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Palaeoenvironmental characterization of a crocodilian nesting site from the Late Cretaceous of Brazil and the evolution of crocodyliform nesting strategies

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ABSTRACT

Despite the vast crocodyliform fossil record, little is known about the reproductive biology and nesting strategies of the extinct members of the group. Here we report a large accumulation of crocodilian fossil eggs from the type-locality of the baurusuchid *Pissarrachampsa sera*. Sedimentary facies and architectural elements of the site support a palaeoenvironmental model with a shallow lacustrine, playa-lake system interacting to ephemeral braided fluvial channels, with aeolian influence and development of sandy soils. The presence of pedogenic calcretes in the palaeosols indicates arid to semi-arid conditions. The crocodilian affinity of the eggs is supported by the thin eggshell which bears wedge-shaped shell units with tabular microstructures. Furthermore, taphonomic data support an autochthonous assemblage of eggs and skeletal remains, hinting at a monotypical stratigraphic horizon and suggesting *P. sera* as the egg-laying taxon. The repeated pattern of four (eventually five) eggs per clutch at the site demonstrates that *P. sera* laid fewer eggs compared to modern crocodilians, indicating that k-selected reproductive strategy pattern is pervasive in the fossil record of Notosuchia. In the crocodyliform phylogenetic framework, the k-strategy and the "egg clutch sizes" optimization of Notosuchia is opposite to the strategy with larger clutches consistently occurring in modern Crocodylia and Neosuchia, the sister clade to Notosuchia. Yet, the lack of data on more early-branching taxa renders unclear which pattern is plesiomorphic for Crocodyliformes as a whole.

1. Introduction

Crocodyliformes achieved high taxonomic diversity through geologic time (Bronzati et al., 2015) and were notably represented in Gondwanan landmasses by the Notosuchia (Pol et al., 2014; Fiorelli et al., 2015), a successful and diverse clade of terrestrial forms (Martinelli and Teixeira, 2015). The Late Cretaceous Brazilian fossil record, particularly that of the Bauru Group, depicts an important episode in notosuchian evolutionary history, when they played major ecological roles, occupying different niches, from first to second level consumers to top predators with complex social behaviour (Avilla et al., 2004; Godoy et al., 2014).

Although crocodilian fossil eggs have been reported worldwide in the past thirty years (Moreno-Azanza et al., 2014, Table 1), their associations with skeletal remains are scarce. The best documented fossil assemblage is reported from the Late Cretaceous notosuchid *Yacarerani boliviensis* (Novas et al., 2009) in Bolivia, and similar associations are known from the Late Jurassic of Portugal (Russo et al., 2014) and the Middle Eocene of Germany (Hastings and Hellmund, 2015), providing insights on their reproductive biology. Moreover, several sites of the Bauru Group are known for the association of fossil eggs and notosuchid skeletal remains (Magalhães Ribeiro et al., 2006; Vasconcellos and Carvalho, 2010; Marsola et al., 2011; Oliveira et al., 2011). However, in contrast to Mesozoic non-avian and avian dinosaurs (e.g. Chiappe et al., 2005; Grellet-Tinner et al., 2006; Grellet-Tinner and Fiorelli, 2010; Fernández et al., 2013; Hechenleitner et al., 2015), combined taxonomic and stratigraphic studies of crocodyliforms nesting sites and strategies are lacking.

Here we report a large accumulation of crocodile fossil eggs, including clustered and isolated elements, from the type-locality of

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the baurusuchid *Pissarrachampsa sera* (Montefeltro et al., 2011), in the Late Cretaceous Adamantina Formation, Bauru Basin, SE Brazil. This study focuses on (1) describe the depositional and pedological context of the fossil-bearing strata, in an attempt to understand the palaeoenvironment; (2) comparatively describe the oological remains; (3) infer the egg-laying taxon; and (4) discuss the possible implications of the gathered data for understanding the evolution Crocodyliformes nesting strategies.

2. Material and methods

2.1. Study area and sampling

This study mainly relies on facies and pedological analyses of outcrops, along with laboratory analyses. The descriptive and photographic documentation of the outcrop where the fossils were found (Fig. 1) – Inhaúmas-Arantes farm, Campina Verde, Minas Gerais, Brazil (19°20′ 41.8″ S; 49°55′ 12.9″ W) – and the elaboration of columnar sections based on field data provided the basis for the identification of the sedimentary processes and pedogenic features. Facies characterization combining field work, petrography, scanning electronic microscopy (SEM), and X-Ray diffractometric analyses were performed, focusing on the texture, colour, sedimentary structures, and mineralogy, to interpret depositional and diagenetic processes. Following Retallack (2001), pedological interpretations are based on macro and micromorphology analyses of the palaeosols.

2.2. Material

The studied specimens are housed at Laboratório de Paleontologia, Universidade de São Paulo, Ribeirão Preto *campus*, and include three clutches with four eggs each (LPRP-USP 0046, 0047, 0048) (Fig. 7), one clutch with at least four compressed eggs (LPRP-USP 0648) (Fig. 7), isolated eggs (LPRP-USP 0638, 0640, 0647) (Fig. 8), and eggshells (LPRP-USP 0641, 0639) (Fig. 8). The eggshell samples were thin sectioned and submitted to LEICA DM4000B optical microscopy (OM) for microcharacterization of the eggshell units, including their general morphology and geometry. In order to generate tridimensional images of the shell ultrastructure, SEM analyses were performed in JEOL JSM 6460 and FEI Quanta 650 FEG.

3. Geological settings and palaeoenvironmental characterization

The above 300,000 km^2 Bauru Basin covers parts of the states of Minas Gerais, Goiás, Mato Grosso do Sul, São Paulo, and Paraná (Fig. 1).This basin was filled with 300 m of continental deposits, divided into the Caiuá and Bauru groups (Fig. 2). The origins of the Bauru Basin is related to subsidence by isostatic adjustment occurred South of the Alto

