# New turtle remains from the Late Cretaceous of Monte Alto-SP, Brazil, including cranial osteology, neuroanatomy and phylogenetic position of a new taxon

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**Abstract:** A high diversity of land vertebrates is known from the Late Cretaceous deposits of the Bauru Basin, Brazil, including at least five turtle taxa, all belonging to the clade Podocnemidoidae. Some of the richest fossil sites of this basin are in the area of Monte Alto, which yielded several squamate, dinosaur, and crocodyliform taxa. Yet, the single turtle reported so far from this area was only briefly described. Here, we further describe that specimen, a complete but very crushed shell, as well as a partial skull, both found in outcrops of the Adamantina Formation. Comparison of the shell to other podocnemidoid taxa reveals its affinities to *Roxochelys wanderleyi*, a turtle originally described from that same stratigraphic unit. The comparative description of the skull and its inclusion in a phylogenetic study, supports the proposal of a new taxon representing a lineage (Peiropemydodda) so far known only from the Marília Formation of the Bauru Basin and the early Paleocene of Bolivia. The digitally reconstructed endocast and inner ear of the new taxon were also described, as not previously done for a fossil pleurodire.

**Keywords:** Podocnemidoidae; Pleurodira; inner ear; neuroanatomy; carotid circulation; Late Cretaceous Brazil; Adamantina Formation

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## Introduction

The Late Cretaceous deposits of the Bauru Basin have yielded a high diversity of land vertebrates, including anurans, lizards, crocodylomorphs, non-avian and avian dinosaurs, and mammals (e.g., Bertini et al. 1993; Alvarenga and Nava 2005; Brito et al. 2006; Bittencourt and Langer 2011; Martinelli and Nava 2011; Báez et al. 2012). The record of freshwater turtles is also rich, including five valid taxa, namely *Bauruemys elegans* (Suárez, 1969), *Cambaremys langertoni* França and Langer, 2005, *Peiropemys mezzalirai* Gaffney et al., 2011, *Pricemys caiera* Gaffney et al., 2011, and *Roxochelys wanderleyi* Price, 1953, two dubious taxa, *"Podocnemis" harrisi* Pacheco, 1913, and *"Podocnemis" brasiliensis* Staesche, 1937, and more fragmentary records that may represent additional taxa (e.g., Gaffney et al. 2011; Kischlat 2015; Menegazzo et al. 2015; Hermanson et al. 2016; but see Romano et al. 2013 for other taxonomic interpretations). All Bauru group turtles belong to the stem-based clade Podocnemidoidae (França and Langer 2006; Podocnemididae of Gaffney et al. 2011), a side-necked turtle lineage that includes the crown-group Podocnemididae and its sister-clade Peiropemydodda (see Phylogenetic Definition and Comments below).

Deposits of the Adamantina and Marília formations crop out extensively in the area of Monte Alto, São Paulo, Brazil, and their study has been chief to improve the knowledge of the vertebrate fauna of the Bauru Basin. The fossil record in the region includes notosuchian (Pinheiro et al. 2008; Andrade and Bertini 2008; Iori and Carvalho 2009, 2011), peirosaurid (Carvalho et al. 2007), and trematochampsid crododyliforms (Iori and Garcia 2012), titanosaur (Bertini et al. 2001; Santucci and Arruda-Campos 2011) and theropod dinosaurs (Mendez et al. 2014; Tavares et al. 2014), as well as squamates (Fachini and Iori 2009; Fachini and Hsiou 2011). A single turtle specimen from the area, assigned to Pleurodira, has been briefly reported in a conference abstract (Iori and Carvalho 2010).

Here, we present additional turtle specimens from the Late Cretaceous deposits of Monte Alto. One of those, an almost complete skull, represents a new podocnemidoid taxon, *The new taxon*. Its osteology and neuroanatomy is described here and the taxon is included in a phylogenetic analysis. Additionally, we further describe the material previously reported by Iori and Carvalho (2010), also presenting new specimens collected in the same region.

**Geological Settings and material**

The Bauru Basin (Fig. 1) is a large depression developed during the Cretaceous in the southeastern portion of the South American Plate (Fernandes and Coimbra 1996). The filling-up of this basin occurred under semi-arid to arid climatic conditions, between the Aptian and the Maastrichtian (Batezelli 2015). Two of its lithostratigraphic units crop out in the area of Monte Alto-SP, the Adamantina and Marília formations. Although the the stratigraphy and age of the Bauru Basin units are controversial, there is a broad consensus that the Adamantina Fm. is older than the Marília Fm. (for a recent review on the issue, see Menegazzo et al. 2016).

The specimens described here were collected from two different sites in the area of Monte Alto that yield the sandy fluvial/lacustrine deposits of the Adamantina Formation (Fernandes and Coimbra 1994, 1996; Dias-Brito et al. 2001; Batezelli et al. 2003, 2005). MPMA 04-0008/89 comes from the "Barreiro" site, along road SP-333, at the entrance to "Sítio da Serra", type-locality of the crocodyliform *Barreirosuchus franciscoi* (Iori and Garcia 2012). This site exposes an approximately 50 m thick sequence, composed mostly of the Adamantina Formation topped by the Marilia Formation. The specimen described herein, along with bivalve, fish, crocodyliform, and sauropod dinosaur remains were recovered from the basal bed (Iori and Garcia 2012), mostly composed of lightly cemented fine reddish sandstones, with sparse carbonate nodules. In the same bed, disarticulated post-cranial remains of at least three other turtles were also found (MPMA 04-0009/89, MPMA 04-0014/89 and MPMA 04-0017/89). The turtle skeletons disarticulated during the biostratinomic phase, but remained concentrated in the same area.

The other specimen described here (MPMA 10-0003/03) was found in a small isolated outcrop of the Adamantina Formation (S 21° 14' 03,6 ", W 48° 30' 27,5 ") in a farm near the urban area of Monte Alto. The bearing rock corresponds to a strongly cemented fine reddish sandstone, with sparse pebbles and carbonate nodules found near the turtle shell. The remains are partially articulated, with numerous cracks formed by the diagenetic processes.

**Institutional Abbreviations AMNH**, American Museum of Natural History, New York, USA; **CPPLIP**, Centro de Pesquisas Paleontológicas "Llewellyn Ivor Price", Peirópolis, Uberaba, Brazil; **MCT (DGM)**, Museu de Ciências da Terra, Divisão de Geologia e Mineralogia, Departamento Nacional de Produção Mineral, Rio de Janeiro, Brazil; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; **MN**, Museu Nacional, Universidade Federal do Rio de Janeiro, Brazil;

**MPMA**, Museu de Paleontologia "Prof. Antonio Celso de Arruda Campos", Monte Alto, Brazil; **LPRP/USP**, Laboratório de Paleontologia de Ribeirão Preto, University of São Paulo, Ribeirão Preto, Brazil.

**Anatomical Abbreviations ii** and **vii**, epidermal scutes (sensu Ferreira et al. 2015); **a.a**, anterior ampulla; **ap**, antrum postoticum; **asc**, anterior semicircular canal; **bo**, basioccipital; **bs**, basisphenoid; **cc**, cavum cranii; **ccv**, canalis cavernosus; **ce.c**, cerebral branch of internal carotid; **cer**, cerebral hemisphere; **cm**, condylus mandibularis; **cnv**, canalis nervi vidiani; **co**, costal plates; **col**, columella auris; **col.f**, columella auris footplate; **cpt**, cavum pterygoidei; **cr**, cartilaginous ridge; **cru**, crus communis; **cst**, canalis stapedio-temporalis; **ct**, cavum tympani; **ent**, entoplastron; **epi**, epiplastron; **ex**, exoccipital; **facci**, foramen anterius canalis caroticus interni; **fcl**, foramen caroticus laterale; **fjp**, foramen jugulare posterius; **fm**, foramen magnum; **fnt**, foramen nervi trigemini; **fnv**, foramen nervi vidiani; **fo**, fenestra ovalis; **fpc**, fossa precolumellaris; **fpo**, fenestra postotica; **fpp**, foramen palatinum-posterius; **fr**, frontal; **hyo**, hyoplastron; **hyp**, hypoplastron;; **ica**, incisura columella auris; **ie**, inner ear; **ju**, jugal; **lag**, lagena; **lsc**, lateral semicirular canal; **ma**, marginal scute; **me**, mesoplastron; **med**, medulla oblongata; **mx**, maxilla; **ne**, neural plates; **nu**, nuchal plates; **op**, opisthotic; **och**, otic chamber; **ofb**, olfactory bulbus; **oft**, olfactory tract; **pa**, parietal; **p.a**, posterior ampulla; **pa.c**, palatal branch of internal carotid; **pal**, palatine; **pe**, peripheral plates; **pf**, prefrontal; **pit**, pituitary fossa; **pm**, premaxilla; **po**, postorbital; **psc**, posterior semicircular canal; **pt**, pterygoid; **ptp**, processus trochlearis pterygoidei; **qj**, quadratojugal; **qu**, quadrate; **rbs**, rostrum basisphenoidale; **scv**, sulcus cavernosus; **so**, supraoccipital; **sot**, septum orbitotemporale; **spp**, sulcus palatino-pterygoideus; **st**, sella turcica; **V**, trigeminal nerve; **VI**, abducens nerve; **VII**, facialis nerve; **VII.p**, palatine (or vidian) branch of VII; **ve**, vertebral scute; **xip**, xiphiplastron.

