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Enigmatic Early Cretaceous ootaxa from Western Europe with signals of extrinsic eggshell degradation

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ABSTRACT

Crocodiloid eggshell is considered to be one of the most conservative among amniotes. This contrasts with the high body diversity observed within the crocodylomorph lineage, which extebds from the Triassic to the present. This incongruence raises a fundamental question in palaeology: is the crocodylomorph eggshell structure that conservative, or are there variations in this structure that have been misidentified in the fossil record or remain undiscovered to taphonomic biases?

In this paper we re-examine eggshells from the Barremian of northern Spain that were previously assigned to chelonians. We erect a new oogenus and oospecies, *Mycomorphoolithus kohringi*, characterized by thin eggshells with mushroom-shaped or inverted cone shell units with blocky extinction with smooth or slightly undulating outer surface, covered by a highly variable number of pores of irregular size and shape. These variations in the pore opening pattern are here interpreted as evidence of degradation of the eggshell during embryo development, a process that has only been described in modern alligatorids. After discarding its chelonian and dinosaurian affinities, we identify them as related to Krokolithidae, but with enough differences to justify exclusion from this oofamily. In addition, eggshells from the Berriasian of England previously reported as dinosaurian-spherulitic eggshells, are here assigned to undetermined oospecies of *Mycomorphoolithus*. Thus, the record of *Mycomorphoolithus* extends throughout most of the Lower Cretaceous. This long-surviving oogenus may represent eggshells of the non-eusuchian crocodylomorphs that are abundant in the microfossil sites where *Mycomorphoolithus* eggshells are found.

1. Introduction

AMNIOTE vertebrate eggshells are biomaterials composed of organic (mostly protein) and inorganic ($CaCO_3$ in the form of calcite or aragonite) phases (Hirsch, 1994a). The relative proportions of the organic and mineralized components determine the physical properties of the eggshell, from its rigidity to its water vapour conductance (Nys et al. 2004; Deeming, 2006). It is important to note that this proportion between mineral and organic components may vary during embryo development as a consequence of extrinsic and intrinsic degradation of the eggshell at least in some recent crocodylomorphs (Ferguson, 1981, 1982; Fernandez et al. 2013). Furthermore, the intricate relations between the protein network and the crystallographic fabric of the mineralized components result in many different textures, denominated ultrastructures, which may vary across the eggshell section, producing different eggshell morphotypes (Mikhailov, 1991). These variations in texture result in an anisotropic response of the eggshell to modifying agents, a characteristic that some crocodilians use to their advantage (e.g. making it easier to hatch the egg through partial degradation of the eggshell; Ferguson, 1981). The main consequence of the above is that the structure of fossil vertebrate eggshell is extremely diverse, and when modern analogues are not available it may be very difficult to relate egg material to taxa specific taxon. Moreover, eggshell in different states of degradation (either biological or diagenetic) may be misidentified as different ootaxa if the studied sample is not large enough.

The development of egg parataxonomy in the last part of the 20th century partially overcame these problems, as eggshells can be classified on the basis of their mineralogical and morphological features (Mikhailov, 1991, 1997; Hirsch, 1996; Köhring and Hirsch,

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1996). Subsequent work has demonstrated that high hierarchy levels of eggshell classification (at the oofamily level) usually correspond to high hierarchy taxonomic levels – usually above the family level (Zelenitsky and Thierrien, 2008; Mikhailov, 2013). This relation also shows that eggshell morphology is partly related with the taxonomy, thus genetic or epigenetic controlled and subject of evolution and natural selection. A canonical case of such a relationship between an oofamily and a high hierarchy taxonomic clade is provided by the oofamily Krokolithidae Köhring and Hirsch, 1996, which contains the eggshells of all fossil crocodylomorphs, which share all diagnostic characters with modern crocodilian eggshell, suggesting that crocodylomorph eggshell (crocodiloid basic type and morphotype, Köhring and Hirsch, 1996) is very conservative and has not changed much from the Jurassic to the present (Hirsch 1994b, Antunes et al., 1998, Marzola et al., 2015). This contrasts sharply with the wide diversity shown by body-fossils of crocodylomorphs, especially during the Mesozoic, when crocodylomorphs populated most of the ecosystems and occupied varied ecological niches, with subsequent adaptations and morphological changes (Stubbs et al. 2013). Nevertheless, recent work has postulated that crocodiloid basic type eggshells may be more variable than previously thought (Oliveira et al. 2011; Moreno-Azanza et al. 2014b).

In this paper we restudy eggshell materials previously assigned to the dinosaur spherulithic and testudoid morphotypes. Careful examination of new specimens does not support these assignments, as they share several characters with crocodyloid eggshells. Furthermore, we observe evidences of extrinsic degradation of the eggshell which provably occurred during incubation, a process seen in modern alligatorids.

