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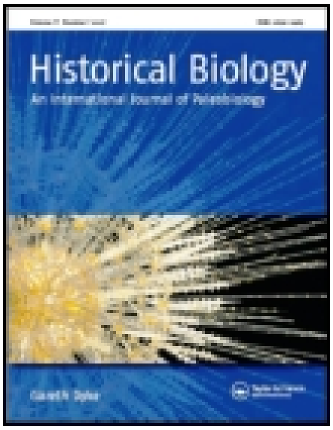

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Identification and comparison of modern and fossil crocodilian eggs and eggshell structures

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Identification and comparison of modern and fossil crocodilian eggs and eggshell structures

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Eggshells from the three extant crocodilian species *Crocodylus mindorensis* (Philippine Crocodile), *Paleosuchus palpebrosus* (Cuvier's Smooth-fronted Caiman or Musky Caiman) and *Alligator mississippiensis* (American Alligator or Common Alligator) were prepared for thin section and scanning electron microscope analyses and are described in order to improve the knowledge on crocodilian eggs anatomy and microstructure, and to find new apomorphies that can be used for identification. Both extant and fossil crocodilian eggs present an ornamentation that vary as anastomo-, ramo- or the here newly described rugosocavate type. The angusticaniculate pore system is a shared character for Crocodylomorpha eggshells and some dinosaurian and avian groups. Previously reported signs of incubated crocodilian eggs were found also on our only fertilised and hatched egg. *Paleosuchus palpebrosus* presents unique organization and morphology of the three eggshell layers, with a relatively thin middle layer characterised by dense and compact tabular microstructure.

Keywords: Extant and fossil crocodyliform eggshells; *Crocodylus mindorensis*; *Paleosuchus palpebrosus*; *Alligator mississippiensis*; eggshell structures; rugosocavate pore canals type

Introduction

Numerous references have been focused on crocodile reproduction; however, very little is known about extant crocodilian eggs and eggshells morphological structure: Ferguson (1982), Grine and Kitching (1987) and Deeming and Ferguson (1990) report of *Alligator mississippiensis* (Daudin, 1802); Zhao and Huang (1986) and Wink and Elsey (1994) report of *Alligator sinensis* Fauvel, 1879; Schlëich and Kästle (1988) and Fernández et al. (2013) report of *Caiman latirostris* (Daudin, 1802); Grine and Kitching (1987) report both of *Crocodylus niloticus* Laurenti, 1768 and *Crocodylus porosus* Schneider, 1801. An example of a rare comparison between eggs of the two extant crocodiles *Caiman latirostris* and *Caiman yacare* (Daudin 1802) has been previously made by Paz et al. (1995).

Our samples belong to three extant crocodilian species, from the infraclass Archosauromorpha and the suborder Crocodyliformes: *Crocodylus mindorensis* Schmidt, 1935, *Paleosuchus palpebrosus* (Cuvier, 1807) and *Alligator mississippiensis*. The Philippine crocodile (*Crocodylus mindorensis*) is a relatively small freshwater crocodile endemic to the Philippines. Both male and female individuals reach their sexual maturity when about 1.5 m long and 15 kg in weight, with the longest individual ever reported of 3.02 m in length; females are slightly smaller than males (Hall 1989; van Weerd 2010). van Weerd (2010) reports that the average number of laid eggs by a female in two different localities in the wild is 20.1 and 26.0, while for two different localities in captivity is, respectively, 15.7 and 25.6, with an incubation time of 65–78 days in the wild and 77–85 days in captivity. Cuvier's smooth-fronted caiman or musky caiman (*Paleosuchus palpebrosus*) is an endemic to South America crocodile, the smallest of all living crocodilians; males can reach a length of 1.5 m while females are slightly smaller, reaching 1.2 m; an adult typically weighs around 6–7 kg (Magnusson 1992). Around 10–19 eggs are laid, usually white, oblong, weighing between 61 and 70 g and that hatch after about 90 days (Medem 1971; Magnusson and Campos 2010). The American alligator or common alligator (*Alligator mississippiensis*) is the largest of the two extant species in the genus *Alligator* and it is endemic to the southeastern USA. Grown-up males can reach about 5 m in length, females 3 m, with the largest individuals up to 450 kg in weight. Nesting and egg-laying are initiated during the early part of the warm, wet summers (Ross and Ernst 1994; Elsey and Woodward 2010). Females construct a mound nest of vegetation and lay 30–50 eggs. Incubation takes 63–84 days, depending on temperature (Lang and Andrews 1994).

This study aims (1) to describe the morphology, the micro- and the ultrastructure of the eggshells from three extant crocodilian species; (2) to improve the general view over crocodilian eggshells, by comparing our samples with the known extant and fossil crocodilian eggshells and (3) to point out new apomorphies for crocodilian eggs that may

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help eggshell identification and further cladistic analyses. One other output is an overview of egg characteristics within the framework of the general consensus phylogeny of Amniotes.

State of art about egg characters and eggshell ultrastructure

In extant crocodile eggs, the shell units start to outgrow from the uppermost fibres of the shell membrane (Mikhailov 1997). The entire eggshell is characterised by a tabular ultrastructure forming regular striations (Mikhailov 1997); the presence of this characteristic laminated tabular structure in the middle layer (ML) is given by most authors as the diagnostic condition for crocodylomorph eggshell, both extant and fossil (Hirsch 1985; Schlëich and Kästle 1988; Mikhailov 1997; Jackson and Varricchio 2010). No organic core is present at the base of the inner layer (IL); instead, an aggregation of calcite plates that serve as the nucleation centre is evident (Mikhailov 1997; Carpenter 1999; Rogers 2001), as well as basal plate groups and basal knobs characterising all the inner surface (IS) described in Hirsch (1985). On the contrary, Moreno-Azanza et al. (2013, p. 4) state about nucleation centres that ‘No crystallographic features can be identified either in scanning electron microscope (SEM) or in petrographic photographs, suggesting that the nucleation centres are poorly crystallised aggregates of calcite micro grains and organic matter’, suggesting the possibility of organic matter in the nucleation centres of crocodylomorph eggs. Moreover, the IL presents a series of ‘wedges’ (*sensu* Mikhailov, 1997, p. 15, fig. 5), large radiating subunits characteristic for the entire shell unit, distinguishable in observation with crossed nicols, under polarised light (Moreno-Azanza et al. 2013).

Generally, both extant and fossil crocodilian eggs are associated with a crocodiloid morphotype. The microstructure of this morphotype is characterised by discrete, large and rough shell units having a truncated cone shape, wider at the top (outer surface, OS) than the bottom (IS), with a bulbous base, exhibiting a rosette-like structure in the inner eggshell surface. The ultrastructure is made up of tabular calcite plates. The shell units are built up by large and rough wedges with irregular boundaries; no fan-line pattern can be seen on radial sections (Mikhailov 1997; Carpenter 1999).

The state of the art on crocodilian eggs is given in Moreno-Azanza et al. (2013):

> The micro- and ultrastructure of extant and fossil crocodilian eggshells remains controversial. Ferguson (1982) describes five distinct layers in the *Alligator mississippiensis* eggshell, four of which – the mammillary layer, the organic layer, the honeycomb layer and the outer, densely calcified layer – correspond to the calcified portion of the eggshell, or true eggshell. [. . .] Following Hirsch (1985), Mikhailov (1991, 1997) establishes the crocodyloid basic type and the corresponding crocodyloid morphotype as single-layered eggshell with ‘rough’ shell units. This approach is followed by Kohring and Hirsch (1996) in erecting the Krokolithidae oofamily. [. . .] More recently Jin et al. (2010) confirmed Ferguson’s observation that crocodilian eggshell is composed of several structural layers. [. . .] The presence of three structural layers is patent in *Krokolithes wilsoni* and in the eggshells of extant *Crocodylus porosus* and *Crocodylus niloticus*.

The ultrastructures of few extant crocodilians have been so far described: *Alligator mississippiensis* and *Crocodylus niloticus* are described in Grine and Kitching (1987) as similar to one another. The eggs of these two species are described as made by an innermost layer consisting of mammillary processes densely packed. The mammillary crystals radiate outwards from a basal centre and become gradually extinguished by tabular crystal lamellae. A second upper layer (‘palisade layer’) is then described, made of tabular aggregates with the lamellae disposed parallel to the OS of the egg. *Alligator sinensis* is described in Zhao and Huang (1986) as made by three differentiate layers: a mammillae layer, where the tips of each mammilla is a spherulitic aggregate of aragonite crystals radiating from the mammilla core, a cone layer and a columnar layer, characterised by small erosion pits on incubated eggs; however, aragonite is currently known only from turtles eggshells (see Hirsch 1996; Kohring 2000), and Zhao and Huang (1986) do not present any chemical analyses for the identification of aragonite in *Alligator sinensis* eggshell and no acicular aragonite crystal seems evident in their plates: because of this, the possible presence of aragonite in crocodilian eggs remains a dubious hypothesis, unless supported by future specific analyses. *Caiman latirostris* is described in Fernández et al. (2013) as made up of one single calcareous ultrastructural layer characterised by ‘units formed from the irregular radial growth of tabular wedge-like crystals with a basal plate group (rosette); the organic core is absent’.

Incubation has an influence on the eggshell morphology and preservation (Oliveira et al. 2011). An extrinsic degradation, characterised by many erosion pits (‘craters’ in previous literature) and stepped concentric erosion rings around the pore openings, has been reported for incubated eggs of *Alligator mississippiensis* (Ferguson 1981a, 1982; Hirsch 1985; Deeming and Ferguson 1989, Wink et al. 1990a), *Alligator sinensis* (Zhao and Huang 1986; Wink and Elsey 1994) and *Crocodylus niloticus* (Grine and Kitching 1987). Also, it has been previously documented on *Alligator mississippiensis* that the initial porosity of unfertilised eggshell is related to the density of mammillae on the IS of the shell and that incubation destroys the original relationship between pores and mammillae (Wink et al. 1990b), as well as that in *Alligator mississippiensis* the eggshell degrades progressively, losing thickness, because of

Table 1. Main parameters of our three eggshell samples.

