



**João Paulo Vasconcelos Mendes Russo**

Licenciado em Geologia



## **Eggs and eggshells of Crocodylomorpha from the Upper Jurassic of Portugal**

Dissertação para obtenção do Grau de Mestre em Paleontologia

Orientador: Octávio Mateus, Professor Auxiliar, Faculdade de  
Ciências e Tecnologia da Universidade Nova de Lisboa

Co-orientadora: Ausenda Balbino, Professora Catedrática,  
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FACULDADE DE  
CIÊNCIAS E TECNOLOGIA  
UNIVERSIDADE NOVA DE LISBOA

**Janeiro 2016**

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## Abstract

Crocodylomorph eggs are relatively poorly known in the fossil record when compared with skeletal remains, which are found all over the world, or when compared with dinosaur eggs. Herein are described crocodyloid eggshells from the Upper Jurassic Lourinhã Formation of Portugal, recovered from five sites: Cambelas (clutch), Casal da Rola, Peralta (eggshell fragments), and Paimogo North and South (three partial crushed eggs and eggshell fragments). The clutch of Cambelas, composed of 13 eggs, is the only sample not found in association with dinosaur eggshells. Morphological characters of the eggshells described herein, such as shell units and microstructure, are consistent with the crocodyloid morphotype. As such, this material is assigned to the oofamily Krokolithidae, making them the oldest known crocodylomorph eggs so far and the best record for eggs of non-crocodylian crocodylomorphs. Two new ootaxa are erected, *Suchoolithus portucalensis* oogen. et oosp. nov., for the clutch of Cambelas, and *Krokolithes dinophilus*, oosp. nov., for the remaining eggshells. The basic structure of crocodylian eggshells has remained stable since at least the Late Jurassic. Additionally, the findings suggest previously unknown biological associations with contemporary archosaurs, shedding light on the poorly understood egg morphology, reproduction strategies and paleobiology of crocodylomorphs during the Late Jurassic.

**Keywords:** Crocodyloid; eggs and nest; nesting and reproduction; eggshells; Late Jurassic; Lourinhã Formation; Crocodylomorpha; Krokolithidae.



## Resumo

Ovos de crocodilomorfos são relativamente pouco conhecidos no registo fóssil, quando comparados com os restos esqueléticos, muito mais comuns, encontrados por todo o mundo. Apresentam-se aqui cascas de ovos de crocodilomorfos da Formação da Lourinhã, do Jurássico Superior de Portugal, recolhidas em cinco jazidas: um ninho de Cambelas e vários fragmentos de Casal da Rola, Paimogo (N e S), e Peralta. Três ovos esmagados parcialmente completos provêm também de Paimogo. O ninho de Cambelas, composto por 13 ovos, é a única amostra encontrada desassociada de cascas de ovos de dinossauro. A pesquisa revela que caracteres morfológicos diagnósticos, como unidades de casca e microestrutura, são consistentes com o morfótipo crocodilóide. Assim sendo, atribui-se este material à oofamília Krokolithidae, tornando-o nos mais antigos ovos de crocodilomorfos conhecidos até agora e também o melhor registo de crocodilomorfos não crocodilianos. Criam-se dois novos ootaxa, *Suchoolithus portucalensis* oogen. et oosp. nov., para os ovos do ninho de Cambelas, e *Krokolithes dinophilus*, oosp. nov., para as restantes cascas. A estrutura básica de cascas de ovos crocodilianos mantém-se estável desde pelo menos o Jurássico Superior. Adicionalmente, os dados sugerem associações biológicas desconhecidas previamente com arcossauros contemporâneos, incidindo uma nova luz sobre as pouco conhecidas morfologias de ovos, estratégias de reprodução e paleobiologia de crocodilomorfos durante o Jurássico Superior.

**Palavras-chave:** Crocodilóide; ovos e ninho; nidificação e reprodução; cascas de ovo; Formação da Lourinhã; Jurássico Superior; Crocodylomorpha; Krokolithidae.



## Abbreviation List

### Institutional

**FCT-UNL** – Faculdade de Ciências e Tecnologia da Universidade Nova de Lisboa;

**ML** – Museu da Lourinhã;

**UE** – Universidade de Évora;

### Nomenclatural

**dl** – diagenetic layer;

**ei** – elongation index;

**il** – inner layer;

**ml** – middle layer;

**n** – sample size or number;

**ol** – outer layer;

**sd** – standard deviation;

**st** – shell thickness;

**SEM** – scanning electron microscope



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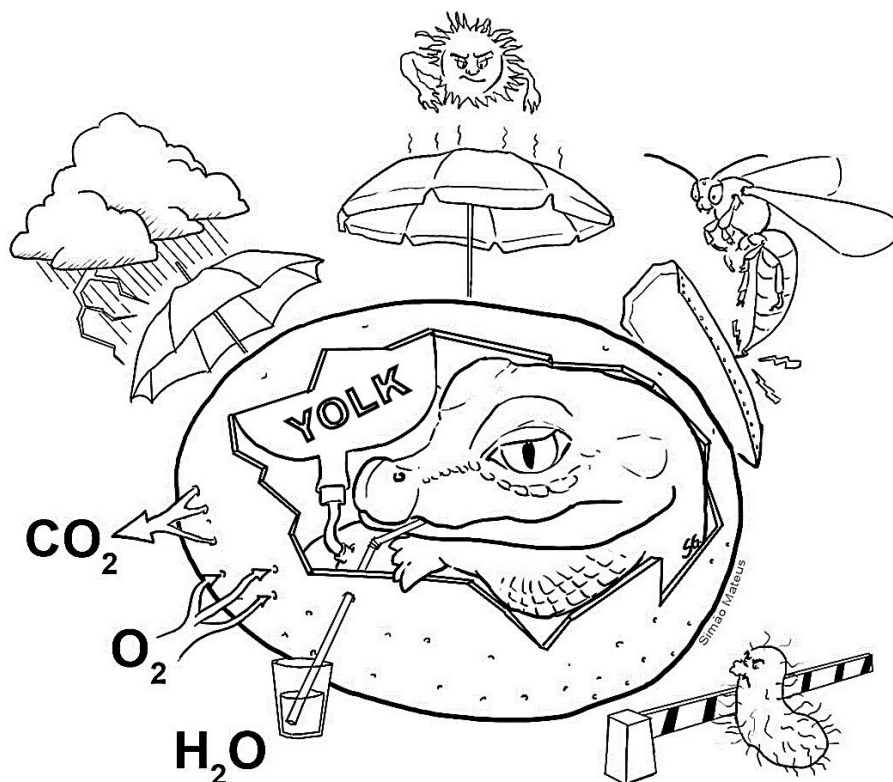
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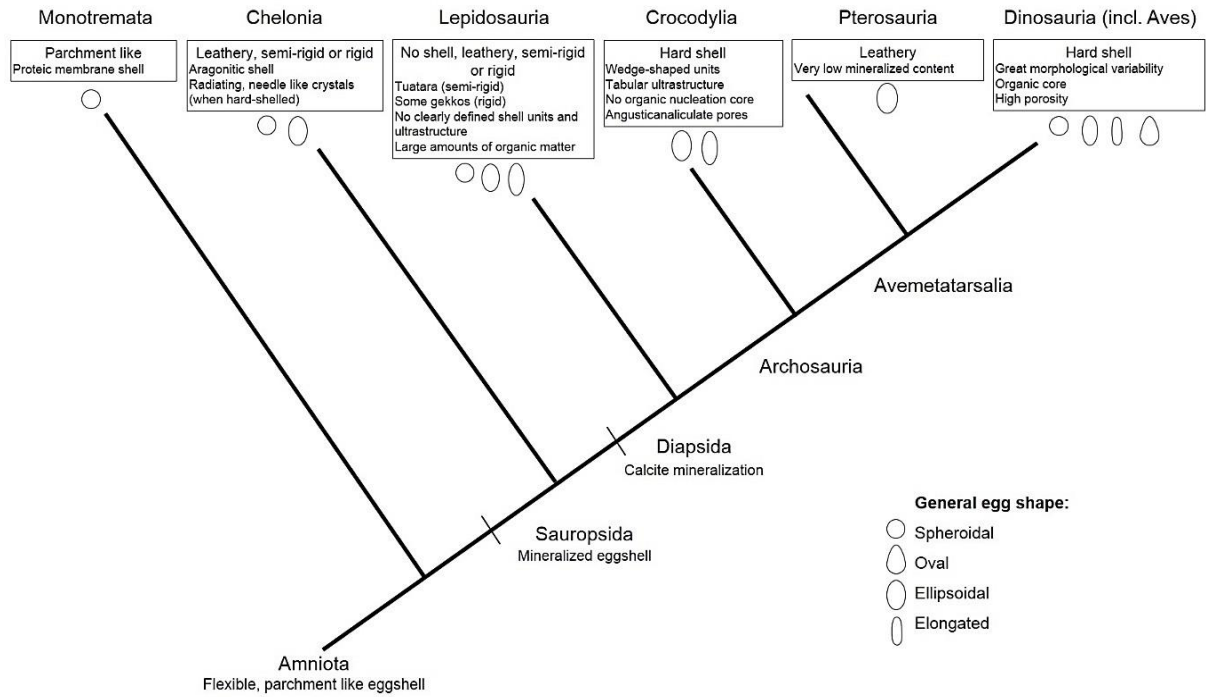
## 1. Introduction

The egg is much more than a mere means to an end, this being the birth of a new organism. It is a life pod, a self-sustaining capsule that provides a stable and safe environment in which the new life can grow and develop. This is even truer in the case of amniotes, a group of animals that spread across the globe and conquered every land ecosystem, becoming the dominant land vertebrates, due to one main factor: the appearance of extraembryonic membranes (i.e. Carroll, 1988; Kohring, 1995; Packard & Seymour, 1996; Carpenter, 1999; Benton, 2005; Sander, 2012). The appearance of a sturdy, porous outer layer encasing all the vital developmental structures is one of the most important developments marking the transition from a water dependent reproduction to a complete dry land environment. Carpenter (1999:31) elegantly summarizes “Shelled eggs are Nature’s way of packaging food for the embryo [...] in a neat, recyclable package”. The advantages of having a hard-shelled egg are illustrated in Figure 1.1. More importantly, the evolution of the hard-shelled egg can be traced throughout the evolution of the Amniota (Fig. 1.2). For example, Amniotes show a general trend for increased mineralization and complexity of the egg shell morphology (Kohring, 1995; Stewart, 1997; Carpenter, 1999; Marzola *et al.*, 2014), albeit this relationship is often not linear and extremely variable. Therefore, the study of the eggshell provides fundamental clues and insights not only into the reproductive strategies of the different groups of organisms, their evolution and paleoenvironment, but also, in groups such as crocodiles (*sensu* Crocodylomorpha), a direct correspondence between eggshell morphology and groups of egg-laying amniotes.



**Figure 1.1:** The hard-shelled egg as a life capsule, protecting the embryo from weather extremes, insects and nefarious microorganisms while allowing for gas and water exchanges. Illustration by Simão Mateus.



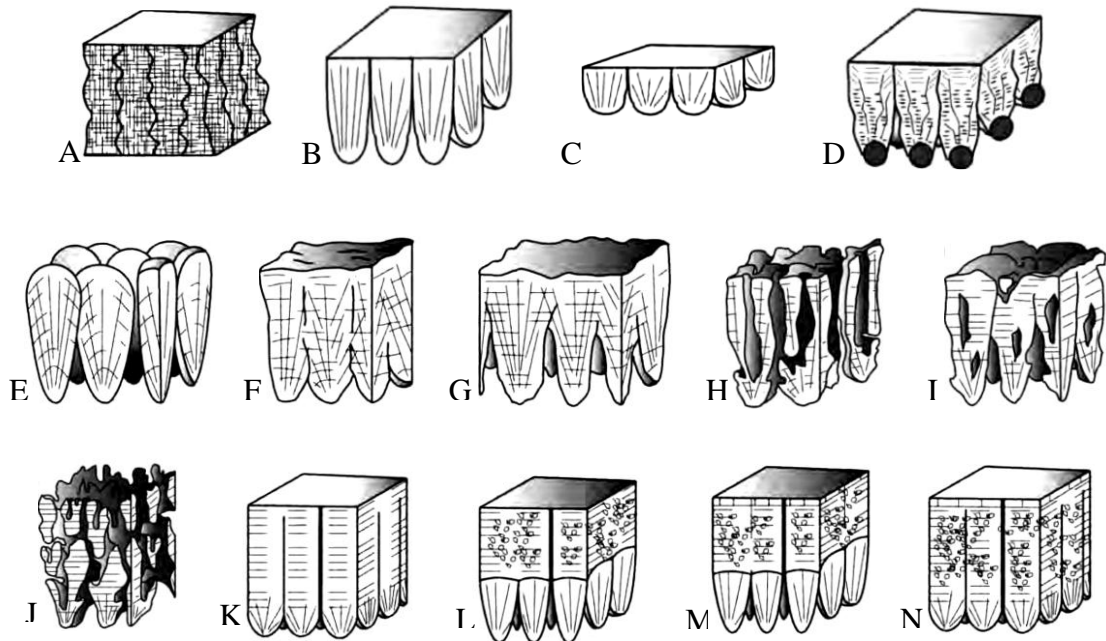


**Figure 1.2:** Phylogeny of the shelled egg based on most relevant morphological characters, according to the most consensual tree of the Amniota. See Marzola *et al.*, 2014, and references therein for further details.

