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In contrast to the rich record of eggs from non-avian dinosaurs, complete eggs attributable to Mesozoic birds are relatively scarce. Nevertheless, several well-preserved specimens have been discovered over the last three decades revealing functional and phylogenetic characters that shed light on the breeding strategies of extinct birds. Here we report the first fossil avian egg from Brazil, which was discovered in Upper Cretaceous strata of São Paulo in the southeastern part of the country. The taxonomic identity and structural features of the biomineralized tissues were determined using a combination of Scanning Electron Microscopy, Wave Dispersion Energy analyses and Computed Tomography. These show that the 125.5-μm-thick shell of the 31.4 × 19.5 mm egg incorporates three structural layers of similar thickness with both prismatic and aprismatic boundaries. Close similarity between the Brazilian bird egg and those of enantiornithines from the Upper Cretaceous Bajo de la Carpa Formation (Río Colorado Subgroup) of Argentina advocates affinity with basal Ornithothoraces. Furthermore, coherency of their depositional contexts might imply a compatible preference for breeding and nesting environments.

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THE MESOZOIC fossil record includes more than 120 species of birds found worldwide (Brocklehurst *et al*. 2012). Moreover, the last 30 years has also witnessed important discoveries of fossil bird eggs including those of *Gobipteryx* and possible neognathids from Mongolia (Elzanowiski 1981, Mikhailov 1991, 1997, Grellet-Tinner & Norell 2002), Ornithothoraces from Argentinean Patagonia (Schweitzer *et al*. 2002, Grellet-Tinner *et al*. 2006, Fernández *et al*. 2013), Enantiornithines from China (Zhou & Zhang 2004) and bird-like theropods from Spain (Lópes-Martines & Vicens 2012). In contrast, the Brazilian record of Mesozoic avians is restricted to putative enantiornithine skeletal fragments from the Upper Cretaceous Bauru Group of Minas Gerais (Candeiro *et al*. 2012) and São Paulo (Alvarenga & Nava 2005), and two possible specimens from the Lower Cretaceous Crato Member of the Araripe Basin (Naish *et al*. 2007). In addition, feathers from the Araripe Basin were tentatively attributed to birds (Kellner 2002). Here, we contribute an important new occurrence to this record—the first Brazilian fossil avian egg (LPRP-USP 0359) recovered from Upper Cretaceous deposits of the Vale do Rio do Peixe Formation in the Bauru Group of São Paulo.

Institutional abbreviations

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

Locality and geological setting

The source site of LPRP-USP 0359 occurs along road SP-270, near Álvares Machado municipality in São Paulo state (22°05′31″S, 51°28′51.4″W). The specimen derived from a well-defined intraformational conglomerate level exposed within white–reddish sandstones attributable to the Vale do Rio do Peixe Formation (Fernandes & Coimbra 1996; Fig. 1). The Vale do Rio do Peixe Formation is laterally equivalent to most of the Adamantina Formation (Soares *et al*. 1980), which varies in age from Turonian to Maastrichtian (Dias-Brito *et al*. 2001, Santucci & Bertini 2001, Gobbo-Rodrigues *et al*. 2003, Zaher *et al*. 2006). In general lithology, the Vale do Rio do Peixe Formation consists of fine-grained sandstones locally intercalated with siltstones and mudstones. According to Fernandes (2004), the

