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The first Pan-Podocnemididae turtle egg from the Presidente Prudente Formation (Late Cretaceous, Bauru Group), Brazil

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Abstract

Pan-Podocnemididae turtles are ubiquitous in Late Cretaceous rocks of the Bauru Group in southeastern Brazil. This group of side-necked turtles is particularly abundant in a turtle-bearing site of the Presidente Prudente Formation known as Tartaruguito. Here, we describe the first turtle egg (LPRP-USP 0052) from the Tartaruguito site. LPRP-USP 0052 is nearly complete but misses a pole and measures 5,1 and 2,9–2,2 centimeters due to its flattened minor axis. The egg morphology and microstructure were analyzed by observations performed with CT, Optic Microscopy, Scanning Electronic Microscopy and Wave Dispersion Energy analyses. The eggshell ranges from 145 to160 micrometers thick. Considering the matching morphology of the new specimen and its provenance from the stratigraphic horizon that yielded only the podocnemidids *Bauruemys* and *Roxochelys*, it is most likely that LPRP-USP 0052 was produced by a podocnemidid turtle.

Key words: Turtle fossil eggs, *Bauruemys*, *Roxochelys*, Presidente Prudente Formation, Bauru Group

Introduction

The Bauru Group (Late Cretaceous, southeastern Brazil) has a rich record of Pan-Podocnemididae turtles (= Pan-Podocnemidae Joyce *et al*., 2004; Pleurodira, Pelomedusoides, França & Langer, 2006, Candeiro *et al*. 2006; Gaffney *et al*. 2011). The deposits of the Presidente Prudente Formation at the turtle-bearing site called "Tartaruguito" (colloquial fusion of the word tartaruaga, the Portuguese for turtle and the Greek suffix *líthos*), in southwestern São Paulo, Brazil, yielded the most diagnostic remains, which have been assigned to two species: *Roxochelys wanderleyi* and *Bauruemys elegans* (Suárez 2002; Bertini *et al*. 2006; Oliveira & Romano 2007). Previously, the turtle oological record of the Bauru Group was restricted to a single egg from the Adamantina Formation, at Álvares Machado, São Paulo, described by Azevedo *et al*. (2000) and attributed to *Podocnemis* (Pleurodira, Pelomedusoides, Podocnemididae). Here, we describe a fairly complete egg, the first known from the Tartaruguito site, which we refer to a podocnemidid turtle.

Institutional abreviation

LPRP-USP: Laboratório de Paleontologia, Universidade de São Paulo, Ribeirão Preto, Brazil.

Context

Locality. The material was collected in the site informally known as "Tartaruguito" (Bertini *et al*. 2006), located at

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kilometer 736 of the deactivated railroad *Estrada de Ferro Sorocabana* at Pirapozinho municipality, São Paulo, Brazil (22°13'27,61"S; 51°25'58,22"W) (figure 1). The egg was recovered from deposits with large accumulations of disarticulated fossil turtle remains.

Stratigraphy. The Tartaruguito site is part of the Adamantina Formation in the classic scheme of the Bauru Group stratigraphy (Soares *et al*. 1980). Yet, the current geological framework places the site within the Presidente Prudente Formation (Fernandes & Coimbra 1996). This stratigraphic unit is limited to southwestern São Paulo State (figure 1) and is composed of sandstones deposited in a meandering fluvial system in flood plains (Fernandes 2004). This depositional setting has great preservation potential, as indicated by the record of numerous fossil turtles, and less common fossils of other tetrapod groups (Suárez 1999; Bertini *et al*. 2006; Campos *et al*. 2011). The Presidente Prudente Formation lays atop of the Vale do Rio do Peixe Formation, which corresponds to most of the Adamantina Formation of Soares *et al*. (1980), that may range in age from Turonian to Maastrichtian (Dias-Brito *et al*. 2001; Santucci & Bertini 2001; Gobbo-Rodrigues *et al*. 2003; Zaher *et al*. 2006).