	Crocodylus mindorensis	*Alligator mississipiensis*	*Paleosucus palpebrosus*
PA (mm)	69.3	71.5	–
EA (mm)	37.3	44.8	–
EI (PA/EA)	1.86	1.6	–
Volume (cm^3)	50.48	75.14	–
Average no. of pores/cm^2	21	5	22
Average pore diameter (μm)	100.65	129.75	115.9
Mean pore area (mm^2)	0.009	0.015	0.01
% Pore area	0.19	0.08	0.22
Average shell thickness (mm)	0.43	0.53	0.41
OL to total eggshell thickness (%)	18	35	57
ML to total eggshell thickness (%)	55	45	11
IL to total eggshell thickness (%)	27	20	32
Single cell *w*/*h* ratio	0.58	0.42	0.65

the acidic metabolites of the microorganisms involved in the nest fermentation (Ferguson 1981b).

Materials and methods

A total of three eggs by three different species of extant crocodiles have been analysed, so one eggshell per species. The eggs were provided by Rene Hedegaard (Krokodille Zoo, Denmark) and Jesper Mìlan (Geomuseum Faxe, Denmark). The eggshell thin section slides are stored at Faculdade de Ciências e Tecnologia da Universidade Nova de Lisboa (FCT–UNL) with the repository numbers FCT–UNL 707, 708 and 709, respectively. *Crocodylus mindorensis* and *Alligator mississippiensis* eggs were unfertilised, thus complete, while *Paleosuchus palpebrosus* egg was fertilised and hatched. All the main parameters for the eggshells are reported in Table 1.

From each eggshell, selected samples were prepared for 30 μm thin sections using epoxy resin EpoThin 5 (resin) and 1.95 (hardener). Fragments imaged using a JEOL JSM T330A SEM at the FCT–UNL were previously treated with 10% formic acid for 30 s to dissolve the eggshell membrane, as well as those for observation and imaging under petrographic microscope. Polar axis (PA) and equatorial axis (EA) measures were taken with a caliper from the entire eggshell when possible; pores were counted from direct observation of the samples with a petrographic microscope and opening diameters were measured from the external surface using macro photographs; eggshell and structural layers thicknesses were measured from the thin sections. During the eggshell description, we standardised the orientation of the samples with the external surface (OS) to the top and the internal (inner) surface (IS) to the bottom.

The following acronyms have been used: EA, equatorial axis of the egg (shortest); EI, elongation index (ratio PA/EA); IL, inner layer; IS, inner surface; ML, middle layer; *n*, number of measurements; OL, outer layer; OS, outer surface; PA, polar axis of the egg (longest); SD, standard deviation; *V*, egg volume.

Institutional abbreviation. FCT–UNL, Faculdade de Ciências e Tecnologia da Universidade Nova de Lisboa (Portugal).

Density values in Table 2 were measured using different sets of data for masses and volumes. Due to this, they are merely indicative.

Table 2. Egg mass, volume and density of modern crocodilian eggs.

	Mass (g)	Volume (cm^3)	Density (g/cm)
Family Alligatoridae			
A. mississippiensis	76.6	69.3	1.11
A. sinensis	48.2	41.1	1.17
Paleosuchus palpebrosus	68.6	56.7	1.21
Paleosuchus trigonatus	67.2	–	–
Caiman crocodylus	62.9	54.4	1.16
Caiman yacare	–	62.8	–
Caiman latirostris	76.2	64.1	1.19
Melanosuchus niger	143.6	–	–
Family Crocodylidae			
Crocodylus acutus	112.8	95.1	1.19
Crocodylus cataphractus	146.0	–	–
Crocodylus intermedius	110.4	–	–
Crocodylus johnstoni	69.7	59.5	1.17
Crocodylus mindorensis	73.6	–	–
Crocodylus moreletii	79.5	–	–
Crocodylus niloticus	107.1	94.0	1.14
Crocodylus novaeguinae	88.5	73.5	1.20
Crocodylus palustris	99.5	83.1	1.20
Crocodylus porosus	109.2	109.1	1
Crocodylus rhombifer	104.3	–	–
Crocodylus siamensis	106.9	103.5	1.03
Osteolaemus tetraspis	55.0	45.1	1.22
T. schlegelii	139.9	148.81	0.94
Family Gavialidae			
G. gangeticus	161.4	134.6	1.20

Notes: Mass values are taken by Thorbjarnarson (1996, p. 11). Volumes were obtained using PA and EA values in Table 3; when more than one couple of values per species was given, we calculated the mean value. For *T. schlegelii*, we decided to use the value given by Mathew et al. (2011), which is considered more accurate. All the data are merely indicative because mass and volume values were taken from different sets of eggshells.

Main characters and structures in crocodilian eggs

Egg shape, dimensions and eggshell thickness

Modern and fossil crocodilian eggs are generally ellipsoid and our two complete samples (*Crocodylus mindorensis* and *Alligator mississippiensis*) confer with this shape. The eggs are ellipsoid, with both poles equal in curvature and symmetrical to the equatorial plane. All the relative dimensions of our samples are presented in Table 1.

In a generic view, modern crocodilian eggs have a PA between 58 and 102 mm in length, an EA between 34 and 63.5 mm, with an EI between 1.43 and 2. The eggshell thickness varies from 0.30 to 0.85 mm. The mass value ranges between 48.2 g in *Alligator sinensis* and 161.4 g in *Gavialis gangeticus* (Gmelin, 1789) (see data in Thorbjarnarson 1996); volumes are variable in a range between 41.1 cm^3 in *Alligator sinensis* and 189.2 cm^3 in *Tomistoma schlegelii* (Müller, 1838). Finally, modern crocodilian eggs have a very stable density, between 0.94 g/cm^3 in *T. schlegelii* and 1.22 g/cm^3 in *Osteolaemus tetraspis* Cope, 1861 (Table 2). Fossil crocodilian eggs seem to have smaller dimensions than modern ones, with a PA between 30 and 70 mm and an EA between 16 and 54 mm; however, the EI does not differ so much, being included between 1.19 and 2.11, as well as the thickness, which goes between 0.15 and 0.76 mm (Table 3).

On Alligatoridea eggs, the dimensions range goes from 62 mm × 39 mm in *Paleosuchus palpebrosus* (Medem, 1971) to 76 mm × 42 mm in *Alligator mississippiensis* (Hirsch and Kohring 1992) – 71.5 mm × 44.8 mm in our sample – with an EI between 1.43 in *Caiman latirostris* and 1.79 in *Paleosuchus palpebrosus* (Medem 1971; Panadès I Blas and Patnaik 2009). The eggshell thickness ranges from 0.41 mm in *Paleosuchus palpebrosus* (our sample) to 0.85 mm in *Caiman latirostris* (Schlëich and Kästle 1988); Fernández et al. (2013) gave a range of thickness for *Caiman latirostris* between 0.36 and 0.72 mm, calculating the thickness, respectively, without and with superficial ornaments. In Crocodylidae family, the range goes from 58 mm × 40 mm in *Crocodylus johnstoni* Krefft, 1873 (Hirsch and Kohring 1992) to 101.6 mm × 63.5 mm in *T. schlegelii* (Butler 1905), with our sample from *Crocodylus mindorensis* of 69.3 mm × 37.3 mm with an EI between 1.44 in *Crocodylus johnstoni* and 1.86 in *Crocodylus mindorensis* (Hirsch and Kohring 1992, our sample). The thickness ranges from 0.4 mm in *Crocodylus acutus* (Cuvier 1807) and *Crocodylus johnstoni* (Hirsch and Kohring 1992; Panadès I Blas and Patnaik 2009) to 0.60 mm in *Crocodylus porosus* (Hirsch and Kohring 1992), with our sample value from *Crocodylus mindorensis* of 0.43 mm. In Gavialidae family, the only extant species *Gavialis gangeticus* presents dimensions equal to 82 mm × 56 mm, an EI equal to 1.46 and a thickness between 0.30 and 0.59 mm (Panadès I Blas and Patnaik 2009).

External surface

The classification for the external surface ornamentation proposed in Carpenter (1999) for dinosaurian eggs is not commonly used in the extant literature describing modern and fossil crocodilian eggs. The crocodilian eggs present some ornamentations, but those do not fit with the types already described. The studied samples present an external hard and crystallised shell and an internal thin layer, the egg membrane. The colour of the external eggshell surface is whitish in all our three samples; the thin egg membrane presents a leather-like aspect.

In *Crocodylus mindorensis*, the external surface (Figure 1(a),(b)) presents an ornamentation characterised by an irregularly rugose surface scattered by subcircular pits that not always correspond to pore openings: this kind of ornamentation seems unique in its kind and does not resemble any of the known and described type in Carpenter (1999); thus here we propose the rugosocavate as a new type of external surface ornamentation for crocodilian eggs. In *Paleosuchus palpebrosus*, the fragments bear bumps and nodes, more compact than in *Crocodylus mindorensis*, but somewhat resembling the surface of a golf ball (Figure 2(a)). We interpret this ornamentation as a rugosocavate type as well, although it differs from *Crocodylus mindorensis* for the denser and less irregular shape of the pits. Besides the rugosocavate ornamentation, *Paleosuchus palpebrosus* also presents many erosion pits and stepped concentric erosion rings around the pore openings, due to the microbiological degradation of the outer eggshell surface during the incubation (Figure 2(a),(c),(e)). Pits in the rugosocavate ornamentation are not always associated to pore openings and are characterised by smooth pit walls and shallow deepness in comparison to erosion pits, which are always associated to pore openings and present typical irregular and concentric stepped walls. In *Alligator mississippiensis*, the external surface presents an anastomotuberculate-like ornamentation along the equatorial region with curly, ramified, bulbous and polar elongated ridges (Figure 3(a)). On the contrary, the polar regions are smooth with some sporadic bulbs.

