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The largest Cretaceous podocnemidoid turtle (Pleurodira) revealed by an isolated plate from the Bauru Basin, south-central Brazil

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ABSTRACT

The Bauru Basin (south-central Brazil) fossils have largely contributed to understand the faunal composition of South American Cretaceous. Among those, several turtle specimens were retrieved from those deposits, all belonging to Podocnemidoidae, the single group known from the Basin. On the other hand, only incomplete shell elements indicate large turtles such as 'Peirópolis A'. Another shell fragment, a large peripheral plate from the Marília Formation, is described here. Its lack of surface ornamentation, and deep sulci are generally typical for podocnemidoids. The plate exhibits a narrow knob slightly projected onto the pleuro-marginal sulcus, absent in any other Bauru Basin turtle. According to extant and fossil podocnemidoids measures, we estimated this individual reached 1 m of carapace length, exceeding in size all other taxa known from the Basin. This new report reveals a broader size variation among podocnemidoids from the Late Cretaceous of Bauru Basin today, in which inhabits the largest extant podocnemidoid *Podocnemis expansa*. Furthermore, the occurrence of such large turtles implies the presence of perennial streams on the northeastern portion of the Bauru Basin during the Maastrichtian and a richer environment than previously thought.

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Podocnemidoidae; giant turtles; Bauru Basin; Marília Formation; palaeoenvironment

Introduction

Podocnemidoidae is a stem-based taxon that comprises all pleurodiran turtles sharing a more recent common ancestor with Podocnemis expansa than with Bothremys cooki (modified from Podocnemoidae of França & Langer 2006; see Ferreira et al. 2015 for a discussion of the spelling of Podocnemis derived names). Its present diversity is restricted to seven freshwater species from the Amazon Basin, and one from Madagascar (Gaffney et al. 2011), but its fossil record shows a wider geographic distribution, including Africa, southeast Asia, Europe, and North America (Swinton 1939; Tong 1998; Weems 2009; Gaffney et al. 2011), and a broader niche occupation, including sea-dwelling forms (Ferreira et al. 2015). Yet, except for a handful of other Gondwanan forms (Broin 1971; Tong & Buffetaut 1996; Lapparent de Broin 2000; de la Fuente 2003; Gaffney et al. 2011), all known Cretaceous podocnemidoids come from the Bauru Basin, in south-central Brazil (França & Langer 2006). In fact, this is the single turtle group known from the Basin, including taxa on the stem-lineage to Podocnemididae, such as Roxochelys wanderleyi, Bauruemys elegans, Cambaremys langertoni, Pricemys caiera, and Peiropemys mezzalirai (Price 1953; Suárez 1969; França & Langer 2005; Gaffney et al. 2011), as well as dubious forms such as 'Podocnemis' harrisi and 'P'. brasiliensis (Pacheco 1913; Staesche 1937). In addition, disarticulated shell elements were retrieved from the area of Peirópolis, Minas Gerais, and might correspond to two other forms, 'Peirópolis A' and 'Peirópolis B' (Gaffney et al. 2011; Rogério et al. 2013), although those authors also suggested that the specimens could alternatively belong, respectively, to *Pr. caiera* and *Pe. mezzalirai*. Lastly, Menegazzo et al. (2015) reported an unnamed new turtle from the Santo Anastácio Formation, and Kischlat (2015) reported other possible Podocnemididae from the Adamantina Formation.

