vertebrados, Museo Argentino de Ciências Naturales "Bernardino Rivadavia", Angel Gallardo 470, 1405BDB Buenos Aires, Argentina

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ABSTRACT

In this study, we describe a small theropod dorsal vertebra from the Late Cretaceous Bauru Group (Brazil). The specimen is referred to the maniraptoran clade Unenlagiidae based on the following combination of characters: diapophyses short, wide and weakly inclined; dorsal surface of the neural spine transversely expanded; neural spine at least twice as high than it is long at mid-height; and deep lateral excavations of the ventrolateral surface of the neural spine. The vertebra belonged to an ontogenetically mature individual with an estimate total body length of around 1 m. This is the first evidence of Unenlagiidae in Brazil, a clade currently known only from Argentina and possibly Madagascar. The presence of large- to small-bodied forms in the Turonian–Santonian of South America indicates that Unenlagiinae were ecologically disparate during the first half of the Cretaceous. The Bauru vertebra shows a combination of avian-like, *Rahonavis*-like and *Unenlagia*-like features, making it a possible pivotal taxon in future phylogenetic investigations of intra- and interrelationships of unenlagiids.

1. Introduction

Fossil bones of theropod dinosaurs in Late Cretaceous deposits of Brazil are extremely scarce. The putative abelisaurid *Pycnonemosaurus nevesi* from the Adamantina Formation (Turonian–Santonian) of the Cambebe area, Mato Grosso State (Kellner and Campos, 2002), and the spinosaurid *Oxalaia quilombensis* from the Alcantara Formation (Cenomanian) of the Maranhão State (Kellner et al., 2011) are the only theropod taxa known to date. In addition, the Brazilian record also includes isolated bones and teeth which have been referred to suprageneric clades (i.e., abelisaurids, carcharodontosaurids, maniraptorans, spinosaurids; e.g., Vilas Bôas et al., 1999; Medeiros and Schultz, 2001, 2002; Novas et al., 2005; Candeiro et al., 2006; Medeiros, 2006; Candeiro, 2007; Elias et al., 2007; Medeiros et al., 2007; Machado et al., 2009).

Early Cretaceous Brazilian theropods are relatively more diverse and a few taxa are recognized. They include spinosaurids (*Irritator challengeri* and its possible junior synonym *Angaturama limai*; Kellner and Campos, 1996; Martill et al., 1996; Kellner et al., 2011), coelurosaurs (*Santanaraptor placidus* and *Mirischia asymmetrica*; Kellner, 1999; Naish et al., 2004), and isolated remains (Medeiros, 2006; Elias et al., 2007; Medeiros et al., 2007; Machado et al., 2009).

In this contribution we describe an isolated dorsal vertebra of a maniraptoran comparable in size to those of the extant *Anser anser* (Linnaeus, 1758). The specimen was collected from beds of the Adamantina Formation, approximately 12 km northwest of the city of Marilia (São Paulo State). It is housed in the collection of the Museu de Paleontologia de Marilia under the collection number MPM 011. In the same quarry, fish, notosuchian crocodyliform, and indeterminate theropod remains were also unearthed.

Institutional abbreviation. MPM, Museu de Paleontologia de Marilia city, São Paulo State, Brazil.

2. Systematic palaeontology

Dinosauria Owen, 1842
Theropoda Marsh, 1881
Maniraptora Gauthier, 1986
Unenlagiidae Bonaparte, 1999 sensu Agnolín and Novas, 2011

* Corresponding author. Tel.: +51 34 3268 6118.
E-mail address: candeiro@yahoo.com.br (C.R.A. Candeiro).

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Gen. et sp. indet.
Fig. 1

Locality and horizon. Amaden Amaral rural district, Marilia municipality, Sao Paulo State, Brazil; Turonian–Santonian Adamantina Formation, Bauru Group (Fernandes and Coimbra, 1996).

Description. The specimen MPM 011 (Figs. 1 and 2) is a small, isolated vertebra that has been mostly prepared on the left side because of a hard, oxide layer covering the bone surface and because of the size and soft nature of the bone. The vertebra is 39 mm high and 26 mm wide at the maximum point of the neural arch (i.e., at the level of the diapophyses). Based on the relative size of the centrum and neural arch, the presence of a well-developed ventral keel and the position of parapophyses, we assume that it is an anterior–middle dorsal vertebra.