### 1.1. Classification framework

The Crocodylomorpha are represented by 23 extant species of Crocodylia, a group that originated within Eusuchia during the Late Cretaceous (Campanian). Eusuchians themselves derived from mesoeucrocodylians during the Early Cretaceous (Barremian) (Benton & Clark, 1988; Carroll, 1988; Norell & Clark, 1992; Clark, 1994; Thorbjarnarson, 1996; Brochu, 2003; Benton, 2005; Oliveira *et al.*, 2011). Contrarily to the limited diversity of extant taxa, the fossil record of crocodylomorphs is extensive throughout the Mesozoic, originating in the Triassic and estimated in over 300 genera, with numerous different forms and a much more diverse ecological distribution (Oliveira *et al.*, 2011; www.fossilworks.com). However, fossil eggs of Crocodylomorpha are scarce and still poorly understood when compared with skeletal remains (or dinosaur eggs), even though crocodyloid eggshells have been identified worldwide. The crocodyloid morphotype was defined by Mikhailov (1991), but previous authors had already identified and described the diagnostic characters of crocodylian eggshells (Schmidt & Schönwetter, 1943; Erben, 1970; Erben & Newesely, 1972; Packard *et al.*, 1982; Ferguson, 1985; Hirsch, 1985). Since all major groups of egg-laying Amniota (e. g. Testudines, Lepidosauria, Crocodylomorpha, Dinosauria) were found to have a stable, distinct basic eggshell structure, the identification of different types of eggshell morphotypes and its variations (Fig. 1.3) prompted Mikhailov and colleagues (1996) to propose for the first time a uniform parasystematic classification system based on eggshell morphological characters, following a binomial nomenclature first adopted by Chinese paleontologists in 1975 (Zhao, 1975; Mikhailov, 1991; 1997; Mikhailov *et al.*, 1996; Carpenter, 1999) to describe fossil eggs. The same authors proposed adopting the term Veterovata (meaning “old eggs”), introduced by Vialov in 1972, for the parataxonomy of fossil eggs.





**Figure 1.3:** Eggshell morphotypes in Amniotes: A) gekonoid; B and C) testudinoid; D) **crocodiloid**; E – H) dinosauroid spherulitic; I – K) dinosauroid prismatic; L – N) ornithoid. Modified from Moreno-Azanza (2014).

A decade before the proposal for a uniform parataxonomy system, Hirsch (1985) erected the oogenus *Krokolithes* based on the micro- and ultrastructure observed in eggshells from the DeBeque Formation (Eocene) of Colorado and comparisons with eggshell characters of extant crocodiles, naming a new oospecies, *Krokolithes wilsoni*. However, the oofamily Krokolithidae was only named in 1996 by Kohring and Hirsch, who at the same time included another oospecies within *Krokolithes*, *K. helleri*. A third ootaxon, *Bauruoolithus fragilis*, within Krokolithidae was erected in 2011 by Oliveira *et al.*, from the Late Cretaceous Adamantina Formation of Brazil, with enough differences at the micro- and ultrastructural level, shell thickness, and size of the specimens to classify it as a distinct oogenus. Following the work of Moreno-Azanza and colleagues (Moreno-Azanza *et al.*, 2013; Moreno-Azanza, 2014), a new oogenus and oospecies is proposed for crocodiloid eggshells, *Mycomorhoolithus kohringi*. However, Moreno-Azanza (2014) places it as *incertae sedis*, very close to Krokolithidae. The same author recognizes at least one other Krokolithidae indet., in the Maastrichtian of Northern Spain, and two new unclassified oospecies in *Krokolithes* from the Lower Cretaceous of Spain. In spite of these recent discoveries, when comparing the number of known ootaxa referred to all the different groups for which fossil eggshells are known, stands out the extremely low diversity of oogenera and oospecies in the crocodiloid eggshell morphotype, ascribed to crocodylomorphs. Up to this point, there are 139 total accepted oospecies, of which 128 are attributed to dinosaurs, four attributed to Crocodylomorpha, six to turtles, and one to lizards (Appendix 1). This work adds to this knowledge and increases the diversity within Krokolithidae by describing and identifying one new oogenus and oospecies, *Suchoolithus portucalensis*, and one new oospecies of *Krokolithes*, *K. dinophyllus*, from the Lourinhã Formation of Portugal, thus extending the range of crocodiloid eggs to the Late Jurassic, the oldest so far (Appendix 2).



## 1.2. Geological and paleontological framework

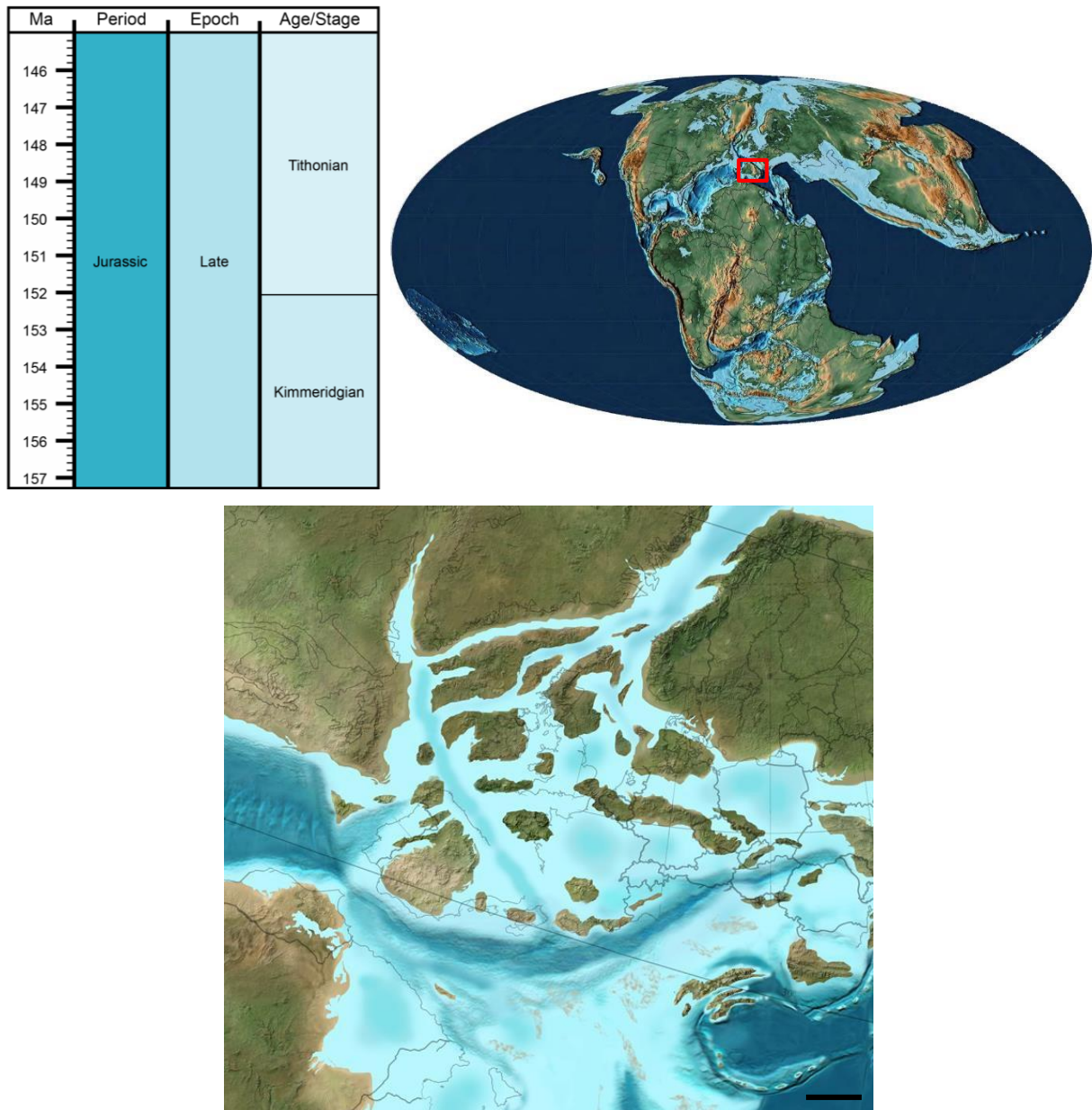
### 1.2.1. Paleogeographical context

The opening of the Central Atlantic Ocean and its northernmost sections, and the separation between the North American and Eurasian Plates occur gradually during the Jurassic. The Southern Pangea landmasses, such as the African and South American Plates (part of Gondwana), are still joined together, contrarily to Laurasia, which starts to break-up as early as the Late Triassic (e.g. Kullberg *et al.*, 2006, 2013; Tucholke *et al.*, 2007), in what is the first of three major phases. The other two take place during the Late Jurassic-Early Cretaceous and Early Cenozoic. The Late Jurassic-Early Cretaceous episode (165-115 Ma) is the most relevant, in terms of paleogeographical changes. It is during this time that the break-up of Pangea accelerates and sets in, with successive rifting events leading to ocean floor formation and spreading. The Iberian Plate is located in a focal point between the proto-Atlantic and the Tethys Sea (Fig. 1.4), and therefore is greatly conditioned by the major tectonic movements that characterize both domains during this period (e.g. Wilson, 1988; Kullberg *et al.*, 2006, 2013; Blakey, 2011; Scotese, 2014). The current position of Iberia is the result of successive northward movements and gradual counterclockwise rotation since the Late Jurassic, as a consequence of the rifting episodes and relative motion of North America, Eurasia, Iberia and Gondwana to each other. During the Late Jurassic, specifically during the Kimmeridgian-Tithonian interval (Fig. 1.4), Iberia was located at a much lower latitude than at present, at around 28° N (Myers *et al.*, 2012a; van Hinsbergen *et al.*, 2015).

The breakup of Pangea originated dramatic shifts in global climate, due to disrupted ocean currents, volcanic activity, eustatic sea level fluctuations (Moore *et al.*, 1992). The Jurassic (and the Mesozoic for that matter) was a significantly hotter period than at present, with higher sea levels. In fact, according to Moore *et al.* (1992), the eustatic sea level maximum for the Jurassic is reached during the Kimmeridgian, Iberia was one of the largest islands of the archipelago that constituted modern day Europe (Fig. 1.4), surrounded by a warm, shallow, epicontinental sea with several transgressive-regressive sequences (see Hill, 1989; Moore *et al.*, 1992; Martinius & Gowland, 2010; Myers *et al.*, 2012a, 2012b). The paleoclimate of Iberia, and more specifically Portugal, was warm and sub-humid, with strongly seasonal precipitation, with an average temperature of 31°C, with pedogenic carbonate deposits also attesting to this seasonality (see Martinius & Gowland, 2010; Myers *et al.*, 2012a, 2012b for further details). Should be noted that the Late Jurassic Morrison Formation, in Central Western United States, shows almost exactly the same characteristics that are observed in Portugal (Mateus, 2006; Myers *et al.*, 2012a, 2012b).

Within this tectonic and paleoclimatic setting, the conditions were in place for the development of multiple marginal Atlantic and Tethyan extensional basins, such as the Lusitanian Basin, that provided the necessary groundwork on which a diverse faunal community could thrive, and a depositional environment suitable during the Late Jurassic for extraordinary fossilization.





**Figure 1.4:** Upper left, standard chronostratigraphy of the Late Jurassic (produced with TSCreator, <http://www.tscreator.org>); upper right, paleogeographical reconstruction of the Tithonian, red rectangle marking the location of Iberia (modified from Scotese, 2014); bottom, European paleogeography during the Late Jurassic (modified from map reconstruction from Ron Blakey, Colorado Plateau Geosystems, Arizona, USA, <http://cpgeosystems.com/paleomaps.html>). Present day country borders represented by a black outline. Scale bar in bottom image: 400 km. Note: the landmasses in the Europe paleomap are slightly dislocated to the Southeast from the original position probably due to an error in the original reconstruction. Actually, the Northwest margins of the main Iberia landmass and country outlines should be aligned.

