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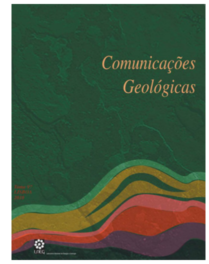
Crocodylomorph eggs and eggshells from the Lourinhã Fm. (Upper Jurassic), Portugal

Ovos e cascas de crocodilomorfos da Formação da Lourinhã (Jurássico Superior), Portugal



J. Russo[1,2,3*], O. Mateus[1,2], A. Balbino[1,3], M. Marzola[1,2]

Artigo Curto
Short Article

Abstract: We here present fossil Crocodylomorpha eggshells from the Upper Jurassic Lourinhã Formation of Portugal, recovered from five sites: one nest from Cambelas with 13 eggs, and three partial eggs and various fragments from, Paimogo N (I), Paimogo S (II), Casal da Rola, and Peralta. All specimens but the nest were found in association with dinosaur egg material. Our research reveals that on a micro- and ultrastructural analysis, all samples present the typical characters consistent with crocodiloid eggshell morphotype, such as the shell unit shape, the organization of the eggshell layers, and the triangular blocky extinction observed with crossed nicols. We assign the material from the Lourinhã Formation to the oofamily Krokolithidae, making it the oldest crocodylomorph eggs known so far, as well as the best record for eggs of non-crocodylian crocodylomorphs. Furthermore, our study indicates that the basic structure of crocodiloid eggshells has remained stable since at least the Upper Jurassic.

Keywords: Crocodylomorpha, Crocodiloid, Eggshells, Upper Jurassic, Krokolithidae.

Resumo: Apresentamos aqui cascas de ovos fósseis de Crocodylomorpha da Formação da Lourinhã do Jurássico Superior de Portugal, recolhidas em cinco locais: um ninho de Cambelas com 13 ovos, e três ovos parciais e vários fragmentos de Paimogo N (I), Paimogo S (II), Casal da Rola, e Peralta. Todos os espécimes excepto o ninho foram encontrados em associação com material de ovos de dinossauro. A nossa investigação revela que, numa análise micro- e ultraestrutural, todas as amostras apresentam caracteres típicos consistentes com o morfótipo crocodilóide de casca de ovo, como a forma das unidades de casca, a organização das camadas da casca, e a extinção triangular em blocos observável com nicóis cruzados. Atribuímos este material à oofamília Krokolithidae, sendo os ovos de crocodilomorfos mais antigos conhecidos até agora e também o melhor registo para ovos de crocodilomorfos não crocodilianos. Além disso, o nosso estudo indica que a estrutura básica da casca de ovos crocodilóides se mantém estável pelo menos desde o Jurássico Superior.

Palavras-chave: Cascas de ovo, Crocodilóide, Crocodylomorpha; Jurássico Superior, Krokolithidae.

[1]GeoBioTec, Departamento de Ciências da Terra, Faculdade de Ciências e Tecnologia, Universidade Nova de Lisboa, Quinta da Torre, 2829-516 Caparica, Portugal.

[2]Museu da Lourinhã, Rua João Luís de Moura, 95, 2530-158 Lourinhã, Portugal.

[3]Departamento de Geociências, Universidade de Évora, Rua Romão Ramalho, 59, 7000-671 Évora.