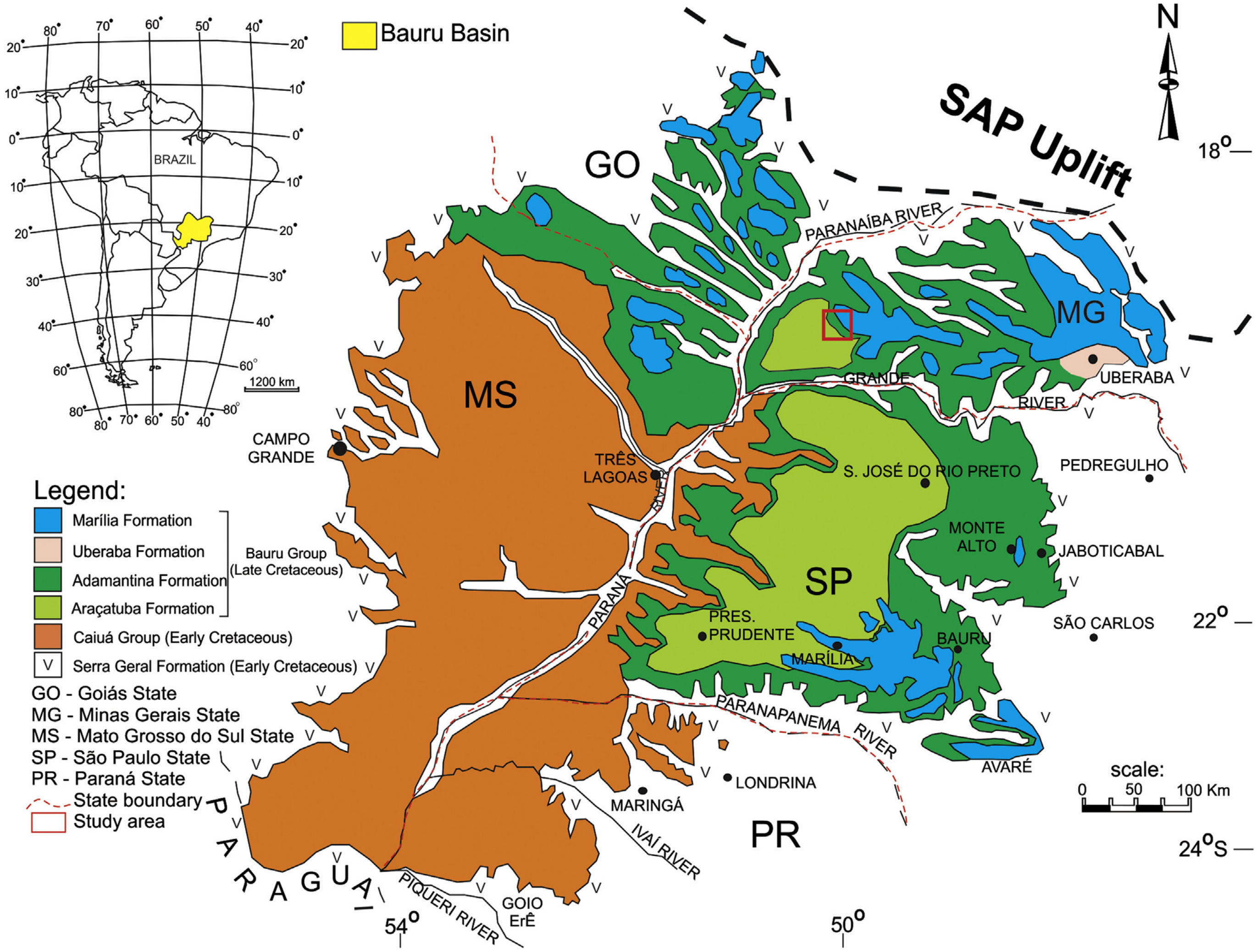

Fig. 1. Surface distribution map of the Bauru Basin lithostratigraphic units. (Edited from Batezelli, 2015.)

Paranaíba Uplift (SAP; Fig. 1) during the Late Cretaceous in Southeastern Brazil (Batezelli, 2015).

The fossils focus of this research were discovered on the top of the Adamantina Formation (Soares et al., 1980) near its contact with the Marilia Formation, in western Minas Gerais. This unit crops-out in the central and western parts of the Triângulo Mineiro region, and is composed of reddish, fine- to medium-grained and moderately-sorted sandstones. These are either massive or exhibit small to medium scale cross-stratifications (up to 3 m-sized foresets), planar stratifications characterized by ripple marks and desiccation cracks (Batezelli, 2010). In the Gurinhatã and Campina Verde areas, the Adamantina Formation also includes well-sorted and fine-grained sandstones, forming large scale (more than 3 m) and high angle (about 25°) cross-stratification foresets. Reddish mudstones, massive or with ripple marks and planar stratifications, often intercalated by centimetric to decimetric layers of very fine-grained sandstones, cemented or not by calcium carbonate, may also occur (Fig. 3). The sandstone layers are lenticular or tabular, sometimes intercalated with centimetric mudstone layers. Trough cross-stratifications and carbonatic cement are common, and bioturbations (krotovinas and root marks) are also frequent, tunnels are mostly filled by well-selected, very fine- to fine-grained sandstone, with low angle cross-bedding (Fig. 3). The geometry of the bodies, the fine texture, and the sedimentary structures of the Adamantina Formation, indicate fluvial flows deposition, with the development of muddy plains. Small aeolian dunes of the sand-sheet type, adjacent to the fluvial deposits, interacted with them during dry periods, partially filling abandoned channels.

A typical trait of the Adamantina Formation is the presence of palaeosols, which profiles occur intercalated in the deposits and are characterized by calcretes. These paleosols allow a general comparison to the present soil orders Alfisol, Aridisol, Entisol, and Vertisol, indicating arid and semi-arid climatic conditions (Dal' Bó et al., 2010; Pereira et al., 2015).

3.1. Depositional environment of the Adamantina Formation

The about 2 m thick and 70 m long fossil-bearing outcrop (Fig. 2) is composed of massive muddy sandstones, fine to medium grained, moderately sorted, and with carbonatic cement. At the base, reddish mudstone and sandstone layers (about 7 cm thick) are intercalated on planar-parallel bedding (Fig. 3). These are characterized by fining-upward rhythmic cycles of up to 40 cm thick, with an erosive-abrupt base. Upwards in the section, the sandstones are mostly massive, but planar stratification and cross beddings are also common. The sandstones are poorly to moderately sorted and the quartz and feldspar grains are rounded to subangular. Rhythmites disappear in the top of the section, sandstones and mudstones are mixed up, and dish structures and convoluted folds are present. From the middle to the upper portions of the section, the muddy sandstone turns into massive sandstones (palaeosols), with carbonatic nodules, root marks, and ped-like structures (Fig. 4). The Marília Formation appears locally above the described lithology, where it is composed by reddish to yellowish, fine to medium grained, and poorly to moderately sorted sandstones. These sandstones are be muddy, massive, cemented by calcium carbonate, and occurs associated with centimetric to decimetric layers of fining-upward conglomerates, composed by rounded to sub-angular pebbles of quartz and quartzite.

In the fossil-bearing site, the rhythmic deposits of sand- and mudstones of the Adamantina Formation indicate episodic sedimentary processes, with slow decrease in energy, as typical of those formed by low viscosity turbidity flows generated during flooding periods on depressed areas ("inundites" sensu Della Favera, 1984). The massive,