## Methods

A phylogenetic data-matrix with 39 taxa and 95 characters (see Nexus file in the Supplementary Data) was compiled using the original matrix of Gaffney et al. (2011), with the addition of MPMA 04-0008/89, *Bairdemys thalassica* (Ferreira et al. 2015), and 21 characters from other sources (see Supplementary Data; Gaffney et al. 2006; Meylan et al. 2009; Cadena et al. 2012; Dumont Junior 2013; Cadena 2015; Ferreira et al. 2015). As MPMA 04-0008/89 is clearly a representative of the Podocnemidoidae, based on the presence of the processus trochlearis pterygoidei and cavum pterygoidei, we chose to use this data-

matrix that focuses on this lineage, instead of more inclusive ones (e.g. Gaffney et al. 2006; Cadena 2015). The matrix was analyzed in TNT v. 1.5 (Goloboff et al. 2008), with Chelidae set as the primary outgroup and parsimony as the search criterion ("traditional search" with 1.000 replicates, hold 20, random seed = 0, collapse of zero length branches). Functions implemented in TNT were employed to summarize the most parsimonious trees (MPTs) in strict consensus, as well as to calculate Bremer support and Bootstrap (GC, 1000 replicates; Goloboff et al. 2003) values.

Micro CT-scan images were obtained using a SkyScan 1176 at Faculdade de Odontologia de Araraquara (FOAr-UNESP), with 721 projections over 360º, exposure time of 540 ms, voltage of 90 kV, current of 275 µA, and a resolution of 17 µm per pixel. NRecon v. 1.6.9.8 and DataViewer v. 1.5.0 were used to process the cross-sectional images. Materialise Mimics Research edition version 18.0 was used for digital reconstructions and measurements of the skull bones and endocasts of the brain and inner ear.

## Systematic palaeontology

**Pleurodira** Cope, 1864

**Pelomedusoides** Broin, 1988

**Peiropemydodda** Gaffney, Meylan, Wood, Simons and Campos, 2011

*Phylogenetic Definition.* Peiropemydodda refers to the branch-based clade that includes all taxa more closely related to *Peiropemys mezzalirai* Gaffney et al., 2011, and *Lapparentemys vilavilensis* (Broin, 1971) than to *Podocnemis expansa* (Schweigger, 1812).

***gen. et sp. nov.***

*Diagnosis*. A small Podocnemidoidae based on the right angle formed by the processus trochlearis pterygoidei and the cavum pterygoidei; a Peiropemydodda based on the anteroventral emargination projecting above the ventral level of the orbit (Gaffney et al. 2011). Compared to other peiropemydod and Bauru Group turtles, it is similar in size to *Bauruemys elegans*, but smaller than all other peiropemydods; the skull is roughly the same height along its entire length, as in *Peiropemys mezzalirai* and *Lapparentemys vilavilensis*, differing from that of *Bauruemys elegans*; the rostral tip of the basisphenoid is acute as in *Pricemys caiera*, but not in *Bauruemys elegans* and *Peiropemys mezzalirai*; the foramen palatinum posterius is formed by the palatine and pterygoid, differing from *Peiropemys mezzalirai*; the

fossa precolumellaris is very large as in *Peiropemys mezzalirai*, in contrast to *Pricemys caiera*; skull dermal scute vii (sensu Ferreira et al., 2015; same as interparietal scute) has the anterior margins on the frontal and lateral edges converging posteriorly as in *Bauruemys elegans*, *Lapparentemys vilavilensis* and *Peiropemys mezzalirai*, but differing from the latter two by an anterior notch on the midline, as also found in *Bauruemys elegans*.

*Material.* MPMA 04-0008/89 (Figs. 2-6), a partial skull lacking both premaxillae and squamosals, most of the maxillae, and portions of several other bones (see Comparative Description) housed at the Museu de Paleontologia "Prof. Antonio Celso de Arruda Campos", Monte Alto, Brazil.

*Stratum and locality.* Reddish sandstones of the Late Cretaceous Adamantina Formation, exposed at the entrance to "Sítio da Serra" (S 21° 15' 06.9'', W 48° 33' 10.4''), Monte Alto-SP, Brazil.

*Description.* The skull of MPMA 04-0008/89 is 35 mm long as preserved, much smaller than other peiropemydods (e.g. the holotype of *Peiropemys mezzalirai* is approximately 90 mm long excluding the crista supraoccipitalis, and the specimen AMNH 14444 referred to *Lapparentemys vilavilensis* is 96 mm long). The adductor chamber is completely filled by matrix, but parts of its roof were imprinted in the sandstone, forming a natural endocast (Fig. 2). The skull is relatively high at the orbital region, with a value of 0.80 for the height at orbit/largest height ratio, approaching the condition of *Lapparentemys vilavilensis* (AMNH 14444) and *Peiropemys mezzalirai* (MCT 147), which have 0.69 and 0.79 ratios, respectively, whereas that of *Bauruemys elegans* (Kischlat and Azevedo 1991) ranges from 0.50 (MCZ 4123) to 0.55 (MCT 1753). Some epidermal scute sulci are poorly preserved, but various features can be observed: based on the preserved borders, scute vii (sensu Ferreira et al. 2015) possibly formed a small and equilateral triangle with smooth edges similar to that of *Peiropemys mezzalirai* and *Lapparentemys vilavilensis*, but the anterior sulcus shared with scute ii on the frontal and postorbital has an anterior notch on the midline, as in *Bauruemys elegans* (Gaffney et al. 2011); part of the posterior edge of scute ii is preserved on the postorbital, but its extension cannot be determined.

**Prefrontal**

The prefrontal is partially preserved and it is therefore possible to identify its posterior contact with the frontal. The bone forms the anteromedial edge of the orbit, as in most podocnemidoids. The interorbital distance is similar to that of *Bauruemys elegans*, *Peiropemys mezzalirai*, and *Lapparentemys vilavilensis* (Gaffney et al. 2011), and the large orbit is directed dorsolaterally as in other peiropemydods.

**Frontal**

As in most podocnemidoids, the frontal contacts the prefrontal anteriorly, the other frontal medially, the postorbital posterolaterally, and the parietal posteriorly. It has an almost squared dorsal outline, with subparallel lateral and medial edges, as in *Bauruemys elegans* and differing slightly from *Lapparentemys villavilensis* and *Peiropemys mezzalirai*, which have diverging lateral and medial edges. The anterior and posterior edges are also subparallel, as in *Peiropemys mezzalirai*, but not in *Hamadachelys escuilliei*, *Lapparentemys villavilensis*, and most *Bauruemys elegans* specimens (although some have subparallel edges, e.g., MCZ 4123 in Gaffney et al. 2011:fig. 13), in which the frontal-prefrontal suture projects anteromedially. The frontal forms the anteromedial margin of the orbit, as in other podocnemidoids.

**Parietal**—Only the horizontal parietal plate is exposed in MPMA 04-0008/89 and its posterior margin is not completely preserved (Fig. 2a). However, the limits of the posterodorsal emargination are preserved in the natural cast of the adductor chamber, and it reached half the length of the cavum tympani, as in *Bauruemys elegans* and *Pricemys caiera*, in contrast to the more extensive emargination of *Hamadachelys escuilliei* and the less extensive ones of *Lapparentemys vilavilensis* and *Peiropemys mezzalirai* (Tong and Buffetaut 1996; Gaffney et al. 2011). The parietal plate meets the frontal anteriorly, the postorbital anterolaterally, the quadratojugal posterolaterally, and the other parietal medially, as seen in other podocnemidoids (Gaffney et al. 2011). As in other peiropemydods, the medial suture between the parietals extends posteriorly, and the supraoccipital either does not take part of the skull roof, or has only a slight exposure on it (Gaffney et al. 2011). With the help of micro CT images (Fig. 3), it is possible to identify the sutures of the processus inferior parietalis with the prootic posterolaterally, on the dorsal surface of the otic chamber, the supraoccipital posteriorly, and the pterygoid anteriorly. As in most other podocnemidoids, the parietal of MPMA 04-0008/89 forms the dorsal margin of the foramen nervi trigemini (Fig. 3c), along with the prootic posteriorly and the pterygoid anteriorly (Gaffney et al. 2011).

**Jugal**

The jugal is fractured on both sides (Fig. 2) of MPMA 04-0008/89. Nevertheless, it is possible to identify some of the contacts seen in most pelomedusoids: with the maxilla anteriorly, the postorbital dorsally, and the quadratojugal posteriorly (Gaffney et al. 2006, 2011). Also, part of the ventral margin of the left jugal is preserved and, together with the natural cast of the quadratojugal on the right side (Fig. 2c), allows inferring the extension of the anteroventral emargination, which is composed by the jugal and

quadratojugal, as in other pelomedusoids (Gaffney et al. 2006, 2011). This emargination surpasses the ventral level of the orbit dorsally (about half the height of the cavum tympani), as seen in *Peiropemys mezzalirai* and *Lapparentemys vilavilensis*, and is likely synapomorphic of Peiropemydodda (unknown in *Pricemys caiera*), differing from the less extensive anteroventral emarginations of *Hamadachelys escuilliei* and *Bauruemys elegans*, which do not surpass the ventral margin of the orbit (Tong and Buffetaut 1996; Gaffney et al. 2011).

