CROCODYLOMORPH EGGS AND EGGSHELLS FROM THE ADAMANTINA FORMATION (BAURU GROUP), UPPER CRETACEOUS OF BRAZIL

by CARLOS E. M. OLIVEIRA*†‡, RODRIGO M. SANTUCCI§¶,
MARCO B. ANDRADE**††, VICENTE J. FULFARO*, JOSÉ A. F. BASÍLIO†
and MICHAEL J. BENTON**

*Departamento de Geologia Aplicada, Instituto de Geociências e Ciências Exatas, IGCE-UNESP, Avenida 24-A 1515, Rio Claro, São Paulo 13506-900, Brazil; e-mails edumaiaoli@yahoo.com.br; vfulfaro@rc.unesp.br

†Fundação Educacional de Fernandópolis, FEF, Câmpus Universitário, Avenida Teotônio Vilela, PO Box 120, Fernandópolis, São Paulo 15600-000, Brazil; e-mails edumaiaoli@yahoo.com.br; jabasilio@gmail.com

‡Universidade Camilo Castelo Branco, Unicastelo, Câmpus Universitário, Estrada Projetada s/n, Fazenda Santa Rita, PO Box 121, Fernandópolis, São Paulo 15600-000, Brazil; e-mail edumaiaoli@yahoo.com.br

§Universidade de Brasília, Faculdade UnB Planaltina, Brasília, Distrito Federal 73300-000, Brazil; e-mail rodrigoms@unb.com.br

¶Departamento Nacional de Produção Mineral, S.A.N. Q 01 Bloco B, Brasília, Distrito Federal 70041-903, Brazil

**Palaeobiology and Biodiversity Research Group, Department of Earth Sciences, University of Bristol, Queens Road, Wills Memorial Building, Clifton, Bristol BS8 1RJ, UK; e-mails marcobranda@yahoo.com.br; mike.benton@bris.ac.uk

††Departamento de Paleontologia e Estratigrafia, Universidade Federal do Rio Grande do Sul, Avenida Bento Gonçalves 9500, PO Box 15001, Porto Alegre, Rio Grande do Sul 91501-970, Brazil

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Abstract: Compared with crocodylomorph body fossils, the record of fossil crocodiloid eggs is scarce and poorly understood, a gap partially attributed to their typically thin eggshell, which is not conducive to preservation. A remarkable new association of well-preserved eggs and eggshells from the Adamantina Formation (Bauru Group, Upper Cretaceous) is described and compared to other known materials, while the significance of their unique oological features is discussed. These eggs constitute a new ootaxon, *Bauruoolithus fragilis* oogen. et oosp. nov., diagnosed by the following characteristics: elongate and elliptical egg with blunt ends; length-to-diameter ratio of 1:0.55; outer surface slightly undulating; shell thickness ranging from 0.15 to 0.25 mm; pore openings elliptical or teardrop-shaped, ranging from 30 to 80 μm in diameter; and shell units wider than higher, with the interstices forming an obtuse triangle. Specimens of *Bauruoolithus* also show only slight signs of extrinsic degradation that, coupled with the evidence that some of them constitute hatched eggs, suggests that the egg-laying taxon had a different pattern of egg incubation, in which the hatchling could break through the rather thin eggshell relatively easily and that the extrinsic degradation of the eggshell was not necessary. This contrasts with the pattern of incubation for all other known crocodylomorphs and crocodiloid eggs, where extrinsic degradation is a key component of the hatching process.

Key words: eggs, crocodylomorphs, Upper Cretaceous, Bauru Basin, Adamantina Formation, extrinsic degradation, *Baurusuchus*.

THE past diversity of fossil Crocodylomorpha is compelling (over 200 taxa), ranging from the Triassic to the Recent and with occurrences on almost all continents, contrasting with the limited range of extant taxa, which are all members of the eusuchian lineage (e.g. Buffetaut 1979, 1982; Benton and Clark 1988; Carroll 1988; Clark 1994; Benton 2005). The record of fossil crocodylomorph eggs is even more limited and poorly understood. So far, only two oospecies have been assigned to a single oogenus (*Krokolithes*), within the oofamily Krokolithidae (Hirsch 1985; Kohring and Hirsch 1996). These, along with a small amount of unnamed oological material known so far (e.g. Kohring 1990; Novas *et al.* 2009; Antunes *et al.* 1998;

Rogers 2000), most likely provide a poor representation of the diversity of fossil crocodylomorphs in terms of eggshell morphology, egg-laying and reproductive strategy.

Hirsch (1985) proposed the name *Krokolithes wilsoni* to accommodate the relatively small eggs and eggshells from the DeBeque Formation (Eocene) of Colorado, USA. A second oospecies, *K. helleri*, was described by Kohring and Hirsch (1996) on the basis of six badly damaged eggs from the middle Eocene of Geiseltal, Germany. Crocodiloid eggs have also been reported from the Bridger Formation (middle Eocene), Wyoming, USA (Hirsch and Kohring 1992), and from the Glen Rose Formation (Albian), Texas, USA (Rogers 2000). The oldest known

crocodylomorph eggshell comes from the Upper Jurassic of Portugal, consisting of badly damaged eggs unearthed at the Pai Mogo Site, in Lourinhã (Antunes *et al.* 1998). Crocodylomorph eggs and eggshells are also known from the lower Barremian of Galve, Spain (Kohring 1990), and from the Upper Cretaceous of Bolivia (Novas *et al.* 2009).

In Brazil, occurrences of fossil eggs and eggshells are rare and known materials are poorly understood. Crocodylomorph eggs have generally been briefly mentioned in short abstracts. Magalhães-Ribeiro *et al.* (2003, 2006) and Magalhães-Ribeiro and Nava (2005) reported crocodylomorph eggs from the city of Marília (Adamantina Formation) and assigned them to the oofamily Krokolithidae. These eggs and eggshells were putatively attributed to *Mariliasuchus*, based on their close proximity to skeletal remains of this crocodylomorph (Magalhães-Ribeiro *et al.* 2006). Arruda *et al.* (2004) and Vasconcellos and Carvalho (2010) also briefly mentioned some crocodylomorph eggs from the Adamantina Formation near General Salgado (São Paulo State), without additional remarks concerning their morphology.

The unexpected discovery of a remarkable association of egg clutches in early 2006 (see Oliveira *et al.* 2008), during a fieldtrip to Jales (São Paulo State, Brazil; Text-fig. 1), substantially increased the diversity of fossil eggs from Brazil. Subsequent fieldwork by CEMO and RMS successfully recovered no fewer than 17 egg clutches, arranged in at least three horizons, from a remarkably small area (Oliveira *et al.* 2008). These were in close association with several skeletal and dental remains of the notosuchian *Baurusuchus*, a well-known predacious crocodylomorph (e.g. Price 1945; Romer 1966; Riff and Kellner, 2001).