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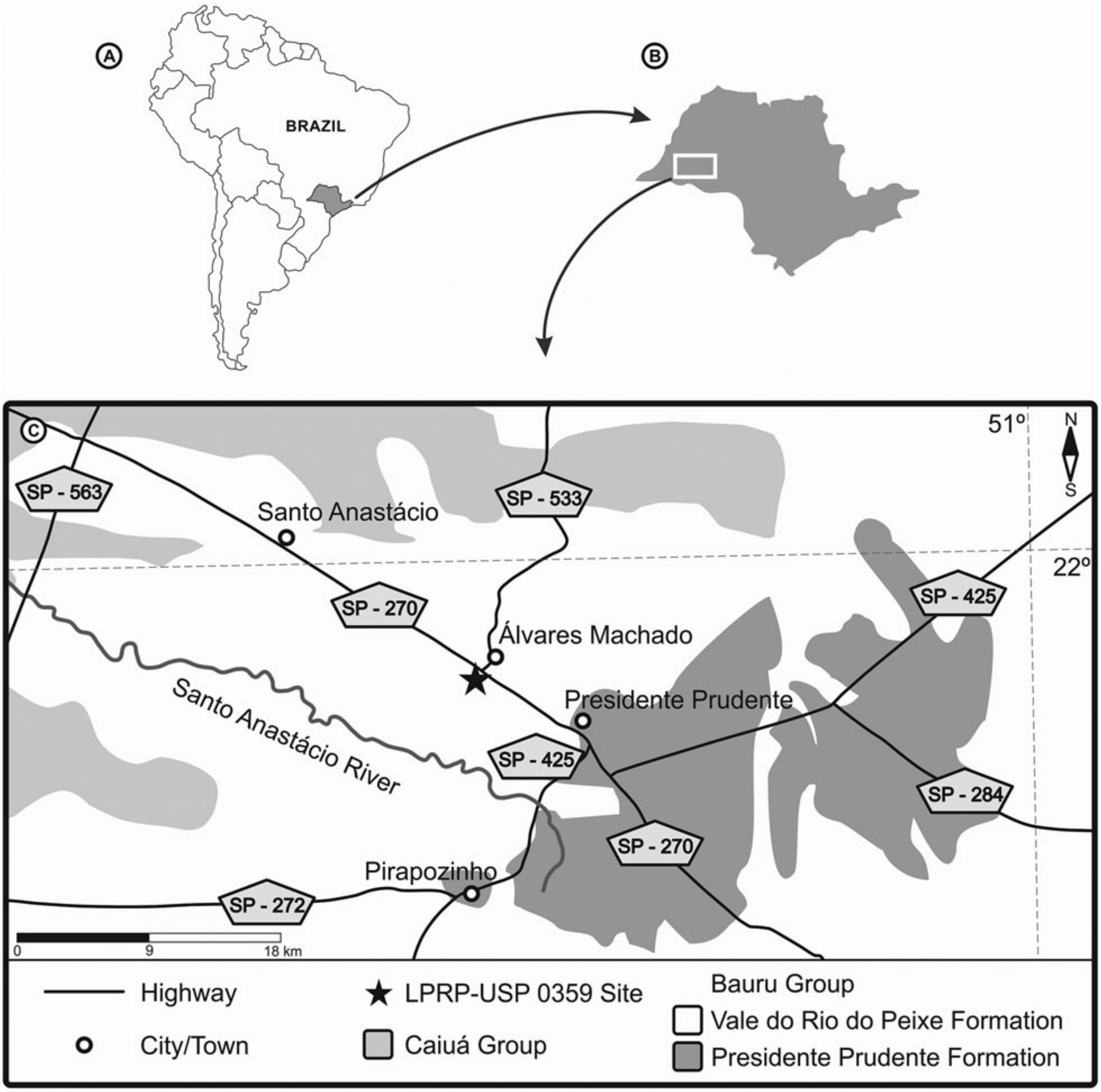

Fig. 1. Composite map showing Brazil (**A**) and São Paulo State (**B**) and the outcrop distribution (**C**) of the Caiuá and Bauru groups (Upper Cretaceous) in southwestern São Paulo State, southeastern Brazil. Black star indicates the fossil locality in Álvares Machado (after Fernandes & Coimbra 1996).

palaeoenvironmental setting represents mainly eolian sand sheets and low dune fields adjacent to ephemeral water bodies alternating with loess. Alternatively, Batezelli (2003) considered this sedimentary package to be predominantly fluvial.

Methods

Eggshell samples for Scanning Electronic Microscopy (SEM) and Wave Dispersion System (WDS) analysis were completely prepared from the matrix prior to carbon coating so as to avoid contamination. The WDS highlighted chemical profiles and permitted examination of mineral zonation within the eggshell; SEM was used to image the shell ultrastructure (Grellet-Tinner *et al.* 2006). Computed tomography (CT) was also employed to detect any possible embryonic remains (Ketcham & Carlson 2001, Grellet-Tinner *et al.* 2011). For descriptive purposes, we adopt the terms 'prismatic' and 'aprismatic' in the context proposed by Grellet-Tinner (2006). L1, L2 and L3 correspond to the mammilary, squamatic and external structural layers of the eggshell respectively.

Systematic palaeontology

AVES Linnaeus, 1758

ORNITHOTHORACES Chiappe & Calvo, 1994

Material. LPRP-USP 0359 (Fig. 2A) is a nearly complete egg. A small polar portion was damaged, probably by erosion during exposure in the outcrop.