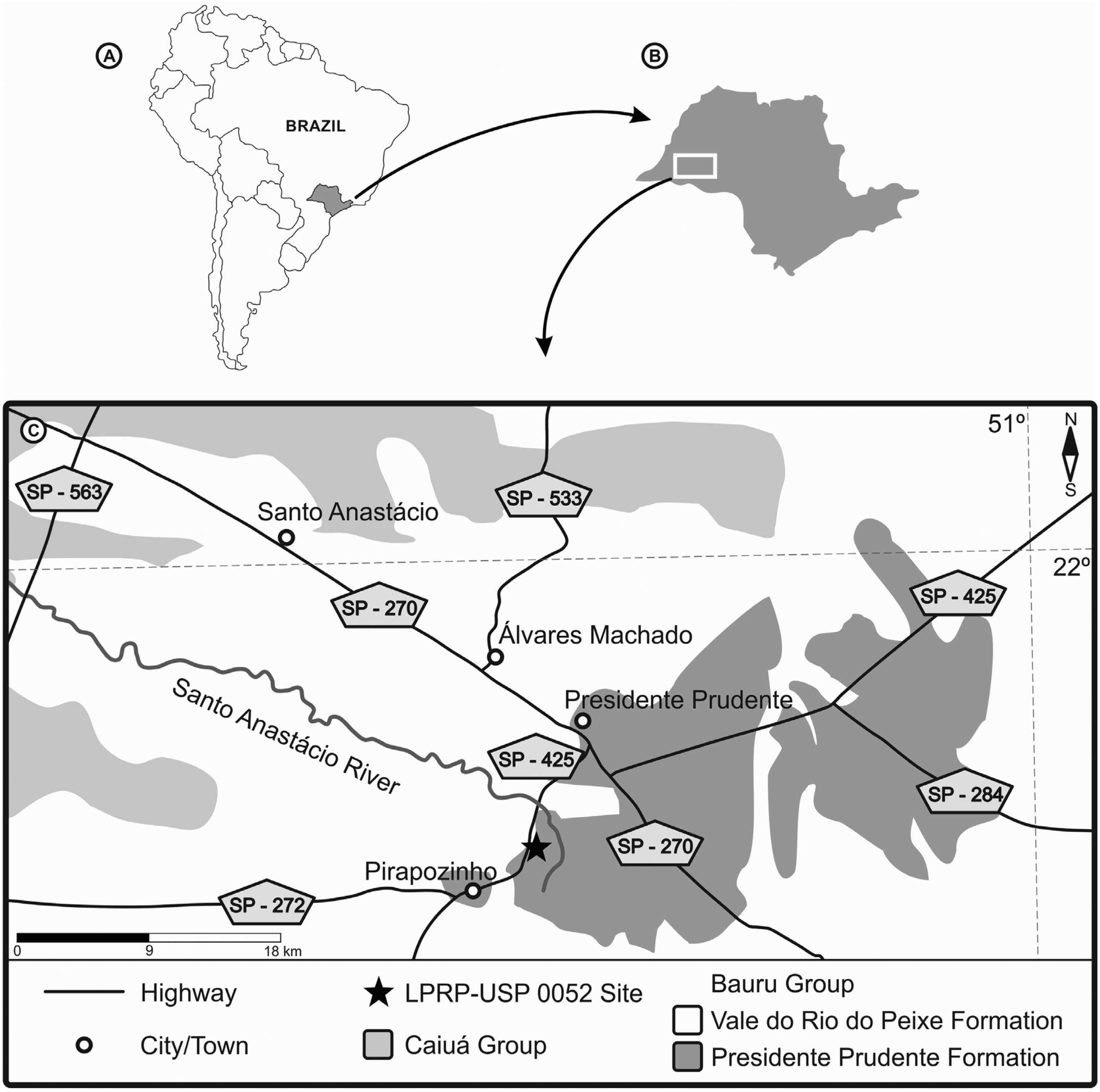

FIGURE 1. Maps of Brazil (**A**), São Paulo State (**B**), and the distribution of Late Cretaceous rock exposures of the Caiuá and Bauru Groups (**C**). Black star indicates the site of LPRP-USP 0052 (edited from Marsola *et al.* 2014).

Material and methods

LPRP-USP 0052 is a nearly complete egg with a damaged pole. Optical Microscope (OM), Scanning Electron Microscope (SEM) and Wave Dispersion System (WDS) were used to observe LPRP-USP 0052 morphology and microstructure. Five mm eggshell fragments were removed and cleaned of excess rock matrix in an Ultrasonic Bath (Quinn 1994). The samples were then divided in smaller pieces for both thin sectioning and carbon coating procedures. The histostructural and ultra-structural analyses were performed by OM and SEM. WDS provided the chemical profiles of the eggshell and the mineral zonation of its organizational structure (e.g. Grellet-Tinner *et al.* 2006). CT scanning was employed to check for possible embryo remains (Azevedo *et al.* 2000; Ketcham & Carlson 2001; Grellet-Tinner *et al*. 2011). Finally, the nomenclatural terms adopted for descriptive purposes are based on Hirsh (1983) and Winkler (2006).