Here, we (1) introduce the general morphology of the eggs and eggshells found in this new locality from the Adamantina Formation; (2) compare them to all other known fossil crocodile-like oological remains and eggshells of extant crocodylians available in the literature; and (3) explore the palaeobiological and functional significance of this new ootaxon. The combination of a thin eggshell and absence of signs of extrinsic degradation in all samples, coupled with evidence of hatched eggs, is of particular interest and suggests a new pattern of egg incubation among crocodylomorphs. The significance of aspects regarding egg-clutch structure and nest distribution will, however, be presented elsewhere.

GEOLOGICAL SETTING

The eggs and egg clutches were recovered from the Adamantina Formation, the richest vertebrate-bearing unit in the Bauru Group (Bertini *et al.* 1993; Kellner and Campos 1999, 2000). In São Paulo State, the Bauru Group (*sensu* Batezelli *et al.* 2003) includes the Araçatuba, Adamantina
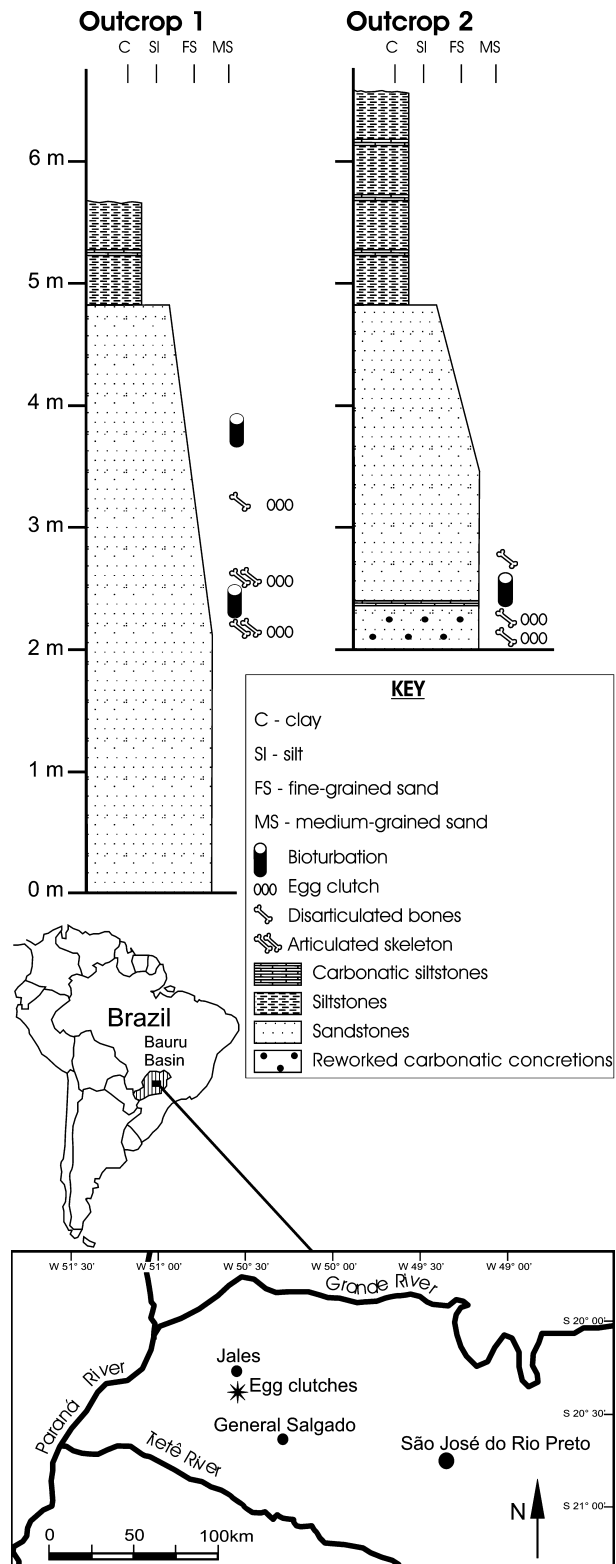
TEXT-FIG. 1. Map depicting the locality where *Bauruoolithus fragilis* egg clutches were collected, with two stratigraphical sections of the same outcrop.

and Marília formations. Of these, the Adamantina Formation has the greatest outcrop area. The rocks of this formation are interpreted as deposited by a fluvial depositional system created by braided rivers (Fernandes and Coimbra 2000; Batezelli *et al.* 2003). Mezzalira (1974, 1989) and Gobbo-Rodrigues *et al.* (1999*a*) reported well-preserved remains of ostracods, conchostraceans and molluscs from the Adamantina Formation. The vertebrate record is also noteworthy and comprises turtles, crocodylomorphs, theropods, sauropods and, most recently, birds (Bertini *et al.* 1993; Kellner and Campos 1999, 2000; Alvarenga and Nava 2005).

The outcrop where the eggs were discovered consists of massive reddish, immature, fine-grained sandstones, with reworked carbonate concretions of millimetric size at the base. This egg-bearing layer is approximately 3 m thick and the grain size decreases, from fine grained to very fine-grained sandstones, towards the top, where it contacts a layer of siltstones with incipient parallel bedding interbedded with thin layers of carbonate-rich siltstones (Text-fig. 1). Remains of *Baurusuchus* were found within the egg-bearing horizons, with many scattered small elements. About 1 m from well-preserved clutches, two reasonably complete skeletons of *Baurusuchus* were unearthed, both from the same horizon. Several small and elliptical coprolites have also been recovered. Rare burrows infilled with mud occur at the base of this layer. They are vertically oriented, straight and nearly elliptical, with the largest axis not exceeding 10 mm. Such burrows fit well within the ichnogenus *Skolithos* (Text-fig. 1).

Abbreviations. BRSUG, Department of Earth Sciences, University of Bristol; FEF, Fundação Educacional de Fernandópolis, São Paulo, Brazil; HEC, Hirsch Eggshell Catalogue, National Museum of Natural History, Smithsonian Institution, Washington, DC; SMU, Southern Methodist University, Texas; UCM, University of Colorado Museum, Colorado; UFRJ-DG, Departamento de Geologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; USNM, National Museum of Natural History, Washington, DC.

MATERIAL AND METHODS

All eggs and eggshells were unearthed from one large outcrop about 300 m in length. Some of the egg clutches were found close to each other, whereas others were isolated and slightly above the main egg layer. Data and samples in this study include four egg clutches (FEF-PV-8/1, FEF-PV-8/2, FEF-PV-8/3, FEF-PV-8/5) and an isolated egg (FEF-PV-8/13-a). FEF-PV-8/1 is the most complete clutch and includes the best preserved eggs.

Shell fragments were studied using light and polarizing microscopy (PLM) and scanning electron microscopy (SEM). Samples for SEM analysis from the holotype (FEF-PV-8/1-a, the most complete egg from clutch FEF-PV-8/1) included eggshell from both equatorial and polar regions. This procedure allowed us to evaluate morphological variation in different portions of the same egg and ensured that all other samples (from the same clutch or from other clutches) pertain to the same oospecies. Additionally, samples from clutches FEF-PV-8/1, FEF-PV-8/3, FEF-PV-8/5, and FEF-PV-8/8 were prepared for SEM analysis.