[*]Corresponding author / Autor correspondente: jpvmrusso@gmail.com

1. Introduction

Despite the limited diversity of extant taxa, the extensive fossil record of crocodylomorphs is estimated in over 200 taxa (Oliveira *et al*., 2011). Fossil eggs of Crocodylomorpha are, compared to dinosaurs, scarcer and still poorly understood, even though fossil crocodiloid eggs and eggshells (Mikhailov, 1991, 1997; Mikhailov *et al*., 1996; Carpenter, 1999; Marzola *et al*., 2014), have been identified worldwide. We hereby identify crocodiloid eggs from the Upper Jurassic (Upper Kimmeridgian-Tithonian), from five sites in the fossil rich Lourinhã Formation, making these findings the oldest known so far. The Lourinhã Formation is a thick syn-rift siliciclastic succession, ranging from 200 to 1100 meters, dated from the Upper Kimmeridgian to Tithonian-earliest Berriasian, of fluvial-deltaic origin with some shallow marine incursions (Hill, 1988; Kullberg *et al*., 2013; Mateus *et al*., 2014), providing not only a suitable environment for a thriving and diverse fauna during the Late Jurassic, namely dinosaurs and crocodylomorphs, but also the conditions for the fossilization of extremely rare specimens, such as eggs and embryos (Mateus *et al*., 1997, 1998; Antunes *et al*., 1998; Martins *et al*., 2011; Araújo *et al*., 2012, 2013; Ribeiro *et al*., 2013).

2. Material and methodology

Eggshells were recovered from five localities in the Lourinhã Formation (Fig. 1): Paimogo N (ML760) and S (ML1795), Casal da Rola (ML1194), Peralta (ML195), and the nest from Cambelas (FCT-UNL706, replica stored at Museu da Lourinhã with collection number ML1582) (Fig. 2A-B). Stratigraphically, the highest sample is specimen FCT-UNL706, which was found in the Upper Tithonian Assenta Member, the uppermost unit of Lourinhã Formation. The samples from Peralta and Casal da Rola were collected in the Praia Azul Member, dated from the Upper Kimmeridgian-earliest Tithonian. The Paimogo samples are also from Upper Kimmeridgian age, but stratigraphically lower, from the base of the

Praia Azul Member (Paimogo S) and from the top of the Praia da Amoreira-Porto Novo Member (Paimogo N). From each locality, samples were selected, cleaned, and prepared for 30 µm thin sections as well as for SEM imaging. Macrophotographs were taken of the outer and inner surfaces of the eggshells, using both reflected and transmitted light; observation under transmitted light allowed for the observation of the pores (whenever present), and distribution and organization of the shell units (Fig. 2C). The observations under the petrographic microscope were done at Museu da Lourinhã (ML) and Faculdade de Ciências e Tecnologia da Universidade Nova de Lisboa (FCT-UNL). The SEM imaging was done at FCT-UNL and Universidade de Évora (UE).

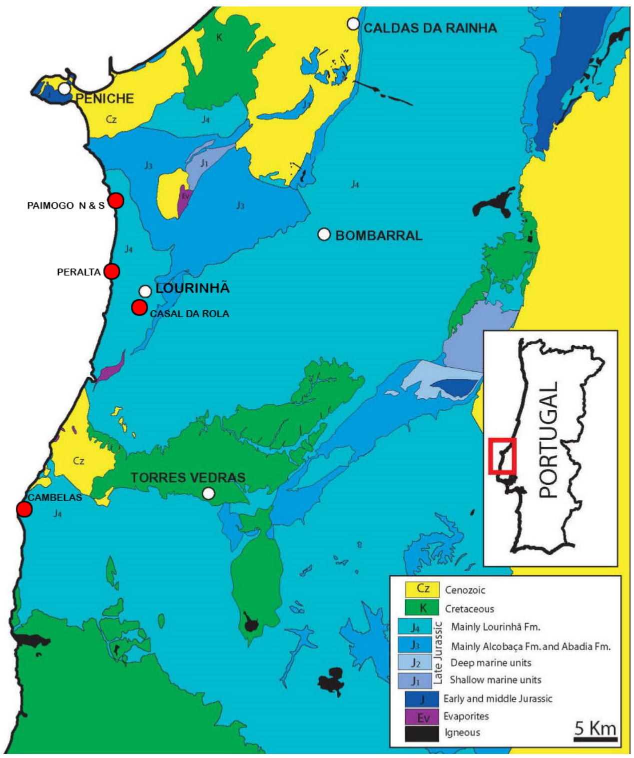


Fig. 1. Regional geological map, with the location of the fossil sites. Sites and specimens: Paimogo N: ML760; Paimogo S: ML1795; Casal da Rola: ML1194; Peralta: ML159; Cambelas: FCT-UNL706. Modified from Mateus, 2006.