**Quadratojugal**

The quadratojugal has preserved contacts with the postorbital anteromedially, the parietal medially, the quadrate posterolaterally, and possibly the jugal anteriorly, as in other peiropemydods. The suture with the squamosal is not preserved and that with the quadrate follows the anterior curvature of the cavum tympani, as in other pelomedusoids (Gaffney et al. 2006, 2011). Compared to other non-Podocnemididae podocnemidoids, the quadratojugal of *the new taxon* more similar to those of *Hamadachelys escuilliei*, *Peiropemys mezzalirai* and *Lapparentemys vilavilensis*, differing from that of *Bauruemys elegans*, in which it is antero-posteriorly compressed (Tong and Buffetaut 1996; Gaffney et al. 2011).

**Postorbital**

The postorbital is antero-posteriorly elongated, forming the posterodorsal margin of the orbit and contacting the frontal medially, the parietal posteromedially, the quadratojugal posterolaterally, and the jugal laterally (Fig. 2i, j). This differs from the very reduced postorbital of the different species of *Podocnemis*, which is sometimes not even exposed in dorsal view (Gaffney et al. 2011). In *the new taxon* it has a ventral projection that forms most of the septum orbitotemporale, contacting the jugal ventrolaterally and the pterygoid ventrally at the anterior base of the processus trochlearis pterygoidei, where it forms the posterodorsal part of the sulcus palatino-pterygoideus roof (Fig. 3b, c), as in other pelomedusoids (Gaffney et al. 2011). In the anterior part of the septum orbitotemporale, the postorbital contacts the frontal dorsomedially, the jugal ventrolaterally, and the palatine ventromedially (Fig. 3b, c).

**Maxilla**

Only small fragments of the right maxilla are preserved in MPMA 04-0008/89. It is possible to identify its contact to the jugal posterodorsally and to the palatine posteroventrally (Fig. 2c).

**Palatine**

The anterior portion of the palatine is not preserved and only the posterior part of the horizontal plate is exposed in MPMA 04-0008/89, with the vertical structures covered by matrix. It contacts the maxilla anterolaterally, its counterpart medially, and the pterygoid posteriorly. The palatine appears to be exposed on the orbital floor (Fig. 2a), covering the medial part of the maxilla, as typical of non-Podocnemididae Podocnemidoidae, but not very clear in *Peiropemys mezzalirai*. The foramen palatinum posterius reaches the palatine-pterygoid suture (Fig. 2e, 3a) as in *Lapparentemys vilavilensis* and some specimens of *Bauruemys elegans*, differing from *Peiropemys mezzalirai*, in which it is restricted to the palatine (Gaffney et al. 2011). The position of this foramen, however, may be variable within the same taxon, as is the case in *B. elegans* (Gaffney et al. 2011).

**Quadrate**

As in other pleurodires, the quadrate of *the new taxon* forms the entire cavum tympani (Gaffney 1979; Gaffney et al. 2006, 2011), contacting the lateral surface of the quadratojugal anteriorly. On the roof of the otic chamber, the quadrate contacts the prootic anteriorly and the opisthotic posteromedially (Fig. 3a, c). The fossa precolumellaris is very large, as in *Peiropemys mezzalirai*, and larger than those of other non-podocnemidid podocnemidoids (Tong and Buffetaut 1996; Lapparent de Broin 2000; Gaffney et al. 2011). The antrum postoticum is also well-developed (Fig. 2k, l), comparable in size to those of *Podocnemis unifilis* and *Galianemys emringeri* (Gaffney et al. 2006, 2011). The incisura columellae auris is completely closed by the contact of the dorsal and ventral processes of the quadrate, as in other Podocnemidoidae (Gaffney et al. 2011).

As in other pelomedusoids, the ventral surface of the quadrate of *the new taxon* meets the basioccipital posteromedially and the basisphenoid medially, its anteromedial projection contacting the pterygoid (Fig. 2e, f). It also forms part of the roof of the cavum pterygoidei, where it contacts the pterygoid anterolaterally, the prootic anteromedially, and the basisphenoid posteromedially, as typical of podocnemidoids (Lapparent de Broin 2000; Gaffney et al. 2011). Although the condylus mandibularis is not preserved in MPMA 04-0008/89, it is possible to infer that it was anterior to the basisphenoid-basioccipital suture, as in all other known podocnemidoids, except for some Stereogenyina (Gaffney et al. 2011; Ferreira et al. 2015). Very little is preserved of the posterior surface of the quadrate. Only an outline of the fenestra postotica is seen (Fig. 2k), which is wide as in other podocnemidoids, differing from the slit-like fenestra of Cearachelyini (Gaffney et al. 2006).

**Pterygoid**

As in most podocnemidoids, the pterygoid of *the new taxon* contacts the palatine anteriorly, its counterpart medially, the quadrate posterolaterally, and the basisphenoid posteromedially. As synapomorphic for pleurodires, the pterygoid forms the processus trochlearis pterygoidei laterally, which is nearly perpendicular to the midline in MPMA 04-0008/89. This latter condition is typical of Pan-Podocnemididae, compared to Chelidae or Pelomedusidae (Gaffney et al. 2006, 2011). Yet, the angle formed by the lateral margin of the process is almost 90°, as in *Podocnemis expansa*, *Portezueloemys patagonica*, *Peltocephalus dumerilianus*, *Peiropemys mezzalirai*, and other podocnemidids (de la Fuente 2003; Gaffney et al. 2011; Cadena 2015), whereas that angle is more oblique in *Bauruemys elegans*, *Lapparentemys vilavilensis*, *Hamadachelys escuilliei*, *Cearachelys placidoi*, and most bothremydids (Tong and Buffetaut 1996; Lapparent de Broin 2000; Gaffney et al. 2011). The pterygoid of *the new taxon* also forms a well-developed pterygoid flange, typical of Podocnemidoidae (França and Langer 2006), developing a complete cavum pterygoidei (Fig. 2e, 3e). The thin plate that forms the floor of the cavum pterygoidei is very fragile and usually broken in fossil specimens (Gaffney et al. 2011), but it is partially preserved in MPMA 04-0008/89 (Fig. 2f).

The cavum pterygoidei is also formed by the basisphenoid, prootic, and quadrate, in addition to the pterygoid, as in all podocnemidoids (Gaffney et al. 2011). Its anterior opening is large and corresponds to the foramen caroticum laterale (Fig. 3d), which is enlarged in *The new taxon*, as in other peiropemydods and *Podocnemis* spp. (Gaffney et al. 2011). The cavity is roofed by the prootic and, hence, not continuous to the canalis cavernosus as in *Peltocephalus dumerilianus* and *Erymnochelys madagascariensis* (Lapparent de Broin 2000; Gaffney et al. 2011). Anteriorly to the foramen cavernosum formed by the prootic and the quadrate, the sulcus cavernosus extends on the dorsal surface of the pterygoid, running laterally to the rostrum basisphenoidale (Fig.3e). The foramen caroticum laterale also opens in this sulcus (Gaffney 1979). Finally, the very small foramen nervi vidiani can be seen in the 3D model as a perforation on the pterygoid inside the cavum pterygoidei as in other podocnemidoids (Gaffney et al. 2011), lateral to the foramen caroticum laterale (Fig.3d). The canal for this branch of the facialis nerve (Gaffney 1979) could only be reconstructed partially; it extends anteriorly along the pterygoid, but its anteriormost portion cannot be determined (Fig. 3e).

**Supraoccipital**

The supraoccipital is not exposed on the skull roof of MPMA 04-0008/89 (Fig. 2a, 3c). This matches the condition of all known Peiropemydodda, the parietals of which cover almost the entire dorsal surface of that bone, in contrast to other podocnemidoids such as *Bauruemys elegans* and the different species of *Podocnemis* (Gaffney et al. 2011). Other parts of the supraoccipital of MPMA 04-0008/89 are covered by matrix and can only be seen in the micro CT images (Fig. 3). The bone forms the dorsal edge of the foramen magnum, contacting the exoccipitals posteroventrally, the prootic anterolaterally, the opisthotic posterolaterally, and the parietals anterodorsally (Fig.3c).

**Exoccipital**

The exoccipital of MPMA 04-0008/89 contacts the supraoccipital dorsally, the opisthotic laterally, and the basioccipital ventrally (Fig. 2k, l). The contact with the quadrate cannot be seen in this specimen, but the exoccipitals form the lateral edges of the foramen magnum. The foramina nervi hypoglossi are not preserved and the foramen jugulare posterius seems partially preserved on its right side (Fig. 2k), but it is not clear if it is continuous with the fenestra postotica as in *Bauruemys elegans* and *Portezueloemys patagonica* (de la Fuente 2003; Gaffney et al. 2011), or closed as in peiropemydods and podocnemidids (Gaffney et al. 2011).