In modern crocodilian eggs, the texture and the ornamentation are smooth to rough, depending on the species and, in case of incubated eggs, on the grade of the degradation undergone during incubation (Schmidt and Schönwetter 1943; Ferguson 1982, 1985). The *Caiman latirostris* egg in Fernández et al. (2013, fig. 1(C)) seems to have an ornamentation characterised by pronounced isolated bumps (‘towers of ornamentation’) and deep craters or pits of erosion. In Paz et al. (1995), eggs from both *Caiman latirostris* and *Caiman yacare* present an external surface made by a layer of craters and corresponding columnar structures formed by deposits of calcite crystals and with an anastomosed appearance.

Table 3. Egg size, elongation index and eggshell thickness of modern and fossil crocodilian eggs.

	Egg size: PA × EA (mm)	EI	Eggshell thickness (mm)	Source
Modern crocodiles				
Family Alligatoridae				
Alligator mississippiensis	68.2 × 41.1	1.66	0.51–0.53	Hirsch and Kohring (1992)
	71.5 × 44.8	1.60	0.53	Our sample
	74 × 43	1.72	0.51–0.53	Panadès I Blas and Patnaik (2009)
	76 × 42	1.81	0.53	Hirsch and Kohring (1992)
Alligator sinensis	–	–	0.30–0.38	Wink and Elsey (1994)
	68 × 34	2	–	Panadès I Blas and Patnaik (2009)
Paleosuchus palpebrosus	62 × 39	1.59	–	Medem (1971)
	66 × 42	1.58	–	Panadès I Blas and Patnaik (2009)
	71.5 × 40	1.79	–	Medem (1971)
	–	–	0.41	Our sample
Caiman crocodylus	65 × 40	1.63	–	Panadès I Blas and Patnaik (2009)
Caiman yacare	68 × 42	1.62	–	Panadès I Blas and Patnaik (2009)
Caiman latirostris	63 × 40.9	1.54	0.36–0.72	Fernández et al. (2013)
	66 × 46	1.43	–	Panadès I Blas and Patnaik (2009)
	–	–	0.85	Schlëich and Kästle (1988)
Melanosuchus niger	67.71 × 39.78	1.70	–	Herron et al. (1990)
Family Crocodylidae				
Crocodylus acutus	77 × 48	1.60	0.40–0.52	Panadès I Blas and Patnaik (2009)
	77.8 × 48.9	1.59	0.52	Hirsch and Kohring (1992)
Crocodylus johnstoni	58 × 40	1.45	0.40	Hirsch and Kohring (1992)
	65 × 45	1.44	0.40	Hirsch and Kohring (1992)
	66 × 42	1.57	0.40	Panadès I Blas and Patnaik (2009)
Crocodylus mindorensis	69.3 × 37.3	1.86	0.43	Our sample
Crocodylus niloticus	74 × 43	1.72	0.58	Panadès I Blas and Patnaik (2009)
	78 × 51	1.53	0.53	Hirsch and Kohring (1992)
	79.2 × 50.1	1.58	0.58	Hirsch and Kohring (1992)
Crocodylus novaeguinae	76 × 43	1.77	–	Panadès I Blas and Patnaik (2009)
Crocodylus palustris	75 × 46	1.63	–	Panadès I Blas and Patnaik (2009)
Crocodylus porosus	77 × 52	1.48	0.53	Panadès I Blas and Patnaik (2009)
	80 × 50	1.60	0.53	Hirsch and Kohring (1992)
	80.1 × 50.8	1.58	0.60	Hirsch and Kohring (1992)
	81 × 52	1.56	0.53	Hirsch and Kohring (1992)
Crocodylus siamensis	76 × 51	1.49	–	Ferguson (1985)
Osteolemus tratraspis	63 × 37	1.70	–	Panadès I Blas and Patnaik (2009)
Tomistoma schlegelii	90–94 × 55	1.64–1.71	–	Mathew et al. (2011)
	98.4 × 63.5[a]	1.49	–	Butler (1905)
	101.6 × 63.5[a]	1.60	–	Butler (1905)
Family Gavialidae				
G. gangeticus	82 × 56	1.46	0.30–0.59	Panadès I Blas and Patnaik (2009)
Fossil crocodiles				
Pliocene – India (Silwalik Sequs.)	64 × 54	1.19	(0.19–0.66)	Patnaik and Schleich (1993; after Moreno-Azanza et al. 2013)
Miocene – Pakistan (Chinji Beds)	Fragments	–	0.15–0.75	Panadès I Blas and Patnaik (2009)
Eocene – Germany	53 × 35	1.51	–	Kohring and Hirsch (1996)
	40 × 19	2.11	0.29–0.36	
	35 × 30	1.17	0.30	
	52 × 25	2.08	0.30–0.35	
	60 × 35	1.71	0.35–0.45	
Eocene – Germany	44 × 44	1	0.36–0.45	Kohring and Hirsch (1996)
Eocene – USA (DeBeque Formation)	50 × 30	1.67	0.25–0.45	Hirsch (1985) and Hirsch and Kohring (1992)
	Fragments	–	0.48–0.58	
Eocene – USA (Bridger Formation)	68 × 44	1.55	0.76	Hirsch and Kohring (1992)

(*Continued*)

Table 3 – *continued*

	Egg size: PA × EA (mm)	EI	Eggshell thickness (mm)	Source
Upper Cretaceous – Brazil (Adamantina Formation)	57 × 35 (estimated)	1.63	–	Oliveira et al. (2011)
	58 × 32	1.81	–	
	65 × 36	1.81	0.15–0.25	
Upper Cretaceous – Bolivia	30 × 16	1.88	0.20	Novas et al. (2009)
Upper Cretaceous – France	Fragments	–	0.29 (0.21–0.38)	Garcia (2000)
		–	0.64	Hirsch and Kohring (1992)
Upper Cretaceous – Spain	Fragments	–	0.40	Garcia (2000)
		–	0.75	Moreno-Azanza et al. (2013)
Upper Cretaceous – USA (Two Medicine Formation)	Fragment	–	0.66	Jackson and Varricchio (2010)
Late Cretaceous – Brazil (Araçatuba Formation)	40 × 35	1.14	0.24–0.36	Ribeiro et al. (2006)
	50 × 30	1.67		
Late Cretaceous – Morocco	45 × 30	1.50	0.45	Panadès I Blas and Patnaik (2009)
Late Cretaceous – Spain	Fragments	–	0.25	Buscalioni et al. (2008)
		–	0.30	Canudo et al. (2010)
		–	0.50–0.70	Kohring (1990)
Late Cretaceous – India (Malabar Hill section)	Fragments	–	0.35	Panadès I Blas and Patnaik (2009)
Late Cretaceous – USA (Glen Rose Formation)	49 × 28	1.75	0.60–0.70	Rogers (2001)
Upper Jurassic – Portugal (Paimogo)	70 × 40	1.75	0.20–0.35	Antunes et al. (1998)
Uncertain eggs				
Upper Cretaceous – Lance Formation	58 × 36	1.61	0.18	Hirsch and Kohring (1992)

[a] Approximate dimensions, originals expressed in inches.

Fossil crocodilian eggs usually present a smooth external surface due to the weathering and dissolution processes (Hirsch and Kohring 1992; Antunes et al. 1998; Novas et al. 2009). However, there are some fossil crocodilian eggs still presenting a slightly undulated external surface with few depressions and small pits: the sample from the Eocene of the Bridge Formation (Hirsch and Kohring 1992, fig. 2(C), p. 61) resembles the ramotuberculate ornamentation described in Carpenter (1999), with irregular chains of nodes splitting and joining other nodes spreading all over the surface. The sample from the Upper Miocene of Chinji Beds of Pakistan in Panadès I Blas and Patnaik (2009, fig. 3, p. 3) presents 'cracks, smooth and patchy surfaces, and craters containing pores', characterising an ornamentation that resemble the rugosocavate type described for *Crocodylus mindorensis*, with a golf ball-like general aspect made of rugose surface pitted by subcircular depressions.

Pores

In modern and fossil crocodilian eggs, pores always form between shell units and extent from the external surface through the calcified layers to the IS to end between the eggshell unit cones usually straight and with a simple shape, other times with an inclined angle and irregular shapes and pore openings (Hirsch 1985; Wink et al. 1990a; Wink and Elsey 1994; Antunes et al. 1998; Panadès I Blas and Patnaik 2009).

The *Crocodylus mindorensis* has an angusticanaliculate pore canal system (*sensu* Carpenter 1999, p. 141; Figure 1(g),(h)). Pores mean diameter is 101 μm ($n = 20$, SD = 44 μm). The distribution of pores is uneven: the average density is 21 pores/cm^2; however, in the polar regions the value decreases to 10 pores/cm^2. Mean individual pore area is 0.009 mm^2 ($n = 20$, SD = 0.008 mm^2) and the relative pore area is 0.19% (Table 3). On the OS, pores present subcircular openings (Figure 1(a)), while on the IS openings have triangular, trapezoidal or irregular shape (Figures 1(h) and 4).

Paleosuchus palpebrosus presents an angusticanaliculate pore system. Pores have a diameter of 115 μm ($n = 20$, SD = 25 μm) and the mean density is 22 pores/cm^2. Pores mean area is 0.01 mm^2 ($n = 20$, SD = 0.005 mm^2) and the relative pore area is 0.22%. Pore openings are circular to subcircular in shape both on the OS and the IS (Figures 2 and 5).