2. Geological setting

The eggshells included in this study come from several Lower Cretaceous (Barremian) localities in the Maestrazgo Basin, a part of the larger Iberian Basin (Fig. 1) in the east Iberian Peninsula (Spain). Mesozoic sedimentation in the Iberian Basin took place within an intraplate extensional tectonic framework with two main rift stages (Late Permian to Early Jurassic and Late Jurassic to Early Cretaceous). During this second rifting stage, differential subsidence was caused by reactivation of late and post-Variscan or Triassic faults, and the formation of NW–SE and NE–SW normal faults (Liesa et al. 2006 and references within). This rifting cycle led to the creation of the Maestrazgo Basin, which can be subdivided into seven smaller sedimentary sub-basins. Sedimentation in these sub-basins was tectonically controlled and diachronous, and was not homogenized at the basin level until the Albian (Salas et al. 2001).

This complex tecto-sedimentary framework resulted in the partitioning of depositional environments, which supported the proliferation of vertebrate-rich ecosystems that have been recorded in some geological units from the Early Cretaceous (Estes and Sanchiz, 1982; Buscalioni et al. 2008; Canudo et al. 2010; Cuenca-Bescos et al. 2011). Of especial interest are some microfossil bonebeds (Buscalioni et al. 2008; Canudo et al. 2010; Gasca et al. 2012) from the Iberian Chain outcrops that have been regarded as time-averaged samples of their source communities (sensu Rogers and Brady, 2010) –i.e. they record the faunal and floral association of the ecosystem during periods of hundreds or thousands of years, instead of recording single punctual events. Fossil eggshell fragments are almost ubiquitous in the Lower Cretaceous microfossil bonebeds of Spain, and are usually present in high numbers, forming a significant part of the fossil assemblage (Moreno-Azanza et al. 2009a, 2009b; Canudo et al. 2010; Cuenca-Bescós et al., 2011; Gasca et al. 2012; Moreno-Azanza et al. 2014b, 2014c). The eggshells described in this study come from several early Barremian localities from the Maestrazgo Basin. The type material comes from the La Cantalera locality, located 2 km west of the village of Josa (Teruel, NE Spain), in an outcrop of the Barremian Blesa Formation (Canudo et al. 2010; Moreno-Azanza et al. 2014b, 2014c), within the Oliete Sub-basin. Additional material been collected from other microfossil sites from the Galve Sub-basin, more precisely from the upper part of the El Castellar Formation in the Galve Sub-basin (Canudo et al., 2012) and from the Morella Sub-basin (Mirambel Formation, Barremian in age, Castellote, Teruel). These bonebeds formed as attritional deposits through the progressive accumulation and concentration of disarticulated remains within low-energy depositional settings; more specifically, on a poorly drained floodplain in the case of the La Cantalera locality (Canudo et al. 2010; Moreno-Azanza et al. 2014b), and on shallow lacustrine deposits in others (Cuenca-Bescós et al. 2011).

The La Cantalera locality has yielded thousands of skeletal remains from at least 31 taxa (Canudo et al. 2010), and previous estimates based on preliminary studies suggest the presence of at least eight ootaxa are present (Moreno-Azanza et al. 2009a). However, the results presented here reduce this diversity to seven ootaxa, including the recently described Guegoolithus turolensis (Moreno-Azanza et al., 2014c). The La Cantalera site is the type locality of *Trigonoolithus amoae* (Moreno-Azanza, Canudo and Gasca 2014b). An oogenus of the oofamiliy Prismatoolithidae.

3. Materials and methods

The eggshell fragments included in this study were obtained by washing and sieving the deposits from four different localities. Over three tons of rocks from the La Cantalera locality were washed and sifted, whereas only 500 kg of rocks were processed each from the Menires and Camino Canales 2 localities. The sedimentary deposits were processed using 2% hydrogen peroxide and sieves of 2.0, 1.0 and 0.5 mm mesh. The eggshell fragments were sorted under a binocular microscope, and a total of 150 fragments were selected for this study. Thirty fragments were mounted, gold-coated and viewed with a JEOL 6400 SEM at the University of Zaragoza, using both secondary and backscattered electrons. X-ray diffraction analyses were used to confirm the calcite composition of the eggshells.

Twenty eggshell fragments were prepared as radial sections, and studied under an Olympus BX 41 petrographic microscope. In addition, cathodoluminescence (CL) analyses were performed with a Nikon Eclipse 50i POL optical microscope coupled with a cathodoluminescence system (model CL8200 Mk5-1) at the Institut Català d'Arqueologia Clàssica (ICAC; Tarragona, Spain). Cathodoluminescende images where edited using Adobe Photoshop, overexposing the whole picture + 5, due to the low general luminescence of the samples. .

The eggshell measurements were obtained from a sample of 96 eggshells, representative of each category, using a digital calliper. The pore surface areas were measured by digital analysis of scanning electron microscopy images using the software ImageJ. Due to the small mean size of the eggshell fragments (1.99 mm^2, SD = 0.89), and the fact that eggshell fragments tend to break at pore openings, two different approaches were used to estimate the number of pores of the eggshell (Table 1). First, only complete pore openings were counted, which is considered to underestimate the total pore opening count. Secondly, partially preserved pore openings were also counted. This number may be closer to the real porosity, but it overestimates the actual density of pores per square