Preparation of specimens followed Hirsch and Kohring (1992) and the descriptive nomenclature for the eggshell is from Mikhailov (1991, 1997). As thin section analysis is destructive, samples were removed from an incomplete egg from clutch FEF-PV-8/1, which was in close association with the holotype (Text-fig. 2A, F). Further samples were taken from other egg clutches, where incomplete eggs were found (FEF-PV-8/2, FEF-PV-8/3 and FEF-PV-8/5), comprising a total of five samples. The samples were taken from portions of the clutches where several eggshells were found in close association, generally stacked eggshells, to maximize the number of eggshells per thin section and mitigate the effects of diagenesis at the eggshell/sediment boundary.

Fifteen shell fragments were measured to determine the shell thickness both under PLM and under stereoscopic zoom microscope with a reticular lens. To evaluate the differences between this new oospecies and those previously reported, we used the following material from the literature for comparison: UCM 47523 A and UCM 47523 D, eggs attributed to *Krokolithes wilsoni*, from the DeBeque Formation (Hirsch 1985); USNM 12597, HEC 128-1 and HEC 128-2, from the Bridger Formation (Hirsch and Kohring 1992); unidentified eggs, attributed to *Krokolithes helleri*, from the Geiseltal quarry Neumark-Süd XXII, Germany (Kohring and Hirsch 1996); unnamed egg from the Pai Mogo site, Portugal, no catalogue number provided, housed at Lourinhã Museum, Portugal (Antunes *et al.* 1998); SMU 74977, unnamed egg from the Glen Rose Formation (Rogers 2000); UFRJ-DG 298 IcV, unnamed eggs from the Araçatuba Formation, Brazil (Magalhães-Ribeiro *et al.* 2006); uncategorized unnamed eggs attributed to *Yacarerani boliviensis*, from the Cajones Formation, Bolivia (Novas *et al.* 2009). Estimated sizes and length-to-diameter ratios were used for *Krokolithes helleri* and *K. wilsoni* (Table 1) and were taken from Hirsch (1985) and Kohring and Hirsch (1996). However, it must be noted that taphonomic alteration can compromise morphometric data sampling on fossil eggs as (1) they may be incomplete, or (2) lithostatic pressure may lead to an increase in length and/or diameter. Therefore, the use of estimated measurements is more likely to reflect accurate information than raw
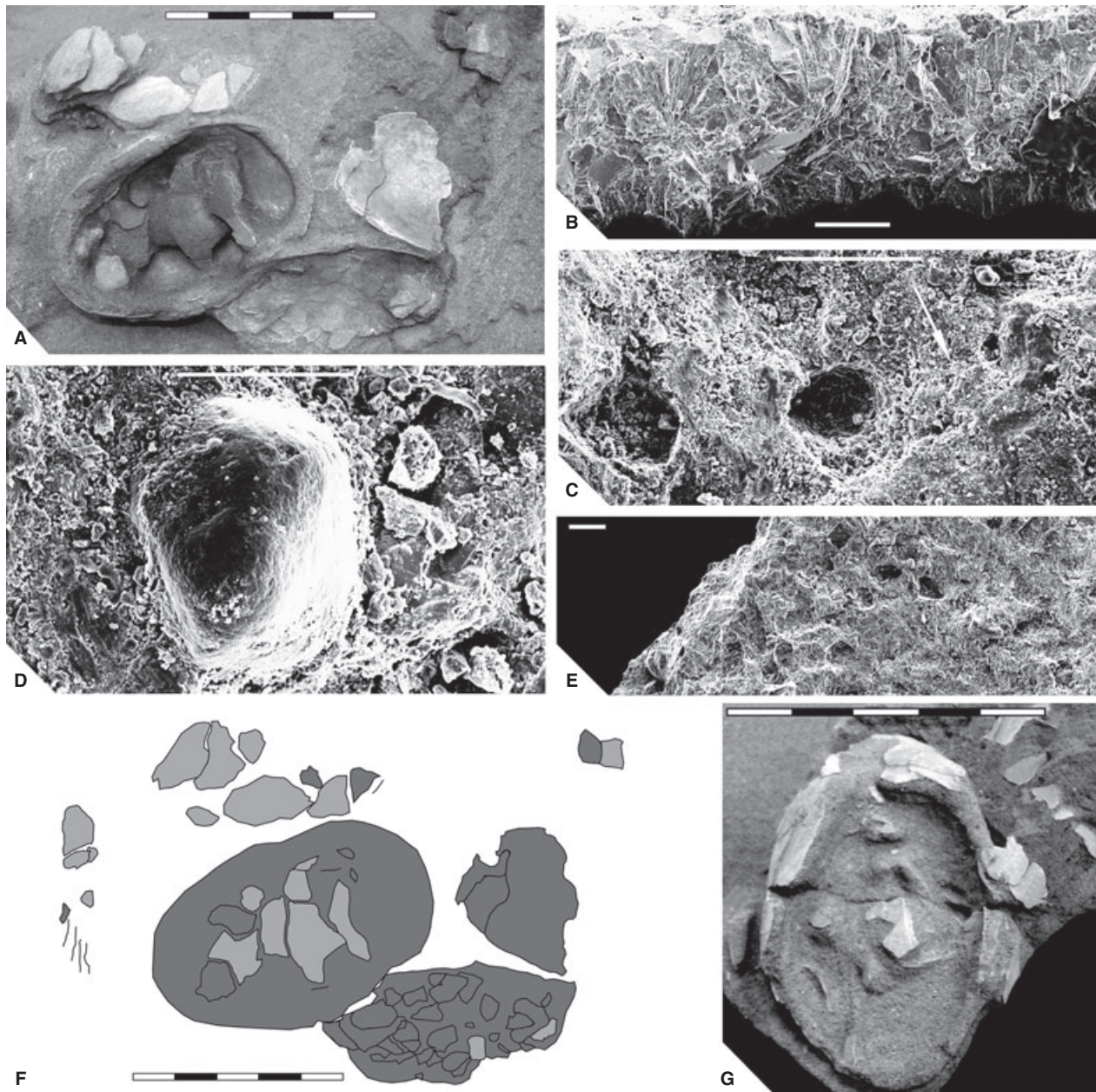
TEXT-FIG. 2. *Bauruoolithus fragilis* oogen. et oosp. nov., Adamantina Formation, Upper Cretaceous, Brazil. A, holotype FEF-PV-8/1. B, SEM, radial view showing the shell units, holotype FEF-PV-8/1. C, SEM, outer surface with pore openings and small signs of extrinsic degradation (arrow), holotype FEF-PV-8/1. D, SEM, outer surface, drop-shaped pore, holotype FEF-PV-8/1. E, SEM, inner surface with pore openings, holotype FEF-PV-8/1. F, sketch of the holotype FEF-PV-8/1 highlighting the concave up (dark grey) and concave down (light grey) eggshell fragments. G, specimen FEF-PV-8/10, showing one end and part of the equatorial portion. Scale bars in A, F and G represent 5 cm; B–E, 100 μm.

measurements of specimens, whenever taphonomic alteration is known to affect such data. This is certainly the case for *Krokolithes* (Hirsch 1985; Kohring and Hirsch 1996), where raw measurements were produced from flattened eggs.