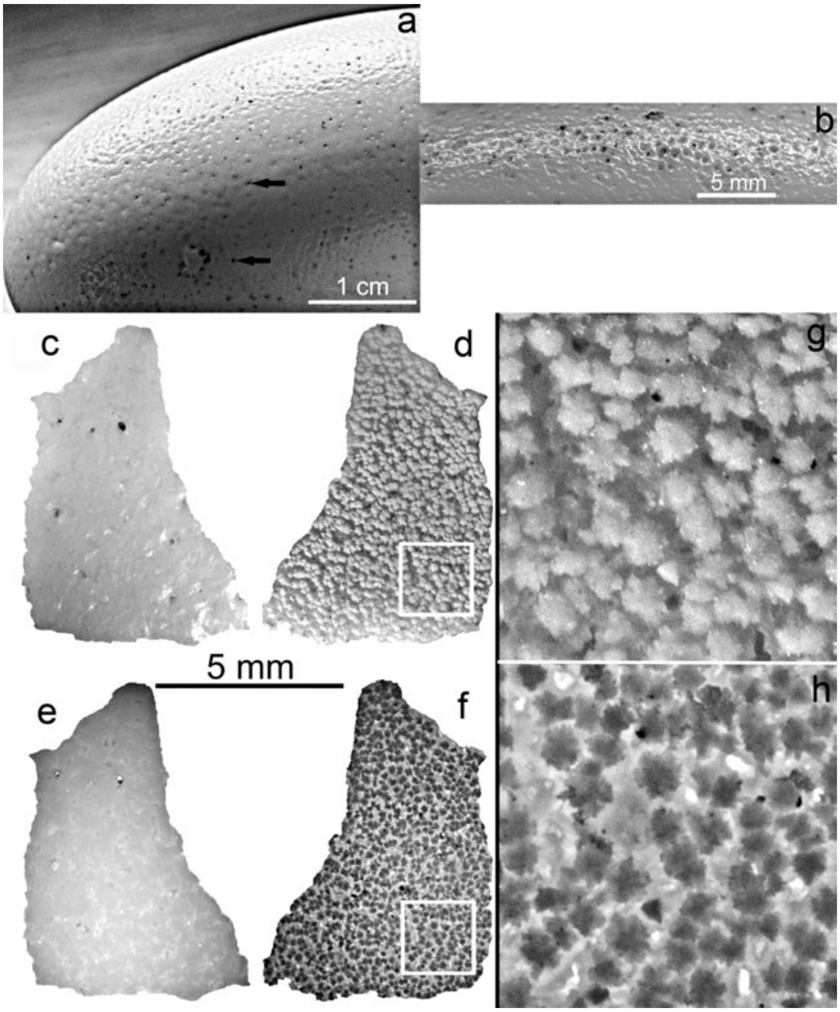

Figure 1. *Crocodylus mindorensis* eggshell FCT–UNL 707. (a) Macro of the OS, ornamentation and pores (arrows). (b) Close-up image of the external surfacing showing the rugosocavate ornamentation. (c–f) Sample of FCT–UNL 707 observed under petrographic microscope: (c) OS under reflected light; (d) IS under reflected light showing nucleation centres; (e) OS under transmitted light; (f) IS under transmitted light showing nucleation centres. (g, h) Inset of (d) and (f), respectively, showing nucleation centres; white holes in (h) are pore openings on the IS, right in between the nucleation centres.

In *Alligator mississippiensis* pores distribution is much more uneven than in *Crocodylus mindorensis* and *Paleosuchus palpebrosus*, without any relevant change between polar and equatorial regions porosity. The pore system is angusticanaliculate and pore openings are subcircular both on the OS and in the IS (Figures 3(a),(b), (d) and 6). Pores average diameter is 129 μm ($n = 20$, SD = 42 μm) and the mean density is 5 pores/cm^2. Pores mean area is 0.015 mm^2 ($n = 20$, SD = 0.009) and relative mean area is 0.08%.

Eggshell sections

In *Crocodylus mindorensis*, the discrete shell units have a trapezoidal shape (Figure 7(a)), wider at the top (external surface), with a width to height ratio of 0.58 for the single unit and a nucleation centre and basal knobs at the bottom of each (Figures 1(d),(f), 4 and 7(b)). The entire eggshell presents three distinct structural layers (Figure 8): (1) a dark IL, consisting of nucleation centres characterising the entire IS; (2) a pale ML, with noticeable linear brown growth lines and (3) an OL, darker than the ML probably for the higher presence of organic material. The typical crocodilian tabular ultrastructure is less visible on the thin section sample and can be only seen on SEM images, especially on the upper part of the OL. The growth lines are faint at the basal part of the ML and get more pronounced in outward direction, as well as there is not a clear distinction between the IN and the ML. The IL, ML and OL to total eggshell thickness ratios are, respectively, 18%, 55% and 27% calibrated to 100% of the eggshell total thickness (Figure 7(a)). Visible with crossed nicols, single extinction wedges can be distinguished, with the tip

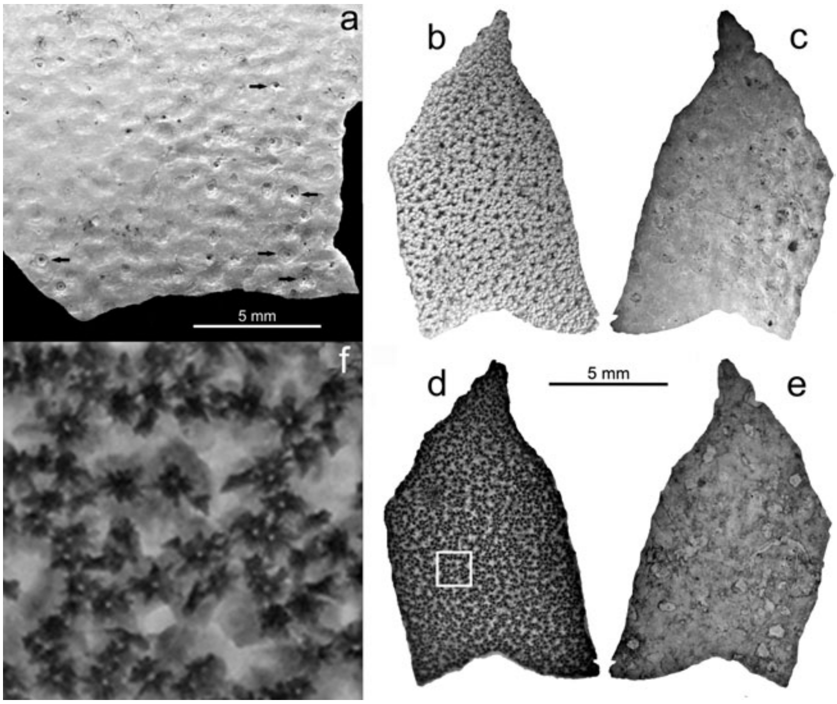

Figure 2. *Paleosuchus palpebrosus* eggshell FCT–UNL 708. (a) Macro of the OS showing pores (arrows) and the rugosocavate ornamentation; concentric erosion pits due to the incubation process are noticeable associated to pores. (b–e) Sample of FCT–UNL 708 observed under petrographic microscope: (b) IS under reflected light showing nucleation centres; (c) OS under reflected light; (d) IS under transmitted light showing nucleation centres; (e) OS under transmitted light. (f) Inset of (d) with clear pinholes at the centre of each nucleation centre.

at the base of the ML and the base at the upper part of the OL; the wedges present irregular shape and the typical crocodilian blocky extinction with an upside down triangular shape (Figure 8).

In *Paleosuchus palpebrosus*, the discrete shell units have a trapezoidal shape, wider at the top, with a height to width ratio of 0.65 for the single unit and a nucleation centre at the bottom of each (Figures 2(b),(d),(f) and 9(a)). The entire IL observed under transmitted light on a petrographic microscope presents pinholes in the middle of each nucleation centre (Figure 2(d)), which are not or rarely visible under reflected light or SEM (Figures 2(b) and 5). These pinholes are similar to those presented in Garcia et al. (2008, Plate 1(c)) for *Megapodius nicobariensis* Blyth, 1846, the Nicobar scrubfowl, and interpreted as marks of a possible reabsorption of calcite by the growing embryo or by weathering. The structure of this eggshell seems unique among all those described and known so far. Three different layers can be distinguished, like in the previous sample, but their organization is different than any other eggshell we observed: at the base of the shell units, there are nucleation centres made by an aggregation of calcite plates; all the IL of the eggshell is characterised by the presence of these nucleation centres. Above this level, there is a middle, thin, dark, irregular layer (ML), probably an aggregation of fibres. The fibrous nature of the IL seems to be a unique feature of *Paleosuchus palpebrosus*, when compared to the other samples and also to the so far described extant crocodilian eggshells (Figure 9(a)). On SEM observation (Figure 10), above the basal layer, a clear horizontal tabular ultrastructure can be observed for about a fourth of the entire eggshell thickness. No evidence of vertical lamination and fibres is present. Above this layer, there is a thick OL (approximately half of the entire eggshell thickness) characterised by a faint horizontal lamination, growth layering and a more evident vertical lamination, corresponding to a fibrous fabric disposed perpendicularly to the eggshell surface, not radially like the tabular ultrastructure. Layer to entire eggshell thickness ratios are 32%, 11% and 57%, respectively, for the IL, ML and OL, calibrated to 100% of the eggshell total thickness (Figure 10). In crossed nicols observation, single wedges can be distinguished by the triangular shape (large side up), with the tip endorsed on the upper part of the ML and the base at the upper part of the OL; the wedges present regular shape and the typical blocky extinction (Figure 9(b)).