**Basioccipital**

In ventral view, the basioccipital of MPMA 04-0008/89 contacts the basisphenoid anteriorly and the quadrate laterally (Fig. 2f). The posterior most portion of the bone is not preserved and the contacts with the opisthotic and exoccipital are not clearly seen (Fig. 2k). Although not entirely preserved, the tubercula basioccipitale are smoother than in *Bauruemys elegans* and the different species of *Podocnemis* and the space between the tubercula appears to be wider than in those taxa (Gaffney et al. 2011), and more similar to the condition found in *Lapparentemys vilavilensis* and *Peiropemys mezzalirai* (Fig. 2e, f).**Prootic**

Most of the prootic is covered by matrix in MPMA 04-0008/89, but the micro-CT scan images and our 3D reconstructions reveal its contacts and several structures (Fig. 3). As in all podocnemidoids, the prootic is completely covered in ventral view by the pterygoid, except inside the cavum pterygoidei, in which it forms the dorsomedial portion of its roof (Gaffney et al. 2011) and contacts the basisphenoid medially, the quadrate laterally, and the pterygoid anterolaterally. On its dorsal portion it also contacts the opisthotic posteriorly, the supraoccipital posteromedially, and the parietal anteromedially. Together with

the parietal and pterygoid, it forms the border of the foramen nervi trigemini, which opens laterally on the fossa temporalis inferior, as in other pleurodires (Gaffney et al. 2006, 2011).

Due to the poor contrast between fossil and matrix some smaller structures are difficult to identify in the micro-CT images. The foramen nervi facialis in the prootic inside the cavum pterygoidei, as found in *Pricemys caiera*, *Peiropemys mezzalirai*, and other podocnemidoids (Gaffney et al. 2011) could not be identified. On the other hand, the canalis cavernosum, between the prootic and quadrate, as well as the canalis stapedio-temporalis, could be completely reconstructed. The former starts posteriorly, in the fenestra postotica, and extends anteriorly to the foramen cavernosus, bordered by the prootic medially and quadrate laterally, following on the pterygoid as the sulcus cavernosus. The canalis stapedio-temporalis, branches from nearly half-way the length of the canalis cavernosus, carrying the arteria stapedialis to the foramen stapedio-temporalis (Gaffney 1979). The latter is also bordered by the prootic and quadrate, opening dorsally on the external surface of the otic chamber on the fossa temporalis superior, as in other podocnemidoids (Gaffney et al. 2011).

**Opisthotic**

Only small parts of the opisthotic of MPMA 04-0008/89 are visible, but its dorsal surface can be seen in the micro-CT images (Fig. 3). It is possible to identify the contacts to the prootic anteriorly, supraoccipital medially, exoccipital posteromedially, and quadrate laterally, as in other podocnemidoids (Tong and Buffetaut 1996; Lapparent de Broin 2000; Gaffney et al. 2011).

**Basisphenoid**

The basisphenoid differs from that of most non-podocnemidid podocnemidoids (Suárez 1969; Tong and Buffetaut 1996; Lapparent de Broin 2000), except for *Pricemys caiera*, in having an acute anterior tip exposed in ventral view (Fig. 2e, f). This could be an ontogenetic variation, as the sutural contact between the pterygoids could extend posteriorly to cover that tip in older specimens. As in other podocnemidoids, the basisphenoid of *The new taxon* has a pentagonal shape (Fig. 2e). It contacts the pterygoids anteriorly and, inside the cavum pterygoidei, a small ventral exposure of the prootic anterolaterally. It also contacts the quadrate laterally and the basioccipital posteriorly. The latter suture is smoother than in *Bauruemys elegans* (Suárez 1969) and similar to those of peiropemydods (Gaffney et al. 2011).

On the dorsal surface of the basisphenoid of *The new taxon*, as revealed by our 3D model (Fig. 3e), the rostrum basisphenoidale projects anteriorly over the dorsal surface of the pterygoids. Posteriorly,

the sella turcica is preserved on the midline and its posterolateral walls are pierced by the foramen anterius canalis carotici interni, through which the internal carotid artery enters the cavum cranii (Gaffney 1979). The foramen nervi abducentis is smaller and opens slightly posterior to the foramen anterius canalis carotici interni, also laterally on the basisphenoid and inside the cavum pterygoidei.

**Cranial endocast**

The brain endocast reconstructed for MPMA 04-0008/89 exhibits a tubular shape (Fig. 4a), as in other known extinct and extant turtles (Zangerl 1960; Gaffney 1977; Wyneken 2001; Paulina-Carabajal et al. 2013, 2017; Mautner et al. 2017). The medulla oblongata is located slightly below the level of the cerebral hemispheres, similar to the extant *Dermochelys coriacea*, *Malacochersus tornieri*, and *Macrochelys temminckii*, as well as to the extinct *Corsochelys haliniches* (Hopson 1979; Paulina-Carabajal et al. 2013; Mautner et al. 2017). Yet, in these taxa and in *The new taxon* the braincase elements are found almost in the same horizontal plane (Fig. 4a), differing from the condition of other podocnemidoid turtles such as *Bothremys cooki* and *Chedighaii barberi* (Hopson 1979; Gaffney et al. 2006), and some sea turtles (Wyneken 2001), in which the pontine and cephalic flexures of the brain position the medula oblongata well below the cerebral hemispheres (Hopson 1979). The latter are easily discernible in MPMA 04-0008/89 and more laterally expanded than in *Plesiochelys etalloni*, as also seen in *Bothremys cooki* and *Corsochelys haliniches* (Hopson 1979). The olfactory bulbs project laterally just anterior to the cerebral hemispheres, and the endocast continues anteriorly forming the slender olfactory tract (Fig. 4a, b). Projecting ventrally from the ventral surface of the endocast it is possible to identify the pituitary cast, in which the pituitary gland is located (Fig. 4a).

Dorsal to the cerebellum, a subtle subtriangular area is found (Fig. 4a, b), corresponding to the cartilaginous ridge (Paulina-Carabajal et al. 2013), or cartilaginous “rider” (Gaffney and Zangerl 1968; Gaffney 1982).. Among extinct turtles, *Bothremys cooki*, *Corsochelys haliniches*, and the baenid *Plesiobaena antiqua* (Hopson 1979; Gaffney 1982), as well as meiolaniids (Paulina-Carabajal et al. 2017) seem to possess a more prominent version of this ridge, as in *The new taxon*, but not in *Plesiochelys etalloni* (Paulina-Carabajal et al. 2013).

Only some of the cranial nerves could be reconstructed in MPMA 04-0008/89 (Fig. 4). The canal for the trigeminal nerve (V) projects laterally from the endocast, posteroventrally to the cerebral hemispheres and dorsally to the pituitary cast (Fig. 4a). The facialis nerve (VII) leaves the endocast more

posteriorly, just anterior to the endosseous labyrinth, and extends laterally inside the prootic, to the canalis cavernosus (Fig. 4b, c). The latter, after branching off from the dorsal canalis stapedio-temporalis (Fig. 4a), extends anteromedially. As in peiropemydods and *Podocnemis* spp. (Gaffney et al. 2011), it turns into the sulcus cavernosus after leaving the foramen cavernosum, where it communicates with the ventral cavum pterygoidei (Fig. 4a). The canalis cavernosus contains the lateral head vein in pleurodires (Gaffney 1979), which runs anteriorly through the sulcus cavernosus, lateral to the rostrum basisphenoidale (Fig. 3e). The canal for the palatine (or vidian) branch of the facialis nerve (Gaffney 1979) could be partially identified inside the pterygoid. It leaves the anterior wall of the cavum pterygoidei and extends anteriorly (Fig. 3e, 4c). A small canal anteroventral to the nerve facialis could be identified in the micro-CT scan images, and could correspond to the abducens nerve (VI), which runs anteriorly (Paulina-Carabajal et al. 2013).

Finally, the cerebral and palatine branches of the internal carotid leave the cavum pterygoidei anteromedially and anteriorly, respectively (Fig. 4c), as in all peiropemydods and podocnemidids (Gaffney et al. 2011). The cerebral artery enters the pituitary fossa on the basisphenoid, and the palatine artery runs anteriorly to the sulcus cavernosus on the dorsal surface of the pterygoid (Fig. 3e, 4c). Thus, the split between the two branches of the internal carotid artery occurs inside the cavum pterygoidei, floored by the pterygoid flange, which extends ventrally to that split (Gaffney et al. 2011). As in all crown-turtles, the split of the internal carotid artery is, therefore, floored by bone (Sterli et al. 2010; Müller et al. 2011), but this occurs in an open space (i.e., inside the cavum pterygoidei), and not within its own canal (the canalis carotici interni; Gaffney 1979). The patterns of carotid circulation are well documented in cryptodires and stem-turtles (Albrecht 1976; Sterli et al. 2010; Müller et al. 2011; Rabi et al. 2013), but descriptions or both extant and extinct pleurodires are still lacking

**Inner ear**

The digitally reconstructed inner ear of *The new taxon* shows a morphology that generally resembles that of other turtles (Wever 1978; Walsh et al. 2009; Paulina-Carabajal et al. 2013, 2017): the semicircular canals are dorsoventrally low, subequal in size, and their cross-section is sub-eliptical, with a globose lagena (Fig. 4d).