We adopt the system of 'levels of confidence', as proposed by Grellet-Tinner (2005, 2006), to establish a relation between oological material and egg-laying taxa. Of

these, associations Levels 1 and 2 are the only ones to provide reliable links with an egg-laying taxon, whereas Levels 3 and 4 (i.e. without embryonic remains/direct contact; putative association) are considered unreliable, thus not providing grounds for the use of standard taxonomy or cladistic framework (*contra* Grellet-Tinner 2005).

Considering these remains as ichnological, we adopt the parataxonomic nomenclatural system in accordance

TABLE 1. Size and shell thickness of modern and fossil crocodylomorph eggs.

Identification and possible egg-laying taxon	Number	ST	Size	LDR	References
Extant crocodylians					
Crocodylus acutus	HEC 6	0.45	48 × 77	1:0.62	Hirsch and Kohring (1992)
Crocodylus niloticus	HEC 175	0.53	51 × 78	1:0.65	Hirsch (1983)
Crocodylus porosus	HEC 526	0.53	52 × 81	1:0.64	Hirsch and Kohring (1992)
Crocodylus johnstoni	HEC-1	0.40	40 × 58	1:0.69	Hirsch and Kohring (1992)
Alligator mississippiensis	HEC 174	0.53	42 × 76	1:0.55	Hirsch and Kohring (1992)
Alligator mississippiensis	HEC 33	0.51–0.53	41.1 × 68.2	1:0.60	Hirsch (1983)
Fossil crocodiloid eggs					
Krokolithus wilsoni (Neosuchian)	UCM 47523A	0.25–0.45	36 × 56 (50*)	1:0.64/1:0.60*	Hirsch (1985)
Krokolithus helleri (Neosuchian)	HEC 411-1	0.36–0.45	44 × 44	–	Kohring and Hirsch (1996)
	HEC 411-2	0.30	30 × 35	–	
	HEC 411-4	0.29–0.36	19 × 40	–	
	HEC 443-1	0.35–0.45	35 × 60 (63*)	1:0.58/1:0.55*	
	HEC 443-6	–	30 × 53	–	
	HEC 443-13	0.30–0.35	25 × 52	–	
Bridger Fm eggs (Neosuchian, Atoposauridae?)	USNM 12597	0.60–0.70	44 × 65	1:0.68	Hirsch and Kohring (1992)
	HEC 128	–	44 × 68	1:0.65	
Pai Mogo eggs (Neosuchian?)	–	0.20–0.35	40 × 70	1:0.57	Antunes *et al.* (1998)
Araçatuba Fm eggs (*Mariliasuchus amarali*?)	UFRJ-DG 298	0.24–0.36	30 × 50	1:0.60	Magalhães-Ribeiro *et al.* (2006)
	UFRJ-DG 298	0.24–0.36	30 × 45	1:0.66	
Cajones Fm eggs (*Yacarerani boliviensis*?)	–	0.20	30 × 16	1:0.53	Novas *et al.* (2009)
Bauruoolithus fragilis (*Baurusuchus pachecoi*?)	FEF–PV–8/1	0.15–0.25	36 × 65	1:0.55	This paper
	FEF–PV–8/5	–	32 × 58	1:0.55	
	FEF–PV–8/13	–	35 × 57*	1:0.61	

Morphological comparisons with *Bauruoolithus* considered corrected data for size and shape, based on estimated measurements provided by original descriptions.

LDR, length-to-diameter ratio; ST, shell thickness.

*Estimated values.

with the rules of the International Code of Zoological Nomenclature (ICZN, 1999; article 66.1), and following Mikhailov (1991, 1997) and Mikhailov *et al.* (1996). It should be noted that the name *Krokolithus* is an incorrect subsequent spelling of *Krokolithes* (see Hirsch 1985), under article 33.3 of the ICZN (1999).

SYSTEMATIC PALAEONTOLOGY

KROKOLITHIDAE Kohring and Hirsch, 1996

BAURUOOLITHUS oogen. nov.

Type species. *Bauruoolithus fragilis.*

Derivation of name. Generic name after Bauru Group, the unit in which the material was found; *Oo* (Ωov), meaning 'egg', and *lithus* (Λιθoς), meaning 'rock' or 'stone'.

Diagnosis. As for type oospecies.

Bauruoolithus fragilis oosp. nov.
Text-figures 2A–F, 3A–C

Holotype. FEF-PV-8/1a (Text-figs 2A–F, 3A), the most complete egg from clutch FEF-PV-8/1.

Referred materials. FEF-PV-8/1, besides the holotype, four partial eggs and several eggshells; FEF-PV-8/2, a partial egg; FEF-PV-8/3, two incomplete eggs and several eggshells; FEF-PV-8/4, eggshells; FEF-PV-8/5, a partial egg with stacked eggshells within; FEF-PV-8/6, scattered eggshells; FEF-PV-8/7, scattered eggshells; FEF-PV-8/9, an incomplete egg and several eggshells; FEF-PV-8/10, an incomplete egg and several eggshells; FEF-PV-8/11, several eggshells; FEF-PV-8/13, an incomplete egg; FEF-PV-8/14, scattered eggshells FEF-PV-8/15, scattered eggshells FEF-PV-8/16, an incomplete egg and several eggshells; FEF-PV-8/17, scattered eggshells FEF-PV-8/18, an incomplete egg and several eggshells.

Derivation of name. The specific epithet '*fragilis*' is Latin for thin or slender, in reference to the remarkable reduced shell thickness of the eggs.

Locality and horizon. A locality 12 km south the city of Jales, in Northern São Paulo State, South-eastern Brazil. Adamantina Formation, Bauru Group, Upper Cretaceous; Campanian to Maastrichtian (Gobbo-Rodrigues *et al.* 1999*a*, *b*).

Diagnosis. Crocodiloid egg with the following association of characteristics: elongated and elliptical egg with blunt ends; length-to-diameter ratio 1:0.55; outer surface slightly undulating; shell thickness ranging from 0.15 to 0.25 mm; pore openings elliptical or drop-shaped, ranging from 30 to 80 μm; shell units wider than higher, with the interstices forming an obtuse triangle; and average value for pore count of 3/mm^2.

Description

All egg clutches were recovered from a large, nearly horizontal eroded area. As the erosion process contributed to the exposure of the egg clutches, it also progressively destroyed them. Thus, none of the eggs collected is complete and most of them consist of less than half the egg. Although none of the clutches is completely preserved, many small eggshell fragments occur in close association or even inside the eggs. There are no signs of compaction. This can be deduced from the state of the most complete eggs (FEF-PV-8/1, FEF-PV-8/5, and FEF-PV-8/10), which are undistorted. Additionally, most of the measurements were taken from the clutches FEF-PV-8/1, FEF-PV-8/5, and FEF-PV-8/10, which consists of nearly complete eggs.