In *Alligator mississippiensis*, the discrete shell units are wedged shaped, widening to the OS, with a width to

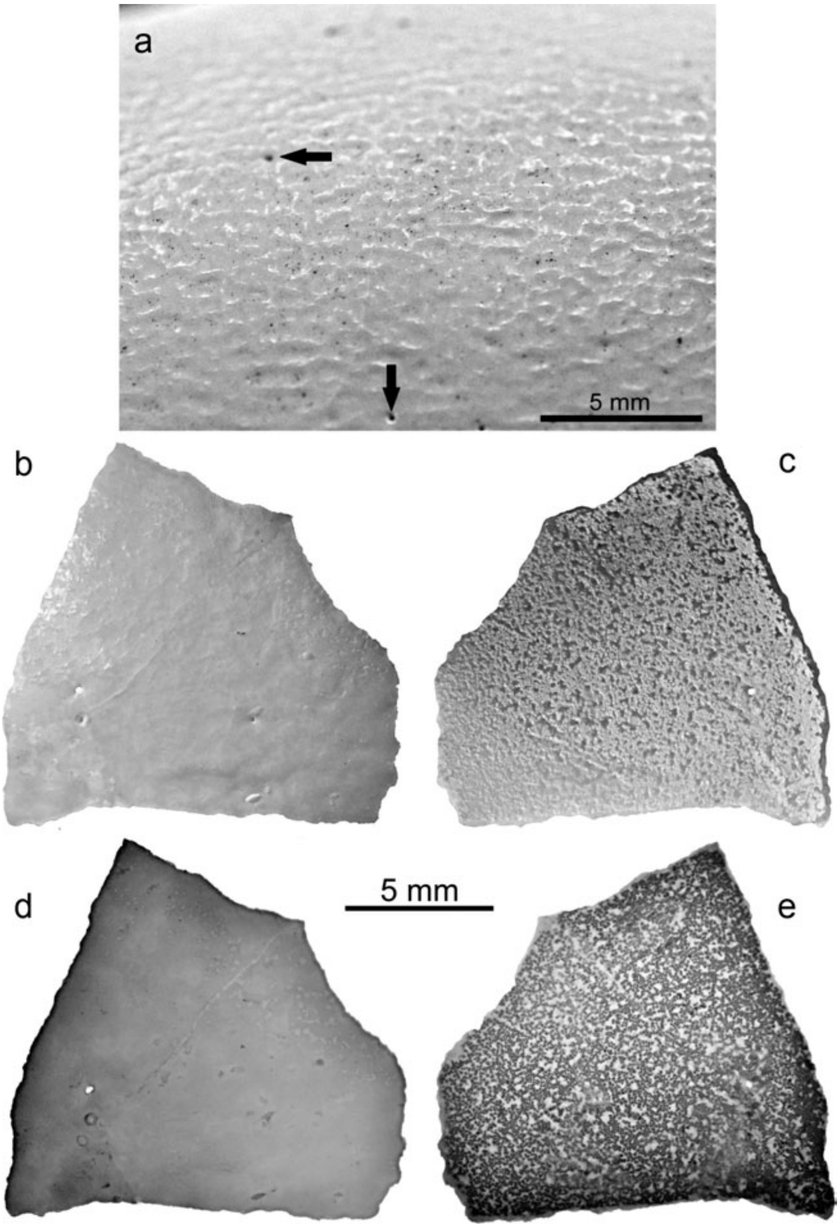

Figure 3. *Alligator mississippiensis* eggshell FCT–UNL 709. (a) Macro of the OS of showing pores (arrows) and an anastomotuberculate ornamentation type. (b–e) Sample of FCT–UNL 709 observed under petrographic microscope: (b) OS under reflected light; (c) IS under reflected light showing nucleation centres; (d) OS under transmitted light; (e) IS under transmitted light showing nucleation centres.

height ratio of 0.42 and a nucleation centre at the bottom of each. Three different layers can be distinguished (Figure 11(a)), organised in a IL made of tightly packaged nucleation centres and basal knobs (Figure 3(c),(e)), which are approximately one-third in size than those observed in the previous two samples (see Figures 1(d),(f), 2(b),(d) and 3(c),(e)). Both ML and OL are characterised by growth lines, a compact tabular ultrastructure and an evident fibrous vertical fabric, perpendicular to the eggshell surface (Figure 12). The growth lines are more evident in the ML, while the fabric made by fibres is better defined on the OL. The IL, ML and OL to total eggshell thickness ratios are, respectively, 20%, 45% and 35% calibrated to 100% of the eggshell total thickness (Figure 12). With crossed nicols, a blocky extinction can be noticed, shaped by irregular single extinction wedges, with an upside down triangular shape protracting from the upper part of the IL to the external surface (Figure 11(b)).

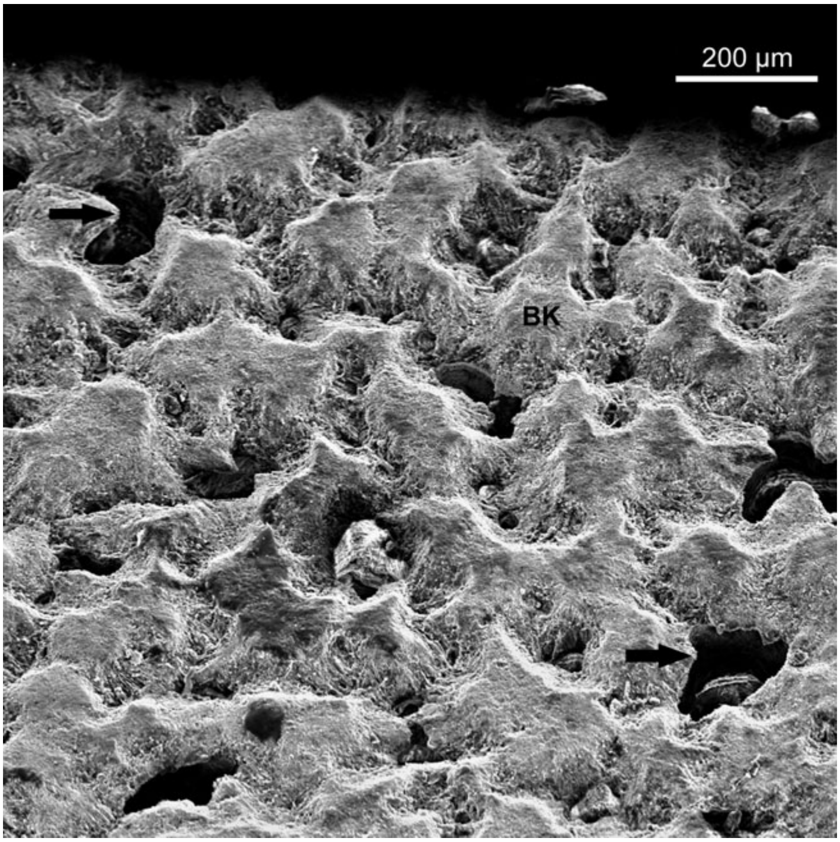

Figure 4. *Crocodylus mindorensis* eggshell. SEM image of the IS of FCT–UNL 707 showing pores (arrow) and the packing of the BKs of the IL. BK, basal knob; IL, inner layer; IS, inner surface.

Discussion

Among our samples, the external surfaces present two different kinds of ornamentation: *Alligator mississippiensis* presents an anastomotuberculate type of ornamentation, while both *Crocodylus mindorensis* and *Paleosuchus palpebrosus* present a new identified type of ornamentation, here called rugosocavate (Figures 1(a),(b) and 2(a)), characterised by an irregularly rugose surface scattered by subcircular pits. This ornamentation seems characteristic also for a fossil crocodilian sample described from the Upper Miocene of Chinji Beds of Pakistan (Panadès I Blas and Patnaik 2009, fig. 3, p. 3). We exclude this pattern to be a simple product of the degradation throughout incubation, because it is present on two different modern crocodilian samples, one unfertilised and the other incubated and hatched. The dissolution pits and stepped concentric erosion rings around the pore openings, identified on our only hatched samples (*Paleosuchus palpebrosus*) and previously documented for *Alligator mississippiensis* in Ferguson (1981a, 1981b, 1982), are a good evidence for distinguishing the incubated eggs from the unincubated ones.

Our samples show an angusticanaliculate type of pore system which is typically associated to crocodiloid eggshells (Ferguson 1982; Mikhailov 1991, 1997; Zelenitsky and Hirsch 1997; Carpenter 1999). Crocodiles, however, share this character with some groups of dinosaurs and birds: the angusticaniculate type is described (1) for the theropodian oofamilies Prismatoolithidae and Elongatoolithidae, including the oospecies *Elongatoolithus andrewsi* Zhao, 1975, *Macroelongatoolithus carlylei* Jensen, 1970, *Macroelongatoolithus xixianensis* Li, Yin and Liu, 1995, *Macroolithus yaotunensis* Zhao, 1975, *Macroolithus rugustus* Young, 1965, *Preprismatoolithus coloradensis* (Hirsch, 1994), *Prismatoolithus levis* Zelenitsky and Hills, 1996, *Prismatoolithus jenseni* Bray, 1999, *Pseudogeckoolithus* Vianey-Liaud and Lopez-Martinez, 1997, *Spheruprismatoolithus condensus* Bray, 1999, *Spongioolithus hirschi*; (2) for the ornitid oofamilies Laevisoolithidae, Oblongoolithidae, Medioolithidae, Struthiolithidae and Ornitholithidae (see Antunes et al. 1998; Bray 1999; Garcia 2000; Zelenitsky et al. 2000; Deeming 2006; Ribeiro et al. 2013) and (3) for the unassigned oofamily Ovaloolithidae, including the oospecies *Ovaloolithus tenuisus* Bray, 1999, and *Ovaloolithus utahensis* Bray, 1999, tentatively associated to ornithopod dinosaurs by Mikhailov (1991) based on some similarities in the microstructure to hadrosaur eggs. *Alligator*

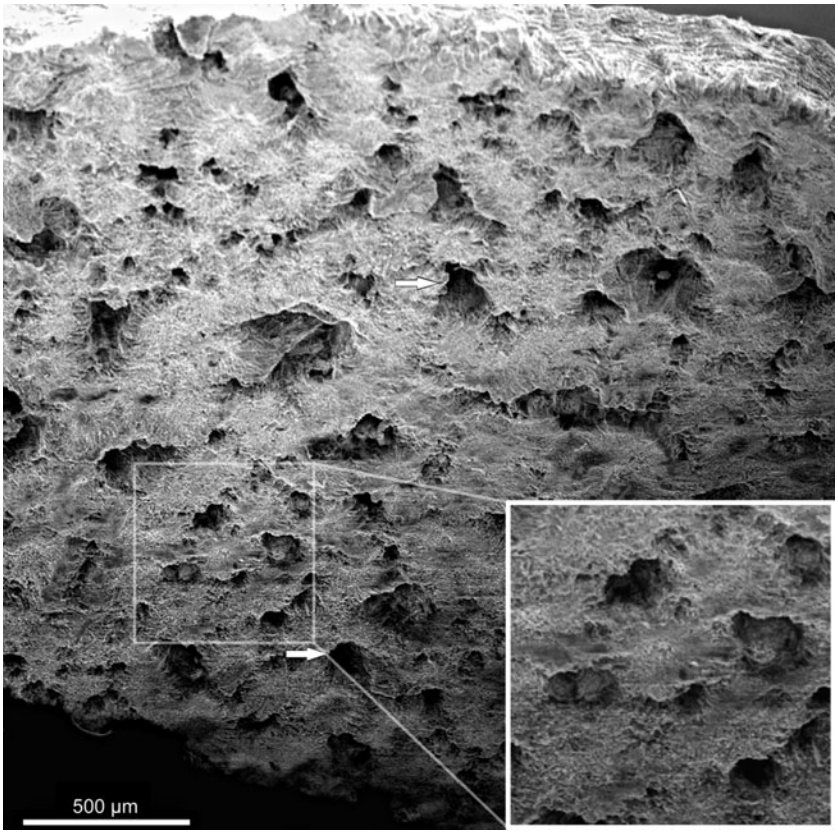

Figure 5. *Paleosuchus palpebrosus* eggshell. SEM image of the IS of FCT–UNL 708 showing pores (arrows) and an inset of a nucleation centre with a pinhole.