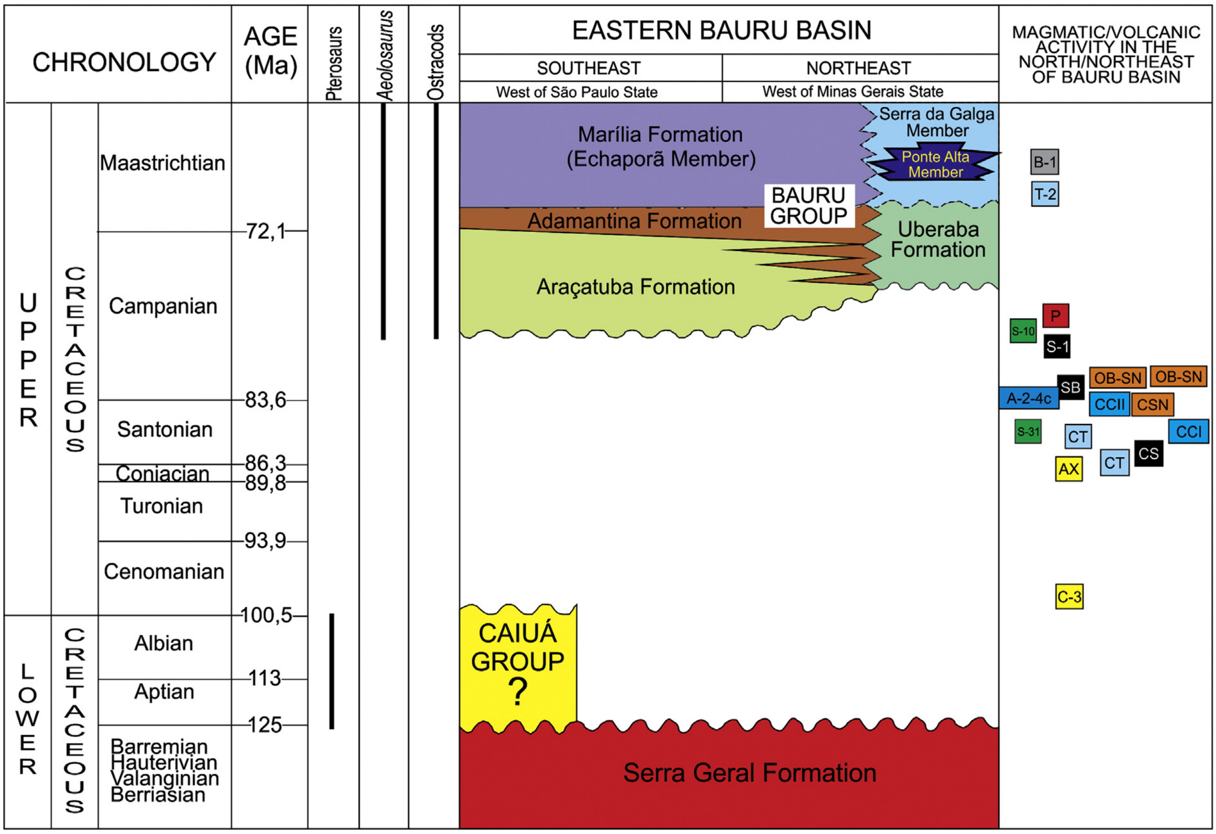

Fig. 2. Chronostatigraphic chart of the Cretaceous sequences of the Paraná/Bauru basins, based on Amaral et al., 1967 (sample CSN); Hasui and Cordani, 1968 (samples AX, C-3, S-10, S-31, A-2-4c,OB-SN, SB, S-1, P, T-2, B-1); Sonoki and Garda, 1988 (samples CT, CS, CCI); Machado Júnior, 1992 (sample CCII); Guimarães et al., 2012 and Fragoso et al., 2013 (Pterosaurs); Gobbo-Rodrigues, 2001 and Dias-Brito et al., 2001 (Ostracods); Santucci and Bertini, 2001 and Martinelli et al., 2011 (*Aelosaurus*).
(Edited from Batezelli, 2015.)

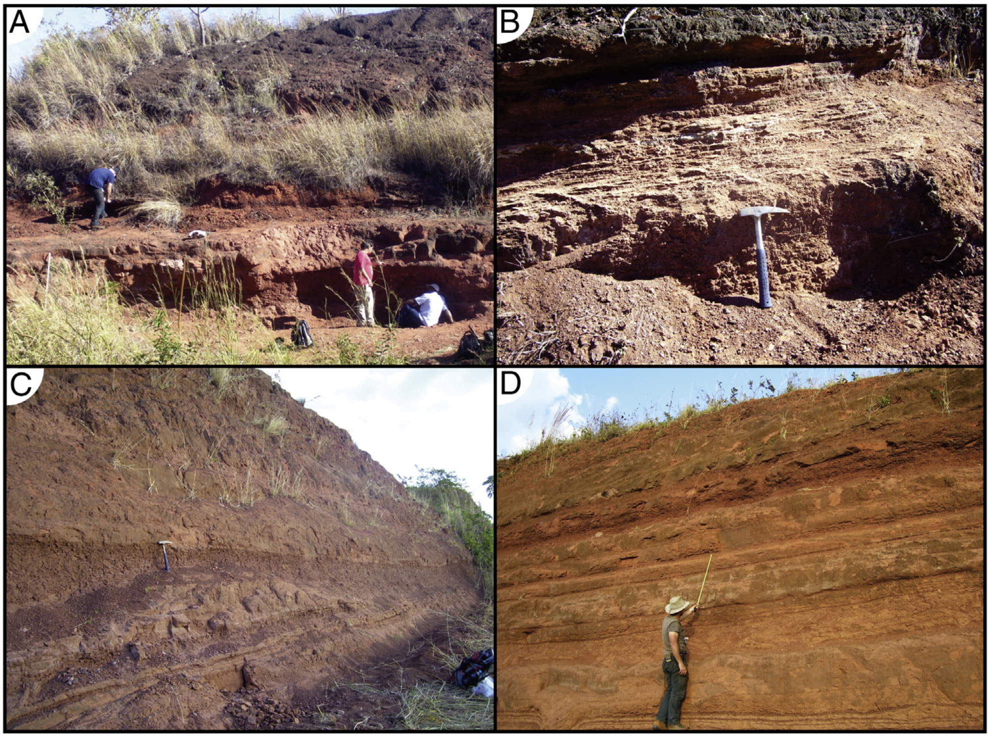

Fig. 3. Adamantina Formation. A, Sand bars deposits with trough cross bed, interlayered with mudstone (Prata-Campina Verde road, 20 km from Prata-MG). B, Very fine sanstone with low-angle trough cross bed. C, Channel deposits (BR 364 road, 5 km from Gurinhatã-MG). D, Tabular sand bars interlayered with mudstones (BR 364 road, 5 km from Gurinhatã-MG).

muddy sandstones that appear above the rhythmic facies show root marks and carbonatic nodules, both of which indicate pedogenic processes. The superimposed Marília Formation is formed by high-energy fluvial deposits. This includes channel-geometry conglomerates and sandstones, as well as downstream and lateral accretion macroforms. The depositional geometry and prevalence of bottom sediments suggests a braided river system, whereas the occurrence of thick palaeosol horizons indicate that the sediment-transporting flows were ephemeral. Indeed, the thick massive conglomerates are typical of density-detrital flows associated to rapid, high-energy events (Ramos and Sopeña, 1983; Miall, 1985, 1988a, 1988b, 1996).

Palaeocurrent data (cross stratification front measurements) from the Campina Verde area (Batezelli, 2003) indicate a prevalent east/northeast to west/southwest sedimentary transport, with base level positioned at the central/south part of the Basin. The high variability of the paleocurrents, together with the identified facies and architectural elements, shows an alluvial-fan system, dominated by low-sinuosity braided rivers, as discussed by Stanistreet and McCarthy

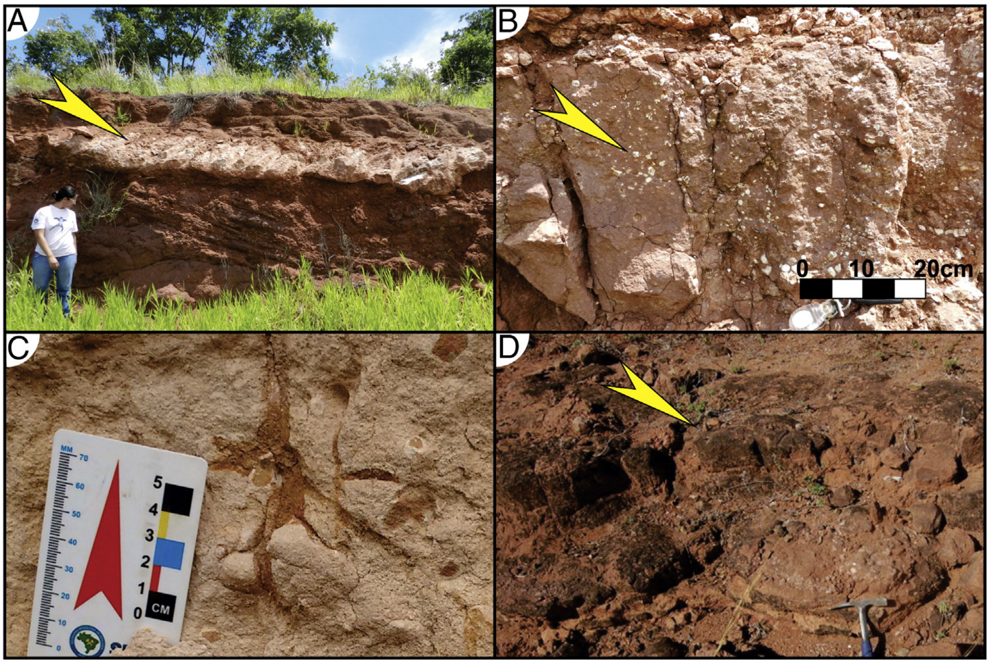

Fig. 4. Adamantina Formation. A, Calcrete overlying channel deposits. B, Carbonate nodules in palaeosol profile. C, Root mark. D, Prismatic ped structure in palaeosol.