The centrum is amphicoelous with the posterior articular surface wider than the anterior one (Fig. 1A, C). The anterior surface is subcircular whereas the posterior surface is oval (wider than high). In lateral view (Fig. 1B), the ventral edge of the posterior surface is ventrally projected in comparison with the anterior border of the centrum, suggesting a slight anterior upturning of the vertebral column in that region, and supporting the interpretation of MPM 011 as a vertebra close to the cervicodorsal transition (Taylor et al., 2009). In ventral view, the centrum is transversely concave and constricted in the middle. The ventral surface bears a narrow keel. On the left lateral side of centrum (Fig. 1B), an oval pleurocoel is located on the cranial haft of the centrum, immediately below the base of the neural arch. The elliptical pleurocel is deep and with distinct margins. There is no clear suture between the centrum and the neural arch, suggesting that the vertebra belongs to a mature animal.

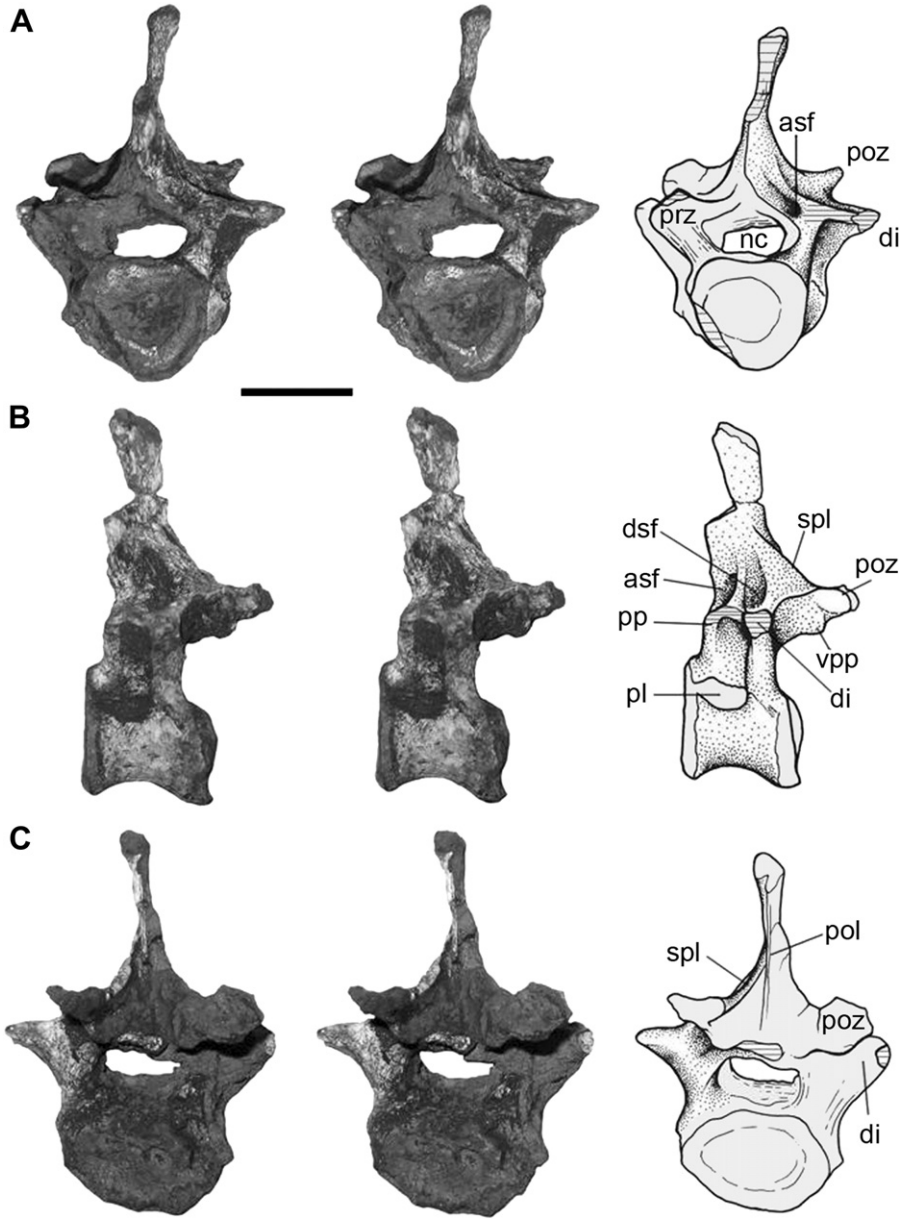

Fig. 1. Dorsal vertebra of Unenlagiidae gen. et sp. indet., MPM 011. Stereopairs and schematic drawings in A, anterior, B, left lateral and C, posterior views. Abbreviations: asf, anterior spinal fossa; di, diapophysis; dsf, dorsal spinal fossa; nc, neural canal; pol, postspinal lamina; poz, postzygapophysis; pp, parapophysis; prz, prezygapophysis; spl, spinopostzygapophyseal lamina; vpp, ventral process of postzygapophysis. Scale bar represents 1 cm.