mississippiensis presents a lower porosity (5 pores/cm^2) than *Crocodylus mindorensis* and *Paleosuchus palpebrosus*. This low porosity seems, however, synapomorphic for this genus because *Alligator sinensis* presents a pore density between 3 and 6 pores/cm^2 (see Wink and Elsey 1994). The number of pores seems to change, however, by many environmental factors: Wink et al. (1990b) report 94 pores/cm^2 per unincubated fertile eggs of wild alligators. Furthermore, Wink et al. (1990b) and Bryan (2005) registered very low porosity values for *Alligator mississippiensis* in a wide range of environmental conditions lending additional support to the value described for this study. The pore diameter of the three samples ranges between 100 and 130 µm. The relative mean pore area percentage on the entire eggshell area is very similar for *Paleosuchus palpebrosus* and *Crocodylus mindorensis*, respectively, 0.22% and 0.19%, and lower for *Alligator mississippiensis*, about 0.08% (Table 3).

While an eggshell thickness between 0.30 and 0.59 mm seems to be typical for the extant Crocodyliformes, it does not appear to be a distinctive and useful character to identify specific taxa within this suborder. Our *Alligator mississippiensis* sample thickness is in agreement with the recorded range of this species, between 0.51 and 0.53 mm (Hirsch 1983; Hirsch and Kohring 1992), but is higher than a previous captive, fertile and unincubated sample described in Wink et al. (1990a), 0.43 ± 0.0236 mm.

Characteristic trapezoidal wedge-shaped shell units are clearly noticeable in our samples, with a width to height ratio between 0.42 and 0.65 (Table 3). While all the three ILs are characterised by basal knobs with basal plate groups clearly distinguishable (Figures 1(d),(f)–(h), 2(b),(d)–(f) and 3(c),(e)), the other two layers differ for the three samples. In *Crocodylus mindorensis* and *Alligator mississippiensis* can be recognised a thick ML, scarce in fibres, in contrast with an OL rich in fibres (so, darker on observation in thin section with normal light). On the contrary, *Paleosuchus palpebrosus* eggshell presents a characteristic and unique organisation of the ML and OL among extant and fossil crocodiles described so far. The thin ML appears fully dark observed on thin section under direct light, while the OL, relatively thick compared to the entire eggshell thickness, appears lighter in colour. There is no direct observation of fibres in the ML, so the darker colour of this layer could only depend on the dense

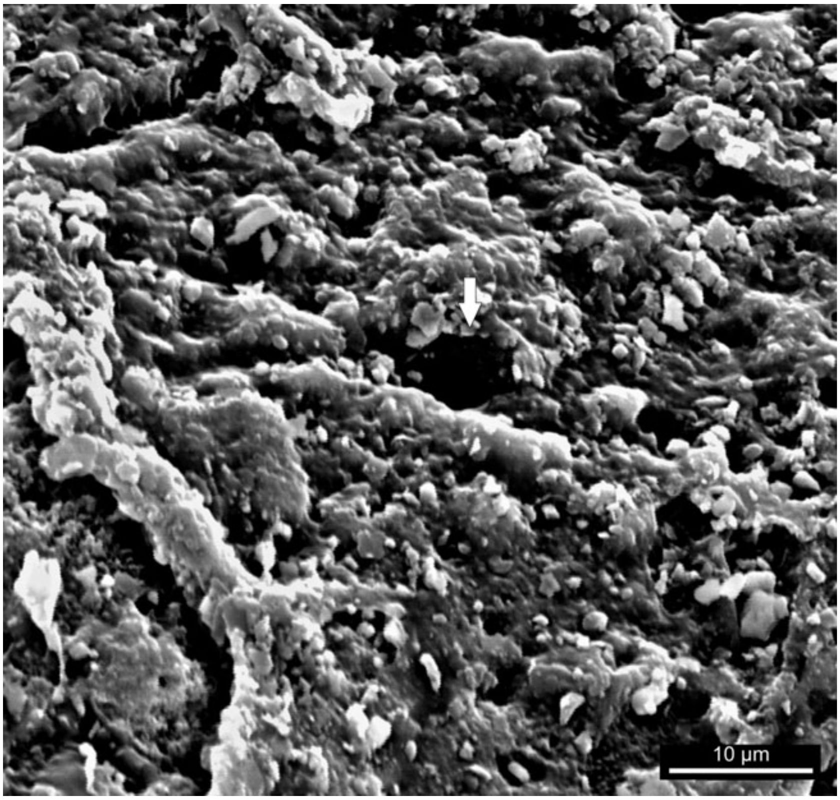

Figure 6. *Alligator mississippiensis* eggshell. SEM image of a pore (arrow) on the outer surface (OS) of FCT–UNL 709.

microtabular horizontal lamination, in opposition to the sparse lamination present on the OL.

The absence of fibres and, subsequently, organic material in the ML is unique in *Paleosuchus palpebrosus* and differs from the general microstructure of crocodylomorph eggs, which show '… an aggregate of prismatic calcite crystals that grow parallel to the shell surfaces, interwoven with protein fibers' (see Ferguson 1982). On thin section and SEM images observation (Figures 9 and 10), the ML is absent of all the characteristic that recall the presence of proteic fibres, evident in most of crocodylomorph eggs, as well as in our other two samples (Figures 7 and 12).

On SEM observation, the three samples present a similar organization of the layers: the IL presents the characteristic crocodilian basal knobs with basal plate groups; both the ML and the OL have the presence of a tabular horizontal ultrastructure, typical for crocodilian eggshells, denoting growth levels. Moreover, the OL presents a distinct vertical lamination, designating a fibrous

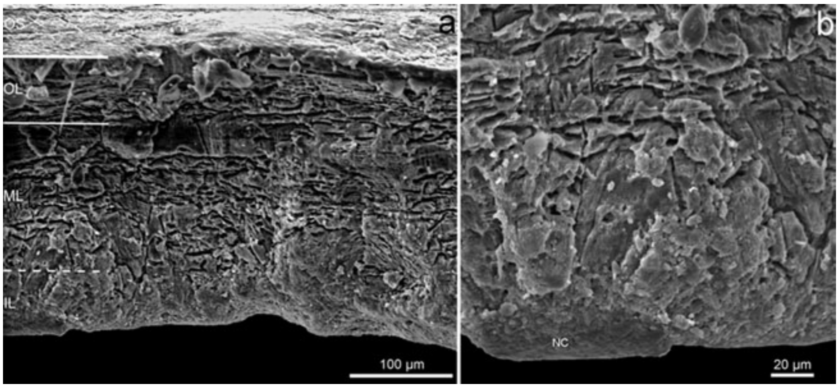

Figure 7. *Crocodylus mindorensis* eggshell. (a) SEM image of an eggshell fragment in radial section of FCT–UNL 707. (b) Detail of (a) showing calcite plates on a NC. IL, inner layer; ML, middle layer; NC, nucleation centre; OL, outer layer; OS, outer surface.

Figure 8. (Colour online) *Crocodylus mindorensis* eggshell. Crossed nicols image with pore section of FCT–UNL 707.

fabric. In *Paleosuchus palpebrosus*, the ML presents a denser horizontal lamination than the other two species, probably a unique characteristic of the eggshell of this species.

The crocodilian blocky extinction described in our samples is characterised by a V-shaped wedges that, on thin sections, appear like shaded triangular upside down areas in the upper part of the eggshell. This particular extinction pattern is indicative of an irregular distribution of the shell units that superimpose one to another among the eggshell. On the contrary, the sweeping and columnar extinction pattern observed in dinosaurian eggs shows a more organised distribution of the shell units, packed one close to each other but with no superimposition (see Jackson and Varricchio 2010; Ribeiro et al. 2013).

Figure 13 compares the three types of eggshell here described.

Crocodilians exhibit a stable and well-defined eggshell morphology, with only very slight variations at the structural level throughout the entire clade, as observed in this study. A cladogram summarising the evolution of the egg in Amniotes was constructed in order to understand the relationships among the various oviparous groups and eggshell characteristics (Figure 14). Packard et al. (1982, p. 142) recognise that 'grouping of eggs on the basis of similarities in structure of eggshells is somewhat artificial'. Nonetheless, according to Carpenter (1999), Amniotes show a trend in hardening through further mineralisation and an increase in the eggshell morphology complexity (see also Kohring 1995). Even though there is

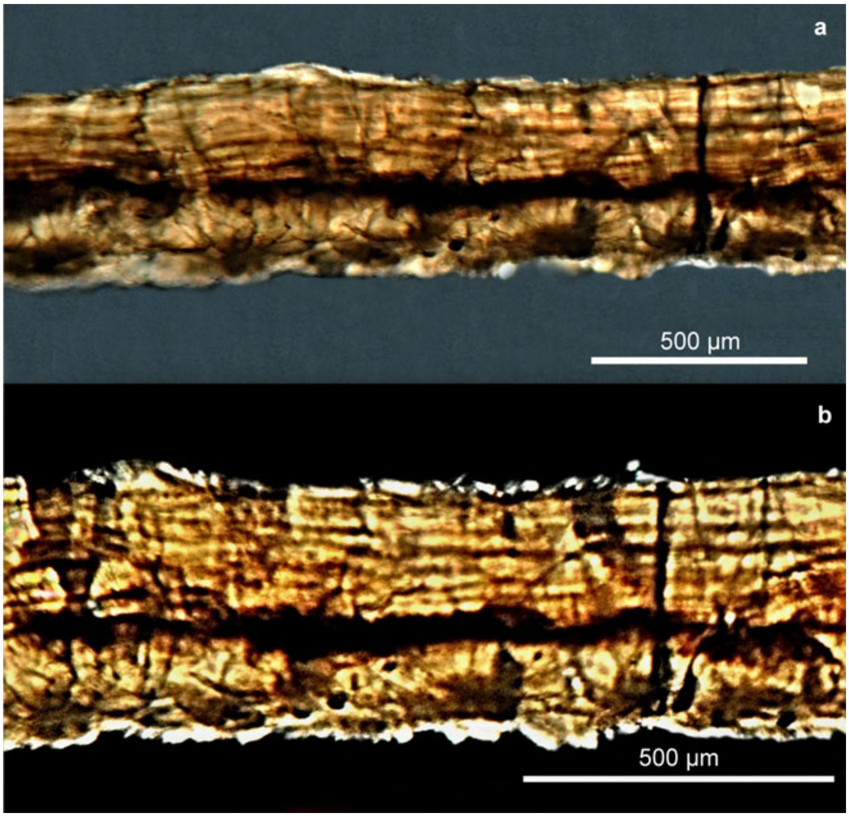

Figure 9. (Colour online) *Paleosuchus palpebrosus* eggshell. Thin section under polarised light (a) and under crossed nicols (b) of FCT–UNL 708.