Testudines are known to attain large sizes, with living forms such as the leatherback sea turtle (Dermochelys coriacea) and the Galápagos tortoise (Chelonoidis nigra) reaching about 200 cm of total length (Fritts 1983; Wood et al. 1996). Among extant pleurodires, only *Podocnemis expansa* (the giant Amazon turtle) approaches 100 cm of carapace length (Vogt 2008). Larger fossil forms include the Miocene podocnemidid Stupendemys spp. from Venezuela and northern Brazil (Wood 1976; Bocquentin & Melo 2006), Cretaceous marine turtles such as Archelon ischyros, Protostega gigas, and Gigantatypus salahi (Cope 1872; Wieland 1896; Kaddumi 2006), and the tortoise Megalochelys atlas from the Eurasian Neogene (Brown 1931), all with carapace lengths surpassing 200 cm. The carapace from the Cretaceous nearshore marine bothremydids Nigeremys gigantea and Arenila krebsi (Lapparent de Broin & Werner 1998; Gaffney et al. 2006; Rabi et al. 2012), known only by skull material, would also exceed this length. Regarding continental (terrestrial or freshwater) testudines, some Cretaceous forms such as Asian (e.g. Nanhsiungchelys wuchingensis and Basilochelys macrobios) and North American (e.g. Basilemys spp.) nanhsiungchelyids would also have reached 100 cm of carapace length size range (Yeh 1966;

Brinkman & Nicholls 1993; Tong et al. 2009) as well as the South American chelid *Mendozachelys wichmanni* (de la Fuente et al. 2017). The occurrence of such large pelomedusoids, however, was previously reported only to the Cenozoic (e.g. Wood 1976; Bocquentin & Melo 2006; Cadena et al. 2012; Dumont Júnior 2013; Cadena & Jaramillo 2015). In the Cretaceous Bauru Basin, only incomplete shell remains indicate the presence of relatively large podocnemidoid turtles, including a set of disarticulated elements cited briefly in Broin (1991, p. 515), later labelled as 'Peirópolis A' by Gaffney et al. (2011), and a peripheral plate from the São José do Rio Preto Formation reported by Ferreira and Langer (2013).

Here, we describe a new isolated peripheral bone from the Marília Formation, representing the largest Bauru Basin podocnemidoid. We used regression analyses to estimate and compare sizes among different podocnemidoid taxa to explore the spectrum of size range attained during their evolution. Furthermore, the occurrence of this large turtle helps understanding the depositional environment of the northeastern border of Marília Formation, traditionally considered as an alluvial fan deposit with ephemeral lakes and braided rivers (Fernandes & Ribeiro 2015), which could be characterized instead by the presence of perennial fluvial systems (Basilici et al. 2016), likely suitable for such larger testudines.

Materials and methods

The specimen CPPLIP 1486 (see Appendix 1 for institutional abbreviations) is housed at the Centro de Pesquisas Paleontológicas 'Llewellyn Ivor Price', Complexo Cultural e Científico de Peirópolis, UFTM, Peirópolis, Uberaba, MG, Brazil. Figures were prepared using Adobe Photoshop CC and Illustrator CC softwares.

In order to estimate the size of the carapace to which CPPLIP 1486 belonged, we obtained approximate measures of carapace and right peripheral 7 lengths from extant and fossil podocnemidoid specimens (see Appendix 2 for the list) and employed those to produce a linear regression analysis. Prior to this analysis, we tested our data for normality with the Shapiro-Wilk's test and, since they were normally distributed, there was no need to logarithmically transform those measures.

We also measured the nuchal bone length of several podocnemidoid specimens and regressed them to total carapace length to estimate the size of specimens possessing only nuchal bones,



Figure 1. CPPLIP 1486. Photographs and respective outline drawings of right peripheral 7 in dorsal (A–B) and ventral (C–D) views. Abbreviations: ma=marginal scutes; pl=pleural scutes. Scale: 2 cm.



Figure 2. CPPLIP 1486. Photographs and outline drawing of right peripheral 7 in caudodorsal (A–B) and laterocranial (C) views. Abbreviations: ma = marginal scutes; pl=pleural scutes. Scale: 1 cm (A–B) and 2 cm (C).

e.g. CPPLIP 348, CPPLIP 731 (assigned to 'Peirópolis A' by Rogério et al. 2013), and CPPLIP 746 (assigned to 'Peirópolis B' by the same author). Similarly, to estimate the carapace length of taxa known only by their skulls (e.g. *Peiropemys mezzalirai* and *Pricemys caiera*) we regressed skull width (measure B in Gaffney et al. 2006: Fig. 315) to total carapace length of our sampled taxa. All statistical analyses were conducted in R environment software (R Core Team 2016).