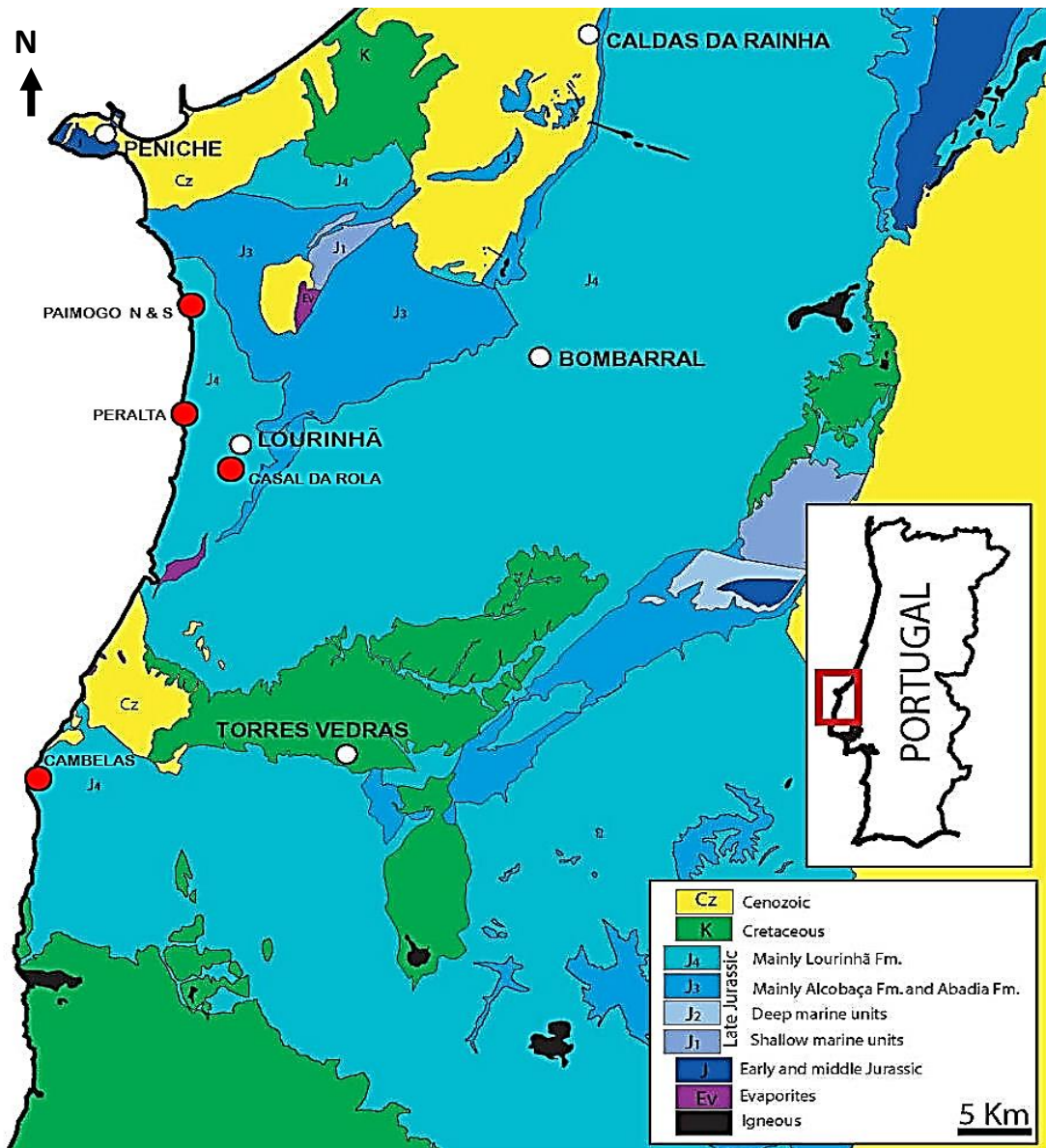
### 1.2.2. Geology of Lourinhã Formation

The study area (Fig. 1.5) comprises a massive continental depositional sequence, with some shallow marine intercalations, informally defined by Hill (1988) as the Lourinhã formation, replacing the designation used until then of “Grés Supérieures” named by Choffat in 1882 (Zbyszewski & Almeida, 1960; França *et al.*, 1961; França & Zbyszewski, 1963; Zbyszewski *et al.*, 1966; Mouterde *et al.*, 1979; Hill, 1988, 1989; Leinfelder, 1993; Leinfelder & Wilson, 1998; Rasmussen *et al.*, 1998; Kullberg, 2000; Kullberg *et al.*, 2006, 2013; Mateus, 2006; Schneider, 2009; Taylor *et al.*, 2013). It is a thick syn-rift



siliciclastic succession, ranging from 200 to 1100 meters, of Late Kimmeridgian to latest Tithonian-earliest Berriasian age (Wilson, 1979, 1988; Hill, 1988; Ravnås *et al.*, 1997; Reis *et al.*, 2000; Martinius & Gowland, 2010; Myers *et al.*, 2012a; Kullberg *et al.*, 2013; Mateus *et al.*, 2013; Salminen *et al.*, 2013; Taylor *et al.*, 2013). It was deposited during the third rifting episode of an extensional event related to the opening of the North Atlantic that climaxed during the Late Oxfordian-Early Kimmeridgian. The distensive regime conditioned the evolution of the Lusitanian Basin, from its inception during the Late Triassic (?Carnian) to the basin-fill influx in the earliest Late Cretaceous (Cenomanian), and compartmentalized it in smaller sub-basins (see Wilson, 1979, 1988; Leinfelder, 1986, 1993; Ravnås *et al.*, 1997; Leinfelder & Wilson, 1998; Rasmussen *et al.*, 1998; Kullberg, 2000; Kullberg *et al.*, 2006, 2013; Rey *et al.*, 2006; Myers *et al.*, 2012a; Mateus *et al.*, 2013; Taylor *et al.*, 2013). The exact lithostratigraphy of the Lourinhã Formation is complex, and even though it has been thoroughly studied, there is no general consensus regarding its formal lithostratigraphical units (for further details, see França & Zbyszewski, 1961; Mouterde *et al.*, 1972, 1979; Wilson, 1979; 1988; Hill, 1989; Leinfelder & Wilson, 1998; Manuppella *et al.*, 1999; Schneider, 2009; Martinius & Gowland, 2011; Mateus *et al.*, 2013; Taylor *et al.*, 2013). Herein the most recent stratigraphy is used, defined by Mateus *et al.* (2013) that describe three units in the Lourinhã Formation. The lowermost is the Praia da Amoreira-Porto Novo Member (Fig. 1.5), with marked upper delta, floodplain and alluvial facies, representing the uppermost Kimmeridgian (i. e. Hill, 1989; Mateus *et al.*, 2013, and references therein for further details). The Paimogo North specimen ML760 comes from the top of this unit, just below the boundary between it and the overlaying unit. The latter unit is the Praia Azul Member (also appearing in literature as Sobral Member, i.e., Manuppella *et al.*, 1999; Ribeiro *et al.*, 2013), a mainly marl-mudstone unit with few sandstone levels, which was deposited in the latest Kimmeridgian to earliest Tithonian. This unit is defined by three marly-carbonate layers, rich in brackish bivalve associations, which indicate brief yet relevant transgressive episodes, the lower and upper levels used as base and ceiling markers (Fig. 1.6). The Kimmeridgian-Tithonian boundary and a maximum flooding surface in the Lusitanian Basin is defined, according to Schneider *et al.* (2010), by the middle carbonate layer with *Protocardia gigantea*. Specimen ML1795, from Paimogo South, was recovered from the lowest mudstone level, at the base of this unit. The uppermost unit of the Lourinhã formation is the Assenta Member (Fig. 1.6), dominated by mudstones, often with levels of caliche, pedogenic carbonate concretions evidence of paleosoils (either forming high resistance levels or the reworked nodules forming conglomerates at the base of channels), intercalated with channelized cross-bedded sandstones, including large scale point-bars, and thin flat lenses or tabular crevasse and levee bodies (Mateus *et al.*, 2013). This unit represents the late Early Tithonian to earliest Berriasian (Mateus *et al.*, 2013; Salminen *et al.*, 2013). The clutch FCT-UNL706 was recovered in this unit, on a loose block coming from an alternating sequence of mudstone and fine to very fine sandstone, which stratigraphically were identified as CB01 through CB15 (Fig. 1.7).





**Figure 1.5:** Regional geological map, with the location of the fossil sites (red circles). Sites and specimens: Paimogo N: ML760; Paimogo S: ML1795; Casal da Rola: ML1194; Peralta: ML159; Cambelas: FCT-UNL706. Modified from Mateus, 2006.

### 1.2.3. Faunal assemblage (crocodylomorphs and associated fauna)

The Kimmeridgian-Tithonian formations of Lourinhã and Alcobça are known by the rich vertebrate assemblage increasingly reported since the 19<sup>th</sup> century (Lapparent & Zbyszewski, 1957). This includes at least 34 species of Mammaliaformes, 18 taxa of Dinosauria, 7 of Crocodylomorpha, 6 of Lepidosauria, and 5 of Testudines (see Mateus, 2006, 2008; Ribeiro & Mateus, 2012, and the online database at [www.fossilworks.org](http://www.fossilworks.org), but numbers may change according to the accepted validity for each taxa). Moreover, numerous tracks, trackways (see, as example, Milàn *et al.*, 2005), and eggs have been reported. The faunal assemblage is somewhat similar to that of the Morrison Formation (USA) with shared genera such as *Allosaurus*, *Ceratosaurus*, *Goniopholis* and others. Myers *et al.* (2012b) show that the paleodiversity of these two formations is correlated with soil  $p\text{CO}_2$  productivity and positively linked to water availability.





**Figure 1.6:** Outcrops of Paimogo (top), Peralta (middle) and Cambelas (bottom). The red arrows in the photos of Peralta and Cambelas indicate the site of the eggs. In Peralta, the red line marks one of the three shallow marine levels that characterize the Praia Azul member.

#### 1.2.4. Record of fossil crocodyloid eggs

Fossil crocodyloid eggs and eggshells have been identified worldwide (Appendix 4, Table 3). In Europe, eggshells referred to this morphotype are reported from the Lower Miocene of Ulm and Middle Eocene of Geiseltal, Germany (Heller, 1931; Kohring, 1992b; Kohring & Hirsch, 1996), from the Upper Cretaceous of France (Kerourio, 1987; Garcia, 2000), from the Upper and Lower Cretaceous of Spain (Kohring, 1990b, 1992a; Moratalla, 1993; Buscallioni *et al.*, 2008; Canudo *et al.*, 2010; Moreno-Azanza *et al.*, 2013, 2014; Moreno-Azanza, 2014), and possible crocodylian eggshells from the top of the Lulworth Formation (Berriasian) of the Purbeck Limestone Group (Wealden) of England (Ensom, 1997); in North America, eggshells were found in the Middle Eocene DeBeque and Bridger Formations, from Colorado and Wyoming, respectively (Hirsch, 1985; Hirsch & Kohring, 1992), in the Upper Cretaceous Two Medicine and Fruitland Formations, from Montana and New Mexico, respectively (Hirsch & Quinn, 1990; Jackson & Varrichio, 2010; Tanaka *et al.*, 2011), and in the Lower Cretaceous (Albian) Glen Rose Formation from Texas (Rogers, 2001). Erikson (1978) described what he considered





a probable crocodylian egg from the Upper Cretaceous of Wyoming, but that identification is highly doubtful based on the inner filling of the specimen (Hirsch & Kohring, 1992). It should also be noted that Hirsch (1994:143) mentions very badly preserved, highly uncertain crocodylian-like eggshells from the Upper Jurassic Morrison Formation which according to the author "... show large shell units with indications of wedge-like structures similar to those in crocodylian eggs [...] the extinction pattern is also similar to that seen in crocodylian eggs. However, before a final identification is made, the specimens must be studied in more detail". In South America, crocodylomorphs eggshells are reported from the Upper Cretaceous Araçatuba and Adamantina Formations of Brazil (Ribeiro *et al.*, 2006; Oliveira *et al.*, 2011) and Cajones Formation of Bolivia (Novas *et al.*, 2009), and from the Lower Cretaceous (Aptian) Crato Member of the Santana Formation of Brazil (Ribeiro *et al.*, 2011). In Asia, Patnaik & Schleich (1993) report crocodyloid eggshells from the Pliocene in the Upper Siwaliks of India. In the Upper Miocene Chinji Formation from Pakistan, a complete crocodylomorph egg was described by Panadés I Blas & Patnaik in 2009. Crocodylian eggshells were found also in the K-Pg boundary Intertrappean Beds and the Maastrichtian Lameta Formation from India (Singh *et al.*, 1998; Prasad *et al.*, 2015; Srivastava *et al.*, 2015).