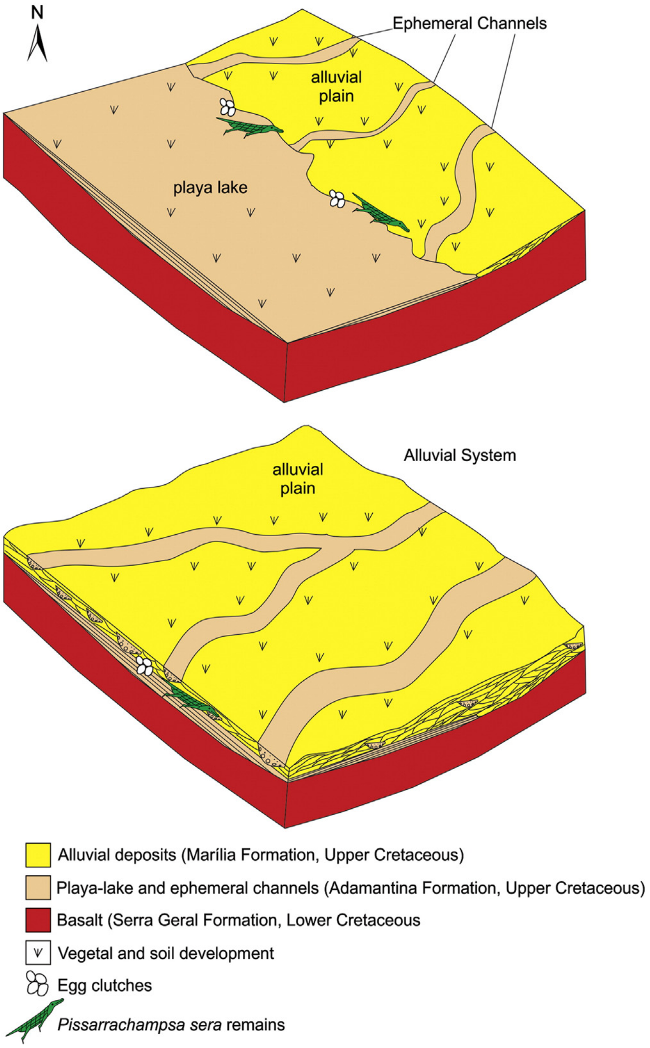

Fig. 5. Depositional model to the study area.

(1993), or a distributive fluvial system according to Weissmann et al. (2010). In general, architectural elements of the Bauru Group resemble those described by Bromley (1991) from the Kayenta Formation, Colorado, and by Jones et al. (2001) from the Rio Vero Formation, Spanish Pyrenees, both related to intermediate to distal alluvia-fan systems (Batezelli, 2003). The proposed depositional model also resembles that of the Huesca alluvial system, Ebro Basin (Spain), where the braided fluvial channels are distributaries, evolving from alluvial-fans that enter the basin from the Pyrenees (Hirst, 1991). A general palaeoenvironment model for the area would include a shallow lacustrine environment, such as a playa-lake, acting as the base level and interacting with ephemeral braided fluvial system, with aeolian influence and the development of sandy soils (Fig. 5). Accordingly, Batezelli (2015) states that the sedimentary characteristics of the Adamantina Formation indicate a playa-lake setting with high sedimentation rate, dominated by suspension settlings in the more internal portions. Finally, density flows generated during floods may be responsible for the upward fining rhythmic deposits, i.e., Tb-d Bouma's sequence turbidity (Bouma, 1962) or "inundites" (Della Favera, 1984). Low-density mudflows were responsible for the muddy deposits. Carbonate cementation and vegetation development would be responsible for the obliteration of sedimentary structures. Fauna and flora (palynomorphs, ostracods, conchostraca, and charophyta) show that the environment had long-lasting waters (Gobbo-Rodrigues, 2001; Dias-Brito et al., 2001).

3.2. Paleosols and paleoenvironments consideration

The most striking feature of the fossil-bearing outcrop is the occurrence of paleosols. The profiles have undeveloped "B" (commonly lacking) and "C" horizons, high carbonate content, and colours ranging from 7.5 R to 10 R (Fig. 4). The horizons display light colours, carbonate nodules, medium to large prismatic structures, and have sandy-clay textures, with millimetre- to centimetre-sized clasts and abundant root marks (Fig. 4). The root marks range from 0.3 to 90 cm in length, are tubular in shape and filled with $CaCO_3$ or clay (Fig. 4B). Quartz occurs at 50% levels and corresponds to the main detrital phase in the rock. Both poli- and monocrystalline forms are present, with undulated extinction. Calcite substitution is common, generating massive calcrete

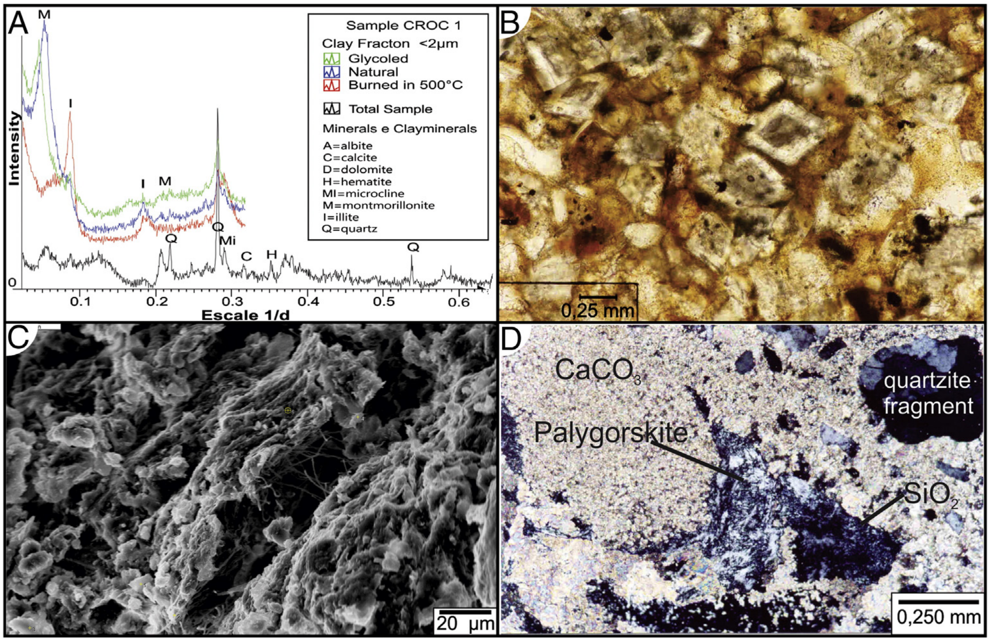

Fig. 6. A, X-ray diffractogram showing minerals and clay minerals. B, Photomicrography: micritic cement, authigenic palygorskite (Pa) and silex (Si) (from Batezelli, 2015). C, Detail of the fibrous aggregates of the palygorskite (image obtained by SEM). D, Dolomite and hematite cement.

layers (Fig. 4 and 6A). Illite, montmorillonite, and palygorskite are the most common clay minerals. Palygorskite occurs in intertwining fibrous aggregates forming nodular structures (Fig. 6B).

3.3. Pedogenic considerations

The presence of palaeosols in the Bauru Groups is ubiquitous (Suguio et al., 1975; Suguio and Barcelos, 1983; Dal' Bó et al., 2009; Pereira et al., 2015). The described section displays root marks, blocks structures, and is heavily cemented by $CaCO_3$, indicating pedogenic processes with calcrete formation (Watson, 1992; Klappa, 1980; Wright, 2007). Pedogenic calcretes are formed in shallow soils, above the phreatic level, and are variably developed (Alonso-Zarza, 2003). This allows for the thick calcrete profiles of the site, which may also result from the superposition and repetition of such environments over time. The presence of calcretes is a clear indication of arid to semi-arid conditions, because they are formed by soil accumulation of $CaCO_3$ due to intense evapotranspiration and changes in the CO_2 partial pressure.