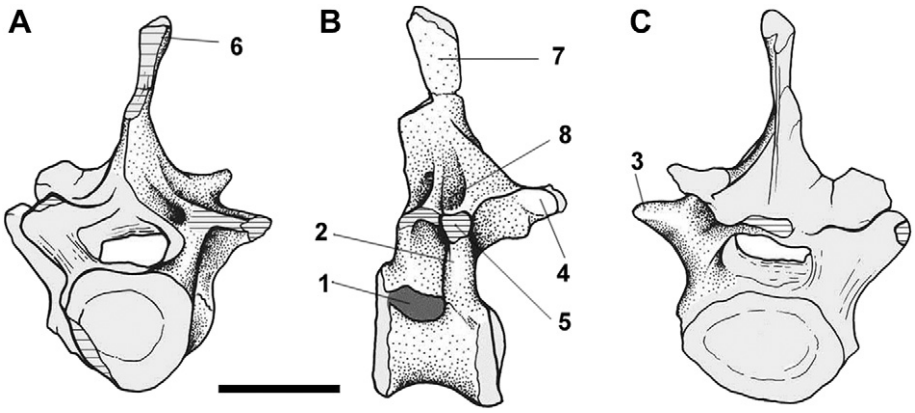

Fig. 2. Dorsal vertebra of Unenlagiidae gen. et sp. indet. in A, anterior, B, left lateral and C, posterior views. 1–8, theropod, maniraptoran and unenlagiine synapomorphies in MPM 011. Theropoda: 1, pneumatic foramen on centrum; 2, well-developed centrodiapophyseal laminae. Maniraptora: 3, widely spaced zygapophyses; 4, posterior margin of postzygapophyses placed posterior to centrum end. Unenlagiidae: 5, diapophyses short, wide and weakly inclined; 6, apex of neural spine expanded mediolaterally. "*Unenlagia* + MPM 011" node: 7, neural spine more than twice as high than long; 8, deep lateral excavations of the ventrolateral surface of the neural spine. Scale bar represents 1 cm.

The neural arch is high and mediolaterally broad at its base (Fig. 1A). The neural canal is wide, about 50% the width of the posterior centrum facet. Only the left diapophysis is partially preserved (Fig. 1B). It is anteroposteriorly short and laterally projected. The preserved proximal end of the diapophysis is quadrangular in lateral view. The diapophysis is located slightly anterior to the level of the posterior articular surface, connecting the centrum through a prominent descending, posterior centrodiapophyseal lamina. This lamina runs vertically and forms the posterior border of the deep infradiapophyseal fossa. The paradiapophyseal lamina is broken off. There are few data on the parapophyses and prezygapophyses. The right prezygapophysis is covered with hard matrix and not completely preserved and the left one is totally lost. The centroprezygapophyseal lamina is relatively strong, with a broad base (about 30% of the ventral width of the neural arch). The postzygodiapophyseal lamina is preserved on the left side. It is thin with a concave contour when observed dorsally. The postzygapophyses are well offset from the neural arch, and project posterolaterally. A subtle spinopostzygapophyseal lamina is present. On the ventral margin of the postzygapophyses, there is a projection of bone that reaches the border of the neural canal (Fig. 1B). A bone connection between both postzygapophyses is evident, but the preservation of this region does not permit rigorous interpretation. Accordingly, the available evidence suggests that the hyposphene–hypantrum accessory articulation is absent. A deep fossa, transversely oriented, is present between the base of the neural spine and the dorsal surface the diapophysis. It slopes gradually both dorsally (towards the spine) and laterally (on the diapophysis). Anterior to that fossa, a second, shallower fossa, separated by a spinodiapophyseal ridge, slopes towards the prezygapophysis.