The eggs are elongate and elliptical with blunt ends. The greatest length varies from 58 to 65 mm, and the equatorial diameter ranges from 32 to 36 mm (Text-fig. 2A). The length-to-diameter ratio was calculated for the three most complete eggs. It is 1:0.55 for both the holotype FEF-PV-8/1-a and FEF-PV-8/5-a, which is an almost complete egg. A ratio of 1:0.61 was estimated for the isolated incomplete egg FEF-PV-8/13-a, but because this egg is not complete this difference in ratio may reflect damage by erosion (see Table 1). Shell thickness varies from 0.15 to 0.25 mm. As previously reported by Kohring and Hirsch (1996), a putative shell membrane seems to be preserved in some eggshells. This possible shell membrane corresponds to a thin layer on the inner surface of the eggshell without signs of internal structure, differing from both the shell units and the sediment by being dark grey or black, with no extinction pattern under PLM. This can be seen mostly in the thin sections, where several eggshells contact each other (Text-fig. 3A) under PLM, but not under SEM.

In most instances, where the egg is in contact with the sediment, quartz grains seem to have deformed the eggshell (Text-fig. 3B–C), creating shallow subcircular craters
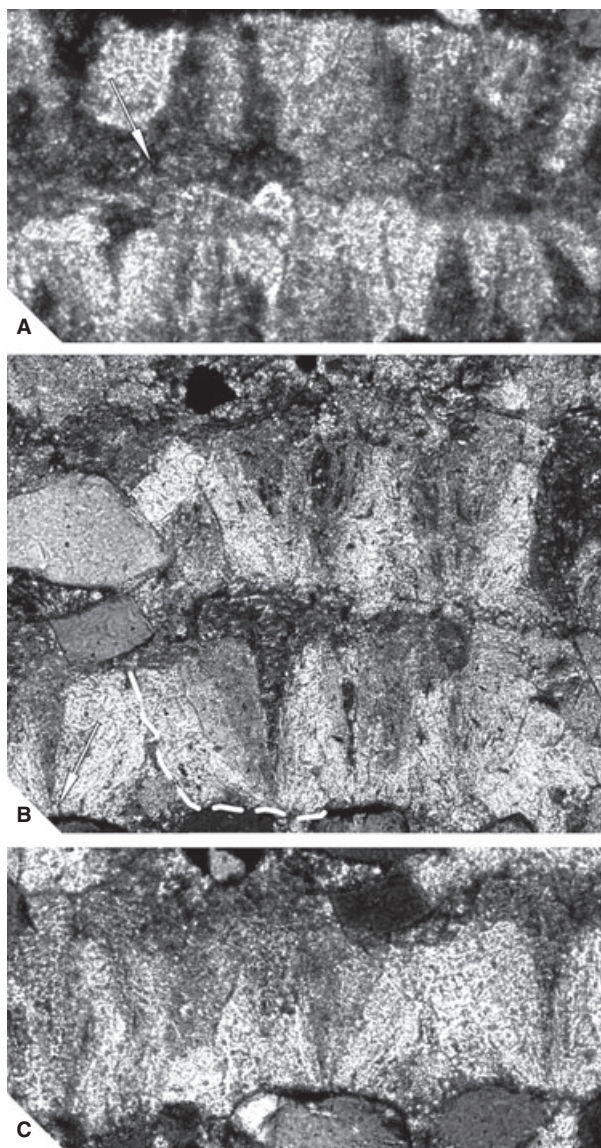
TEXT-FIG. 3. *Bauruoolithus fragilis* oogen. et oosp. nov., Adamantina Formation, Upper Cretaceous, Brazil. Radial thin section under polarized light, outer surface up. A, holotype FEF-PV-8/1-a, 20×, with a putative shell membrane (arrow). B, specimen FEF-PV-8/3, 20×, with radiating crystalline wedges (arrow). C, specimen FEF-PV-8/3, 20×, white dashed lines highlight the shell units.

in the eggshell surface (Text-fig. 2E). These crater-like structures are interpreted as artefacts, because they can be distinguished from true morphological features by their irregular distribution and shape. In some specimens, a thin layer of iron oxide is present at the interface between the eggshell and the sediment. The outer surface is slightly undulating with irregularly distributed pores (Text-fig. 2C–D). The outer surface and the pores show no clear signs of the typical extrinsic degradation that

extensively affects the eggshells of crocodylians (see Comparison and Discussion section). However, rare irregularly depressed areas next to a few pores may be considered as feeble signs of extrinsic degradation (Text-fig. 2C), but these are only incipient and may be merely the result of a taphonomic process. In fact, these depressed areas only differ from the crater-like depressions (produced by grains of quartz) by being more irregular.

True pores are present both on the outer and on the inner eggshell surface, irregularly spaced, and relatively large (30–80 μm, along main axis). In all instances, pores are sharply defined, allowing their distinction from other depressions present on the eggshell. The external opening ranges from slightly elliptical to teardrop-shaped, with a broad rounded and a sharp end. Typical pore spacing is <100 μm, and average pore count is 3/mm^2.

The inner surface of the eggshell is undulating and, like the outer surface, has the shallow crater-like structures produced by contact with quartz grains (Text-fig. 2E). Several pore openings can be observed, showing no signs of dissolution. The basal plate groups could not be distinguished, but sharp radiating ridges can be clearly seen in some samples (Text-fig. 3B–C), indicative of their presence *in vivo*.

Thin section analysis reveals that the structure of the shell units is mainly intact, generally allowing observation of their internal structure. Distortion of the eggshell-sediment interface is ruled out because the same morphology is observed in stacked eggshells. In all cases, thin sections show the same morphological pattern (e.g. shell thickness and shell unit shape), under both ordinary and polarized light. An undulating extinction pattern of irregular and divergent massive edges can be seen under polarized light, consistent with the typical crocodiloid extinction pattern (Text-fig. 3A–C). Under PLM and SEM, the radiating pattern of the crystalline wedges can be clearly identified (Text-figs 2B, 3A–C). They radiate from the portion of the shell that presumably once included the basal plate groups and interlock for almost half their height (Text-fig. 3B–C). Horizontal accretion lines are not observed either in the thin sections or in the SEM images. In one of the thin sections from egg clutch FEF-PV-8/1 (the clutch containing the holotype), an indistinct thin layer between two stacked eggshells is tentatively attributed to the shell membrane (Text-fig. 3A). In contrast to some eggshells of *Krokolithes helleri* (Kohring and Hirsch 1996), fibre-like tracks are not observed. Although pores are present in both the inner and the outer shell surfaces, pore canals were not observed in either PLM or SEM.