Systematic Paleontology

TESTUDINES Batsch 1788

PLEURODIRA Cope 1865

PELOMEDUSOIDES Broin 1988 (*sensu* Joyce, Praham & Gauthier 2004)

PAN-PODOCNEMIDIDAE Joyce, Praham & Gauthier 2004

Gen. et sp. indet.

Comparative description.

LPRP-USP 0052 (figure 2 A) is elliptic (0,5 width/length ratio) with a missing pole. Its main axis is 5,1 cm long, whereas the minor axis range from 2,9 to 2,2 cm due to compression. Although taphonomicaly distorted, the elongation of LPRP-USP 0052 still matches that of chelids such as *Elseya* sp., *Chelodina* sp. and *Hydromedusa maximilliani* (Winkler 2006). This differs from the rounded shape of almost all described turtle fossil eggs (Azevedo *et al*. 2000; Jackson *et al*. 2008, table 1; Knell *et al*. 2011), except for those from the Jurassic of England (Hirsch 1996; Bray & Hirsch 1998), United States (Bray & Hirsch 1998) and China (Wang *et al*. 2013). The outer surface of the egg shows folded areas that suggest that the eggshell was flexible before its fossilization (figure 2 A). A different type of sediment fills the egg from its damaged portion compared to that surrounding the egg, suggesting that it was buried and fossilized without the pole, thus helping keeping its biological shape intact. The missing pole may also indicate that the egg had hatched, which is independently supported by CT analysis not revealing any embryonic remains. The WDS analysis of the eggshell indicate calcium as the main component of the eggshell crystalline structure, suggesting that diagenetic modifications had been minimal.

The egg outer surface is smooth, differing from the undulated and rough surfaces of turtle eggs from the Jurassic of the United States (Bray & Hirsch 1998) and the Cretaceous of Brazil (Azevedo *et al.* 2000). The eggshell is relatively thin (145–160 µm thick), including the biomineralized layer and an additional cuticle layer of about 7 µm thick (figures 2 B, D–E). Turtle fossil eggshells with a similar thickness are inferred to have either flexible or rigid eggs, e.g. *Testudooflexoolithus bathonicae* (Hirsh 1996; Bray & Hirsch 1998), *Testudoolithus hirschi* (Kohring 1999), eggs from the Jurassic of Colorado (Bray & Hirsch 1998), *Haininchelys curiosa* (Schleich *et al*. 1988) and *Testudinarum ovum* (Schleich & Kästle 1988; Schleich *et al*. 1988). Hirsch (1983) noticed that, along with to the degree of rigidity, eggshell thickness may be ecological and biological indicators. The sea turtle *Lepidochelys kempi* lays highly pliable eggs, with eggshells about 40 µm thick; the tortoise *Geochelone elephantopus* lays rigid-shelled eggs, with eggshells about 400 µm thick; the fresh-water turtle *Chelydra serpentina* has moderately flexible eggs, with 110 µm thick eggshells, although other fresh-water turtles also have rigid eggshells. The *Chelydra serpentina* condition best compares to that of LPRP-USP 0052, which is congruent with the host freshwater deposits. In addition, the thickness of the additional cuticle layer of LPRP-USP 0052 resembles that of the other freshwater taxon *Erymnochelys madagascariensis* (Winkler 2006). The functionality of the cuticle layer in turtles is rarely mentioned, however, analogous cuticle structures in bird eggs are directly