The inner ear cast is 9.2 mm long. The anterior (ASC) and posterior (PSC) semicircular canals are not as dorsoventrally low as in *Plesiochelys etalloni* (Paulina-Carabajal et al. 2013), meiolaniids

(Paulina-Carabajal et al. 2017), and some other cryptodires (e.g. *Chelonoidis nigra*, *Chelonoidis chilensis*, *Trachemys scripta*, and *Carettochelys insculpta*; Georgi and Sipla 2008; Paulina-Carabajal et al. 2017), but more elevated as in *Gopherus berlandieri*, *Chelydra serpentina* and *Malacochersus tornieri* (Walsh et al. 2009; Mautner et al. 2017; Paulina-Carabajal et al. 2017). The vertical canals (ASC and PSC) are elongated in the anteroposterior axis (Fig. 4), which could indicate an aquatic behaviour according to Georgi and Sipla (2008). As in *Plesiochelys etalloni* and most known turtles (Paulina-Carabajal et al. 2013, 2017), the crus communis is located at the midline of the vestibular organ (Fig. 4). The angle formed between the ASC and the PSC is 87.8º, wider than that described for *Plesiochelys etalloni* or *Trachemys scripta* (Paulina-Carabajal et al. 2013), but lower than that of any terrestrial taxa (Paulina-Carabajal et al. 2017). The lateral semicircular canal (LSC) is the thickest (1.1 mm) of the three, as in *Plesiochelys etalloni*, followed by the ASC (0.8 mm) and the PSC (0.6 mm). The ASC is slightly more elongated than the PSC (2.2 mm and 2.1 mm, respectively). As in *Plesiochelys etalloni* (Paulina-Carabajal et al. 2013), the anterior ampulla is well developed whereas the posterior is much slender (Fig. 4e), in contrast to that of several testudinids (Paulina-Carabajal et al. 2017).

The lagena in *The new taxon* is well-developed ventrally (Fig. 4d), similarly to those of *Plesiochelys etalloni*, *Gopherus berlandieri*, and *Testudo hermanni*, in contrast to those of *Rhinoclemmys funerea* and *Kinixys belliana* (Paulina-Carabajal et al. 2013, 2017), in which this region is more rounded. The fenestra ovalis is smaller than that of *Malacochersus tornieri* (Mautner et al. 2017). The columella auris is preserved on both sides (Fig. 4), except for the distal portion. Its shaft is thinner than in *Plesiochelys etalloni*, and projects anterolaterally, in contrast to the posterolaterally projection of the latter (Paulina-Carabajal et al. 2013). The foot plate is broad and concave medially, towards the fenestra ovalis.

**Podocnemidoidea** Broin, 1988

***Roxochelys*** Price, 1953

*Type species*. *Roxochelys wanderleyi* Price, 1953.

*Diagnosis (emended)*. A medium-size Podocnemidoidae (more than 300 mm of carapace length) with a shell surface with fine sculpturing composed of small polygons; vertebral scutes 2-4 hexagonal and narrower than the pleural scutes; a relatively short and wide nuchal bone (in comparison to other non-Podocnemididae Podocnemidoidea), with a wide anterior edge; four-sided first neural bone; axillary buttress extending onto costal bones 2 and reaching the peripheral bones 3 anteriorly; suture for axillary

buttress medially broad and laterally narrow; costal bones 2 thickened around the axillary buttress suture; bridge peripheral bones unguttered; iliac scar on costal bone 7 with concave anterior outline that crosses from costal bone 8 onto costal bone 7 both medially and laterally; internal gutter of posterior peripheral bones and pygal bone absent; gular scutes restricted to the epiplastra; intergular scute relatively wide; long midline contact between humeral scutes; pectoral scutes reach the entoplastron but not the epiplastra or mesoplastra.

***Roxochelys wanderleyi*** Price, 1953

Figure 5

*Holotype*. MCT (DGM) 216-R housed at Museu de Ciências da Terra, Rio de Janeiro, Brazil.

*Diagnosis*. Same as for genus.

*Studied material*. MPMA-10-0003/03 (Fig. 5) an almost complete, but heavily crushed and partially disarticulated shell.

*Locality and Horizon*. A reddish sandstone of the Late Cretaceous Adamantina Formation, exposed near the urban area of Monte Alto, São Paulo, Brazil (S 21° 14' 03,6", W 48° 30' 27,5") (Fig. 1).

*Description*. MPMA-10-0003/03 consists of a large (approximately 50 cm long) partially articulated, but very cracked and crushed shell (Fig. 5), preventing the analysis of its visceral structures. The right costal plate 7, both costal plates 8, the suprapygal, pygal, and some peripheral plates are not preserved. Some of the scute sulci are seen on the carapace, allowing a partial reconstruction of the scute pattern (Fig. 5b). All the plastral bones are preserved, except for parts of the right epiplastron and xiphiplastron. The ventral surface of the plastron is somewhat eroded, preventing the identification of scute sulci (Fig. 5d). The typical ornamentation of braided lines and small polygons found in the outer surface of *Roxochelys wanderleyi* shells (Broin 1971, 1991; Gaffney et al. 2011) is also seen in the carapace of MPMA-10-0003/03 (Fig. 5a). However, similar ornamentation patterns can also be found in some non-Podocnemidoid taxa (e.g., the different species of *Hydromedusa*) and some extant podocnemidids (e.g. *Peltocephalus dumerilianus* and the different species of *Podocnemis*; pers. comm. E. Cadena), and may not be a reliable feature to identify turtle taxa.

Only a partial contour of the left edge of the nuchal bone can be seen (Fig. 5a, b). It reveals a relatively broad plate without an anterior narrowing margin, as in other specimens referred to *Roxochelys wanderleyi* (Price 1953; Romano et al. 2013), and differing from other taxa found in the Bauru Basin (Gaffney et al. 2011). The neural series is partially preserved (the fifth element missing). The neural bone

1 is four-sided, not contacting the costal bones 2 (Fig. 5b). This is seen in *R. wanderleyi* (Price 1953; Romano et al. 2013) and *Cambaremys langertoni* (França & Langer 2005), but not in *Bauruemys elegans*, the four-sided neural plate of which is the second (Suárez 1969; Kischlat 1994; Romano and Azevedo 2007; Gaffney et al. 2011; Romano et al. 2013). The last preserved neural bone is the hexagonal sixth plate. Usually the last neural plate of a complete series is pentagonal or heptagonal in shape, due to the converging posterior contact with the costal plates. Thus, the last neural plate is probably missing from MPMA-10-0003/03, which would have a neural series composed of seven bones (Fig. 5a, b). Intraspecific variation in the length of the neural series is not uncommon within podocnemidoids and *R. wanderleyi* are known from specimens with six and seven plates (Gaffney et al. 2011; Romano et al. 2013).

The scute pattern is the same as in all so far known specimens of *Roxochelys wanderleyi* (Price, 1953; Gaffney et al. 2011; Romano et al. 2013). The marginal scutes 1 are antero-posteriorly short, but their lateral limits are not preserved, so that their total width is unclear. The vertebral 1 is medio-laterally shorter than vertebral scutes 2 and 3 (Fig. 5a, b), and these are hexagonal in shape (sulci are only partially preserved in vertebral 4). The pleural scutes are wider than the vertebral scutes. As in *Bauruemys elegans* (Suárez 1969) and other *Roxochelys wanderleyi* specimens (Gaffney et al. 2011; Romano et al. 2013), the pleuromarginal sulci of MPMA-10-0003/03 are restricted to the lateral third of the peripheral bones (Gaffney et al. 2011; Romano et al. 2013). However, the characteristic guttering in the marginal scutes of *B. elegans* (Gaffney et al. 2011) is absent in MPMA-10-0003/03.

The plastron of MPMA-10-0003/03 shows the common Podocnemidoidae morphology (Fig. 5c), seen in all Bauru Basin taxa. The entoplastron is diamond-shaped and contacts the epiplastra anteriorly and the hyoplastra posteriorly. The mesoplastron is rounded and located laterally, sutured to the hyoplastron anteriorly, peripherals 5 and 6 laterally, and the hypoplastron posteriorly (Fig. 5c, d). The pectoroabdominal sulcus apparently does not cross the mesoplastron, as in MCT 1787-R, referred to *Roxochelys wanderlyi*. However, this region is poorly preserved in MPMA-10-0003/03 and the identification of this sulcus is not clear (Fig. 5c, d).

**Additional specimens**

Three more fragmentary specimens (Fig. 6) have been found in the same locality as MPMA 04-0008/89. The more complete of these, MPMA 04-0009/89, is composed of several carapace fragments, including costal and peripheral plates. MPMA 04-0014/89 is an articulated carapace fragment, including

three partially preserved left costal plates and two neural plates. Neither of them possess diagnostic features of any particular subclade and are hence considered Testudines indet. MPMA 04-0017/89 is represented by a costal bone, a left hyoplastron fragment, and a pelvic girdle fragment, including mostly parts of the ilium, but also fragments of the ischium, and pubis, and can be assigned to Pleurodira. The latter is comparable in relative size to MPMA 04-0008/89, but those were not found closely associated and, hence, we refrain from referring them to the same specimen. The two other specimens are somewhat larger. The peripheral plates of MPMA 04-0014/89 bear the same reticulation pattern found in MPMA-10-0003/03.