### 1.2.5. Fossil eggs in Portugal

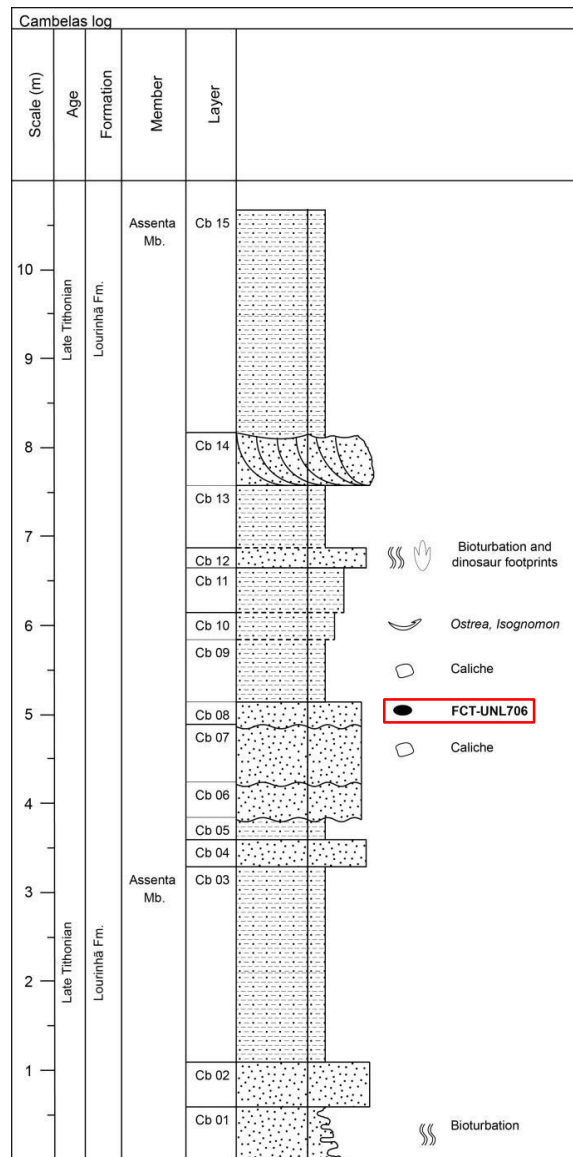
The fossil record of egg material from Portugal is extensive and exceptionally preserved, albeit almost exclusively temporally restricted to the Late Jurassic. The only mention of fossil eggshells in Portugal from a different age is from Rodrigues *et al.* (2008) that in passing refers to undetermined eggshell fragments recovered from the Lower Barremian Boca do Chapim Formation. So far, there are nine localities that produced eggshells and eggs, eight of which are in the Lourinhã formation, where the fossil egg and embryo record is well documented (Mateus *et al.*, 1997, 1998; Antunes *et al.*, 1998; Manupella *et al.*, 1999; Ricqlès *et al.*, 2001; Castanhinha *et al.*, 2009; Martins *et al.*, 2011; Araújo *et al.*, 2012, 2013; Ribeiro *et al.*, 2013). Only the eggshells from the site of the Guimarães coal mine, in Leiria, and described as testudinoid by Kohring (1990, 2000), are from the Alcobaça Formation. In the sites of the Lourinhã Formation, complete eggs and nests were found at Paimogo, Peralta, Porto das Barcas, and Cambelas, with additional eggshell fragments recovered from Casal da Rola, Porto Dinheiro, Porto das Barcas I and II, Zimbral and Valmitão. With the exception of Cambelas, an isolated clutch herein identified as of crocodylomorph origin, every other locality produced dinosaur eggshells as well. Furthermore, the nests recovered at Paimogo, Peralta and Porto das Barcas revealed embryo bone fragments that allowed a more accurate classification of the specimens as *Lourinhanosaurus antunesi* Mateus 1998 and *Torvosaurus gurneyi* Hendrickx & Mateus 2014 (Mateus *et al.*, 1997, 1998; Ricqlès *et al.*, 2001; Castanhinha *et al.*, 2009; Martins *et al.*, 2011; Araújo *et al.*, 2012, 2013; Hendrickx & Mateus, 2014). In Paimogo, Peralta and Casal da Rola, thinner, smaller eggshell fragments were recovered, associated with the dinosaur specimens. These eggshells are analyzed and identified in this



study as crocodyloid morphotype (Schmidt & Schönwetter, 1943; Mikhailov, 1991, 1996, 1997; Carpenter, 1999).

### 1.2.6. Sites with crocodylomorph eggs in Portugal

Fossils crocodylomorph eggs are herein described from five locations in Portugal (Fig. 1.4), from North to South, which are also older northwards: 1) Paimogo North (ML760), Lourinhã, Late Jurassic (latest Kimmeridgian) top of the Praia da Amoreira-Porto Novo member; 2) Paimogo South (ML1795), Lourinhã; Late Jurassic (latest Kimmeridgian) base of the Praia Azul Member, Lourinhã formation,  $152.1 \pm 0.9$  Ma; 3) Casal da Rola (ML1194), Lourinhã, Late Jurassic (latest Kimmeridgian-earliest Tithonian) Praia Azul Member,  $152.1 \pm 0.9$  Ma; 4) Peralta (ML195), Lourinhã, Late Jurassic (latest Kimmeridgian-earliest Tithonian) Praia Azul Member,  $152.1 \pm 0.9$  Ma (*sensu* Mateus *et al.*, 2013); 5) Cambelas, Torres Vedras. Assenta Member, Lourinhã formation, Upper Jurassic (Tithonian), 145 Ma.



**Figure 1.7:** Stratigraphic log of the Cambelas section. The red rectangle marks the provenance layer of specimen FCT-UNL706.



## 2. Objectives

The main aim of this study is to thoroughly describe and identify eggs and eggshells recovered from 5 localities in the Lourinhã Formation, considered to have a crocodylian affinity in a previous preliminary analysis. One of the goals of this project is to confirm the previous diagnostic of the crocodylian origin, and add newer findings to the material studied before, through comparisons with the published literature of crocodylian eggs and eggshells from all over the world. Furthermore, by characterizing the eggshell morphological structure and correctly ascribing the material to an eggshell morphotype and specific ootaxa, the study will shed a new light on the evolution of the crocodyloid eggshell in the last 150 Ma while, at the same time, revealing what will be the oldest known crocodyloid eggshells. Finally, based on the known Crocodylomorpha diversity for the Lourinhã Formation and correlations in extant representatives of the group between egg and body morphometric parameters, this study tries to determine if it is possible to use the same morphometric correlations in fossils and, if so, assign the eggs to a putative parent crocodylomorph, or at least narrow down the size interval of the animal.



### 3. Material and methods

The crocodyloid eggshells reported herein were found and collected between 1987 and 2012 from five localities in the Lourinhã Formation: Paimogo North (ML760) and South (ML1795), Casal da Rola (ML1194), Peralta, and the clutch from Cambelas (FCT-UNL706). The latter also has a cast replica stored at Museu da Lourinhã, specimen number ML1582. The nest presents the only preserved clutch, with 13 mostly well preserved eggs and eggshells, and it is the only specimen not found associated with dinosaur egg material. In the other four localities, crocodylomorphs eggshells have been found associated with theropod dinosaur eggs and nests. Only three partial crushed eggs were recovered, all of them from the Paimogo localities. The rest of the material is the most abundant and consists of numerous weathered, very small fragments (less than 25 mm<sup>2</sup>), making an estimation of the eggs original size and exact shape impossible. The fragments from Casal da Rola and some of the Paimogo material were found loose and were collected at the surface or by sieving sediment from the sites. From each locality, samples were selected and cleaned using an ultrasound bath, and prepared for standard 30 µm thin radial sections using EpoThin resin and hardener, mixed in a proportion of 5:2, as well as for scanning electron microscopy (SEM). Macro photographs were also taken of the outer and inner surface of the eggshells, using both reflected and transmitted light in order to observe the pores and the distribution of the shell units. Backlighting has been used with tangential eggshell samples in order to identify when possible the distribution of shell units, mammillae and nucleation centers, and detect the presence and shape of pores. Marzola *et al.* (2014) have used this technique with extant crocodylian eggshells (see Marzola *et al.*, 2014, Fig. 1f–h, 2d and f, and 3e). The observations under the petrographic and binocular microscopes were done at ML and FCT-UNL. The SEM imaging was done at FCT-UNL using a JEOL JSM T330A scanning electron microscope and at UE using a Hitachi SN-3700 scanning electron microscope. Finally, comparisons were done, whenever possible, with known fossil crocodyloid eggshells already published and the morphometric parameters were compiled in Table 2 (Appendix 2), as well as body and egg data for 23 extant species of crocodylomorphs (Appendix 3). For purposes of providing a clear picture of the state of parataxonomy classification for eggshells, Table 1 (Appendix 1) gathers all the accepted ootaxa for all the basic shell types. Additionally, information on the Late Jurassic Crocodylomorpha present in the Lourinhã Formation was collected in order to perform a theoretical exercise to see if it would be possible to establish putative correlations between eggs and parent taxa, through linear regressions based on previous works.



## 4. Systematic Paleontology

### 4.1. *Suchoolithus portucalensis* oogen. et oosp. nov.

#### SYSTEMATIC PALEONTOLOGY

REPTILIA Laurenti 1768

LORICATA Merrem 1820

CROCODYLOMORPHA Hay 1930

Genus indet.

#### PARA-SYSTEMATIC PALEONTOLOGY

Oofamily KROKOLITHIDAE Kohring &

Hirsch, 1996

*Suchoolithus portucalensis* oogen. et oosp. nov.

**Diagnosis of oogenus** – Krokolithid eggs with small ellipsoid shape with blunt poles with an ei of 1.62 (average polar and equatorial length, 42 and 26 mm, respectively); smooth outer surface; shell thickness averaging 163  $\mu\text{m}$ ; absence of pore openings and canals; shell units tightly packed together and mostly wider than higher, with almost no interstices; absence of tabular ultrastructure.

**Diagnosis of the oospecies** – Same than oogeneric diagnosis.

**Etymology** – *Suchoolithus* derives from *suchus*, the Latinized Greek word for crocodile, and *oolithus* means “egg stone”, from Ancient Greek. *Portucalensis* refers to the country of origin.

**Holotype** – FCT-UNL706, a clutch with 13 eggs on a very fine gray sandstone block. Replica stored at Museu da Lourinhã, specimen number ML1582

**Type locality** – 39° 04' 58,84" N; 9° 25' 01,58" W, Cambelas, Torres Vedras.

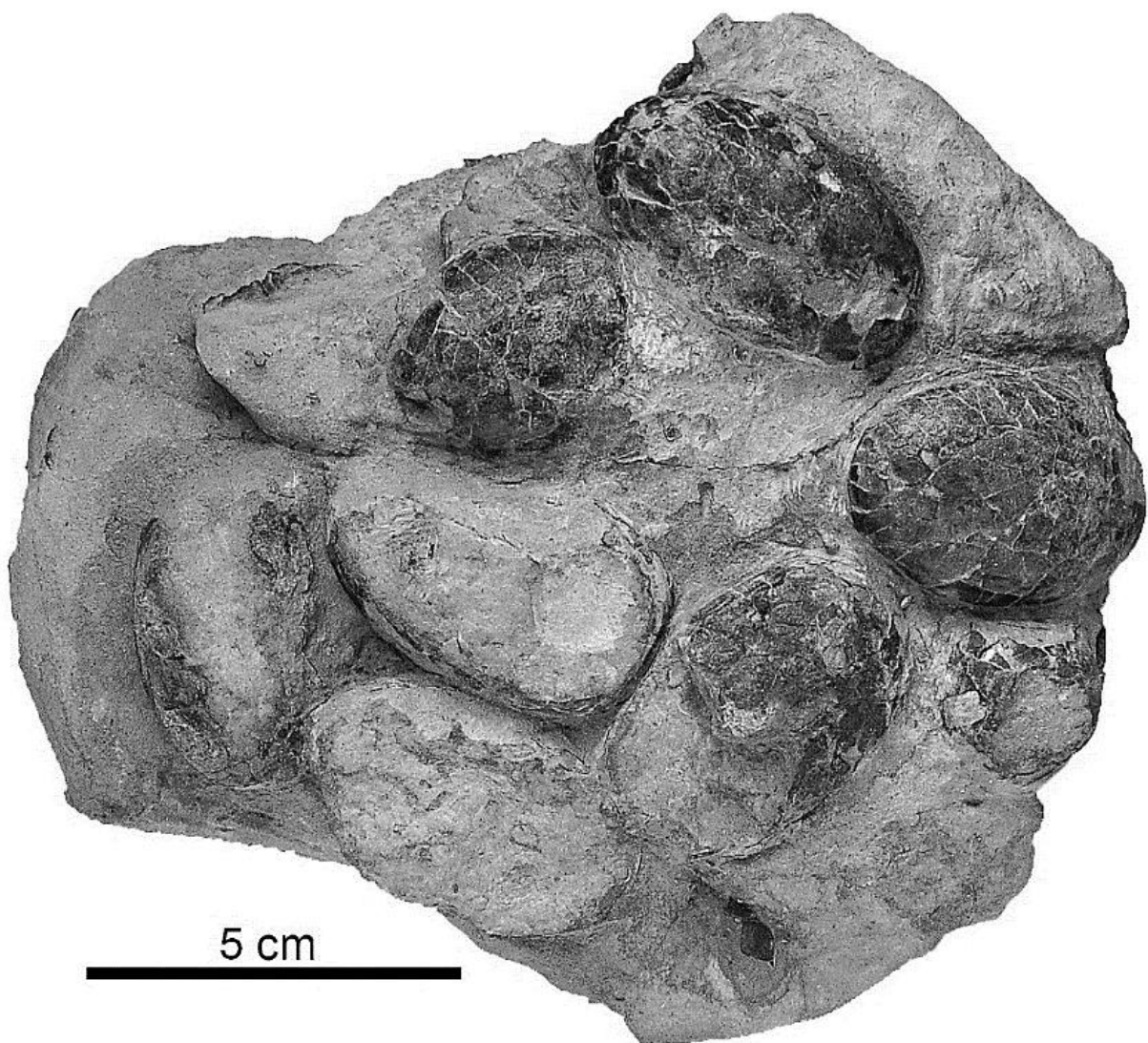
**Type horizon and age** – Assenta Mb., Lourinhã Fm., Upper Jurassic (Tithonian), 145 Ma.