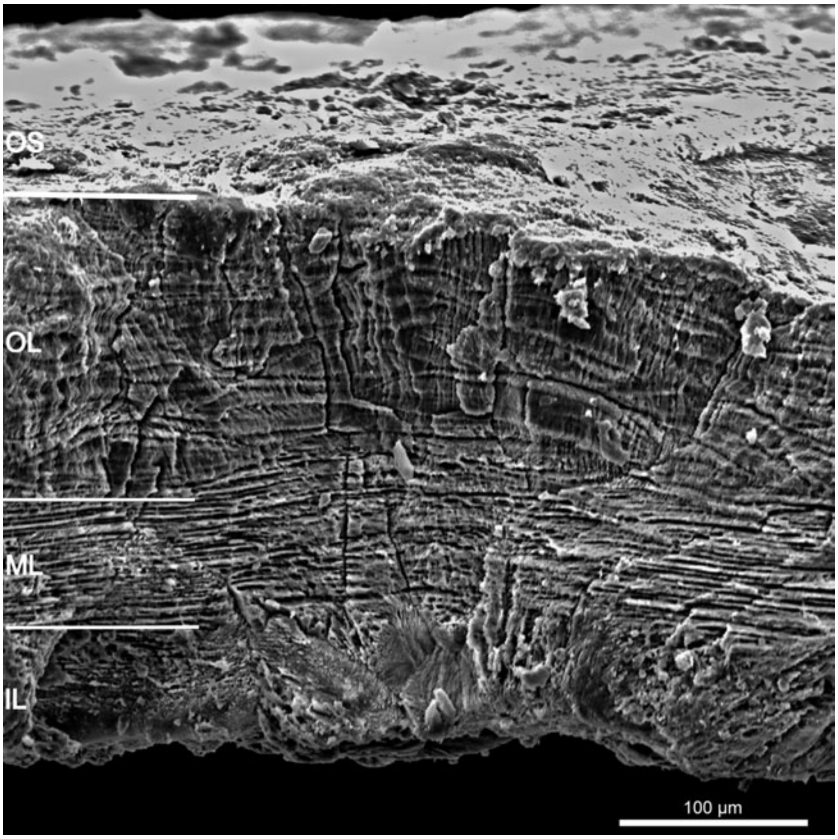

Figure 10. *Paleosuchus palpebrosus* eggshell. SEM image of an eggshell fragment in radial section of FCT–UNL 708. IL, inner layer; ML, middle layer; OL, outer layer; OS, outer surface.

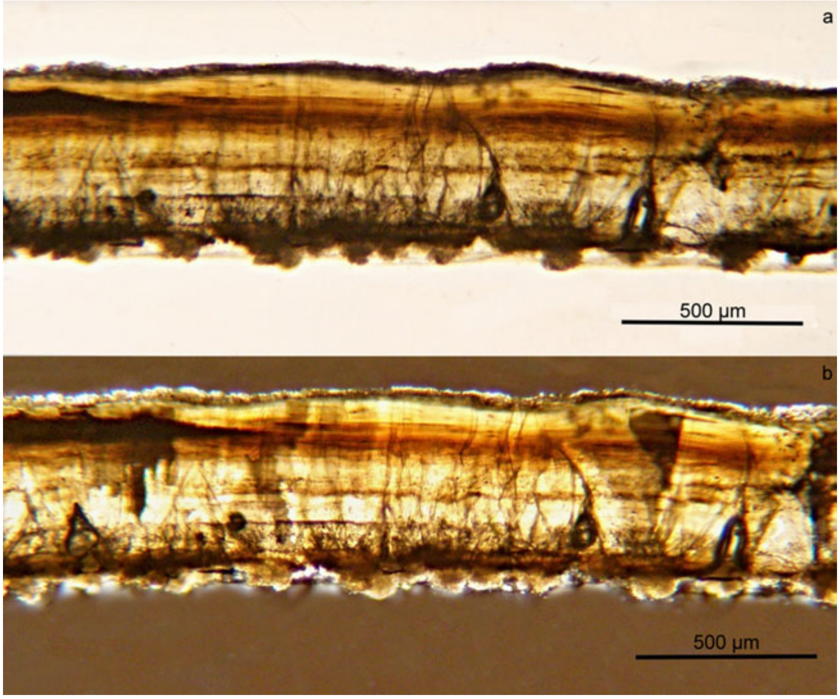

Figure 11. (Colour online) *Alligator mississippiensis* eggshell. Thin section under normal light (a) and crossed nicols (b) of FCT–UNL 709.

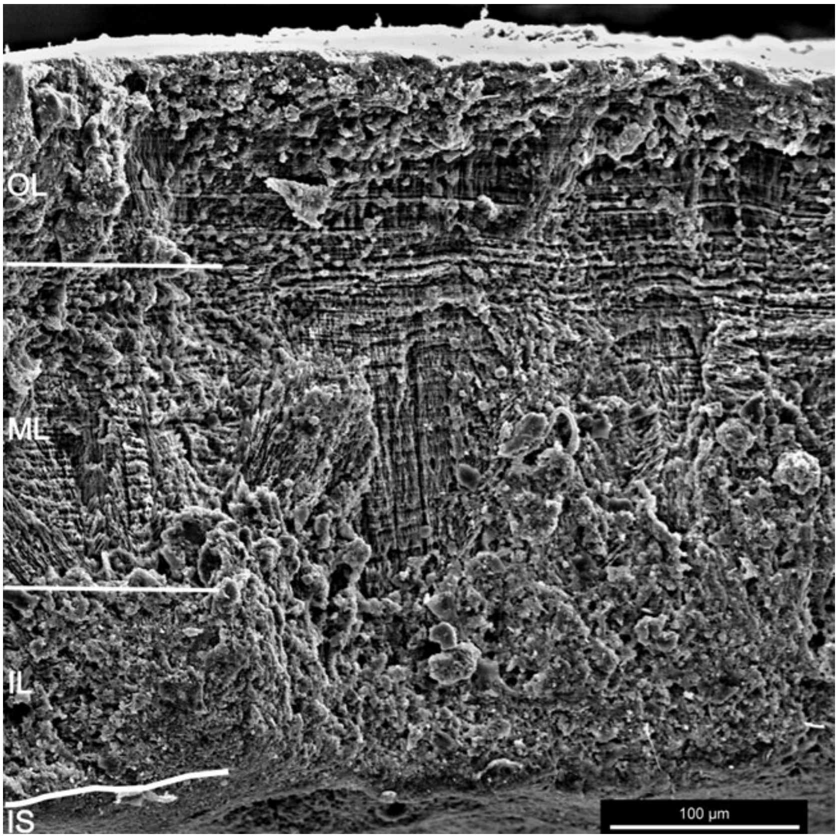

Figure 12. *Alligator mississippiensis* eggshell. SEM image of an eggshell fragment in radial section of FCT–UNL 709. IL, inner layer; IS, inner surface; ML, middle layer; OL, outer layer.

a wide array of eggshell morphologies within some groups, by comparing our samples with other amniotic eggs, we are able to infer such a pattern. However, this analysis also reveals a complex evolution, with several groups developing a broad range of eggshells independently from each other (i.e. Chelonia, Lepidosauria) (Packard et al. 1977; Packard et al. 1982; Packard and Seymour 1997; Stewart 1997; Carpenter 1999; Kratochvíl and Frynta 2006; Unwin and Deeming 2008). The primitive condition seems to be a leathery or parchment-like, flexible, most likely thin proteic membrane enveloping the egg (Grine and Kitching 1987; Kohring 1995; Packard and Seymour 1997; Stewart 1997; Carpenter 1999; Oftedal 2002); nowadays, this condition can be observed in Monotremata (Grine and Kitching 1987; Packard 1994; Packard and Seymour 1997; Stewart 1997; Oftedal 2002; Kratochvíl and Frynta 2006). A mineralised eggshell is considered a synapomorphy of Sauropsida (‘Reptilia’ in Packard 1994). It is plausible to assume that the leathery and semi-rigid eggshells in Chelonia, Lepidosauria and Pterosauria were either a retained primitive condition, as in the very primitive tuatara, or a secondary loss during the evolution of the group, as assumed for some more derived turtles or squamatans (Packard et al. 1977; Packard and Packard 1980; Packard et al. 1982; Kohring 1995; Stewart 1997; Carpenter 1999). In archosaurs, Pterosauria are the only group with a major change in eggshell morphology, characterised by a very thin, low mineralised, leathery eggshell but even so with some low degree of variation throughout the clade (Unwin and Deeming 2008). Crocodilians and dinosaurs (including birds) have very mineralised, rigid eggshells, although the Dinosauria show a greater variability in the eggshell structure, an organic core and a higher porosity (i.e. Grine and Kitching 1987; Antunes et al. 1998; Ribeiro et al. 2013).