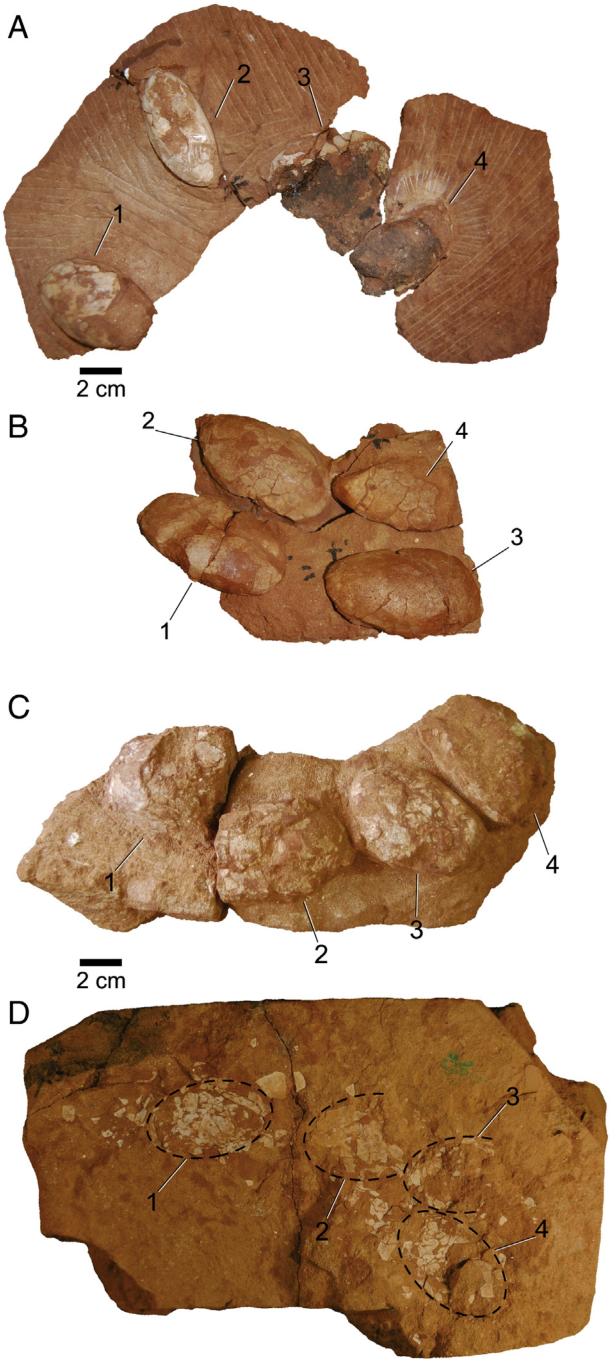

Fig. 7. *Pissarrachampsa sera* egg clutches LPRP/USP 0046 (A), 0047 (B), 0048 (C) and 0648 (D). In D, dashed lines indicate the possible limits of the collapsed eggs.

Nowadays, pedogenic calcretes occur as $CaCO_3$ accumulations near or at the surface; are uniform and continuous over several kilometres; are typical of semi-arid and temperate climates; form on low declivity (below 25°) areas; are substrate independent and may occur in any rock type; are impoverished in $CaCO_3$ towards the base of the horizons; and rarely overcome six metres thick (Klappa, 1983). Soil water may have the Mg^{2+}/Ca^{2+} relation increased under severe evapotranspiration, allowing for authigenic precipitation of dolomite, as described in the Coorong lagoon, near Adelaide, Australia (von Der Borch, 1965). During hot summers, the Mg^{2+}/Ca^{2+} ratio may surpass 10.0, leading to dolomite precipitation. The studied samples bear pedogenic dolomites related to calcrete accumulation, with magnesium source related to palagonitization processes and/or alteration of mafic rock fragments from the northeast border of Bauru Basin (Fig. 1) (Batezelli, 2003). The presence of palygorskite has been associated with arid conditions, because its formation occurs under high Mg and Si concentrations in high pH waters. According to Batezelli (2015), the palaeosol profiles of the Bauru Basin indicate of arid to semi-arid conditions, with a maximum rainfall interval between 500 and 1000 mm (Jenny, 1941; Wright and Tucker, 1991; Retallack, 2005).

4. Egg description and comparisons

The three clutches LPRP/USP 0046–0048 are composed by four eggs each, horizontally distributed in the same plane with no overlapping of elements (Fig. 7). Specimens in the clutches are overall well preserved, but LPRP-USP 0048 was heavily weathered due to water percolation, precluding the analysis of its morphology beyond general shape and measurements. A fourth clutch, LPRP/USP 0648, preserves at least four vertically collapsed eggs also arranged in the same plane, with the possible preservation of a fifth egg (Fig. 7). The larger eggs are clustered in LPRP-USP 0047, measuring in average 7.2 by 4.2 cm. Smaller eggs are also present, as seen in the LPRP-USP 0638, a nearly complete isolated egg which is 5.9 by 3.17 cm in size (Table 1, Fig. 8). The LPRP-USP 0047 eggs are much larger than other crocodyliform eggs described for the Bauru Group, including *Bauruoolithus fragilis* (Oliveira et al., 2011) and those possibly associated to *Mariliasuchus amarali* (Magalhães Ribeiro et al., 2006). Indeed, they are one of the largest

Table 1
Preservation status and measurements of *Pissarrachampsa sera* eggs.

Specimen		Preservation status	Egg length (cm)	Egg width (cm)
LPRP-USP 0046	1	Nearly complete eggs	5.94	3.92
	2		6.46	2.94
	3	Weathered eggs	6.78	3.90
	4		6.26	3.59
LPRP-USP 0047	1	Nearly complete eggs	7.24	4.21
	2		7.26	4.20
	3		7.02	4.16
	4	Partial egg	4.90	3.00
LPRP-USP 0048	1	Weathered eggs	5.65	4.81
	2		5.80	4.82
	3		6.88	4.74
	4		6.34	4.61
LPRP-USP 0638	Single egg	Nearly complete egg	5.90	3.17
LPRP-USP 0640	Single egg	Partial, compressed egg	6.26	3.92
LPRP-USP 0647	Single egg	Egg with damaged pole	4.66	3.40
LPRP-USP 0648	1	Partial, compressed eggs	5.92	3.90
	2		5.62	3.64
	3		6.90	4.07
	4		5.57	4.21

known crocodile eggs, both fossil and extant (Marzola et al., 2015, Table 3). In general, the sampled eggs are elongated with blunt ends (Fig. 7), presenting the common elliptical shape to crocodyliform eggs (Hirsch, 1985; Kohring and Hirsch, 1996; Marzola et al., 2015). Likewise, the outer surface appears smooth in macroscopic observation, as seen in other crocodilians eggs (Ferguson, 1982, 1985; Hirsch, 1985; Marzola et al., 2015). However, stereoscopy shows a complex slightly rugose/undulating surface, as in *B. fragilis* (Oliveira et al., 2011) and in *M. amarali* eggs (Magalhães Ribeiro et al., 2006), also resembling the rugosocavate condition observed in *Crocodylus mindorensis* and *Paleosuchus palpebrosus* eggs (Marzola et al., 2015). No extrinsic degradation pits are seen in the samples, but eggshell thickness is much reduced, although some size-related variation occur; i.e. LPRP-USP 0047 eggshells are about 150 μm thick, whereas smaller eggs (LPRP-USP 0046, 0638, 0640 and 0647) have thinner eggshells, ranging from 130 to 150 μm (Fig. 9). Putative *M. amarali* eggs, which are much smaller, have eggshells about twice thicker (Magalhães Ribeiro et al., 2006), and are closer in thickness to *B. fragilis*, which range from 150 to 250 μm thick (Oliveira et al., 2011). Crocodyliform eggshells about five times thicker than those dealt with here have been reported, reaching up to 750 μm thick (Panadès I Blas and Patnaik, 2009; Moreno-Azanza et al., 2014). The here newly described eggs are among the thinnest known for crocodilians, considering both fossil and extant records (Marzola et al., 2015).