**Discussion**

Our phylogenetic analysis found six most parsimonious trees (MPTs) with 238 steps each (see Supplementary Data). The MPTs differ in the relative position of some outgroup taxa (i.e., *Araripemys barretoi*, Pelomedusidae), as well as *Hamadachelys escuilliei* and *Portezueloemys patagoinica*, and some species of *Podocnemis*. All most parsimonious trees (Fig. 6; Supplementary Data) shows *The new taxon* nested within Peiropemydodda, in a polytomy including *Peiropemys mezzalirai* and the clade formed by *Pricemys caiera* and *Lapparentemys vilavilensis*. Peiropemydodda is supported by an anteroventral emargination reaching above the ventral level of the orbit (ch. 13, state 2). The scoring of *The new taxon* in the data matrix differs from that of *Peiropemys mezzalirai* by two conditions: the foramen palatinum posterius on the palatine-pterygoid suture, rather than restricted to the palatine (ch. 37) and a larger antrum postoticum (ch. 40). The size of the antrum postoticum also sets the taxon apart from *Pricemys caiera* and *Lapparentemys vilavilensis*. The larger foramen nervi abducentis (ch. 65) of the former and the shallow fossa precolumellaris (ch. 41) of the latter also differentiate those peiropemydods from *The new taxon*. Those distinct features, associated with its smaller size and stratigraphic provenance further supports the assignment of MPMA 04-0008/89 to a distinct peiropemydod taxon. As such, it extends the record of Peiropemydodda to pre-Maastrichtian times (Fig. 7), with the clade surviving until the early Paleocene (Broin 1971, 1991; Gaffney et al. 2011).

Although some authors used Computed Tomography to study osteological traits (e.g. Brinkman et al. 2006; Lipka et al. 2006; Sterli et al. 2010; Cadena and Jaramillo 2015; Lively 2015) of extinct turtles, only four other studies were published so far with digital reconstructions of their soft tissue organs

(Georgi and Sipla 2008; Paulina-Carabajal et al. 2013, 2017; Mautner et al. 2017). Indeed, this is the first study to employ these tools to assess the inner ear and neuroanatomy of an extinct pleurodire. The endocast and inner ear of *The new taxon* are similar to those of other turtles. However, some differences are noted, such as the position of the medulla oblongata almost on the same level as the cerebral hemispheres (Fig. 4a), whereas the condition in the bothremydids *Bothremys cooki* and *Chedighaii barberi* (Hopson 1979) resembles that of sea turtles (Wyneken 2001), in which the medulla oblongata is located well below the cerebral hemispheres, with stronger pontine and cephalic flexures. Those differences could be related to the adaptations of bothremydids to marine environments, as suggested by some authors (e.g. Gaffney et al. 2006; Rabi et al. 2012; Joyce et al. 2016). However, with such a small sample, especially for pleurodires, it is premature to infer phylogenetic or behavioural trends from the neuroanatomy of fossil turtles. Future, more comprehensive studies may employ the data presented here to better explore the evolution of those organs in Pleurodira and Testudines. We also provided a detailed account of the cranial nerves and arteries in *The new taxon*. As noted above, the patterns of carotid circulation in turtles has been mainly studied in stem-turtles and cryptodires. Given that several phylogenetic characters are related to the circulatory and nerve systems, such as skull foramina and canals (e.g. Joyce 2007; Sterli et al. 2010; Müller et al. 2011; Gaffney et al. 2006, 2011; Rabi et al. 2013), our study adds new data to understand the patterns in Pleurodira.

The assignment of MPMA-10-0003/03 to *Roxochelys wanderleyi* is based on the general podocnemidoid morphology of the shell, the four-sided neural plate 1, the broad nuchal plate, and the reticulation pattern of ornamentation on its external surface (Broin 1991; Gaffney et al. 2011; Romano et al. 2013). *Roxochelys wanderleyi* was previously recorded in the Adamantina Formation from the type-locality in Mirandópolis, as well as in the area of Presidente Prudente, both in São Paulo, Brazil (Price 1953; Broin 1971; Gaffney et al. 2011; Romano et al. 2013; Menegazzo et al. 2015). The new specimen extends the putative record of this taxon to another Adamantina Formation site. In addition, most of the specimens so far referred to *R. wanderleyi* are smaller than 50 cm of carapace length (Romano et al. 2013), so that the new specimen represents one of the largest yet attributed to the taxon.

## Conclusions

A partial skull from the Late Cretaceous Adamantina Formation represents the first extinct pleurodire and one of the few fossil turtles to have its neuroanatomy described based on digitally reconstructed endocast and inner ear. The large antrum postoticum and fossa precolumellaris, the foramen prepalatinum formed by the pterygoid and palatine, and the triangular dermal scute vii with an anterior notch on the midline, as well as its smaller size and distinct stratigraphic provenance, support the assignment of this specimen to a new taxon, *The new taxon*, placed inside Peiropemydodda in our phylogenetic analysis . This fossil extends the range of that clade to pre-Maastrichtian times. Other fossil turtles from the Monte Alto area include a new *Roxochelys wanderleyi* shell recovered from a different site of the Adamantina Formation, which represents one of the largest specimens referable to that taxon.

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**Figures**

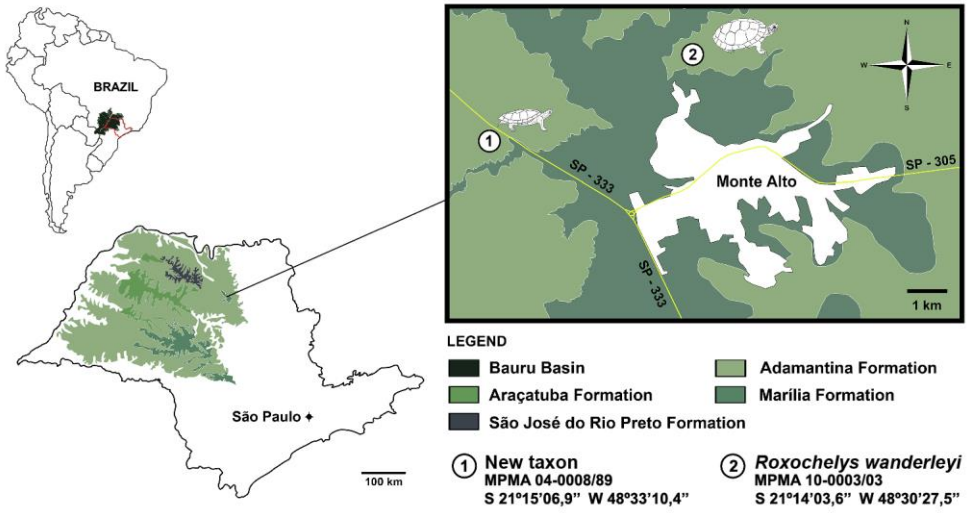


**Fig.1**. Location of the Bauru Basin on a South American map (top left), São Paulo state map showing the surface distribution of the stratigraphic units of the basin (bottom left), and map of the Monte Alto region highlighting the localities were the described fossils were found

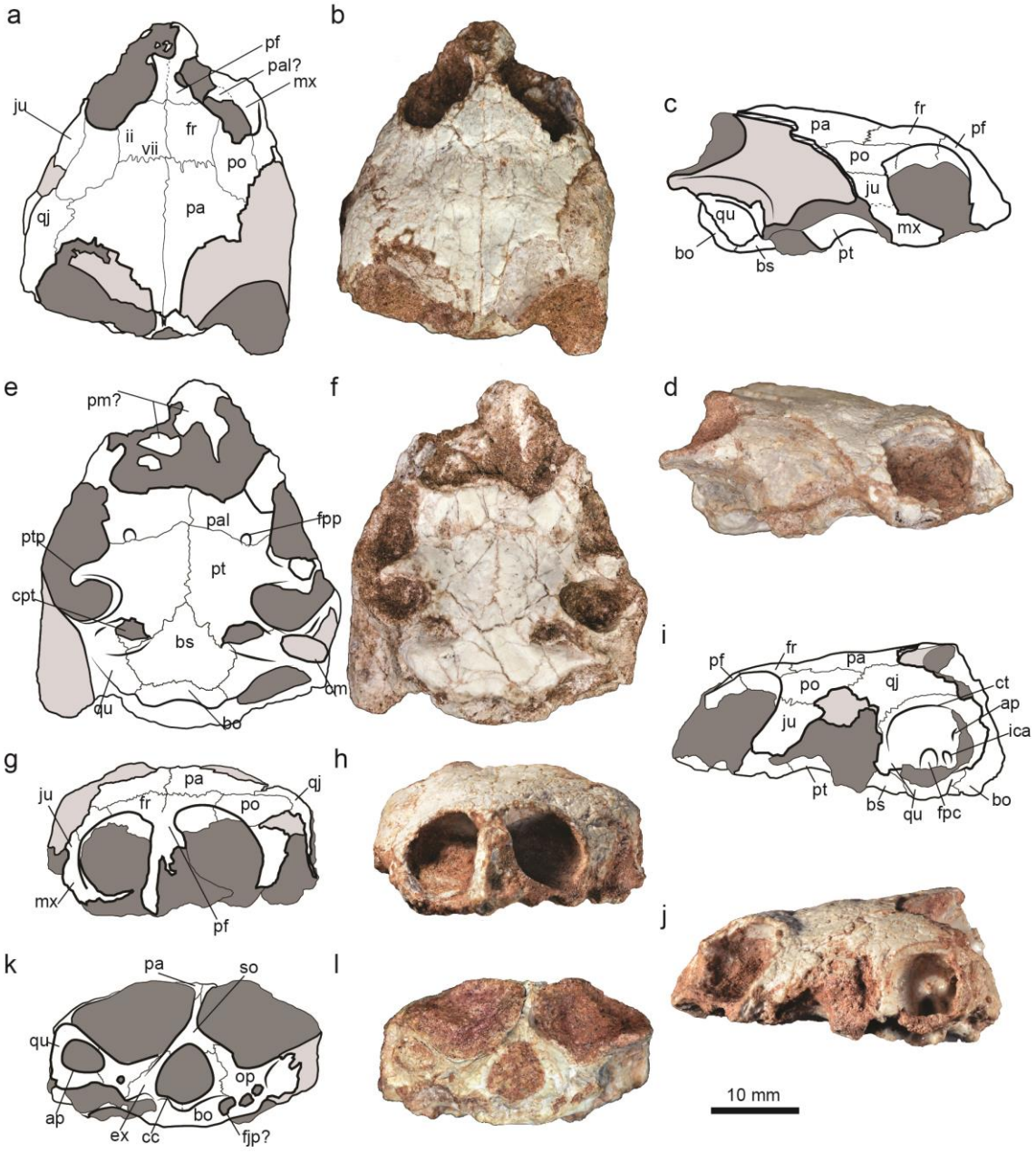


**Fig. 2** *The new taxon*, MPMA 04-0008/89. Outlines and photographs of the skull in (**a, b**) dorsal, (**c, d**) right lateral, (**e, f**) ventral, (**g, h**) anterior, (**i, j**) left lateral, and (**k, l**) posterior views