#### 4.1.1. Description

FCT-UNL706 is a clutch with 13 eggs (Fig. 4.1), seven of which are well preserved and intact whilst the remaining are made up of *in situ* eggshell fragments. Three of the eggs are only visible on the underside of the clutch. With the exception of two eggs, which are oriented vertically, all the others are oriented horizontally. The eggs are dark brown, standing out from the very fine, light gray sandstone matrix, and show a fractured and cracked surface. Nonetheless, the clutch is well preserved and exhibits a low degree of diagenetic alteration. The eggs are ellipsoid, with blunt ends, measuring 42 mm long ( $n = 7$ ,  $sd = 1.5$  mm) and 26 mm wide ( $n = 7$ ,  $sd = 1.3$  mm), with an ei (polar or long axis / equatorial or small axis) of 1.62. The external surface seems smooth on a macroscopic level, but on macro photography and under the binocular microscope, presents a microscopic ornamentation very similar to compactituberculate (Fig. 4.2-A). Mikhailov (1997:36) describes this type of ornamentation as “shell surface is covered completely with dome-shaped tubercles, which are the apical parts of spherulitic shell units”. Pore openings or a pore system were not detected in the areas where the covering sediment was removed, even though in Figure 4.2-C what seems to be a pore canal can be seen. The internal surface

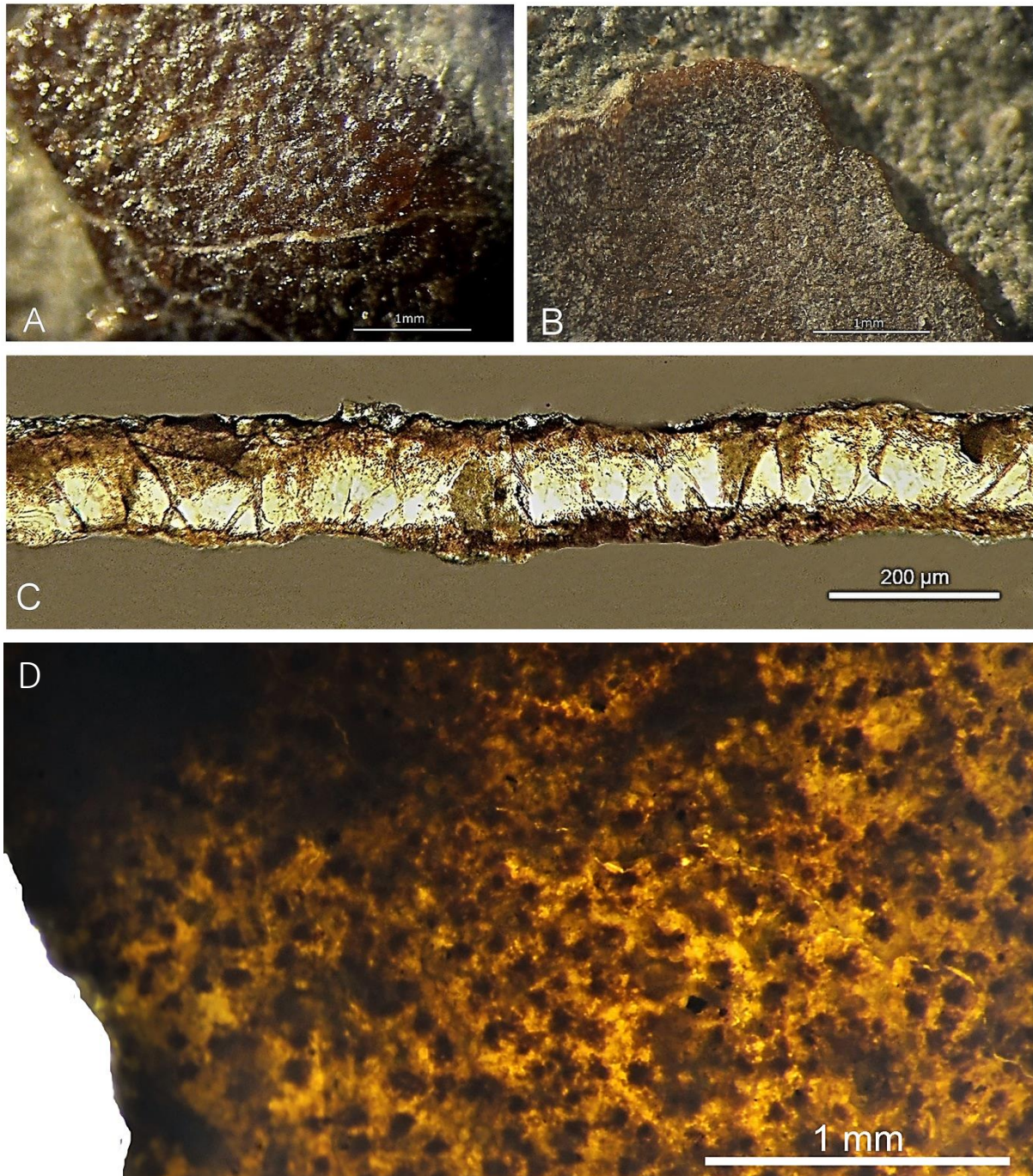


is marked by the constant and abundant presence of the tips of the shell units (Fig. 4.2-B) when not covered by sediment. The shell thickness is  $163\ \mu\text{m}$  ( $n = 80$ ,  $sd = 17.3\ \mu\text{m}$ ). In radial section, the wedges of the shell units are clearly visible, interlocked and closely packed together with little space between them (Fig. 4.2-C). The distinctive crocodyloid tabular ultrastructure is absent. The basal plate groups are observable, although not through the entire section. The triangular extinction pattern is present when observed under cross-polarized light (Fig. 4.2-C). Observations under plane-polarized light were too dark to reveal any useful information. In Figure 4.2-D, through backlighting on a tangential shell section, the darker mammillae tips, corresponding to the basal plate groups, are clearly visible and show a distribution identical to what is observed today in crocodyloid eggs (Marzola *et al.*, 2014, Figures 1f, 2d, and 3e).



**Figure 4.1:** Clutch of *Suchoolithus portucalensis* (FCT-UNL706). The shape and preservation of the specimen indicates an unhatched clutch.





**Figure 4.2:** Macro photographs and thin section of *S. portucalensis*; A) external surface of the shell, B) internal surface of the shell, C) thin section under petrographic microscope in cross-polarized light, D) macro photograph of eggshell under binocular, with backlighting, where the tips of the individual shell units (dark spots) can be seen.

#### 4.2. *Krokolithes dinophilus* oosp. nov.

##### SYSTEMATIC PALEONTOLOGY

REPTILIA Laurenti 1768

LORICATA Merrem 1820

CROCODYLOMORPHA Hay 1930

##### PARA-SYSTEMATIC PALEONTOLOGY

Oofamily KROKOLITHIDAE Kohring and

Hirsch, 1996

Oogenus *Krokolithes* Hirsch, 1985



Genus indet.

*Krokolithes dinophilus* oosp. nov.

**Diagnosis of the oospecies** – *Krokolithes* with an average eggshell thickness of 215  $\mu\text{m}$  and low pore density (one pore per  $\text{cm}^2$  or less).

**Etymology** – *dinophilus* refers to the occurrence of these eggshells with dinosaur eggshells.

**Holotype** – ML760

**Type locality** – Paimogo

**Type horizon and age** – Praia Azul Mb., Lourinhã Fm.,  $152 \pm 0.9$  Ma

**Referred material and localities** – ML195, under 20 eggshell fragments, from Peralta, Lourinhã; ML1194, between 10 and 30 eggshell fragments, from Casal da Rola, Lourinhã; ML1795, two partial crushed eggs and between 147 and 200 eggshell fragments, from Paimogo, Lourinhã.

**Locality and age** – Paimogo N (ML760), Lourinhã, Late Jurassic (latest Kimmeridgian) top of the Praia da Amoreira-Porto Novo Mb.,  $152.1 \pm 0.9$  Ma; Paimogo S (ML1795), Lourinhã; Late Jurassic (latest Kimmeridgian) base of the Praia Azul Mb, Lourinhã Formation,  $152.1 \pm 0.9$  Ma; Casal da Rola (ML1194), Lourinhã, Late Jurassic (latest Kimmeridgian-earliest Tithonian) Praia Azul Mb.,  $152.1 \pm 0.9$  Ma; Peralta (ML195), Lourinhã, Late Jurassic (latest Kimmeridgian-earliest Tithonian) Praia Azul Mb.,  $152.1 \pm 0.9$  Ma (*sensu* Mateus *et al.*, 2013);

#### 4.2.1. Description

Here are described egg or eggshell from four localities, under the numbers ML195, ML760 (oospecies type), ML1795, ML1194, which represent the same basic morphology and are referred as *Krokolithes dinophilus* n. oosp.

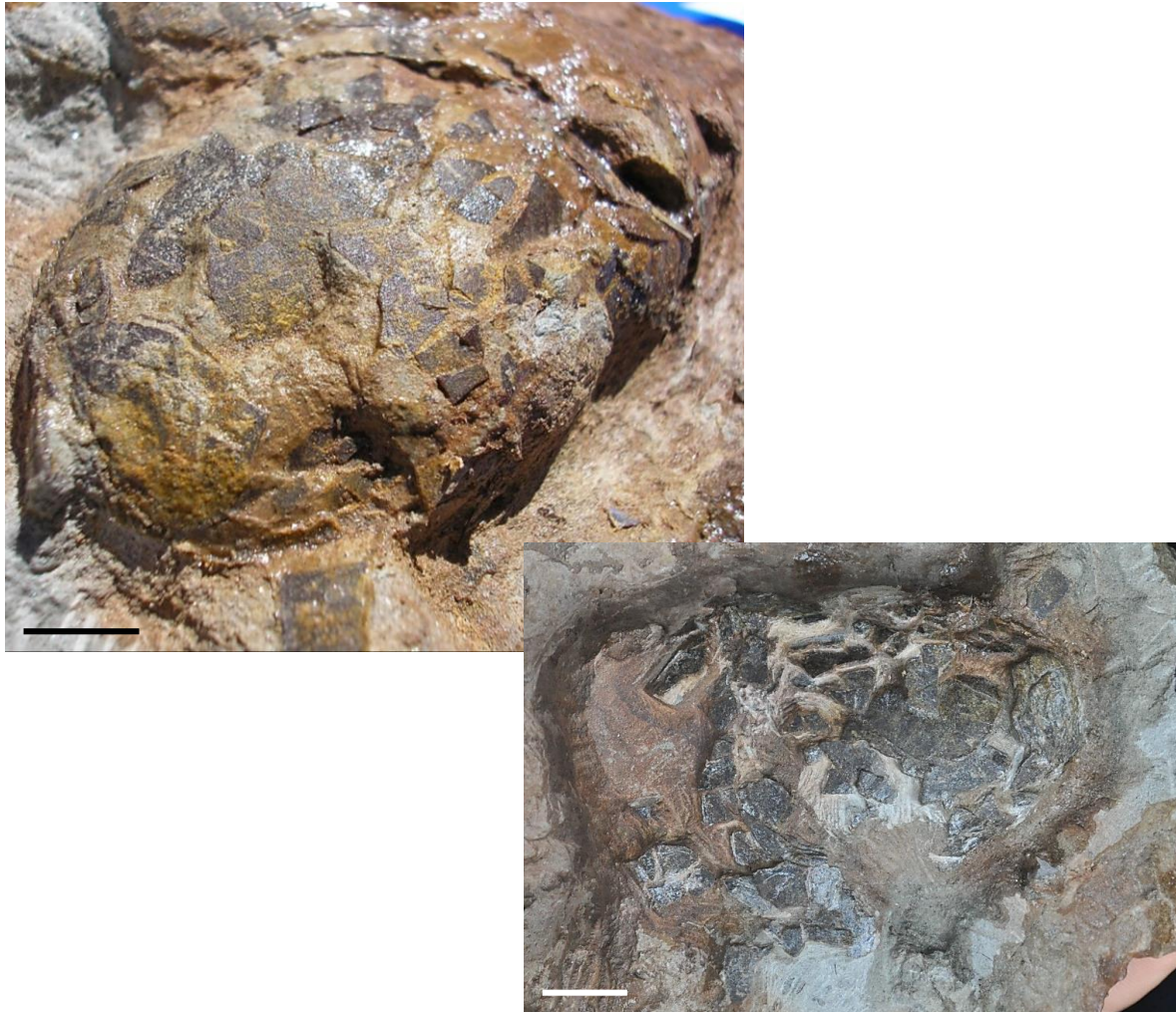
**ML760** – ML760 (oospecies type) is a crushed egg (Fig. 4.3) found in association with a theropod nest, attributed to *Lourinhanosaurus*, in the locality of Paimogo (i.e. Antunes *et al.*, 1998; Mateus *et al.*, 1998; Ricqlès *et al.*, 2001). The egg is encased in a small block of reddish mudstone with some caliche nodules. It measures 70 mm in length (polar axis) and 40 mm in diameter (equatorial axis), with an ei of 1.75. Even though crushed, the egg shows remarkable preservation, retaining a characteristic ellipsoid shape, as well as a smooth eggshell, a common trait in fossil crocodylomorph eggs (Hirsch, 1985; Mikhailov, 1991, 1997; Hirsch & Kohring, 1992; Kohring & Hirsch, 1996; Ribeiro *et al.*, 2006; Novas *et al.*, 2009; Oliveira *et al.*, 2011). The eggshell has an extremely low porosity (less than one pore per  $\text{cm}^2$ ). It seems likely that the reason pores were not observed, at least on the external surface, might be due to an outer dl (average thickness of 71  $\mu\text{m}$ , approximately 30 % of total shell thickness), too crystalline to be exclusively of organic origin (Fig. 4.5) and most likely representing diagenetic secondary deposits of calcite and recrystallization (Hirsch & Kohring, 1992), covering the pore openings therefore resulting in such a low porosity. As such, even though simple pore canals may be expected because of its crocodylian affinity, this cannot be confirmed. The eggshell thickness is 243  $\mu\text{m}$  ( $n = 80$ ,  $\text{sd} = 13.7 \mu\text{m}$ ). Taking into account the thickness of this layer, the eggshell portion displaying





crocodiloid features is 172  $\mu\text{m}$  thick. This dl is also present in ML1795, where it is thicker than in any other sample (144  $\mu\text{m}$ ). In ML 1194 and ML195, the dl is much thinner and almost negligible (20 and 14  $\mu\text{m}$  respectively). In radial section, the basal knobs and nucleation centers are evident, but the shell units are faint and in most cases hard to define due to a strong sub-horizontal fracturing that prevents a clear observation of the tabular ultrastructure (Fig. 4.6). Two layers can be distinguished: a mammillary or il, corresponding to the basal plate groups, which makes up on average 20% of the eggshell thickness, and an ol, between the mammillary and diagenetic layers, on average 50% of the shell thickness. In cross-polarized light, the characteristic irregular triangular extinction pattern present in crocodiloid eggshells is visible, including in the dl.