COMPARISON AND DISCUSSION

The shape, shell thickness, ultrastructure (e.g. shell units, irregularly divergent extinction pattern, and pore shape)

and size clearly indicate that the new eggs are crocodiloid rather than dinosauroid, testudoid or geckoid. *Bauruoolithus fragilis* exhibits the same general shape and outer surface ornamentation as most other crocodiloid eggs, such as *K. wilsoni* and *K. helleri*, or the eggs from the Bridger, Glen Rose and Aracatuba formations. However, *B. fragilis* is considerably more slender when compared to other crocodylian eggs, especially those of extant forms. This distinction is particularly important for the Araçatuba eggs, as these come from the same general area (northern São Paulo State, Brazil) and are roughly the same age (Campanian–Maastrichtian, Upper Cretaceous). This new oospecies has a length-to-diameter ratio of 1:0.55, whereas most other fossil eggs (e.g. *K. wilsoni*, *K. helleri*, and the eggs from the Bridger and the Araçatuba formations) are somewhat broader, ranging from 1:0.60 to 1:0.68. The most rounded fossil crocodiloid eggs are the unnamed specimens from the Bridger Formation (USNM 12597; Hirsch and Kohring 1992), with ratios within the typical range for *Crocodylus*. Among the fossil forms, only the unnamed eggs from the Glen Rose Formation (Rogers 2000), the egg from Pai Mogo site (Portugal) and the eggs attributed to *Y. boliviensis* (Novas *et al.* 2009) have similar ratios, 1:0.58, 1:0.57 and 1:0.53, respectively. However, *B. fragilis* is larger than the Glen Rose and *Y. boliviensis* eggs, and its eggshell is therefore proportionally thinner. The Araçatuba eggs also appear to be smaller than *Bauruoolithus*, but there is some uncertainty because Magalhães-Ribeiro *et al.* (2006) provided two different measurements for the same egg. Nonetheless, the eggs from the Araçatuba Formation are certainly not as slender as *Bauruoolithus*, because both measurements provided indicate a ratio of at least 1:0.60 (Table 1). Comparison to *Krokolithes* eggs on the basis of size is precluded because available specimens of this oogenus are always incomplete and deformed. At least one specimen of *K. helleri* (HEC 443-1; Kohring and Hirsch 1996) has an estimated ratio of 1:0.54, and *K. wilsoni* (UCM 47523A; Hirsch 1985) has an estimated ratio of 1:0.60. Both the shell thickness and the shell unit morphology, however, allow reliable differentiation between *Krokolithes* and *Bauruoolithus*. *Bauruoolithus fragilis* has a quite distinct length-to-diameter ratio when compared with eggs of extant *Crocodylus* (e.g. *C. acutus*, *C. niloticus*, *C. porosus*, and *C. johnstoni*), which varies from 1:0.60 to 1:0.69 (Hirsch 1983; Hirsch and Kohring 1992). The measurements provided by Hirsch and Kohring (1992) for *A. mississipiensis*, however, yielded a length-to-diameter ratio of 1:0.55, which contrasts with the 1:0.60 ratio provided earlier by Hirsch (1983) for the same species, and for all other crocodylians. The problem of size/shape identification of fossil crocodylian eggs highlights the limitation of morphometric data in fossil egg parataxonomy and identification. Size and shape can be profoundly

affected by preservation and, although the use of estimated measurements may be a sensible approach, it is far from accurate. Even in the main literature references (e.g. Hirsch 1985; Mikhailov 1991, 1997; Hirsch and Kohring 1992; Kohring and Hirsch 1996; Mikhailov *et al.* 1996), there is no range, mean or error data for measurements, nor appropriate statistical tests. Overall, it is still poorly understood how shape and size of eggs varies within groups, and even within species.

Despite the problems of macroscopic identification of eggs and eggshells, shell thickness can be used as a more reliable approach. *Baruoolithus fragilis* has a thinner eggshell than most previously known crocodiloid eggs (Table 1). While eggshell thickness in the new oospecies ranges from 0.15 to 0.25 mm, most other fossil forms have shells varying from 0.29 (*K. helleri*) to 0.70 mm (Bridger Formation eggs). *Baruoolithus* is, therefore, less than half as thick as the Glen Rose Formation (Rogers 2000) and Bridger Formation eggs (Hirsch and Kohring 1992). Only the Araçatuba eggs, *K. wilsoni*, and the eggs attributed to *Y. boliviensis* may show a partial overlap of values, but in these cases the overlap is marginal (i.e. smallest values) and in *Baruoolithus fragilis* the same numbers are indicated by the highest values. When compared to the eggs of eusuchian crocodylians, the eggshell of *Baruoolithus* is undoubtedly thinner. Extant eggshells vary between 0.40 and 0.53 mm, (Hirsch 1983; Ferguson 1985) a much tighter range of values than found in fossil forms.

The structural arrangement among shell units is one of the most distinctive features of *B. fragilis*. The shell units are broader than in other reported fossil crocodiloid oospecies (Text-fig. 3A–C). As a result of this pattern, the interstices among the crystalline wedges are proportionally smaller, forming an obtuse triangle (instead of the acute triangle pattern seen, for instance, in *K. wilsoni* and *K. helleri*). Therefore, thin sections of *Baruoolithus* eggshell are easily distinguished from all other crocodylian eggs, under PLM (Text-fig. 3).

Basal plate groups were not found in any sample, although such structures are regarded as a basic feature of the crocodiloid type of eggshell (Mikhailov 1991, 1997). The crystalline wedges radiating from basal plate groups, observed through thin section analysis (Text-fig. 3A–C), support the presence of basal plate groups *in vivo*. Therefore, the absence of these structures in our sample is regarded as the result of taphonomic processes, particularly the deformation of the inner surface by quartz grains. Further collection and preparation of specimens may provide clearer evidence for basal plate groups in *Baruoolithus*.

Unfortunately, there is no information about pore morphology, size and distribution for most previously reported fossil eggs, precluding the use of these features as additional criteria for comparison. This is mainly because of the presence of secondary deposits (e.g. Hirsch and Kohring 1992; Magalhães-Ribeiro *et al.* 2006). However, pore data allow further differentiation of the oogenus *Baruoolithus* from *Krokolithes*. The pore openings in *Baruoolithus* are much smaller (30–80 μm) and show less size variation than those of *K. wilsoni* (50–200 μm). *Baruoolithus* also differs from *K. wilsoni* in pore morphology, showing more elongated, ellipsoid to subtriangular perforations, than the circular pores present on the latter. Moreover, the new oogenus does not have the circular to ovate craters that bear the pore openings in *K. helleri*. Although the pore count is not available for fossil eggs in the literature, in *B. fragilis* the average value for the equatorial area is 3 pores/mm^2.

Mikhailov *et al.* (1996) established criteria for proper erection of oofamilies, oogenera, and oospecies on the basis of egg shape and eggshell structure. According to these authors, oofamilies are based on structural morphotypes, outer surface ornamentation and pore system. Considering these criteria, *B. fragilis* can be assigned to the Oofamily Krokolithidae because it shares the same structural morphotype, outer surface ornamentation and pore system. Mikhailov *et al.* (1996) also stated that oogenera should be based on egg shape and differences within structural morphotypes, outer surface ornamentation and pore systems. The rationale for the establishment of oospecies indicated that eggshell thickness variation, egg size and external pore pattern should be taken into account. Following these criteria and considering the diagnosis for the oogenus *Krokolithes* and the known oospecies (*K. wilsoni* and *K. helleri*), *B. fragilis* does not fit within the same oospecies or oogenus because its shell units have a unique morphology (with a wider base) and the crystalline wedges are tightly packed (Text-figs 3, 4), which is unique among crocodiloid ootaxa. Furthermore, *Baruoolithus* also shows a different length-to-diameter ratio, a thinner eggshell and a more oblong shape than the eggs of most other crocodiloid ootaxa, as well as a distinct pore morphology. All these differences support a new oogenus and oospecies for the Adamantina Formation eggs described here.