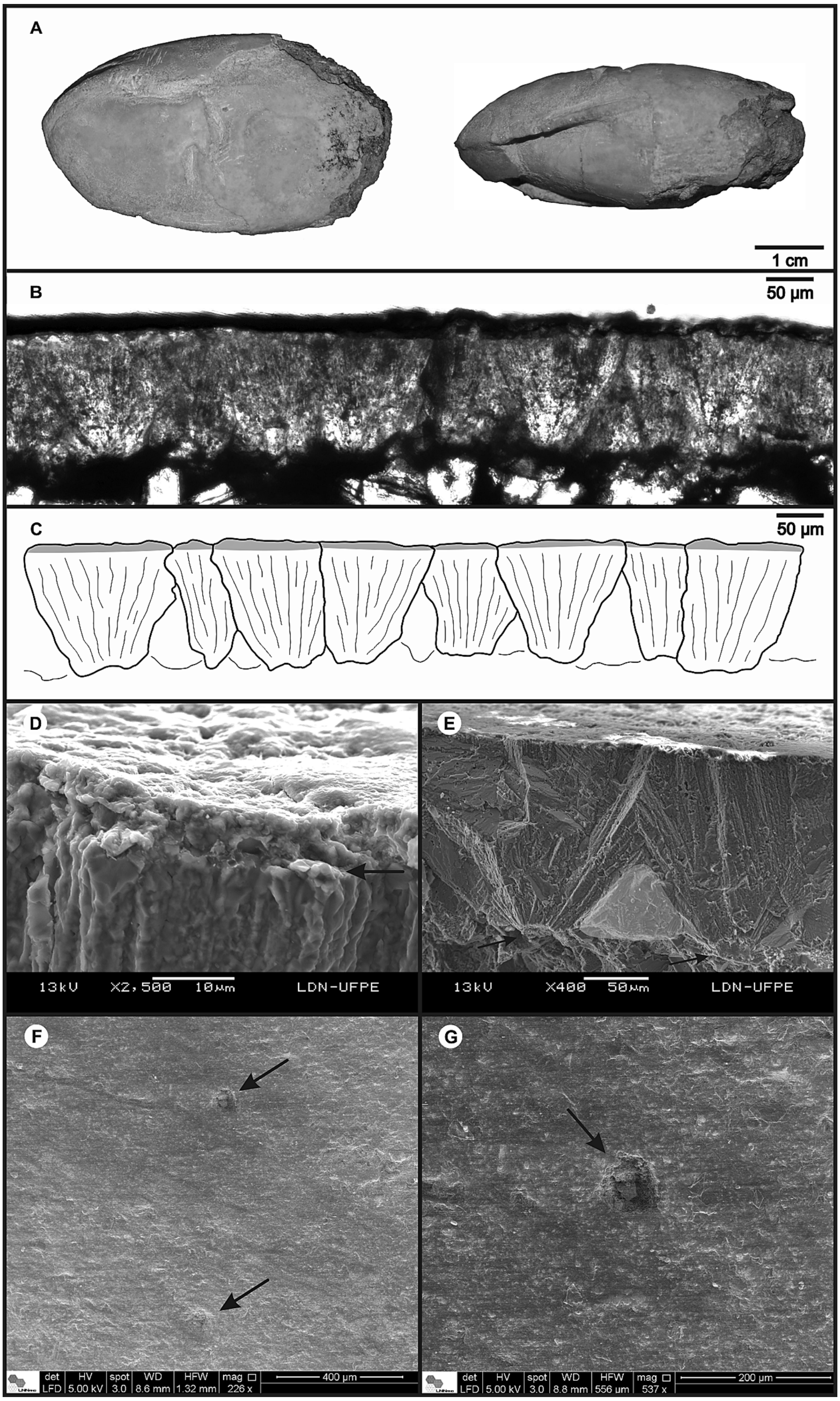

FIGURE 2. **A**, LPRP-USP 0052 in two views showing the missing pole and the folded eggshell. **B**, MO of a thin section of LPRP-USP 0052 eggshell. **C**, interpretative drawing of the thin section. Gray color in represents the additional cuticle layer above the units. **D**, **E**, **F** and **G**, SEM images of LPRP-USP 0052. **D**, eggshell in radial section showing the additional cuticle layer. Black arrow indicates the boundary between the biomineralized eggshell and the cuticle. **E**, eggshell in radial section showing two loosely abutted and triangular basic units and the "cavern" between them (translucent triangle). Black arrows point to the large primary spherites, from which the acicular aragonitic crystals radiate. **F**, outer surface of the eggshell showing two pore apertures (black arrows). Note that the shell basic units outlines are not easily seen. **G**, Enlargment of the rounded pore aperture (black arrow).

related to nesting in wet conditions, as described in Megapodiidae, Podicipedidae and Phoenicopteridae, and are thought to preclude the blocking of pores apertures by foreign material to faciliate gas exchange and limit chemical erosion from microorganisms in the soil (Board 1981; Board *et al.* 1982; Board & Sparks 1991; Booth & Thompson 1991).