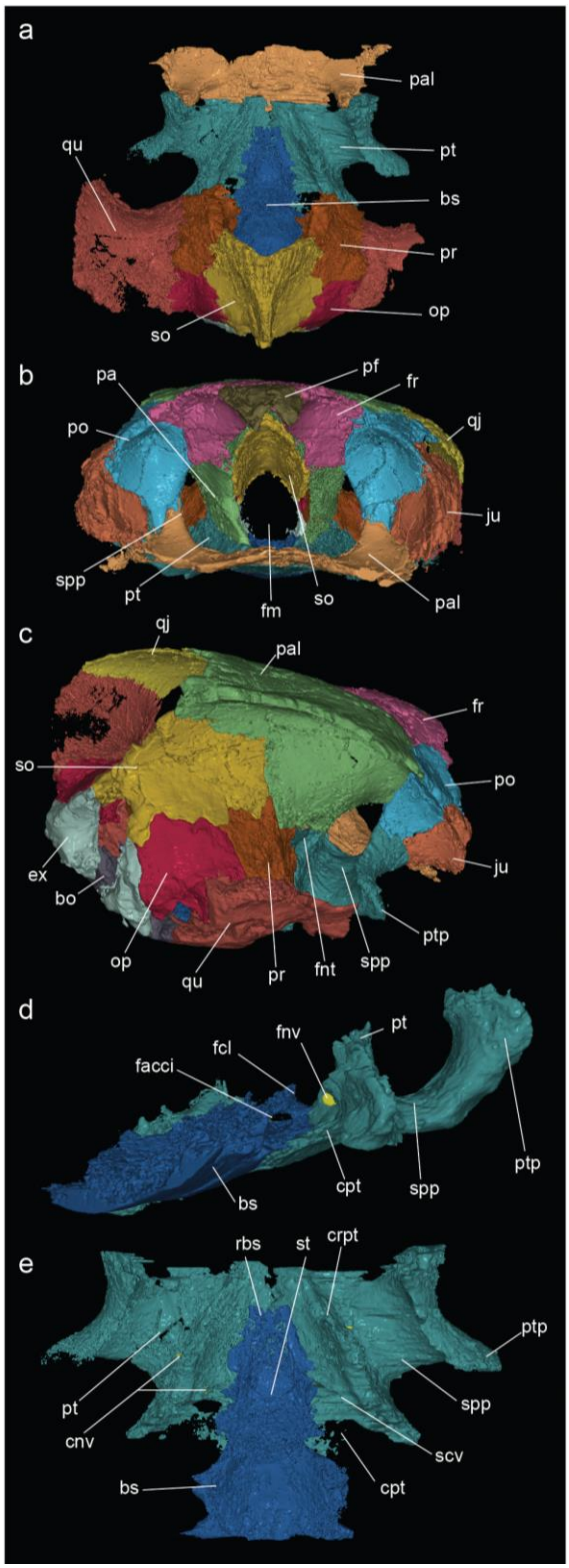


**Fig. 3** *The new taxon*, MPMA 04-0008/89. Micro-CT scan reconstructed 3D models of the skull in (**a**) dorsal view without parietal, frontal and prefrontal bones, (**b**) anterior view, (**c**) oblique right lateral view, and isolated basisphenoid and pterygoid bones in (**d**) oblique left lateral and (**e**) dorsal views

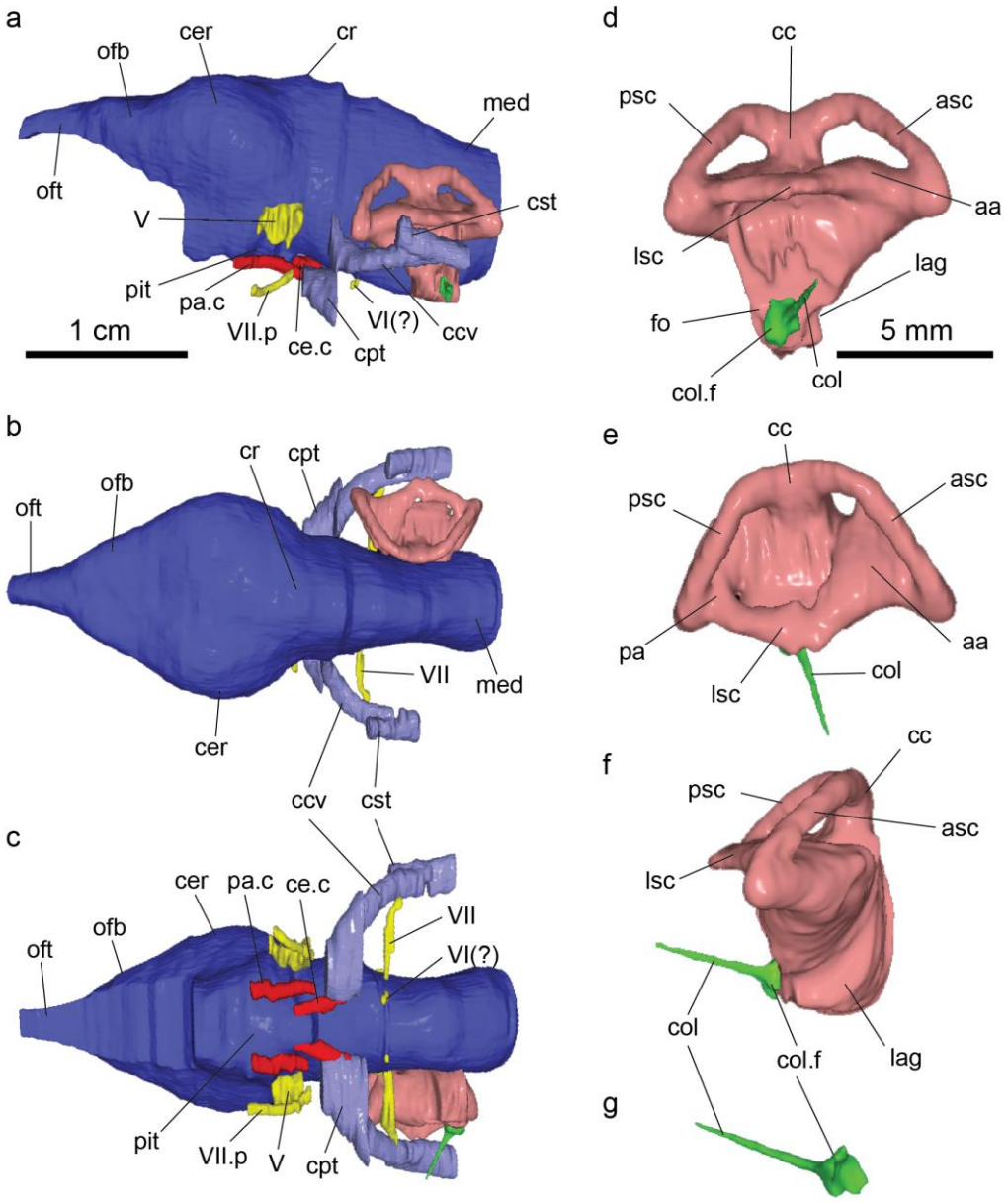


**Fig. 4** *The new taxon*, MPMA 04-0008/89. Digital endocasts of the brain with associated cranial nerves and blood vessels in (**a**) left lateral, (**b**) dorsal, and (**c**) ventral views, and of the endosseous labyrinth with the columella auris in (**d**) right lateral, (**e**) dorsal, and (**f**) anterior views. On the brain endocast models only the right labyrinth is showed for better visualization.