The ultrastructure of the described eggshells is not easily accessed due to diagenetic alterations (weathering and dissolution during fossilization). Fully interlocked shell units are recognized, occasionally intercalated by circular pore openings, similar to those of *Paleosuchus palpebrosus* eggs (Marzola et al., 2015). Pore openings are approximate 40 μm in diameter, visible only in LPRP-USP 0046 and 0047, with average density difficult to stablish due their sparseness (Fig. 9). *Bauruoolithus fragilis* shows pore openings with diameter from 30 to 80 μm (Oliveira et al., 2011), which depart from the pattern described here for their elliptical to subtriangular shape and more abundant distribution. In general, pore openings are evidently more abundant in eggs of living crocodilians, such as in *Crocodylus mindorensis* and *Paleosuchus palpebrosus* (Marzola et al., 2015), than in fossil eggs, as those described here.

The shell units exhibit an irregular morphology, with a trapezoid or wedge-shaped arrangement (Fig. 9), usually regarded as a typical crocodilian feature (Hirsch, 1985; Kohring and Hirsch, 1996; Rogers, 2001). The shell unit height/width ratio ranges from 1.2 to 1.5. However, shell units twice higher than wide or even wider than high are also observed. This height/width ratio resembles that observed for shell units of *B. fragilis* (Oliveira et al., 2011). In addition, wedges are observed in the structure of the shell units in cross section (Fig. 9). The shell inner layer is composed of circular shell units, about 40 to 50 μm in diameter. Only LPRP-USP 0047 preserves basal knobs and surrounding "petal-like" structures (Fig. 9), which resemble those of *Krokolithes helleri* (Kohring and Hirsch, 1996). There is no clear boundary between the middle layer and the outer layer, hampering the precise measurement of their thickness. The typical crocodyliform tabular structures (Ferguson, 1985; Hirsch, 1985; Kohring and Hirsch, 1996; Moreno-Azanza et al., 2014; Russo et al., 2014) are not frequently found in the eggshell ultrastructure, most probably due to the preservation biases. When present (Fig. 9D), however, they are equally spaced, both in the middle and in outer layers, differently of the observed by Moreno-Azanza et al. (2014) in Krokolithidae eggshells from the Late Cretaceous of Spain.

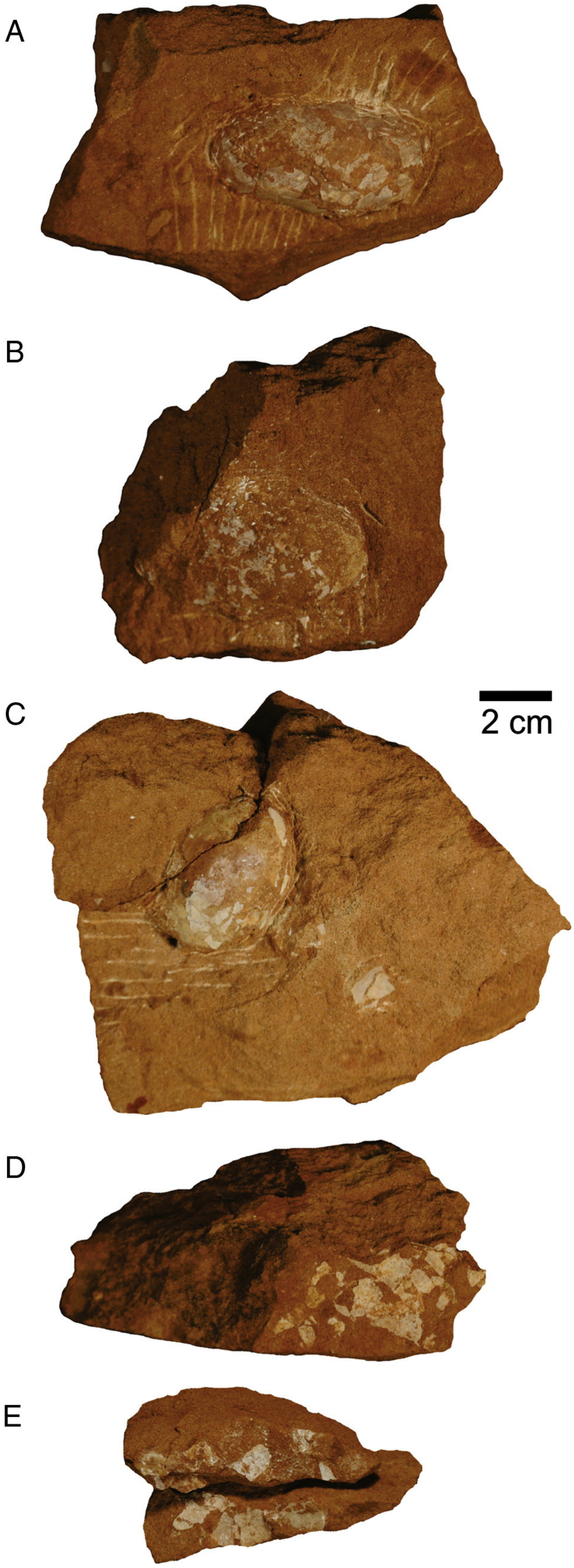

Fig. 8. *Pissarrachampsa sera* isolated eggs LPRP-USP 0638 (A), LPRP-USP 0640 (B), LPRP-USP 0647 (C) and eggshells LPRP-USP 0639 (D) and LPRP-USP 0641 (E).

5. Discussion

5.1. Egg-layer, taphonomic and environmental considerations

Fossil eggs and nests give unique clues to the reproductive biology of extinct organisms and are usually related to exceptional preservation

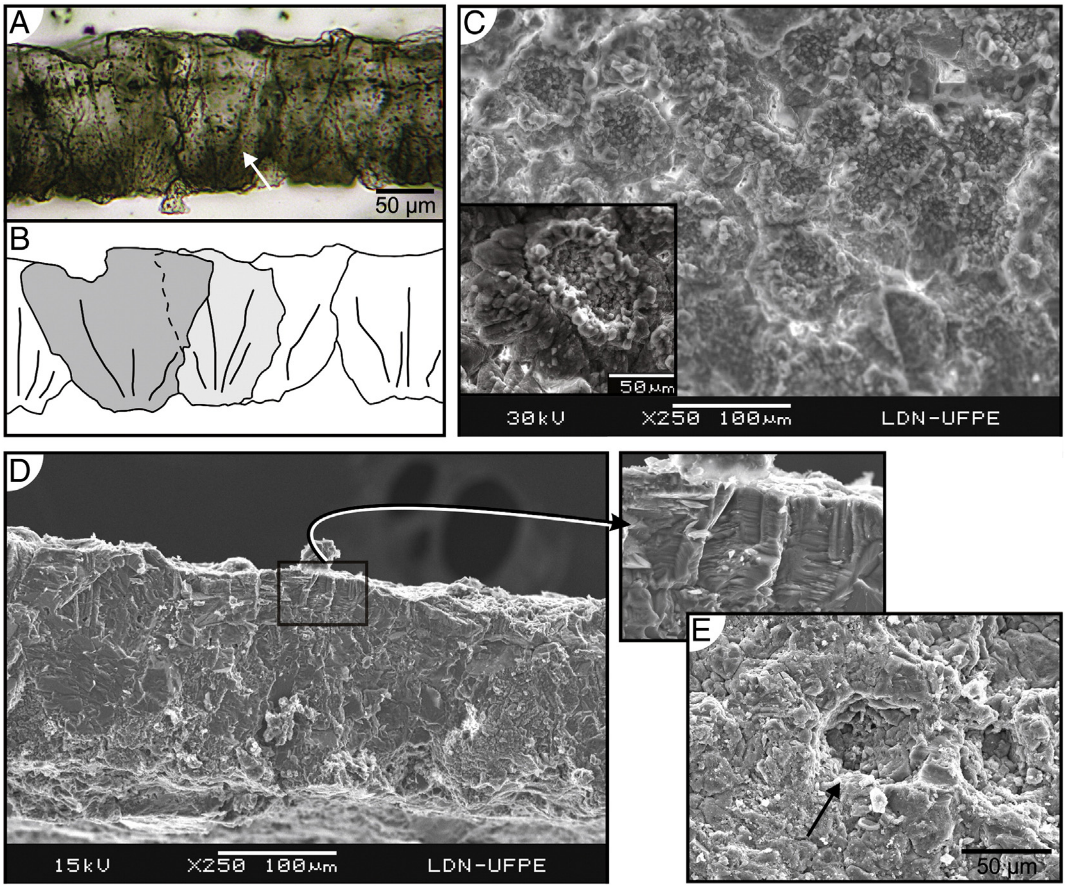

Fig. 9. A, OM of LPRP/USP 0047 eggshell cross section showing the general irregular and trapezoid aspect of the shell units and the presence of wedges (white arrow). B, schematic drawing of the shell units seen in A, depicting the height/width variation of the shell units with the presence of both wider (dark grey) and higher (lighter grey) units in the same eggshell. C and D, MEV of the LPRP/USP 0046 and 0047, respectively. C, inner view of the shell units showing their rounded aspect and the presence of "petal-like" structures at the base (black frame). D, eggshell in cross section detailing the occurrence of tabular structures in its arrangement. E, rounded pore opening indicated by the black arrow.