Description. The specimen is slightly compressed, with its main axes measuring 31.4 mm versus 19.5 mm. This deformation is probably the result of lithostatic compression during sedimentation, which modified the original symmetry to an ellipsoid and now conceals obvious distinction between the poles. No embryonic remains were found *in ovo*, and the WDS qualitative analysis identified calcium as the main chemical component of the shell. This suggests that diagenetic alterations, if present, were limited to the mobilization of existing calcite within the eggshell structure. The shell itself is 125.5 µm thick and externally smooth with rounded pore openings (Fig. 2B). Three structural layers average 38 µm in L1, 42 µm in L2, and 45.5 µm in L3 (Fig. 2C). Spherulites are present at the base of each shell unit and are composed of blade-shaped calcite crystals. These extend close to the L1–L2 boundary and form a semi-circle around a core (Fig. 2C, D). The graded contact between L1 and L2 forms a prismatic transition, whereas an aprismatic transition is evident between L2 and L3 (Fig. 2C). These features indicate that the C axes of calcium carbonate crystals were deposited horizontally in L1 and L2, as opposed to a columnar crystallographic arrangement in L3.

Discussion

LPRP USP-0359 is one of the smallest known Mesozoic bird eggs (Mikhailov 1997, Grellet-Tinner & Norell 2002, Schweitzer *et al*. 2002, Grellet-Tinner *et al*. 2006, López-Martínez & Vicens 2012). Its shell is rather fragile compared with the eggs of modern neognaths, such as *Gallus* and *Anser* (around 500 µm thick), and paleognaths including *Rhea* and *Dinornis* (up to 10 mm thick; Grellet-Tinner 2006). Indeed, LPRP USP-0359 represents one of the thinnest shelled Mesozoic avian eggs documented to date (Mikhailov 1997, Grellet-Tinner & Norell 2002, Schweitzer *et al*. 2002, Grellet-Tinner *et al*. 2006, López-Martínez & Vicens 2012). In extant paleognaths, L1 and L2 typically comprise almost the entire thickness of the eggshell, and L3 and L4, if present, are reduced. Alternatively, neognath eggshells show a different pattern, with L2 being much thicker than L1, and L3 being thinner than L1 (Grellet-Tinner 2006). Grellet-Tinner & Norell (2002) reported a Mesozoic bird egg with L1–L3 thicknesses