**Specimen ML195** – The ML195 samples are small fragments, less than 25 mm<sup>2</sup> each, found in association with dinosaur eggs morphologically very similar to the eggs found at the Paimogo nesting site and, as such, seemingly very close to *Preprismatoolithus*, an oogenus attributed to *Allosaurus* and *Lourinhanosaurus* (Carrano *et al.*, 2013; Ribeiro *et al.*, 2013). The outer and inner surfaces are smooth,



**Figure 4.3:** *Krokolithes dinophilus*, block containing the holotype (ML760). Scale bars: 1 cm.

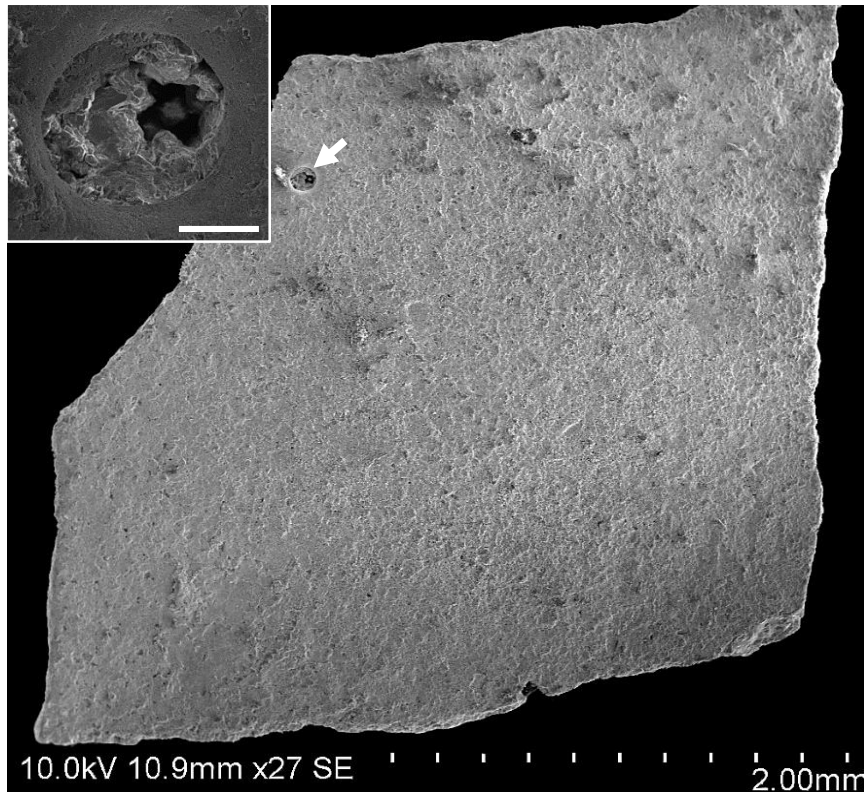
with no discernible internal bumps of the mammillae tips or pore openings. The eggshell thickness is 253  $\mu\text{m}$  ( $n = 80$ ,  $sd = 7.8 \mu\text{m}$ ), with a 14  $\mu\text{m}$  dl present, much less relevant than in both Paimogo samples.



The shell units are very faint and barely distinguishable (Fig. 4.6). On the other hand, the basal knobs and nucleation centers are much more evident and compose the darker il, about 35  $\mu\text{m}$  thick (14% of total shell). Above it, the ml, about 157  $\mu\text{m}$  (62% of total shell), is characterized by a very faint tabular lamination. There is a thin darker band of more compacted horizontal fibers that marks the interface between the middle and outer layers. The ol, approximately 61  $\mu\text{m}$  (24% of total shell), exhibits a more evident tabular ultrastructure, with the fibers closer together, more compact, and more evident horizontal growth structures (Fig. 4.6). In cross-polarized light, the irregular extinction triangles are present, even though less conspicuous as in the samples of Paimogo and Casal da Rola (Fig. 4.6).

**ML1194** – ML1194 samples are small fragments, very similar to the material from Peralta both in dimensions and morphology, found, as ML195, ML760 and ML1795, in association with theropod eggs, morphologically very close to the oogenus *Preprismatoolithus* (Carrano *et al.*, 2013; Ribeiro *et al.*, 2013). As in the other samples, both inner and outer surfaces are smooth. Similar to the Paimogo samples, pores are very scarce (less than a pore per  $\text{cm}^2$ ), but nonetheless Figure 4.4 shows a SEM photograph of the external surface of the eggshell with a detail of a pore with a subcircular opening, with a diameter of 110  $\mu\text{m}$  and a long straight canal, characteristic for the angusticanalicate pore system (*sensu* Carpenter 1999:141) and usually associated with crocodylomorph eggs. The eggshell thickness is 220  $\mu\text{m}$  ( $n = 80$ ,  $sd = 6.5 \mu\text{m}$ ). As in the Peralta samples, the dl is sparse and not observable throughout the whole section, and at most 20  $\mu\text{m}$  thick. The shell units are faint and hard to be distinguished. Three layers can be observed: a basal il (Fig. 4.6), about 35  $\mu\text{m}$  thick (approximately 16% of total shell) and characterized by a darker coloration of the basal knobs and nucleation centers, a ml (Fig. 4.6), about 138  $\mu\text{m}$  thick (approximately 63% of total shell) and characterized by a horizontal tabular lamination that shows an increase in the density of fibers from the bottom to the top, and an ol (Fig. 4.6), about 46  $\mu\text{m}$  thick (approximately 21% of total eggshell) and similar to the ml in structure, but with a less distinct tabular structure and more evident growth lines. With cross-polarized light, the extinction triangles are visible, from the upper part of the ml to the external surface (Fig. 4.6).



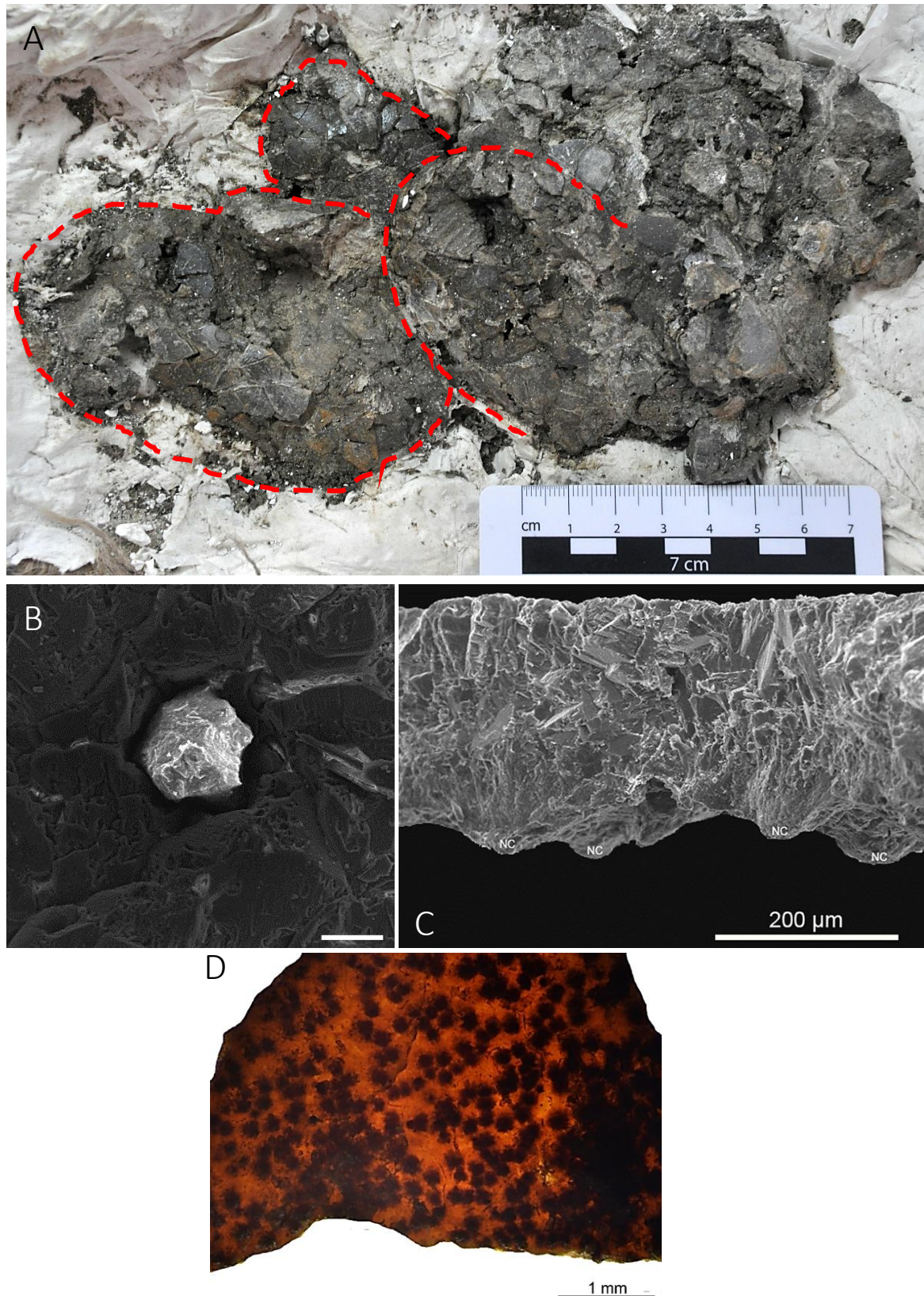


**Figure 4.4:** SEM photo of eggshell of *Krokolithes dinophilus* (ML1194), showing the external surface of the eggshell with a pore (white arrow). Inset: detail of the pore opening. Inset scale bar: 50  $\mu\text{m}$ .

**ML1795** – ML1795 includes three partially crushed eggs and shell fragments (Fig. 4.5-A), also found in association with a theropod nest, as in ML760. Because the specimen is so fragile, it is still partially encased in its plaster jacket as well as supported by a dark brown mudstone matrix (Fig. 4.5-A). As in the other *K. dinophilus* specimens, pores are very scarce (less than one per  $\text{mm}^2$ ) and hard to observe. This might be due to the dl that completely covers the external surface. Nonetheless, in Figure 4.5-B what seems to be an obstructed pore opening can be seen. The hexagonal shape is unique, but it might be a result of the outer dl. The diameter is 42  $\mu\text{m}$ , much less than the pore observed in ML1194 (Fig. 4.4). On the other hand, the internal openings are not visible in the samples which seems to indicate that indeed the porosity is low in these specimens. Total eggshell section thickness is 392  $\mu\text{m}$  ( $n = 80$ ,  $sd = 43.9 \mu\text{m}$ ), but the diagenetic layer is 144  $\mu\text{m}$  (about 36% of total thickness), meaning that the actual portion of the eggshell displaying crocodyloid features is 248  $\mu\text{m}$ . The shell unit wedges are clear (Fig. 4.6), with basal knobs and nucleation centers clearly visible at the base of the inner layer (Fig. 4.6). The eggshell ultrastructure is the same as in the other *K. dinophilus* specimens: an il (35  $\mu\text{m}$ , about 14% of eggshell thickness), composed by the basal plate group knobs and nucleation centers, a ml (138  $\mu\text{m}$ , about 55% of eggshell thickness), with the characteristic crocodyloid horizontal tabular lamination, and an ol (46  $\mu\text{m}$ , about 18% of eggshell thickness), with a darker, more compact lamination. Under SEM, the nucleation centers are observable (Fig. 4.5-C). With cross-polarized light, the typical crocodyloid triangular shaped extinction is clearly observable, extending through all the ol to the uppermost portion