Systematic palaeontology

Testudines Batsch 1788 Pleurodira Cope 1864 Pelomedusoides Cope 1868 Podocnemidoidae Cope 1868

Material. CPPLIP 1486, a right peripheral bone (Figs. 1–2).

Provenance. BR-050 road (19°35'33"S, 48°01'42"W), about 15 km north of Uberaba, Minas Gerais, Brazil. Serra da Galga Member, Marília Formation (Carvalho et al. 2004; Salgado & Carvalho 2008), Maastrichtian of the Bauru Basin (Batezelli 2015; Fernandes & Ribeiro 2015; Menegazzo et al. 2016).

Results

The fossil material CPPLIP 1486 is a nearly complete peripheral bone from the posterior bridge region (13.5 cm long, 8 cm wide and 6.5 cm high, as preserved), probably the seventh right element. The dorsal and ventral surfaces are very smooth as in *Cambaremys langertoni* (França & Langer 2005), lacking ornamentation such as the 'weak pattern of striations' of *Bauruemys elegans* and 'Peirópolis A' and the small polygons sculpture of

Roxochelys wanderleyi (Gaffney et al. 2011). Scale sulci are deep and well-marked, as typical of podocnemidoids (Cadena 2011), indicating little taphonomic modification . These separate marginal scales 7 and 8 and pleural scales 2 and 3, the former of which extends as a lateromedially oriented sulcus to the ventral side of the shell. In some podocnemidoids (e.g. Lapparentemys vilavilensis, C. langertoni, Podocnemis spp.), the pleuro-marginal sulcus nearly matches the costo-peripheral suture, especially at the bridge peripherals (Gaffney et al. 2011), a trait not seen in CPPLIP 1486. The pleural scute in this specimen reaches the medial portion of the peripheral plate, as in most podocnemidoids (Cadena & Jaramillo 2015). In the inner side of the shell, there are no signs of pits or pockets for suturing the distal ends of the ribs, which are seen in cheloniids (Wyneken 2001) and some chelids, but not in Dortoka vasconica (Pérez-García et al. 2012) nor in podocnemidoids. There is also no sign of an inguinal buttress crossing this plate, a feature observed in the seventh peripheral bone of some dortokids (Lapparent de Broin et al. 2004; Pérez-García et al. 2012), although the region is broken in CPPLIP 1486.

The bone is V-shaped in cranial and caudal views, with thick dorsal and ventral laminae, as in *Roxochelys wanderleyi* and *Lapparentemys vilavilensis* (Price 1953; Broin 1971). Their external surfaces meet at a sharp angle, suggesting a low-domed carapace, a common feature of podocnemidoids and other aquatic (freshwater and marine) turtles. Some podocnemidoids, such as *Bauruemys elegans*, *L. vilavilensis*, and 'Peirópolis A', have a guttering on the bridge peripherals (Gaffney et al. 2011), which is lacking in CPPLIP 1486, as well as in *Cambaremys langertoni* and 'Peirópolis B'. Finally, knobs on the carapace dome are common among extant large-sized cryptodires (e.g. testudinids), chelids (Ferreira et al. 2016), and was also reported for



Figure 3. Results of the regression analyses between (A) peripheral and carapace lengths (R²=0.96), and (B) nuchal and carapace lengths (R²=0.97).

a large indeterminate pelomedusoid from the Late Palaeocene of Colombia (Cadena et al. 2012). These are, however, absent in gigantic forms such as *Stupendemys geographicus* and *Protostega gigas* (Cope 1872; Wood 1976). A knob as seen in CPPLIP 1486 (Figures 1–2) is unique among Bauru Group turtles. It is narrow, placed on the rostral portion of the peripheral bone, and slightly projected onto the pleuro-marginal sulcus, followed by a constriction by this sulcus.