The neural spine is tall, about the same anteroposterior length as the remains of the neural arch. Unfortunately, most of the dorsal end of the spine is broken off. Based on the preserved element, it is about four times higher than it is anteroposteriorly long, and rectangular in transverse section. Towards the top, the spine shows a slight mediolateral expansion, suggesting the presence of a mediolaterally expanded dorsal surface. Anteriorly, there is no evidence of a prespinal lamina, whereas in the posterior surface of the spine a thin vertical lamina runs from the dorsal border of the neural canal almost to the dorsal end.

3. Discussion

Specimen MPM 011 is referred to Theropoda based on the presence of the pneumatic foramen on the centrum, and well-developed centrodiapophyseal and spinozygapophyseal laminae (Fig. 2). Among theropods, it cannot be referred to Ceratosauria since it lacks a posterior pleurocoel on the centrum, extensive pneumatic recesses on the neural arch and well-developed postzygodiapophyseal laminae (Bonaparte et al., 1990; Carrano et al., 2002). The presence of a well-developed ventral keel supports a referral to the Tetanurae (Rauhut, 2003). We refer MPM 011 to Maniraptora based on the unique combination of relatively small adult size inferred from the specimen (Turner et al., 2007), the presence of widely spaced zygapophyses (Mackovicky and Sues, 1998), and the posterior margin of postzygapophyses placed well posterior to the end of the centrum (Maryańska et al., 2002). The presence of a relatively wide neural canal and the absence of the hyposphene in dorsal vertebrae are features that occurred independently among small-bodied maniraptoran lineages (paravicursorine alvarezsaurids, *Rahonavis* and avialians; Novas, 1997; Forster et al., 1998). Among maniraptorans, MPM 011 shares with the dorsal vertebrae of the unenlagiid paravian *Unenlagia* (Novas and Puerta, 1997) the following unique combination of features: diapophyses that are short, wide and weakly inclined; dorsal surface of the neural spine transversely expanded, forming a spine table; tall neural spine (at least twice as high as it is long at mid-height); and deep lateral excavations of the ventrolateral surface of the neural spine. Although the first two features are also present in other unenlagiids (Makovicky et al., 2005, fig. 3b; Novas et al., 2008, fig. 1g, h), the second two are only known in *Unenlagia* (Novas and Puerta, 1997; Calvo et al., 2004). Therefore, we refer MPM 011 to a small-bodied unenlagiid maniraptoran closely related to *Unenlagia*.

Based on the dorsal vertebrae of other unenlagiids (Novas and Puerta, 1997, fig. 2e; Forster et al., 1998, fig. 2a, b; Makovicky et al., 2005, fig. 3b; Novas et al., 2008, fig. 1g, h) we estimate that at the time of death the animal to which MPM 011 belonged was larger than the raven-sized holotype of *Rahonavis ostromi*, and about one-third the linear size of the holotype of *Unenlagia comahuensis*. Assuming body proportions similar to the other unenlagiids (Gianechini and Apesteguía, 2011), the body of the Bauru unenlagiid was around 1 m long.

4. Conclusions

MPM 011 represents the first evidence of an unenlagiid theropod in Late Cretaceous deposits of Brazil. Since all diagnosable non-avian paravian remains from South America have been referred to Unenlagiidae (Agnolín and Novas, 2011; Gianechini and

Apesteguía, 2011), the presence in the Adamantina Formation is in agreement with the current palaeobiogeography of that clade (Turner et al., 2007; Novas et al., 2008). The presence of both large (*Unenlagia*) and small (MPM 011) forms in the Turonian–Santonian of South America suggests that the Unenlagiidae were ecologically disparate during the first half of the Late Cretaceous.

The phylogenetic position of the Unenlagiidae (Unenlagiinae of Makovicky et al., 2005; Novas et al., 2008) and *Rahonavis* (Forster et al., 1998) among Paraves is controversial. Unenlagiids have been placed alternatively as basal avialians or basal dromaeosaurids, whereas *Rahonavis* has been referred to both Unenlagiidae and closer to derived avialians than *Unenlagia* (Forster et al., 1998; Makovicky et al., 2005; Novas et al., 2008; Agnolín and Novas, 2011). Although a re-analysis of paravian interrelationships is beyond the aim of our study, we note that MPM 011 shows a combination of both avian-like and *Rahonavis*-like features (small adult body size, wide neural canal, absence of hyposphene) and *Unenlagia*-like features (discussed above), and therefore can support a close relationships between *Rahonavis* and unenlagiids to the exclusion of other paravians. Regardless of its fragmentary nature (Kearney, 2002), MPM 011 could prove to be a pivotal taxon in future phylogenetic analyses of Unenlagiidae and Paraves.

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