contexts (i.e., Norell et al., 1995; Chiappe et al., 1998; Mateus et al., 1998; Schweitzer et al., 2002; Araújo et al., 2013; Ribeiro et al., 2014). Indeed, eggs are usually fragile and prompt to fragmentation during transport (Hayward et al., 2011). In the type-locality of *Pissarrachampsa sera*, all eggs were preserved without biogenic patterns, such as hatching, predation, or trampling signs. LPRP-USP 0639 and 0641 are more fragmentary (Fig. 8), but they represent leftovers of a single collapsed egg, as in the case of the clutch LPRP-USP 0648. Because of the fact that the eggshell fragments still overlap one another, we exclude any transportation of the specimens during sedimentation. As pointed out by Hayward et al. (2000, 2011), if the eggs were subject to any sort of directional transport prior to sedimentation, eggshell fragmentation would be more conspicuous and the fragments may result organized with an orientation pattern . Additionally, Oser and Jackson (2014) show that the edges of eggshell fragments acquire abrasion signs when interact with the sediment during transport, and such features are absent from LPRP-USP 0637, 0639, and 0648. Absence of transport can also be inferred for the three better preserved clutches, LPRP-USP 0046-0048.

Although the described eggs vary in their overall dimension (Table 1), this size disparity cannot be considered a proxy for taxonomic diversity, considering that the average egg size in the extant *Alligator mississippiensis* is directly proportional to the age of the females (with a variation up to 2 cm) (Ferguson (1985). The eggs of the *Pissarrachampsa sera* type-locality are collected from the same stratigraphic horizon preserving several well-preserved skeletal remains of this crocodyliform, including skulls and articulated postcranial elements of different ontogenetic stages (Godoy et al., 2016). This suggests an autochthonous assembly, as corroborated by the evidences disfavouring a long range transport of the eggs and the rhythmic deposits that indicate episodic sedimentary processes with slow decrease in energy and low viscosity turbiditic flows. Though an egg-taxon association is only certain in cases of extraordinary preservation and conditions, such as the presence of embryos and pregnant females (Chiappe et al., 1998; Mateus et al., 1998; Zhou and Zhang, 2004; Sato et al., 2005; Grellet-Tinner et al., 2006; Araújo et al., 2013) or in clear cases of parental care (Norell et al., 1995), the studied locality appears to include a monotypic egg-taxon assemblage that allows inferring *P. sera* as the best potential egg-layer, alike the association egg-taxon between *Bauruoolithus fragilis* and *Baurusuchus pachecoi* described in Oliveira et al. (2011).

The eggs attributed to *Pissarrachampsa sera* are found in deposits that suggest a sedimentary dynamic characterized by short flood periods, intercalated by long periods of subaerial exposure. During these latter periods deprived of sedimentation, deposits were exposed to weathering factors responsible for the pedogenesis. Although long-lasting water was present in the system, the general climatic patter was surely arid to semi-arid. Together with the fact that *P. sera* eggs were found in sandy paleosols, the geological data suggests that this crocodilian nested in dryer environments compared to extant forms, that nest in areas near water bodies and take advantage of surrounding humidity to incubate their eggs (Ferguson, 1981; Ferguson, 1985). A proposed relation between total pore area, eggshell thickness, and water vapour conductance, indicates that, in birds, thicker and more porous eggs lose more water than thinner and less porous ones (Ar et al., 1974). Plus, archosaur hardly mineralized eggshells minimize the loss of water, strongly unlinking the embryo from the hydric potential of the surrounding environment (Packard et al., 1982). Tanaka et al.

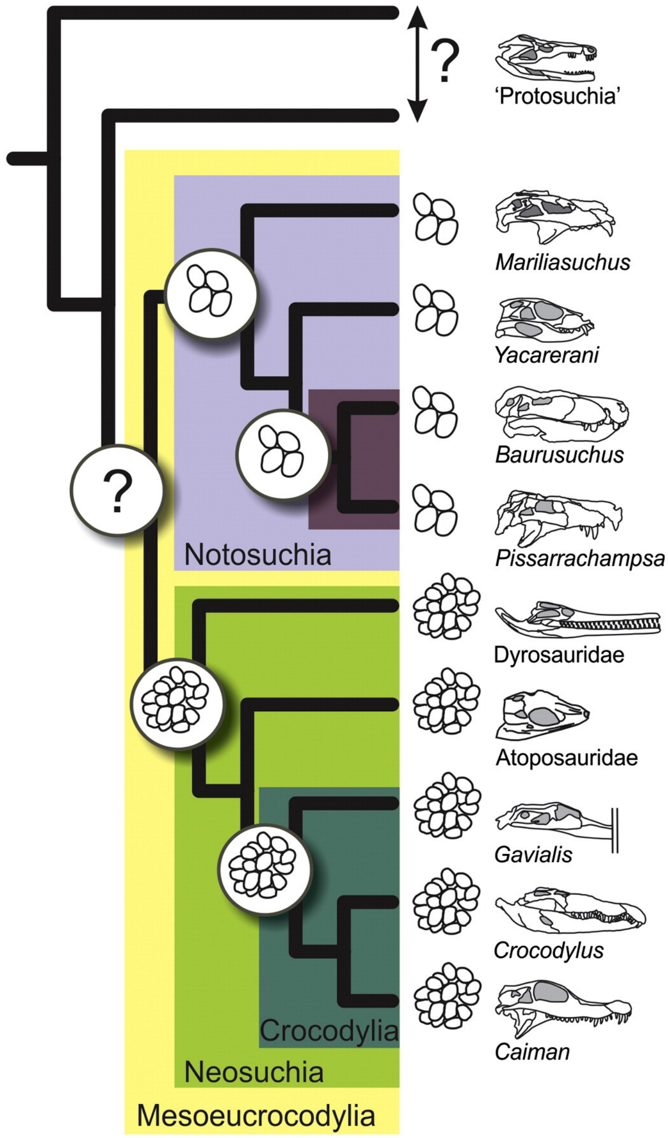

Fig. 10. Simplified phylogenetic framework mapping egg-clutch sizes across Mesoeucrocodylia evolution.

(2015) found covered nesters, such as crocodilians and megapods, to possess more porous eggs than open nesters birds. Accordingly, Seymour (1979) observed that the high porosity of the eggs of some dinosaurs have a clear association with their incubation in nests with quite humid conditions. Accordingly, the scarcity of pores and the thin shells of the eggs described here could also be interpreted as an adaptation for dryer environments, reducing water loss during the embryo development. Therefore, modifications towards a more terrestrial way of life may not be restricted to the skeletal anatomy of baurusuchids (Riff and Kellner, 2011; Godoy et al., 2016), but also include aspects of their reproductive behaviour.