Based on our analyses, we estimated the length of CPPLIP 1486 carapace in over 100 cm, much larger than all other Bauru Basin turtles of which a complete or nearly complete shell is known. In relation to 'Peirópolis A' and 'Peirópolis B' materials, the results indicate that they also fit into the larger spectrum of

ſab	le	1. N	leasures	(in cn	i) of	CPPLIP	1486, 34	48, 1	731,	and	746	lengths.
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Specimen	Peripheral 7	Nuchal	Carapace
CPPLIP 1486	13.5	_	102*
CPPLIP 348 ('Peirópolis A')	_	12**	80.6*
CPPLIP 731 ('Peirópolis A')	-	9.5**	64.5*
CPPLIP 746 ('Peirópolis B')	-	6.2**	43.3*

*Estimates using the equations available on Figure 3; **Measures according to Rogério et al. (2013: Fig. 15).

podocnemidoid sizes (Figure 3), but their estimated carapace length (Table 1) is smaller than that of CPPLIP 1486.

In our estimates, it is noteworthy that values for *Podocnemis* expansa individuals approach those of *Podocnemis* bassleri



Figure 4. Results of the regression analysis between skull width and carapace length of podocnemidoid turtles (R²=0.79).

(Williams 1956) and *Podocnemis medemi* (Wood 1997), the carapaces of which may also have surpassed 100 cm. Affinities between *Po. bassleri* and *Po. expansa* have already been proposed (Williams 1956). The values obtained for *Podocnemis negrii* are close to those of *Podocnemis sextuberculata*, and these taxa were also previously considered to be closely related (Carvalho et al. 2002; Dumont Júnior 2013).

Regarding the Peirópolis turtles, the skulls of *Pricemys caiera* and *Peiropemys mezzalirai* are comparable in size to the expected for the skulls of 'Peirópolis A' and 'Peirópolis B', respectively, but smaller than the expected for CPPLIP 1486 (Figure 4). Finally, despite its broad skull, the estimated carapace length for *Caninemys tridentata* is much smaller compared to *Stupendemys geographicus* carapaces, suggesting it could be a smaller species of *Stupendemys*, as proposed by Meylan et al. (2009).

Discussion and conclusions

The peripheral bone described here belongs to the largest turtle reported for the Bauru Basin and the largest Cretaceous podocnemidoid. Its thickness suggests that it corresponds to an adult individual (Cadena 2011). The presence of forms probably surpassing 100 cm of shell length reveals a broader morphological diversity and size variation than previously hinted for Bauru Basin podocnemidoids. Besides, a knob near the pleuro-marginal sulcus is not present in any other Bauru Group turtle, suggesting that we might be dealing with a different morphotype. Since Cambaremys langertoni, another turtle from the same lithostratigraphic unit, is considered by some authors a juvenile taxon (e.g. Romano et al. 2013), CPPLIP 1486 could represent an older individual of the same species. However, we cannot check this hypothesis with the present data, and the absence of a knob on C. langertoni peripherals suggests otherwise. The other two taxa from the Marília Formation that CPPLIP 1486 could be assigned to are *Pricemys caiera* and *Peiropemys mezzalirai*, but they lack postcranial elements. Even if 'Peirópolis A' and 'Peirópolis B',

respectively, could be associated to these taxa, they also lack the peripheral knob.

The occurrence of a large turtle in the Marília Formation of Minas Gerais presupposes low palaeoelevations in the north-eastern border of the Bauru Basin during the Maastrichtian, as very high altitudes would expose a turtle this size to hypoxia, intense UV radiation, and cold temperatures (Yang et al. 2015), affecting its metabolism. South American tortoises, for instance, are restricted to maximal altitudes of 950 m (Cadena et al. 2015).