Comparisons to fossils

Numerous fossil crocodylomorph eggs were collected and described. The oldest known are from the Late Jurassic of Lourinhã Formation in Portugal, which is known for the dinosaur fauna, including eggs and embryos (Mateus et al. 1998; Castanhinha et al. 2009; Araújo et al. 2013). The eggs bearing horizons are Upper Kimmeridgian/Lower Tithonian. The fossil eggs putatively assigned to Crocodylomorpha from the same formation were found in Paimogo, Peralta, Casal da Rola

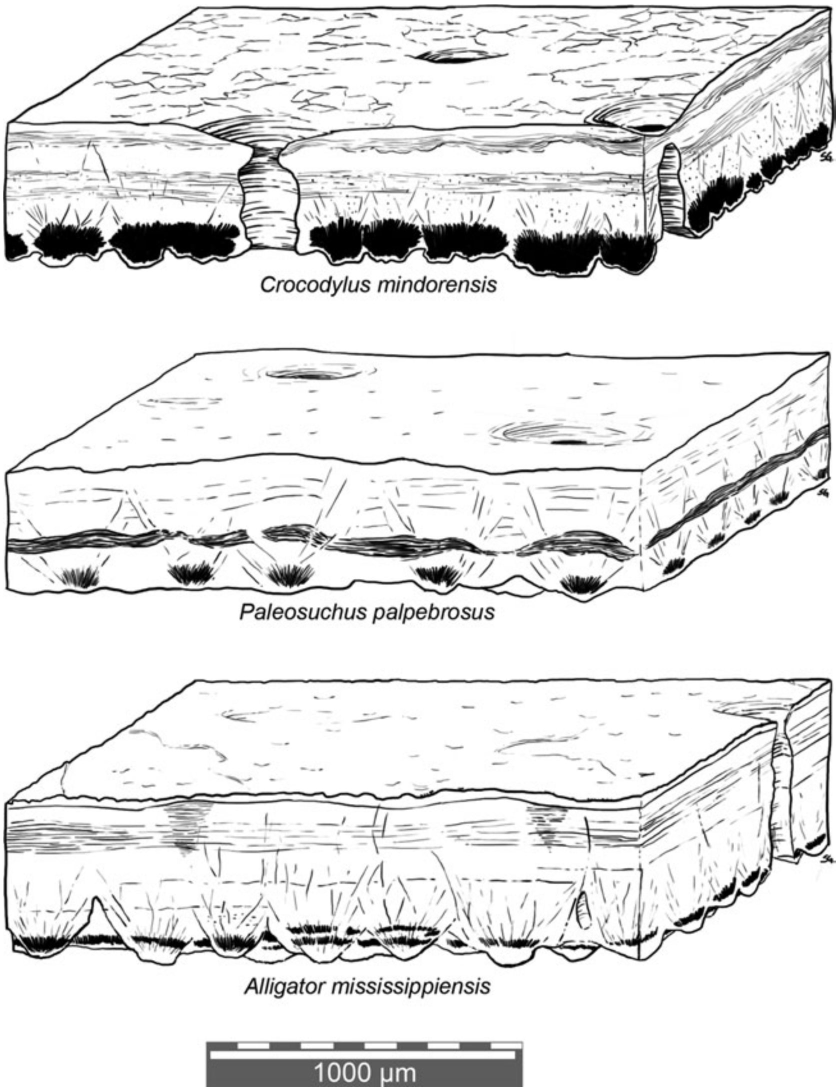

Figure 13. Schematic 3D view of our three eggshell samples. Artwork by Simão Mateus.

and Cambelas. The origin of true crocodilians (members of the clade Crocodylia) occurred in the Late Cretaceous, so our Jurassic samples are not only the oldest known so far, but also the best record for eggs of non-crocodilian crocodylomorphs. The eggs of Paimogo were the only subject of more detailed description by Antunes et al. (1998). These eggs measure 70 mm × 40 mm in dimensions (EI = 1.75) and 0.20–0.35 mm in thickness (Antunes et al. 1998). From the Cretaceous period, there are several crocodilian eggs finds, most of which are preserved only as fragments; from the complete known eggs, dimensions vary from 30 mm × 16 mm from the Upper Cretaceous of Bolivia to 65 mm × 36 mm from the Upper Cretaceous of Brazil (Adamantina Formation), with an EI between 1.14 and 1.88. The thickness goes from 0.15 mm of the Adamantina Formation specimen in Brazil to 0.75 mm of some fragments from the Upper Cretaceous of Spain (Hirsch and Kohring 1992; Rogers 2001; Ribeiro et al. 2006; Novas et al. 2009; Panadès I Blas and Patnaik 2009; Oliveira et al. 2011; Moreno-Azanza et al. 2013). Crocodilian eggs are known from the Cenozoic as well, with dimensions ranging from 35 mm × 30 mm (Eocene, Germany) and 64 mm × 54 mm (Pliocene, Upper Siwaliks, India), with an EI included between 1 and 2.11. The thickness is included between 0.15 mm of some Miocene fragments from the Chinji Beds of Pakistan and 0.76 mm from an Eocene sample from the Bridger Formation of the USA (Hirsch 1985; Hirsch and Kohring 1992; Patnaik and Schleich 1993; Kohring and Hirsch 1996).

All crocodylomorph eggs are ellipsoid in shape. Ovality can be defined as being egg-shaped, i.e. an ellipsoid which bears different pole curvatures and asymmetry to the equatorial plane seems to appear by the first time in

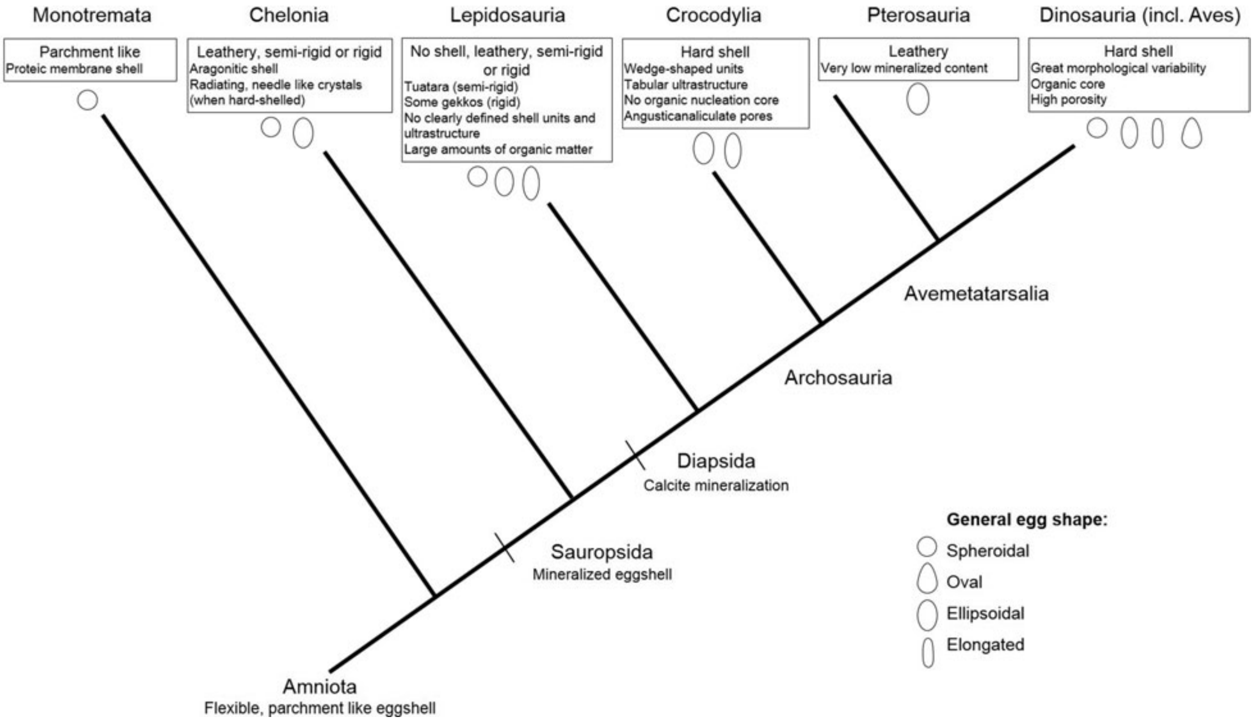

Figure 14. Egg characteristics within the framework of the general consensus phylogeny of Amniotes (see Carroll 1988; Benton 2005; Brusatte et al. 2011; Nesbitt 2011 for major clades relationships). Egg data after Packard et al. (1977), Packard and Packard (1980), Kohring (1995), Packard and Seymour (1997), Stewart (1997), Carpenter (1999) and Unwin and Deeming (2008).

coelurosaurian dinosaurs and is being retained in birds until nowadays.

In general, the extinct crocodylomorph eggs have the same structure and shape than extant crocodile eggs, and synapomorphies for eggs of Crocodylia are also valid for the broader clade Crocodylomorpha. The main observed difference, however, is the smaller values of average eggshell thickness in non-crocodilian crocodylomorph.

Conclusions

We can conclude that (1) anastomotuberculate, ramotuberculate and rugosocavate ornamentation types seem to be the most typical among extant and fossil crocodilian eggs (Crocodylomorpha clade); (2) angusticaniculate pore system is homoplastic for Crocodyliformes clade and some groups of dinosaurs and birds. Pore openings are circular in shape on the outer surface and sub-circular to irregular on the inner surface, having a relatively small diameter between 100 and 130 μm and their relative percentage on the eggshell total area is low (0.08–0.22% per cm^2); (3) *Paleosuchus palpebrosus* presents an autapomorphic eggshell ultrastructure, with a relatively thin middle layer, with a dense and compact tabular microstructure and a thicker upper layer constituting more than half of the total eggshell thickness and (4) dissolution pits and stepped concentric erosion rings around the pore openings are a constant characteristic of crocodylomorph incubated eggs only.

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