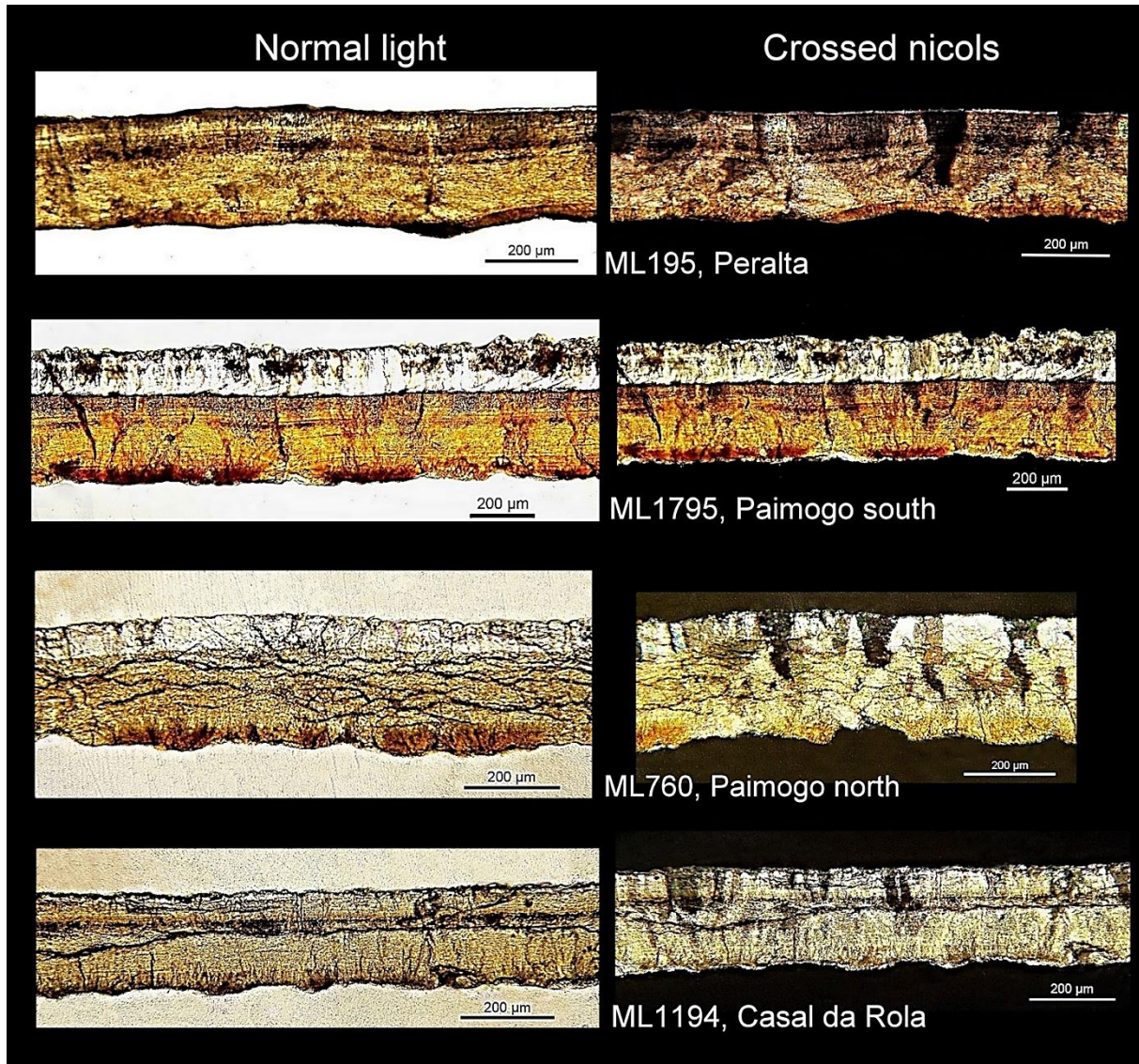


of the ml (Fig. 4.6). Similar to FCT-UNL706, under the binocular and with backlighting, the distribution of the tips of the shell units (Fig. 4.5-D) is evident.



**Figure 4.5:** Eggs and eggshells of *K. dinophilus* (ML1795); A) Block containing specimen ML1795, B) SEM photo of the external opening of a filled pore, C) SEM transversal section of the eggshell, D) Tangential eggshell section with backlighting, showing the darker, smaller spots of the nucleation centers. In C, the nucleation centers or basal knobs (NC) are evident. Red dashed lines in A outline the partial shape of the three crushed eggs. Scale bar in B: 20 µm





**Figure 4.6:** Thin sections of *K. dinophilus* eggshells, with plane-polarized light (left column) and cross-polarized light (right column). Notice the darker basal plate groups at the base of the shell units that define the inner layer, and the tabular ultrastructure with the thin darker band closer to the external surface that marks the boundary between the middle and outer layers (not observable in ML760) as well as the diagenetic layer in ML1795 and ML760.



## 5. Discussion

In general, extinct crocodylomorph eggs have the same basic structure and shape than extant crocodile eggs, and synapomorphies for eggs of Crocodylia are also valid for the broader clade Crocodylomorpha (i. e. Marzola *et al.*, 2014). The main difference, however, is the smaller values of average eggshell thickness in non-crocodylian crocodylomorph. Also, fossil crocodyloid eggshells show a lower number of differentiated shell layers when compared to the extensively studied eggs of *Alligator mississippiensis* which have five identifiable layers (Ferguson, 1982). In the case of the *Krokolithes dinophilus* samples, only three layers were identified. This agrees with the work by Marzola *et al.* (2014) that, in samples of eggshells of three extant crocodylomorph taxa (*Alligator mississippiensis*, *Crocodylus mindorensis* and *Paleosuchus palpebrosus*), only three layers were differentiated.

Specimen FCT-UNL706 shares characters that allow a classification within Krokolithidae, but the absence of a characteristic tabular ultrastructure, shell units that are wider than taller, much thinner eggshell than *Krokolithes* and egg size are sufficient to erect a new oogenus and oospecies, *Suchoolithus portucalensis*.

In *Suchoolithus portucalensis*, the identification of distinct layers at all is extremely difficult. At most, one irregular inner mammillary layer may be identified in some intervals throughout the entire thin section. Whether this is because the thin eggshell did not exhibit such layers originally or because whatever layers it had were erased by diagenesis (rather unlikely considering the preservation of the specimen) it is difficult to know. The first hypothesis seems more likely and may serve as diagnostic character for this oogenus, since in the fossil record this is one of the best preserved diagnostic features of crocodyloid eggshells. These character discrepancies among fossil and extant crocodyloid eggshells are to be expected, and actually observed, even intraspecifically, when considering that oogenesis is ultimately dependent of many environmental and physiological variables (e. g. Thorbjarnarson, 1996; Bryan, 2005). The degree of preservation of specimen FCT-UNL706 rules out transportation. Considering the thickness of 163  $\mu\text{m}$  and breakage propensity of the eggs, and even the inherent preparation issues due to such a fragile eggshell, the clutch was most likely found *in situ*. This suggests the clutch was buried soon after having been laid and suffered very little diagenetic damage. This is contrary to the eggshells from Paimogo, Peralta and Casal da Rola, which are fragmented and, in the case of the eggs ML760 and ML1795, show clear signs of post burial damage, namely vertical compression, as the eggs are flattened and crushed. Because the eggshells date from the Late Jurassic, a crocodylomorph, not eusuchian, origin is the most likely. However, ascribing the egg material to a specific crocodylomorph taxa is extremely difficult, due to the lack of direct skeleton-egg association, more so as the paleodiversity increases. Also, this clutch has the highest number of eggs on record (13), as well as the second smallest crocodyloid eggs, 42 mm in length by 26 mm in width (Appendix 2). The eggs associated to the remains of *Yacarerani boliviensis*, from the Late Cretaceous of Bolivia, are the smallest, 30 mm in length by 16 mm in width (Novas *et al.*, 2009). On the other hand, because of its



morphological similarities, ML195, ML760, ML1194, and ML1795 are hereby assigned to *Krokolithes dinophilus*, oosp. nov., also the oldest known hitherto for this oogenus and the first from Portugal. Antunes *et al.* (1998) had previously shortly described ML760, postulating only though that it was of crocodyloid affinity. Taking into account only complete eggs, ML760 is the second largest crocodyloid egg known, 70 mm in length by 40 mm in width (Appendix 2). The egg described by Panadés I Blas and Patnaik (2009) from Upper Miocene of Pakistan is the largest, 84 mm by 64-54 mm.

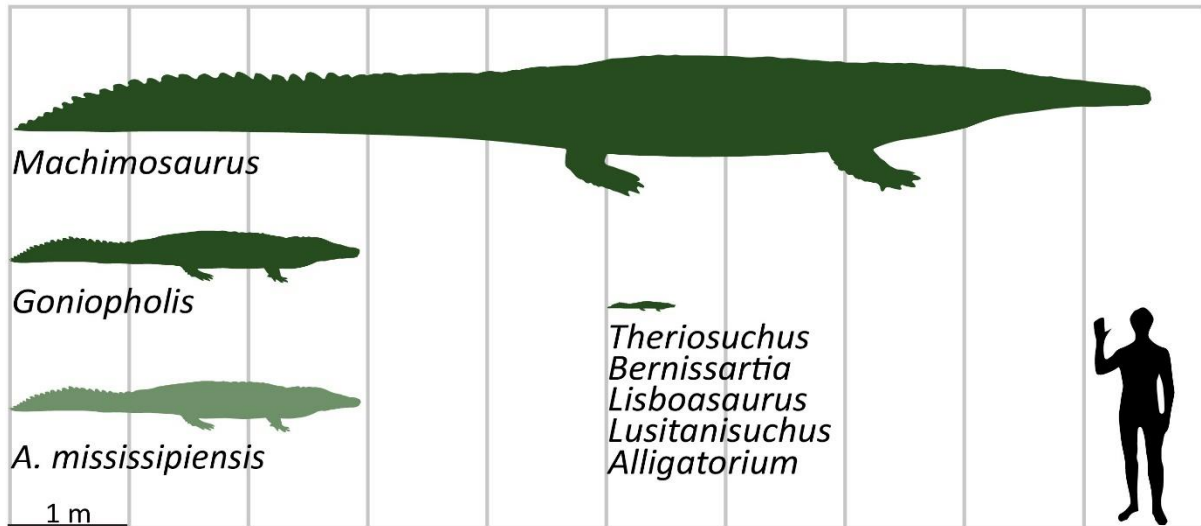
### 5.1. Possible egg layers

The diversity of fossil Mesozoic crocodylomorphs in Portugal is high, with the Late Jurassic forms being better documented, and include the following taxa: *Bernissartia* sp., cf. *Alligatorium*, *Goniopholis baryglyphaeus* Schwarz 2002, *Machimosaurus hugii* von Meyer 1837, *Lisboasaurus estesi* Seiffert, 1973, *Lusitanisuchus mitrocostatus* Schwarz & Fechner 2004, *Theriosuchus guimarotae* Schwarz & Salisbury 2005 (Seiffert, 1973; Schwarz, 2002; Schwarz & Fechner, 2004; Schwarz & Salisbury, 2005; Mateus, 2013). The morphological stability of the eggshells makes a definitive identification of the egg layer impossible whenever associated skeletal remains which can undoubtedly be related to the eggs are not found. As a matter of fact, this is even harder to do when dealing with crocodyloid eggshells since the morphological diversity within the morphotype is extremely low, when compared to the much more diverse dinosaurs and their eggshell morphologies (Appendix 1). According to Hirsch (1985:541), “Fossil eggs can only be linked through circumstantial evidence to a specific genus, unless identifiable embryonic remains are found within the specimen [...] a relationship between the size of the animals and their eggs exists...”. Other authors recognize this as well (e.g. Mikhailov *et al.*, 1996; Zelenitsky & Hirsch, 1997; Carpenter, 1999), making it impossible to exactly ascribe the eggs to a specific egg layer without skeletal remains. On the other hand, a body size / egg size relationship in extant representatives of the group may offer some clues (Appendix 3), allowing at least to restrict the size interval for possible egg layers. Thorbjarnarsson (1996) points out such a body size versus egg size relationships, although with a degree of uncertainty. As such, considering the ratio between adult size and egg size, *Machimosaurus*, over 9 meters long (Krebs & Schwarz, 2000; Young *et al.*, 2014), seems a highly unlikely parent because larger eggs would be expected. Also, material evidence about the reproduction of *Thalattosuchia* (which includes teleosaurids, like *Machimosaurus*, and metriorhynchids) is at this time unknown. Teleosaurids are not as adapted to a fully marine lifestyle as its sister group members, the metriorhynchids, but even so *Machimosaurus* was anatomically well- adapted to a pelagic lifestyle, spending most of its life in open coastal areas and estuarine environments (Krebs, 1967, 1968; Martin *et al.*, 2014), suggesting that dry land incursions were most likely sporadic and probably restricted to the most distal, deeper parts of the river system.

The size of the eggs in FCT-UNL706 suggests as parent taxa one of the small crocodylomorphs from the Lourinhã Formation (Schwarz & Fechner, 2004, 2008; Schwarz & Salisbury, 2005; Mateus, 2013). ML760 and ML1795, on the other hand, because of their similarities to extant crocodylian eggs, and



considering a similar correlation between body size and egg size, might suggest as plausible parent taxa *Goniopholis*, a medium sized (2-4 meters) crocodylomorph ubiquitous throughout the Late Jurassic of Portugal (Schwarz, 2002; Schwarz & Fechner, 2004; Karl, 2006), or at least a *Goniopholis*-sized form. Nevertheless, such assumptions are at this point based solely on poorly supported correlations and known crocodylomorphs present in the Lourinhã Formation. Figure 5.1 shows the estimates of body sizes for the crocodylomorphs in the fossil record of Lourinhã Formation. Appendix 3 has morphometric egg and body data, when available, for 23 extant species of Crocodylomorpha.