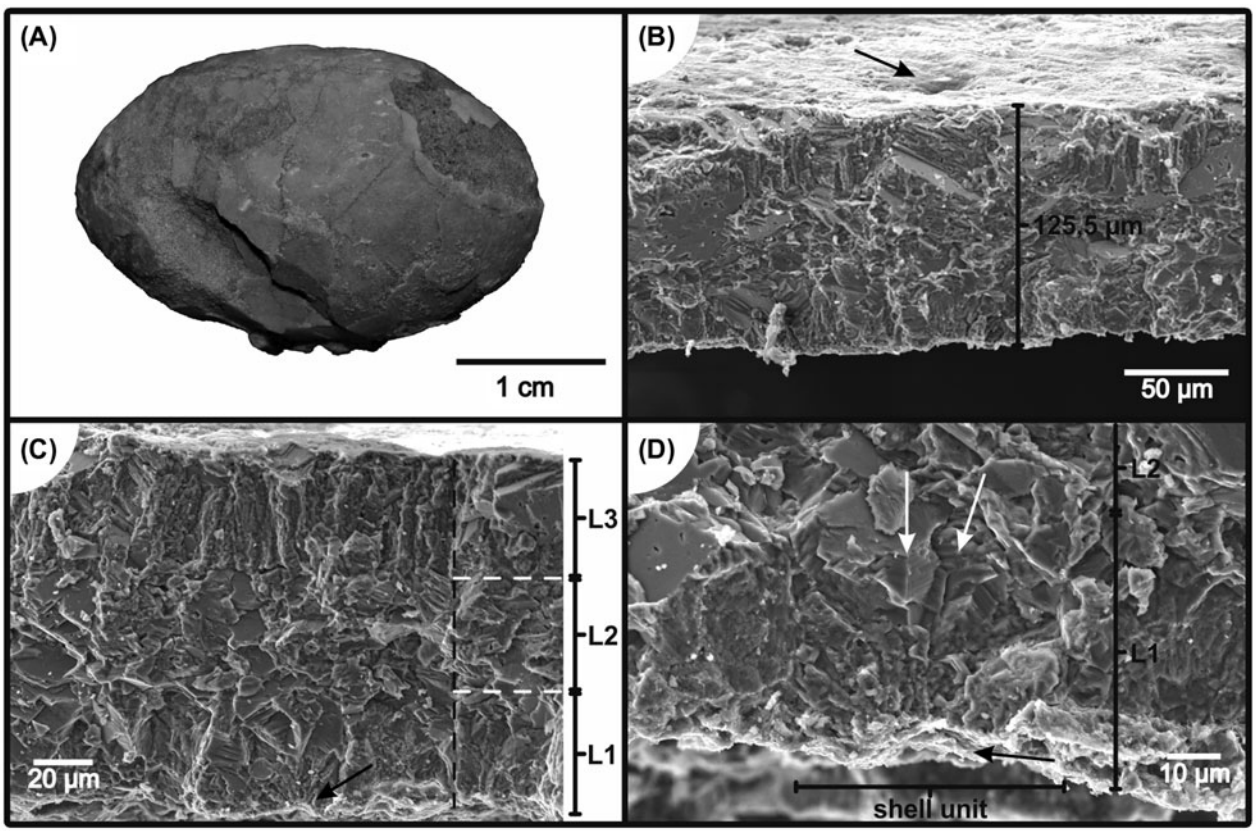

Fig. 2. **A**, LPRP-USP 0359, a nearly complete egg. **B**, **C** and **D**, SEM of the LPRP-USP 0359 shell in radial sections. **B**, Black arrow points to the rounded pore opening. **C**, Arrow indicates a spherulite core. Note also the delimitation of the shell units and the gradual (prismatic) contact between L1 and L2, and the abrupt (aprismatic) contact between L2 and L3. White dashed lines separate the three structural layers, and a black dashed line indicates the boundary of shell units. **D**, Magnification of a spherulite at the base of L1, around the core forming a semi-circle (black arrow). White arrows point to the spherulite calcite crystals that almost reach the contact between L1 and L2.

of 92.9 µm, 58.7 µm and 14.4 µm respectively. Schweitzer *et al.* (2002) and Grellet-Tinner *et al.* (2006) described other eggs collected from the same stratigraphic interval of the Bajo de la Carpa Formation (Río Colorado Subgroup) with L1 and L2 proportionally thicker than L3. On the other hand, López-Martínez & Vicens (2012) identified only two structural layers in theropod eggs that were thought to have possible bird affinities: L1 being 30–40 µm and L2 having >6 times the thickness of L1. We, therefore, interpret the approximately equal thicknesses of L1–L3 in LPRP-USP 0359 to be a unique feature of this specimen. According to Grellet-Tinner (2006), extant neognath eggs have only prismatic transitions between their structural layers, whereas those of paleognaths are always aprismatic. *Gobipteryx* (formally *Gobioolithus* in parataxonomic schema) and bird-like theropods eggs from Spain conversely share the prismatic contact of L1 and L2 with LPRP-USP 0359. However, such specimens have only two structural eggshell layers (possibly a diagenetic artefact at least in *Gobioolithus*) making further comparisons difficult (Mikhailov 1991, 1997, López-Martínez & Vicens 2012). In contrast, Grellet-Tinner & Norell (2002) identified three structural layers together with prismatic transitions in some Mongolian Cretaceous bird eggs, and cited this as evidence for closer affinities with modern avians rather than basal ornithothoracines. Like LPRP-USP 0359, the Bajo de la Carpa bird eggs (Schweitzer *et al.* 2002, Grellet-Tinner *et al.* 2006) manifest a prismatic contact between L1 and L2, and an aprismatic contact between L2 and L3. Fernández *et al.* (2013) mapped dozens of bird eggs with embryos arranged in a breeding colony at this site, and assigned their remains to basal ornithothoracines based on *in ovo* skeletal traits and the occurrence of *Neuquenornis* and *Patagopteryx* body fossils nearby. Schweitzer *et al.* (2002) also described enantiornithine embryos associated with the eggs, which confirmed this eggshell morphotype association. According to Garrido (2010), the palaeoenvironmental context of the Bajo de la Carpa Formation corresponds to a semi-arid landscape with eolian dunes interspersed with wide, shallow and slightly anastomosing river systems that were ephemeral and subject to seasonal fluctuation. Interestingly, this is closely compatible with the Vale do Rio do Peixe Formation depositional setting, and might infer common usage of such habitats as preferred nesting sites by these Late Cretaceous ornithoracine birds.

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