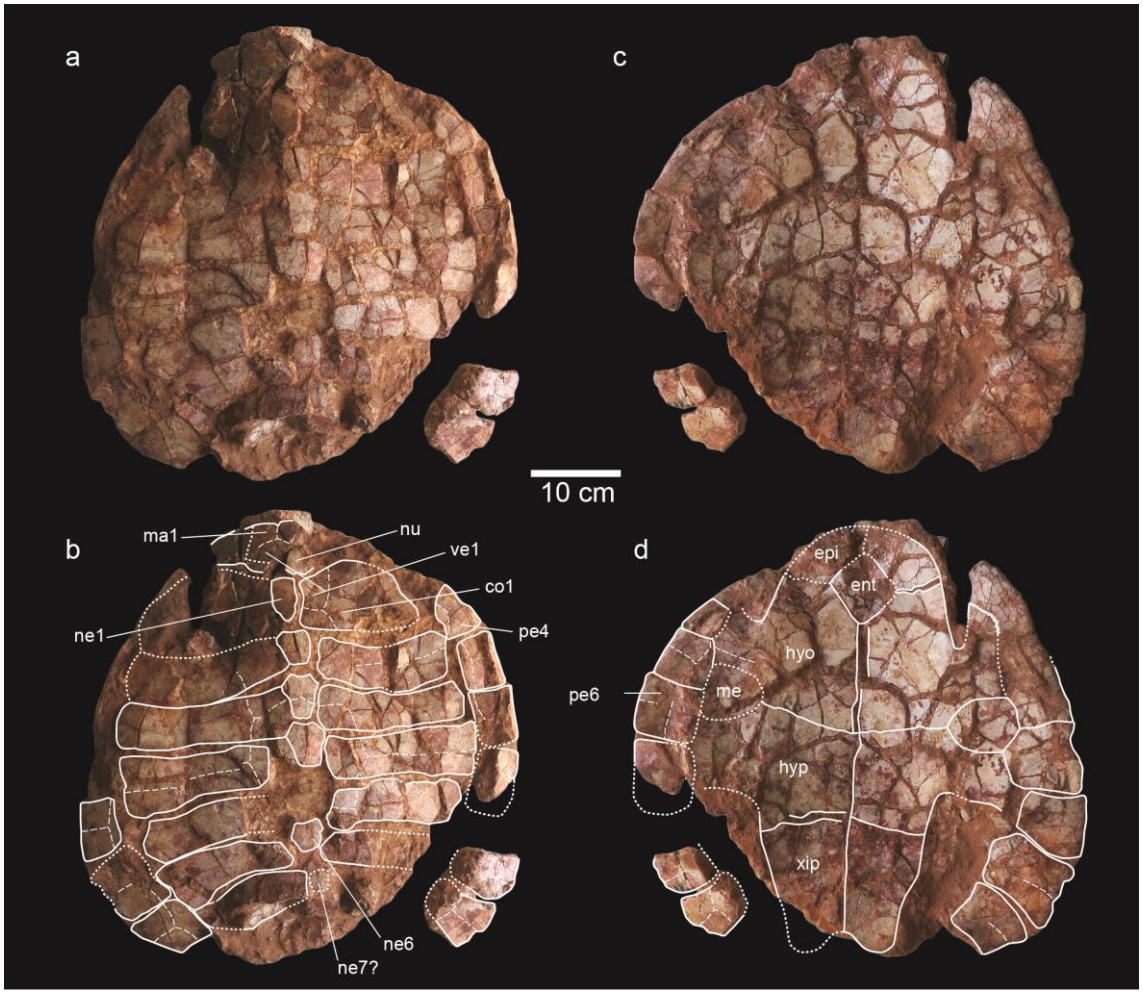


**Fig. 5** *Roxochelys wanderleyi*, MPMA-10-0003/03¸ shell in (**a-b**) dorsal and (**c-d**) ventral views

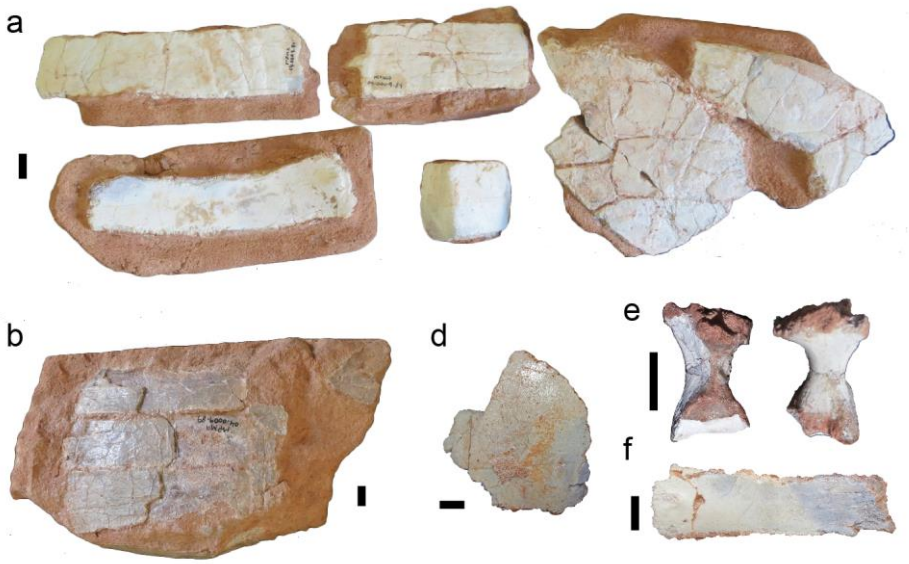


**Fig. 6** Additional turtle specimens from Monte Alto, Brazil. (**a**) Several carapace fragments of a Testudines (MPMA 04-0009/89); (**b**) an articulated carapace fragment of another Testudines indet. (MPMA 04-0014/89); and fragments of (**c**) a left hyoplastron, (**d**) a pelvic girdle, and (**e**) a costal plate of a Pleurodira indet. (MPMA 04-0017/89). Scale bars represent 1 cm.

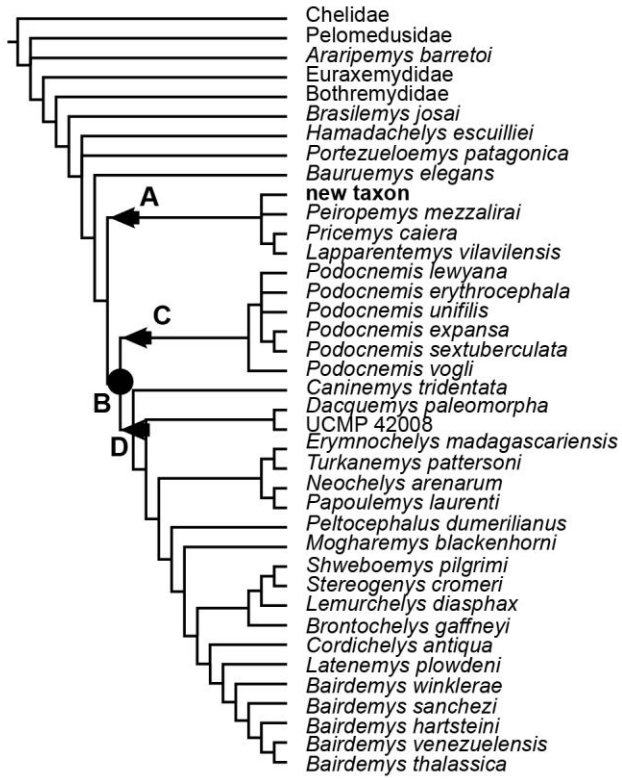


**Fig. 7** Strict consensus tree resulting from the phylogenetic analysis. *The new taxon* (bold) is recovered inside the Peiropemydodda clade, along with *Peiropemys mezzalirai*, *Pricemys caiera*, and *Lapparentemys vilavilensis*. The arrows highlight the branch-based clades (A) Peiropemydodda, (C) Podocnemidinae, and (D) Erymnochelydinae, and the circle indicates the node-based clade (B) Podocnemididae.

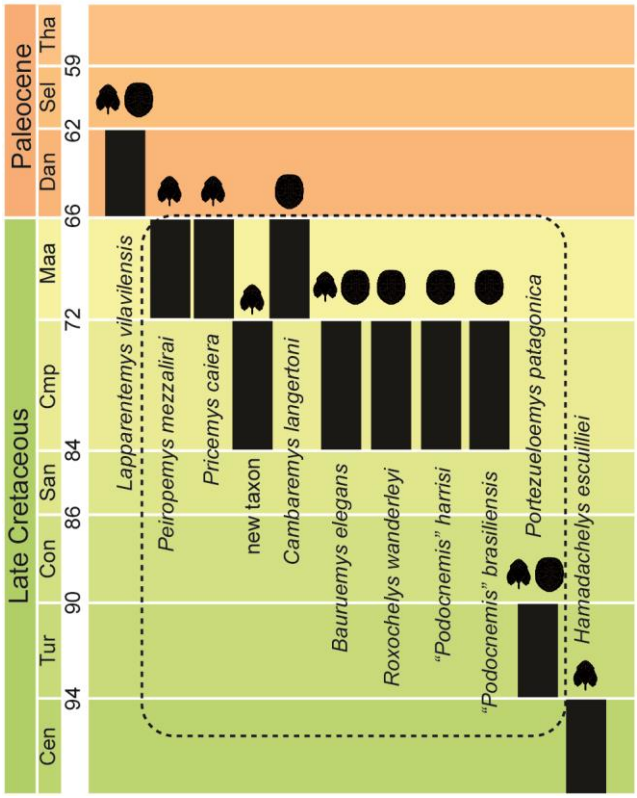


**Fig. 8** Stratigraphic plot of non-Podocnemididae podocnemidoids. Black bars represent their temporal distribution; skulls and carapaces indicated the preserved skeletal parts; dotted rectangle highlights Bauru Basin taxa. Age of the Bauru Basin taxa based on Batezelli (2015)