5.2. Evolutionary significance of *Pissarrachampsa sera* egg

The above mentioned attribution of the egg clutches to *Pissarrachampsa sera*, along with the previous records of such fossils, provides a unique opportunity to discuss the reproductive biology of baurusuchids and its implications for understanding the origin of the reproductive biology of living crocodyliforms. The small number of eggs (four to five maximum) per clutch in *P. sera* differs remarkably from the pattern seen in living crocodilians, ranging from a lower limit of 10 eggs per clutch in *Alligator sinensis*, *Osteolaemus tetraspis*, *Paleosuchus palpebrosus*, and *Crocodylus mindorensis*, to up to 80 eggs in clutches of *Crocodylus niloticus* (Greer, 1975; Platt et al., 2004; see Brazaitis and Watanabe, 2011 for a review). Offspring number is a key factor in determining the life-history strategy of species, but the broadly used k- and r-selected dichotomy is hard to fit in modern crocodilians (Magnusson, 1986; Tucker, 2001; Abercrombie et al., 2001; Grigg and Kirshner, 2015). In one aspect, the group has a greater number of general k-strategists traits (e.g. large size, long-living individuals, slow grow, and long reproductive life), but also presents some typical characteristics of r-selected species, like the numerous eggs per clutch resulting in large offspring (Abercrombie et al., 2001; Tucker, 2001; Grigg and Kirshner, 2015). As for *P. sera*, although much information is lacking to define its life-history strategy, the small number of eggs per clutch pushes the taxon to the k-selected end of the spectrum represented by modern forms (Grigg and Kirshner, 2015).

Considering the entire documentation of crocodyliform egg clutches, the four-egg clutch of *Pissarrachampsa sera* does not depart so much from the pattern seen in the fossil record. All but two Mesozoic crocodyliform egg clutches present a lower number of eggs per clutch than the lowest limit observed in modern crocodilians (Greer, 1975; Brazaitis and Watanabe, 2011); moreover, those with the lowest number of eggs are all from the Cretaceous of South America: two-egg clutches were putatively referred to *Mariliasuchus amarali*, also from the Bauru Group (Magalhães Ribeiro et al., 2006), and to *Yacarerani boliviensis*, from the Late Cretaceous Cajones Formation of Bolivia (Novas et al., 2009). The nesting site reported by Oliveira et al. (2011) from the Adamantina Formation includes one clutch of four eggs (see also Oliveira, 2008). The ootaxon *Bauruoolithus fragilis* was named to encompass these eggs, possibly associated to *Baurusuchus pachecoi* (Oliveira et al., 2011). Two other Adamantina Formation crocodyliform clutches, with four and six eggs, were preliminarily described by Magalhães Ribeiro and Arruda Campos (2009), with no taxonomic or parataxonomic assignment. Finally, Carvalho et al. (2013) reported a presumable adult specimen of *Mariliasuchus amarali* still from the Bauru Group and found in close association to four egg clutches formed by 3–4 eggs each. Thus, the only exceptions to the rule of reduced egg clutches in fossil crocodyliforms are so far from the Late Jurassic of Portugal (Russo et al., 2014; Araújo et al., 2015) and from the Late Cretaceous of India (Srivastava et al., 2015), respectively assigned to Atoposauridae and Dyrosauridae. With 13 eggs each, they represent the largest crocodyliform egg clutches known in the fossil record.

It is possible to identify, therefore, a clear discrepancy between the number of eggs in fossil and living crocodyliform clutches; a pattern that may influence our understanding of the life-history strategies of the group through geological time. In order to further explore this subject, crocodyliform egg clutch sizes were analysed in a phylogenetic framework (Fig. 10). Baurusuchidae (sensu Montefeltro et al., 2011) is a monophyletic group within Notosuchia (Fig. 10), including both *Pissarrachampsa sera* and *Baurusuchus pachecoi* (associated to the oospecies *Bauruoolithus fragilis*). Likewise, *Mariliasuchus amarali* and *Yacarerani boliviensis* are part of the advanced notosuchians clade of Pol et al. (2014). On the other side, Atoposauridae and Dyrosauridae are members of Neosuchia, a broader clade that also includes modern crocodiles (Montefeltro et al., 2013; Pol et al., 2012, 2014; Rabi and Sebők, 2015; Leardi et al., 2015). Notosuchia and Neosuchia are consistently found as sister clades, forming one of the better stablished dichotomies in crocodyliform phylogeny (Montefeltro et al., 2013; Pol et al., 2012, 2014; Rabi and Sebők, 2015; Leardi et al., 2015). Accordingly, the optimization of egg clutch sizes in such phylogenetic framework suggests a reduced number of eggs as the plesiomophic condition at Notosuchia node, and a greater number of eggs as plesiomorphic condition at the Neosuchia node (Fig. 10).

The absence of data on the clutch size for earlier crocodyliform splits precludes identifying confidently the ancestral condition for the Notosuchia/Neosuchia dichotomy. At this point, it is unknown if the great number of egg per clutch of the modern crocodilians is a modification from a condition of smaller egg clutches present in notosuchians. Alternatively, the smaller egg clutches in notosuchians might in fact be a modification from a plesiomorphic condition of larger clutches present in neosuchians. The larger number of eggs per clutch of other archosaur, such as dinosaurs (i.e., Horner and Makela, 1979; Norell et al., 1995; Chiappe et al., 1998; Grellet-Tinner et al., 2012), might support the second scenario. However, given the gap in the knowledge about the egg-clutch size of more basal pseudosuchians, we prefer to take a more conservative approach and do not make this leap. New finds, such as 'protosuchian', basal notosuchian and basal pseudosuchian egg clutches, might help defining the ancestral Mesoeucrocodylia offspring size, shedding light onto origin of the unique reproductive biology of modern crocodilians.

6. Conclusions

Combined stratigraphic and taxonomic studies provided critical information for understanding nesting strategies of archosaurs as a whole. A previously unreported scenario is presented here, where articulated and isolated remains of the baurusuchid *Pissarrachampsa sera* are found in association to several egg clutches. The main conclusions drawn from the palaeoenvironmental characterization of the site and comparative study of the oological remains on a phylogenetic framework are summarized below:

- The rhythmic deposits of sand- and mudstones of the Adamantina Formation in the site indicate episodic sedimentary processes, with slow energy decrease, as typical of low viscosity turbidity flows generated during flooding periods on depressed areas. The muddy sandstones that appear above the rhythmic facies show root marks and carbonatic nodules, both of which indicate pedogenic processes.
- The pedogenic calcretes in the palaeosols are a clear indication of arid to semi-arid climatic conditions, further corroborated by the presence of palygorskite. As a whole, the paleoenvironment is interpreted as a shallow lacustrine system, such as a playa-lake, interacting with an ephemeral braided fluvial system, with aeolian influence and development of sandy soils.
- The combined presence of thin eggshell and wedge-shaped shell units with tabular structures supports the crocodilian affinity of the described eggs. The general egg morphology resembles that of *Bauruoolithus fragilis*, an oospecies assigned to *Baurusuchus*. However, eggs associated to that oospecies are smaller and probably more porous, which along with the elliptical to subtriangular shape of the pore openings, compose their main differences to *Pissarrachampsa sera* eggs.
- Along with the sedimentary patterns discussed above, the scarcity of scattered eggshells and the lack of abrasion signs in their edges, the good preservation of the eggs in clusters, and the presence of articulated remains of *Pissarrachampsa sera*, preclude a long range transport of the remains, indicating an autochthonous assembly. Also, such monotypic deposit allows inferring *P. sera* as the egg-laying taxon.
- The recurring pattern of four (possibly five) eggs per clutch suggest that *Pissarrachampsa sera* laid fewer eggs if compared to modern crocodilians, placing the taxon in the far end of the k-selected spectrum represented in Crocodyliformes.
- The apparent pattern of small egg clutches in notosuchians suggests a peculiar reproductive strategy for this group among crocodyliforms. The optimization of "egg clutch size" in the current phylogenetic framework, however, defines ambiguously if this pattern was already present or not in earlier splits of Crocodyliformes.

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