The outlines of the shell basic units are not easily seen on the outer surface of LPRP-USP 0052 (figure 2 F). Pore openings are very sparse (figure 2 F), a condition also present in the eggs of the extant pleurodires *Podocnemis unifilis* (Winkler & Sánchez-Villagra 2006), *Hydromedusa maximiliani*, *Phrynops hilarii* and *Acanthochelys spixii* (Winkler 2006). The pores apertures are typical of those seen in podocnemidid eggs, but also of some chelids (Winkler 2006). The diameters range from 76 to 95 µm (figure 2 F and G), differing from the podocnemidids *Podocnemis unifilis* (pore openings about 27,7 µm wide) and *Bairdemys* (pores openings about 170 to 200 µm wide, Winkler & Sánchez-Villagra 2006). In radial view, the shell units display the characteristic acicular crystallographic pattern of aragonitic calcium carbonate crystals (figure 2 E), which is considered a Testudines apomorphy (Young 1950; Hirsch 1983, 1996; Packard & Packard 1988; Winkler 2006). The metastable calcium carbonate crystals project radially from the large primary spherites (figure 2 E) differing from the condition in chelids *Elseya* sp. and *Chelus fimbriatus* and the podocnemidids *Peltocephalus dumerliana* and *Erymnochelys madagascariensis*, with no visible spherites (Winkler 2006). Most shell units of LPRP-USP 0052 are roughly triangular, without marked borders, but more columnar unities are also present. This diversity of shapes results in relatively loosely abutting shell units (figure 2 B, C and E). According to Winkler & Sánchez-Villagra (2006), this allows "caverns" (large inter-units spaces) among shell units in some portions of the eggshell (figure 2, E), which are absent from rigid-shelled eggs, such as those of the podocnemidid *Bairdemys* (Winkler & Sánchez-Villagra 2006). On the contrary, the semi-flexible egg of *Podocnemis unifilis* (Foote 1978) has a mix of areas with and without "caverns" (Winkler & Sánchez-Villagra 2006). Finally, shell units of LPRP-USP 0052 are, in average slightly higher than wide (high/width ratio of 1,1–1,2). This is also notable in flexible turtle fossil eggs, as such *Testudooflexoolithus bathonicae* (Hirsh 1996; Bray & Hirsch 1998) and *Testudooflexoolithus agassizi* (Hirsch 1996).

Discussion and concluding remarks

The South American record of freshwater turtles was restricted to Pleurodira until the Miocene, when the first aquatic cryptodirans appeared on this continent (de la Fuente *et al.* 2014). In this context, chelids are the best represented clade of turtles in the South-American Cretaceous, especially in the southernmost part of the continent (de la Fuente *et al.* 2014), except for remains restricted to podocnemidids in the Bauru Group (Oliveira & Romano 2007; Gaffney *et al.* 2011; Romano *et al.* 2013). Accordingly, further morphological comparisons of LPRP-USP 0052 are restricted to pleurodiran turtle eggs.

LPRP-USP 0052 characters elongated eggshape (< 0,6); smooth outer surface; loosely abutting shell units ranging from as high as wide to slightly higher than wide and without visible outlines; large "caverns"; distinct pore apertures sparsely distributed; additional cuticle layer on the outer surface) are consistent with a podocnemidid assignment. However, the elongated profile of LPRP-USP 0052 is mostly shared by Australasian chelids. According to Winkler (2006), pleurodire eggs of Chelidae and Podocnemididae share several characters. Yet, chelids, albeit is the best represented clade of turtle in the South-American Cretaceous in the southernmost part of the continent (de la Fuente *et al.* 2014), are yet to be recovered in the Cretaceous Bauru Group, whereas podocnemidids are the most common freshwater chelonians (Oliveira & Romano 2007; Gaffney *et al.* 2011). Moreover, the notably abundance of podocnemidids at the LPRP-USP 0052 site (Suárez 2002; Candeiro *et al.* 2006; Oliveira & Romano 2007), supports the attribution of LPRP-USP 0052 to Pan-Podocnemididae based on phylogenetics and topotypy.

Azevedo *et al.* reported in 2000 the only turtle egg recovered to date in the Bauru Group. Although the presence of elongate calcite crystals, if interpreted as aragonite pseudomorph, undoubtedly assigns this fossil to Testudines, its *Podocnemis* affiliation remains doubious. In any case, this specimen differs from LPRP-USP 0052 by its rounded shape, seemingly rigid eggshell, and rough outer surface, and for a reevaluation of this specimen, a new analysis is necessary. Other fossil podocnemidid eggshells assigned to *Bairdemys* have been described from the Miocene of Venezuela (Winkler & Sánchez-Villagra 2006) and differ from LPRP-USP 0052 by possessing more abundant pores and a rigid and thicker eggshell, and lack of "caverns". Interestingly, *Bairdemys* is the only podocnemidid known to have nested in marine coastal areas (Winkler & Sánchez-Villagra 2006), contrary to LPRP-USP 0052, which is from a freshwater environment. These ecological preferences probably affected the nesting adaptations of extinct podocnemidids, and could in part explain the variance of their eggshell structures.

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