The likely low-domed carapace of CPPLIP 1486 suggests an aquatic or semiaquatic behavior (Benson et al. 2011), just like extant podocnemidids. Due to its larger size, CPPLIP 1486 may have occupied a different niche from other coeval turtles. This raises comparisons between the podocnemidoid faunas of the Late Cretaceous Bauru Basin and the current Amazon Basin. The latter shows a remarkable niche partitioning among Podocnemis species with different body sizes. Despite the sympatry of the largest forms, Po. expansa and Po. unifilis, all remaining species possess distinct habitats and distributions (Vogt 2008; Eisemberg et al. 2016). A similar situation likely occurred in the Bauru Basin, with smaller taxa like Bauruemys elegans and Cambaremys langertoni occupying niches similar to those of Po. sextuberculata or Po. erythrocephala, and larger forms like CPPLIP 1486 and Pricemys caiera with niches that would correspond to that of Po. expansa.

The Serra da Galga Member of the Marília Formation has been traditionally described as a distal alluvial fan deposit (Fernandes & Ribeiro 2015), with ephemeral braided rivers and lakes on a hot and dry climate (Carvalho et al. 2004; Batezelli 2015). Sudden floods with torrential water flows may have supplied water to lower parts of the region, resulting in large bodies of water (Fernandes & Coimbra 2000). Yet, it has also been suggested that perennial streams of considerable sizes could have been present at the northeastern portion of the Basin (Fernandes & Ribeiro 2015; Basilici et al. 2016). Indeed, Fernandes and Ribeiro (2015) suggested an increase in humidity during the last phases of the Bauru Basin deposition, which includes the Marília Formation (but see Batezelli 2015).

Podocnemis expansa, the most likely extant ecological equivalent of podocnemidoids of the size of CPPLIP 1486, also experiences an alternating regime of water availability in the Amazon and Orinoco Basins (Vogt 2008; Turtle Taxonomy Working Group 2014). During the rainy season, individuals migrate to smaller meandering channels and waterlogged forests in order to feed on seeds and fruits. In the dry season, the adults return to the river channels, whereas juveniles and sub-adults remain in adjacent lakes and large pools resulted of receding waters (Vogt 2008). Yet, the Amazon Basin is currently anything but dry, and water is perennially available in the areas inhabited by Po. expansa. Indeed, this seems a prerequisite to sustain adult freshwater turtles of that size. Accordingly, the record of CPPLIP 1486 in the Marília Formation of the Uberaba area corroborates its interpretation as a perennial river system (Fernandes & Ribeiro 2015; Basilici et al. 2016), which was never completely devoid of large water bodies during the dry seasons.

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Disclosure statement

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Appendix 1. Institutional abbreviations

AMNH American Museum of Natural History, New York, USA; AMU-CURS Alcadía del Municipio Urumaco, Colección Rodolfo Sánchez, Venezuela; BMNH Natural History Museum, London, United Kingdom; BSP Bayerische Staatssammlung für Paläontologie und Historische-Geologie, Munich, Germany; BSZ Bayerische Staatssammlung für Zoologie, Munich, Germany; CRI Chelonian Research Institute, Oviedo, Florida, USA; CPPLIP Centro de Pesquisas Paleontológicas 'Llewellyn Ivor Price', Peirópolis, Uberaba, Brazil; DGM Divisão de Geologia e Mineralogia, Departamento Nacional de Produção Mineral, Rio de Janeiro, Brazil; FMNH Field Museum of Natural History, Chicago, USA; ICN Instituto de Ciencias Naturales, Bogotá, Colombia; IGM Museo Geológico, at the Instituto Colombiano de Investigaciones en Geociencias, Minería y Química, Bogotá, Colombia; INPA-H Instituto Nacional de Pesquisas da Amazônia, coleção herpetológica, Manaus, Brazil; MCF-PVHP 'Museo Carmen Funes of Plaza Huincul', Neunquén Province, Argentina; MCNC Museo de Ciencias Naturales, Caracas, Venezuela; MCT Museu de Ciências da Terra, Departamento Nacional de Produção Mineral, Rio de Janeiro, Brazil; MCZP Museum of Comparative Zoology of Harvard University, Paleontological collections, Cambridge, USA; MGB Museo de Geologia de Barcelona, Catalunya, Spain; MN Museu Nacional, Rio de Janeiro,