Variability and preservation

Morphological variation among egg clutches (e.g. egg number and size, Ferguson 1985), within a clutch, or even in different regions of the same egg was reported by Hirsch and Kohring (1992), Mikhailov *et al.* (1996), and Mikhailov (1997). This phenomenon was seen as a problem that could preclude a proper evaluation of crocodiloid fossil eggs. This is also a concern for other groups, such as dinosaurs (Mikhailov *et al.* 1996, p. 764).
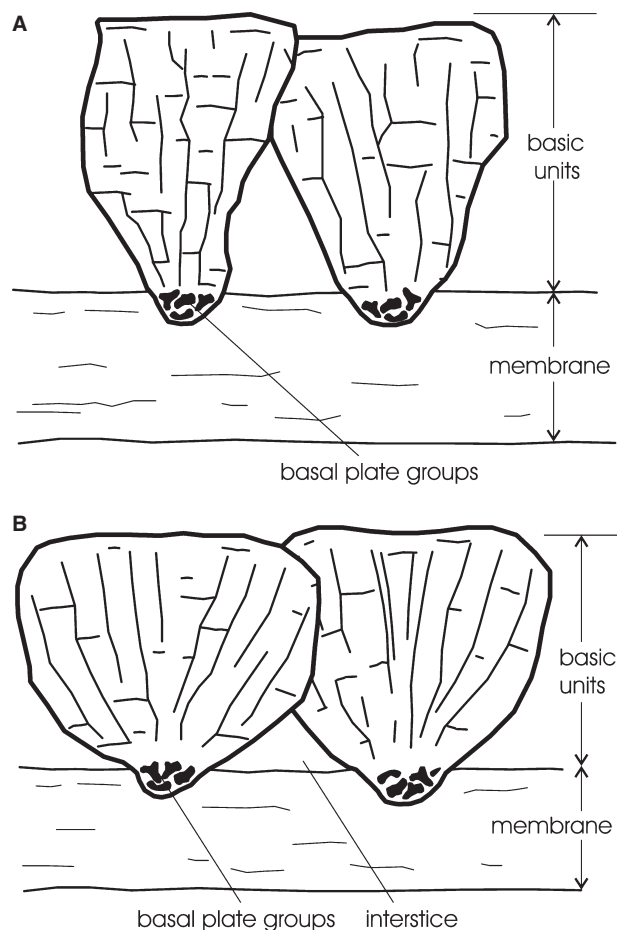
TEXT-FIG. 4. Diagrammatic representation of the basal units of crocodiloid eggs. Note that the overall structure is basically the same, but general morphology is different. A, *Krokolithes helleri*. Note that the shell units display a narrow profile at the base and large interstitial spaces (based on Kohring and Hirsch, 1996). B, *Bauruoolithus fragilis*. Note that the shell units display a wide profile at the base and small interstitial space. Basal plate groups inferred for *Bauruoolithus*. Diagrams not to scale.

Morphological variation was verified for *Bauruoolithus*, with samples analysed from different clutches and from both polar and equatorial regions of the eggs. Taphonomic alteration was also identified as a slight degree of recrystallization over the outer eggshell surface. Recrystallization can alter the configuration of the calcium carbonate microcrystals within the shell units, which could explain the absence of horizontal accretion lines. Nevertheless, recrystallization neither obliterated the general shape of the crystalline wedges nor rearranged the internal position of the acicular crystals, as can be seen by the crocodiloid extinction pattern in thin sections (Text-fig. 3A–C). Although there is some variation in egg size and eggshell thickness, this range is within the ranges reported for previously described eggs (Hirsch 1985;

Hirsch and Kohring 1992; Kohring and Hirsch 1996; Rogers 2000; Magalhães-Ribeiro *et al.* 2006). Moreover, the length-to-diameter ratio is the same for the two most complete and best preserved eggs of *B. fragilis*.

Extensive degradation plays an important role in weakening the eggshell before hatchlings of extant crocodylians emerge from their eggs (Ferguson 1981, 1985). However, this is not the case for *B. fragilis*, as in all samples (eggshells or nearly complete eggs), the shell thickness is the same and signs of extensive extrinsic degradation are virtually absent. In living forms, extrinsic degradation does not occur only in nonhatched immature eggs. Therefore, two hypotheses could explain the absence of extrinsic degradation in *B. fragilis*: (1) all samples of *B. fragilis* collected to date were buried after hatching; or (2) all samples are unhatched eggs that were buried soon after been laid.

To evaluate these scenarios, the distribution, shape and fracture pattern of the eggs and eggshells have been considered. The first scenario assumes damage to the eggshells is the result of the natural process of hatching, where the lack of extrinsic degradation is an unexpected biological signal. The second scenario considers that lack of extrinsic degradation only indicates precocious burial, but damage to the eggs and eggshells demands an alternative explanation.

Transport-related damage would affect both the eggs and the eggshells, where breakage of the eggs would occur during transport. Remains should be scattered, but sorted by size and distributed on a horizontal plane, which is not observed in our sample. This *Bauruoolithus* assemblage encompasses partial eggshells, damaged and reduced to different sizes and shapes, and randomly dispersed around and within the eggs, but set in well-delimited egg clutches. The disposition of elements (including eggshells in vertical position) rules out the possibility of transport and also transport-related damage to eggs and eggshells.

Postburial damage of the eggshells by compression of the sediment, particularly in the vertical axis, would result in 'pancaked' specimens, where most elements would be near their original position, but flattened. Instead, the sample is characterized by many small fragments distributed around and inside eggs, and some larger eggshells inside the egg (following the pattern described by Hayward *et al.* 2000). A few eggs preserve more than 50 per cent of their external perimeter, but these are not crushed or flattened. They instead show a three-dimensional arrangement of eggshells inside the egg, and asymmetrical damage towards one end (consistent with the pattern of hatching in living crocodylians). Indeed, significant signs of deformation are rare in crocodylomorph eggs of the Adamantina Formation.

It is possible also to exclude the effects of predation. The action of extant predators (lizards, snakes, small

mammals, crocodylians) mainly leads to damage at the equatorial region (as the egg is crushed between the jaws, or by other mechanisms), resulting in extensive symmetrical damage to the eggshell. Remains are left exposed and out of place, or ingested. In these cases, the process frequently involves ingestion of whole eggs, leaving few displaced remains behind, particularly when oophagy is observed in crocodylians and snakes (Kushlan and Simon 1981; Hunt 1987; Pough *et al.* 2004).