Fig. 1. Mapa geológico regional, com a localização das jazidas fósseis. Jazidas e espécimes: Paimogo N, ML760; Paimogo S, ML1795; Casal da Rola, ML1194; Peralta, ML159; Cambelas, FCT-UNL706. Modificado de Mateus, 2006.

3. Results

Three layers (four when considering the diagenetic layer) can be differentiated in ML159, ML1194 and ML1795: an inner layer (IL), characterized by the darker coloration of the basal knobs of the mammilae, a medium layer (ML), where the typical crocodiloid tabular ultrastructure is identifiable, and an outer layer (OL), separated of the medium layer by a slightly darker thin band, usually a result of the uneven distribution of fibers that get packed closer together from bottom to top. All the samples observed under polarized light exhibit a wedge-shaped pattern for the shell units, widening from the IL, where the basal plate groups and nucleation centers are clearly distinguishable, to the OL. These wedge shaped shell units are faint and not always clearly defined. With crossed nicols, the samples exhibit a blocky extinction (see Marzola *et al*., 2014), defined by upside down triangles that alternately appear when rotating the samples. The outermost or diagenetic layer (DL) is marked by recrystallized and secondarily deposited calcite that in the FCT-UNL706 sample is almost absent and in the samples from Paimogo S is 144 µm thick on average. The thin sections show a faint, but distinguishable tabular ultrastructure, particularly in the ML of specimens from Paimogo S (Fig. 2D), Peralta and Casal da Rola. Paimogo N, however, displays strong sub-horizontal fractures, precluding an exact description. The very low thickness (163 µm) of FCT-UNL706 does not allow for identification of a clear, discernible ultrastructure. The Paimogo S samples are the thickest, measuring 323 µm, followed by Peralta (253 µm), Paimogo N (243 µm) and Casal da Rola (220 µm).

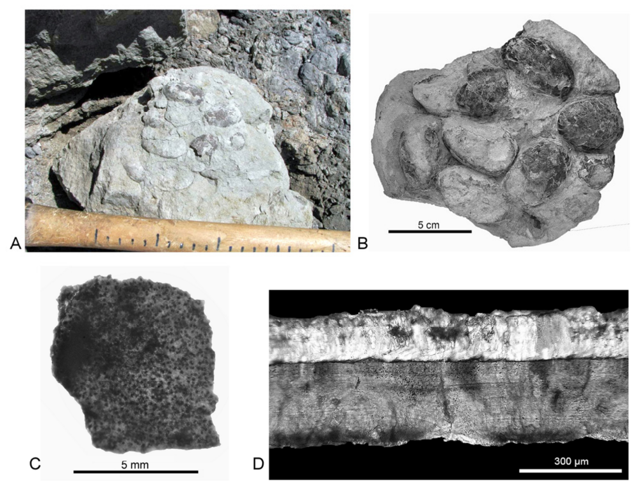


Fig. 2. A) Specimen FCT-UNL706, during excavation; B) Specimen FCT-UNL706, in detail; C) Inner surface of eggshell from FCT-UNL706 under binocular microscope and with transmitted light. No pores are visible, but the nucleation centers at the tip of the mammillae can be observed as the darker small dots on the eggshell, each marking a shell unit; D) 30 µm thin section of Paimogo S eggshell, observed under petrographic microscope (100x), with crossed nicols, where the diagenetic layer (the top layer) and the typical blocky extinction stand out. The tabular ultrastructure extends until the darker inner layer where the basal plate groups forming the mammillae are clearly observable. Faint wedge-shaped shell units widening from bottom to top are also distinguishable.