Brazil; **MNHN** Muséum national d'Histoire naturelle, Paris, France; **MPEG** Museu Paraense Emilio Goeldi, Belém, Brazil; **PCHP** Dr. Peter C.H. Pritchard personal collection; **SGP** Museo do Serviço Geológico de Portugal, Lisbon, Portugal; **SMF** Senckenberg Naturmuseum, Frankfurt, Germany; **UF** University of Florida, Florida Museum of National History Vertebrate Paleontology Collections, Gainesville, Florida, USA; **UFAC-PV** Laboratório de Paleontologia, Universidade Federal do Acre, Rio Branco, Brazil; **USNM** National Museum of Natural History, Smithsonian Institute, Washington, USA; **YPM** Peabody Museum of Natural History, New Haven, Connecticut, USA.

Appendix 2. Specimens examined

Bairdemys harsteini (AMNH 27222), Bairdemys sanchezi (AMU-CURS 186), Bairdemys venezuelensis (MCZ 9418), Bauruemys elegans (MCT 1492-R, MCT unnumbered, MN 6762-V, MN 6807-V), Brasilemys josai (MGB 37991), Cambaremys langertoni (CPPLIP 0252), Caninemys tridentata (MCT 1496-R), Cearachelys placidoi (BSP 1976 I 160), Cordichelys antiqua (YPM 7457), Erymnochelys madagascariensi (AMNH 843120,

BSZ 843-20, BSZ 2518-0, CRI 5206, SMF 33056), Galianemys sp. (AMNH 30551), Lapparentemys vilavilensis (RM 20.5155, MNHN VIL 1, MNHN VIL A), Neochelys franzeni (SMF 1267), Peltocephalus dumerilianus (AMNH 131886, CRI 3295, CRI 3344, ICN 7324, INPA-H 22885), Peiropemys mezzalirai (MCT 1497-R), 'Peirópolis A' (CPPLIP 348, CPPLIP 731, MCT 1499-R), 'Peirópolis B' (CPPLIP 736), Pricemys caiera (MCT 1498-R), Podocnemis bassleri (AMNH 1662), Podocnemis erytrhocephala (CRI 8207, PCHP 7525, UF 57921, USNM 35474), Podocnemis expansa (AMNH 58098, DGM 276-RR, DGM 277-RR, ICN 6319, ICN 8921, UNM 065113, USNM 222270), Podocnemis lewyana (CRI 3230, ICN 1699, ICN 1715, ICN 5769, ICN 7653, MNHN 1944-285), Podocnemis medemi (IGM 1863), Podocnemis negrii (UFAC-PV 441), Podocnemis sextuberculata (AMNH 111068, AMNH 111069, AMNH 111070, BMNH 16075, CRI 5500, DGM 280-RR, INPA-H 21932, INPA-H 8930, INPA-H 8934, MPEG 0397, USNM 065110), Podocnemis unifilis (BMNH 45657, CRI 11120, ICN 6455, INPA-H 11561, INPA-H 31042, MPEG 0489), Podocnemis vogli (ICN 1682, UF 39060, UF 39100, USNM 266206), Portezueloemys patagonica (MCF-PVHP 338), Rosasia soutoi (SGP uncataloged), Roxochelys wanderleyi (DGM 1722-R), and Stupendemys geographicus (MCNC 244, MCZP 4376).