The distribution of the eggshells and the absence of signs of uniform crushing on the radial plane of the eggs are not compatible with compaction of the sediments, even during diagenesis. On the other hand, the distribution, shape and fracture pattern of the eggs and eggshells (e.g. the presence of several eggshells within and outside the eggs; their concave up/concave down ratio; Hayward *et al.* 2000) and the close association of eggs and eggshell fragments of different sizes and shapes are consistent with the interpretation that these are hatched eggs ('Scenario 1'). Hatchlings of extant crocodiles exit their eggs from one end, with the opposite one sustaining less damage or no damage at all (polar asymmetry; see Bellairs 1970, pls 63–64; Ferguson 1985, fig. 4, p. 361). The few mostly preserved specimens of the *B. fragilis* agree with this pattern, where the eggshell seems to be broken outwards at one end, whereas the other one is better preserved (Text-fig. 2G). Although it is not possible to state that all eggs hatched, the evidence suggests this may be the case. On the other hand, it is possible to exclude damage related to diagenesis, transport and predation, and the preservation of remains is not compatible with the idea of precocious burial. We therefore consider the first scenario (i.e. eggs were buried after hatching) as more likely.

Hatched eggs would also not be expected if the morphology of *Bauruoolithus* was the result of an anomalous or pathogenic condition. Therefore, there must have been another mechanism to enable the hatching process, without extensive degradation of the shell, and this is likely to have been the presence of an especially thin eggshell. In fact, if such thin eggshells had shown extensive extrinsic degradation, the eggshell might have ruptured prematurely and the embryos would have died.

The preservation of exceptionally thin eggshells in such great numbers is another unexpected aspect of this assemblage. The relatively thin eggshell of crocodiloid eggs in general already limits their preservation as fossils (Hirsch and Kohring 1992; Mikhailov *et al.* 1996) in comparison with dinosaurian eggshells, which are generally much thicker. The large number of oological remains of *Bauruoolithus* suggests that the quality of preservation at this outcrop of the Adamantina Formation is higher than average and offers prospects for more remarkable finds.

Associated remains

Embryonic remains were not found inside the eggs, providing no secure evidence on the identity of the egg-laying taxon. However, several remains of baurusuchids were found in close association with *Bauruoolithus*. The remains are either fragmentary (e.g. osteoderms, dermal fragments), or fairly complete and articulated (including skull, ribs, vertebrae, and limbs), but show no significant signs of dorsoventral deformation or transport-related damage. The most complete skeletons belong to adult individuals (estimated to be 3–4 m in total length) and were found in the same layer and only 2 m away from some egg clutches. The preservation and distribution of crocodylian remains support the interpretation that the material found in this assemblage has not endured transport or diagenetic deformation. There is currently no indication of other vertebrate taxa in the same outcrop. Nonetheless, the association of crocodiloid eggs, eggshells and egg clutches with notosuchian remains is not surprising, because these crocodylians are the dominant vertebrates in the Upper Cretaceous Bauru Group (Bertini *et al.* 1993). Within the Adamantina Formation, *Baurusuchus* is by far the most common taxon, although other mesoeucrocodylian taxa are known from the same formation in São Paulo State (e.g. *Stratiotosuchus*, *Sphagesaurus*, *Itasuchus*; all rarer findings). This and the proximity to the eggs seem to indicate that *Baurusuchus* is the egg-laying taxon. Even so, it is still quite rare to obtain unequivocal empirical fossil evidence linking fossil eggs or nests to a specific taxon. Examples such as the Mongolian oviraptoroid dinosaur (Osborn 1924; Mikhailov 1991; Clark *et al.* 1999) or the titanosaur embryos of Auca Mahuevo (Chiappe *et al.* 2005; Salgado *et al.* 2005) constitute exceptional cases (for further discussion, see Benton 2010). Until unequivocal evidence becomes available (particularly *in ovo* remains), *Baurusuchus* must only be considered as the most probable candidate for the egg-laying taxon, because of the abundance of remains of this taxon in the outcrop, their close association with the egg clutches and the apparent absence of other crocodylomorph taxa. This association then is assigned a level of confidence of '3' (i.e. without embryonic remains/direct contact; putative association), of Grellet-Tinner (2005, 2006) and is not sufficient to allow a safe taxonomic assignment. Considering the evidence collected, it is not possible to rule out that the *Bauruoolithus–Baurusuchus* association is the result of agonistic interaction between two different taxa, where *Baurusuchus* was present near the egg clutches because it was feeding on them.

Another important element in crocodylian palaeoecology is nesting behaviour. Preliminary evidence exists for burrowing habits in notosuchians, which in at least one case includes the association of a fossil body taxon

(*Yacarerani*) and eggs (see Novas *et al.* 2009; and references therein). However, the relation between nesting behaviour and environment is poorly explored. Extant crocodylians often set their nests near water channels, small islands or sand bars, as in the case of *Crocodylus niloticus* (distance < 200 m), *C. intermedius* and *Alligator mississipiensis* (<10 m), a strategy frequently related to their semi-aquatic habits and parental care (Bellairs 1970; Kushlan and Simon 1981; Hunt 1987; Thorbjarnarson and Hernandez 1993; Pough *et al.* 2004). This facilitates parental care, including protection of the nest, help with the hatching process and transport of younglings from the nest to the water (Hunt 1987; Pough *et al.* 2004). These habits contrast with the strong links of notosuchians (such as *Baurusuchus*, *Notosuchus*, *Sphagesaurus*, *Iberosuchus*) with the terrestrial environment and pose a question of whether these crocodylians also laid their eggs close to water, or if they would choose nesting sites in dryer and higher ground. Unfortunately, we cannot comment further on these environmental questions in the absence of a thorough sedimentological study of the Adamantina Formation.

CONCLUSION

Fossil crocodiloid eggs are rare, and most of them are Paleogene in age. *Bauruoolithus fragilis* is the first oospecies described from South American deposits, and it is also the first crocodiloid ootaxon with several egg clutches recovered. The close association of egg clutches and body fossils suggests that the mesoeucrocodylian *Baurusuchus* may have been the egg-laying taxon, but this association (low level of confidence) should remain tentative until it can be corroborated by embryonic *in ovo* remains (following Benton 2010).

Bauruoolithus fragilis can be distinguished from previously described fossil crocodiloid eggs by being more elongate (length-to-diameter ratio of 1:0.55) and by having a thinner eggshell, with different crystalline wedge morphology and shape of the external pore openings. The striking difference in eggshell thickness displayed by *Bauruoolithus* contrasts with that found in extinct and extant crocodylomorph eggs known to date. Shell thickness and the lack of signs of extrinsic degradation in *Bauruoolithus* might indicate that the reproductive biology of at least one group of notosuchians was different from that seen in extant crocodiles and the vast majority of neosuchians, suggesting that embryos did not need the extrinsic degradation of the eggshell to facilitate the hatching process. In fact, the occurrence of extrinsic degradation would probably imply premature rupture of the eggs. This indicates that reproductive patterns of egg incubation of fossil Mesoeucrocodylia may have been more diverse than previously thought. Even more important, it certainly shows that such studies are both meaningful and necessary if we truly aim to understand the evolution and palaeobiology of fossil crocodylomorphs.

Finally, previous studies introduced the fundamentals for research on fossil eggs, but there is a continuing problem of sampling and lack of proper collection of measurements. This study introduces a few of these elements, but only broader studies on eggshell morphology, particularly in living taxa, can properly explore the key aspects of their functional morphology and environmental control (e.g. deprivation of nutrient, temperature variation during incubation and microclimate conditions).

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