Fig. 2. A) Espécime FCT-UNL706, durante a escavação; C) Espécime FCT-UNL706, em detalhe; C) Superfície interna da casca de FCT-UNL706 sob lupa binocular e com luz transmitida. Poros não são visíveis, mas os centros de nucleação na ponta das mamilas podem ser observados como os pontos pequenos mais escuros, cada um marcando uma unidade de casca; D) Lâmina delgada de 30 µm de casca de Paimogo S, observada em microscópio petrográfico (100x), com nicóis cruzados, onde a camada diagenética (a camada de topo) e a típica extinção em bloco sobressaem. A ultraestrutura tabular estende-se até à camada interna, mais escura, onde os grupos de placas basais que formam as mamilas são claramente observáveis. Unidades de casca ténues em forma de cunha, alargando de baixo para o topo, são também distinguíveis.

The surface ornamentation is smooth, as expected in fossil crocodilian eggs (i. e. Hirsch, 1985; Antunes *et al*., 1998). When observed, as in the samples from Paimogo S and Casal da Rola, pores appear as very simple semicircular openings in the OL, crossing the entire shell in long, straight canals. While all the other samples are from fragmented eggshells, specimen FCT-UNL706 contains complete, well preserved ellipsoidal eggs. Under the SEM, the diagnostic features were not clearly observed, largely in part due to the amount of alteration and external recrystallization in the DL.

4. Discussion and conclusions

The material studied presents diagnostic features that allow us to identify it as crocodiloid morphotype (*sensu* Mikhailov, 1991, 1997) and ascribe it to the Krokolithidae oofamily (Kohring & Hirsch, 1996), and tentatively to the oogenus *Krokolithes*. Yet, the oogenus is at this point still uncertain, requiring a more detailed analysis, considering there seems to be characters, namely in specimen FCT-UNL706, such as thickness lower than 200 µm (167 µm in this case) and shell units wider than taller that closely resemble the oogenus *Bauruoolithus* (Oliveira *et al*., 2011). Nonetheless, the shell thickness, micro- and ultrastructure (i. e. the tabular lamination), ornamentation, and shape, clearly suggest a crocodilian affiliation, thus being the oldest crocodiloid eggshells known. The triangular shaped extinction pattern observed in the samples is a typical feature for crocodiloid eggshells (Hirsch, 1985; Antunes *et al*., 1998; Marzola *et al*., 2014). In general, extinct crocodylomorph eggs present the same basic structure and shape than extant crocodile eggs, and synapomorphies for eggs of Crocodylia are also valid for the broader clade Crocodylomorpha (Marzola *et al*., 2014). The main difference, however, is the smaller values of average eggshell thickness in non-crocodylian crocodylomorph. Because the eggshells date from the Upper Jurassic, a crocodylomorph, not eusuchian, origin is suggested. However, it is not possible to ascribe the egg material to a specific taxa. The diversity of crocodylomorphs in the Late Jurassic of Portugal is high: *Machimosaurus hugii* von Meyer 1837, *Lisboasaurus estesi* Seiffert 1973, *Lusitanisuchus mitrocostatus* Schwarz & Fechner 2004, *Theriosuchus guimarotae* Schwarz & Salisbury 2005, cf. *Alligatorium, Goniopholis baryglyphaeus* Schwarz, 2002 (see Mateus, 2013, and references therein). Considering the ratio between adult size and egg size, *Machimosaurus hugii*, over 9 meters long, seems an unlikely parent for this material. Thorbjarnarsson (1996) underlines such body size versus egg size relationships, although with a considerable degree of uncertainty. This restricts the size interval for possible egg layers, but still makes it impossible an exact correlation. Additionally, the structure of crocodilian eggshells is very conservative and its basic characteristics have remained unchanged since at least the Upper Jurassic. Previous studies have pointed out this morphological stability in crocodilian eggshells (Schmidt & Schöenwetter, 1943; Hirsch, 1985; Marzola *et al*., 2014). This would also explain why the diversity of ootaxa is low, since different species may be represented by the same ootaxon. All the specimens, excluding FCT-UNL706, were found associated with dinosaur eggs, possibly suggesting a reproductive strategy relationship between the two groups.

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