**Figure 5.1:** Body size comparison between the known Crocodylomorpha from the Lourinhã Formation (dark green) and an extant *Alligator mississippiensis* (light green). The *A. mississippiensis* represents the maximum estimated female body size for the species. Data for the fossil forms taken from Buscalioni and Sanz, 1988; Schwarz, 2002; Schwarz and Fechner, 2004, 2008; Schwarz and Salisbury, 2005; Karl *et al.*, 2006; Mateus, 2013.

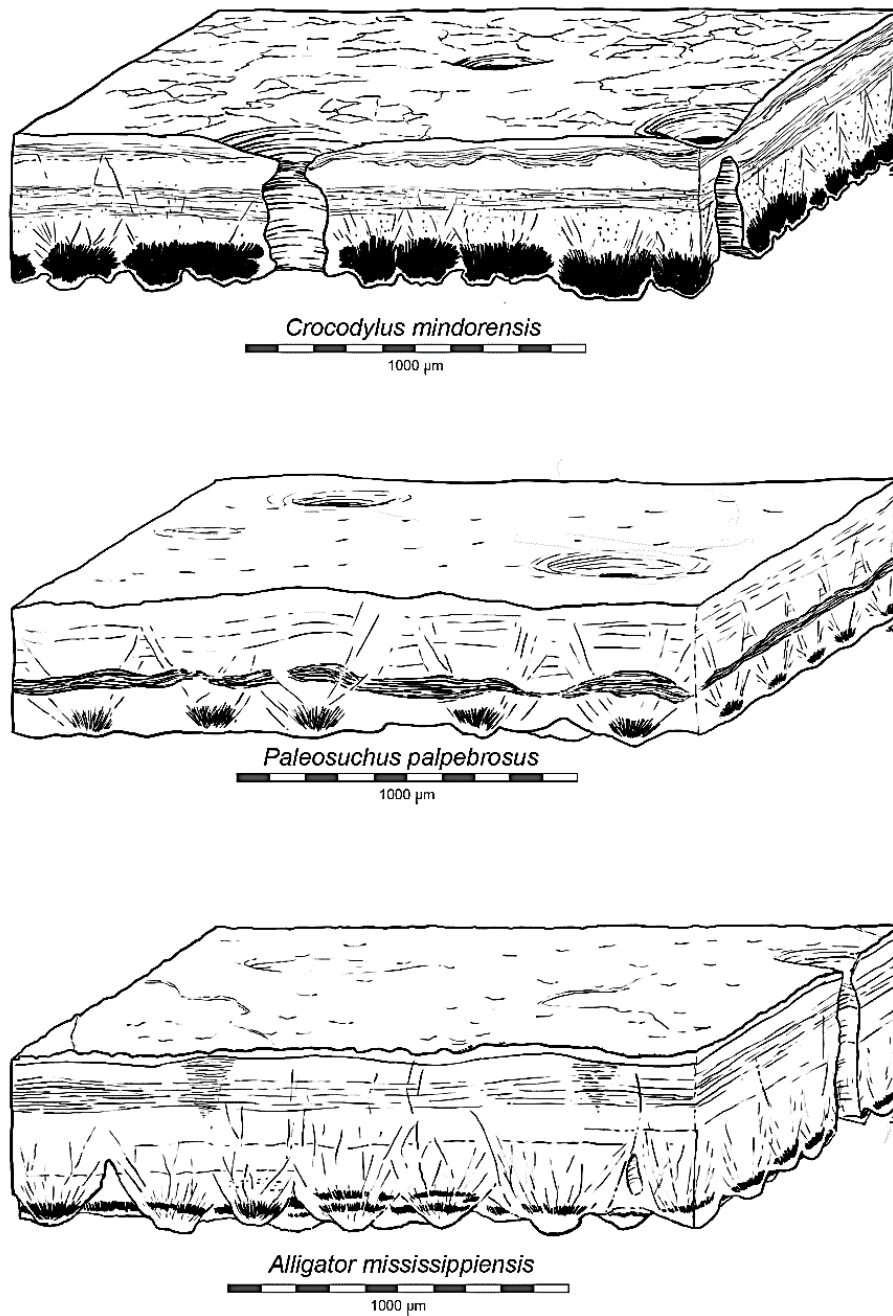
## 5.2. Oophylogeny and low oomorphological disparity in Crocodylomorpha

The crocodyloid morphotype has been shown to be very conservative so far. The low number of ootaxa attributed to confirmed or putative crocodylomorphs is striking when compared with those of dinosaurs. Adding these two new ootaxa, the number of ootaxa ascribed to this morphotype is six oospecies distributed among four oogenera, with only one of those not included in Krokolithidae, *M. kohringi*, from the Early Cretaceous of Spain, and that includes material initially reported by Ensom in the Purbeck of England (Ensom, 1992, 1997; Moreno-Azanza, 2014; Moreno-Azanza, Canudo & Gasca, 2015). This extremely low diversity contrasts with, at least, 53 oogenera and 128 oospecies attributed to dinosaurs (see Appendix 1). These numbers reveal the low diversity of formal ootaxonomical units which is a direct reflex of the low morphological disparity of Krokolithidae eggshells. Moreover, no apomorphies in the eggs or eggshells have been reported to distinguish modern Crocodylia from Jurassic non-crocodylian crocodylomorphs. Contrarily, numerous apomorphies in eggs and eggshells can be identified between birds and more basal dinosaurs. This would help explain such a low diversity, since different species may be represented by the same ootaxon. On the other hand, numerous apomorphies in eggs and eggshells can be pointed between birds and more basal dinosaurs. This shows that crocodylomorph eggs are very conservative in morphology since, at least, the Late Jurassic. Various





studies have pointed out this morphological stability in crocodylian eggshells (e.g. Schmidt & Schönwetter, 1943; Packard & DeMarco, 1982; Hirsch, 1985; Marzola, Russo & Mateus, 2015; Moreno-Azanza *et al.*, 2013; Marzola *et al.*, 2014; Moreno-Azanza, 2014; Moreno-Azanza, Canudo & Gasca, 2015a, 2015b). The reason of the apparent stasis and low evolutionary rate of crocodylomorph eggs in comparison with other egg laying groups is not yet well understood but it is clear that such oomorphology is efficient and functional until today, as seen in modern crocodylians (Fig. 5.2).



**Figure 5.2:** Three samples of extant crocodyloid eggshells used for comparison with the fossil specimens (see Marzola *et al.*, 2014, for further details). The main diagnostic characters are observable, such as the shell units wedges, tabular ultrastructure, dark coloured basal knobs, pores and triangular extinction (the latter visible in *A. mississippiensis*). Illustration by Simão Mateus, from Marzola *et al.*, 2014.



## 6. Conclusions

The eggs and eggshells described by this analysis conclusively show the diagnostic features that allows to identify the material as belonging to the crocodyloid eggshell morphotype (*sensu* Mikhailov, 1991, 1997), as illustrated by Figure 5.2. The shell thickness, micro- and ultrastructure (i. e. the tabular lamination), ornamentation, shape of the eggs, triangular extinction pattern, all indicate a crocodylian affinity (Schmidt & Schönwetter, 1943; Erben, 1970; Erben & Newesely, 1972; Packard *et al.*, 1982; Ferguson, 1985; Hirsch, 1985; Mikhailov, 1991, 1997; Packard & DeMarco, 1991; Hirsch & Kohring, 1992; Kohring, 1995; Kohring & Hirsch, 1996; Antunes *et al.*, 1998; Carpenter, 1999; Moreno-Azanza *et al.*, 2013; Marzola *et al.*, 2014; Moreno-Azanza, 2014; Russo *et al.*, 2014a, 2014b; Marzola *et al.*, 2015; Moreno-Azanza *et al.*, 2015). The diversity within Krokolithidae is increased and the number of crocodyloid ootaxa is now six, by describing and proposing *Suchoolithus portucalensis* oogen. et oosp. nov, and *Krokolithes dinophilus* sp.nov., from the Late Jurassic of the Lourinhã Formation (Portugal), thus extending the range of crocodyloid eggs to the Late Jurassic. As such, these are the oldest crocodyloid eggshells known so far, dated from the Late Kimmeridgian-latest Tithonian, confirming and improving on the analysis and diagnosis performed by Antunes and colleagues (1998). Also, this study verifies and further confirms that the basic crocodyloid eggshell structure has remained essentially unaltered for at least 150 Ma, since the Late Jurassic, with a lesser degree of structural variation than eggshells from other major amniote groups. Fossil crocodylomorph eggs show the same diagnostic characters than extant crocodile eggs (Fig. 5.2), and therefore synapomorphies for eggs of Crocodylia are also valid for eggs of the broader clade Crocodylomorpha. In Archosauria, the group which includes dinosaurs and crocodiles, the latter provides a unique example of evolutionary stasis in eggshell morphology, contrarily to what can be seen in dinosaurs where the evolutionary rate is much higher. Additionally, because of its stability, the identification of isolated fossil eggshells with a specific crocodylomorph taxon is often extremely difficult. Nonetheless, some correlation between body and egg size is possible, using simple regressions with data for extant crocodiles and fossil egg/skeletal remains associations to identify or at least narrow down putative egg laying taxa, based on known Crocodylomorpha diversity of the Late Jurassic of Portugal. Finally, this study allows the creation of two new ootaxa within Krokolithidae, *Suchoolithus portucalensis* (FCT-UNL706) and *Krokolithes dinophilus* (ML195, ML760, ML1194, ML1795).

Finally, it should be mentioned the fact that *K. dinophilus* specimens share so many similarities among each other, possibly pertaining to the same egg laying taxa or at least very closely related forms, raises some interesting questions and possible research routes going forward, the most interesting of which a putative previously unknown reproductive relationship strategy between the crocodylomorph and dinosaur egg layers in those localities. So far, only another occurrence of this type is known, from the Late Cretaceous of India, where crocodylian eggs were found in a sauropod hatching ground (see Srivastava *et al.*, 2015, for further details).



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# Appendixes





**A1. Accepted ootaxa**

**Table 1: Accepted ootaxa for each basic shell type**

| Basic shell type               | Oofamily                            | Oogenus  | Oospecies  |
|--------------------------------|-------------------------------------|--|--|
| Geckonoid                      | Gekkoolithidae Hirsch 1996          | <i>Gekkoolithus</i> Hirsch 1996  | <i>G. columnaris</i> Hirsch 1996   |
|                                | Testudoflexoolithidae Hirsch 1996   | <i>Testudoflexoolithus</i> Hirsch 1996   | <i>T. agassizii</i> Hirsch 1996<br><i>T. bathonicae</i> Hirsch 1996            |
| Testudinoid                    | Testudoolithidae Hirsch 1996        | <i>Chelonoolithus</i> Kohring 1998   | <i>C. braemi</i> Kohring 1998  |
|                                |                                     | <i>Testudoolithus</i> Hirsch 1996  | <i>T. magnirigidus</i> Zelenitsky 1995   |
|                                |                                     |  | <i>T. rigidus</i> Hirsch 1996  |
| Crocodyloid                    | Krokolithidae Kohring & Hirsch 1996 | <i>Bauruoolithus</i> Oliveira, Santucci, Andrade, Fulfaro, Basilio & Benton 2011 | <i>B. fragilis</i> Oliveira, Santucci, Andrade, Fulfaro, Basilio & Benton 2011 |
|                                |                                     | <i>Krokolithes</i> Hirsch 1985   | <i>K. helleri</i> Kohring & Hirsch 1996<br><i>K. wilsoni</i> Hirsch 1985       |
|                                | <i>Incertae sedis</i>               | <i>Mycomorphoolithus</i> Moreno-Azanza, Canudo & Gasca 2014                      | <i>M. kohringi</i> Moreno-Azanza, Canudo & Gasca 2014                          |
| Spherulitic (dinosauroid)      | Phacoolithidae Zeng & Zhang 1979    | <i>Dendroolithus</i> Zhao & Li 1988  | <i>D. dendriticus</i> Fang, Lu & Cheng 1998                                    |
|                                |                                     |  | <i>D. fengguangcunensis</i> Fang 2005  |
|                                | Dictyoolithidae Zhao 1994           | <i>Dictyoolithus</i> Zhao 1994   | <i>D. guoqingensis</i> Fang 2000   |
|                                |                                     |  | <i>D. microporosus</i> Mikhailov 1994  |
|                                |                                     |  | <i>D. shuangtangensis</i> Fang, Lu, Jiang & Yang 2003                          |
|                                |                                     |  | <i>D. verrucarius</i> Mikhailov 1994   |
|                                | Faveoolithidae Zhao & Ding 1976     | <i>Parafaveoolithus</i> Zhang 2010   | <i>D. wangdianensis</i> Zhao & Li 1988   |
|                                |                                     |  | <i>D. sichuanensis</i> Zhao & Zhao 1998  |
|                                | Faveoolithidae Zhao & Ding 1976     | <i>Parafaveoolithus</i> Zhang 2010   | <i>D. xichuanensis</i> Zhao & Zhao 1998  |
|                                |                                     |  | <i>D. neixiangensis</i> Zhao 1994  |
| Spherulitic (dinosauroid)      | Megaloolithidae Zhao 1979           | <i>Megaloolithus</i> Mikhailov 1991  | <i>D. hongpoensis</i> Zhao 1994  |
|                                |                                     |  | <i>D. jiangi</i> Liu & Zhao 2004   |
|                                | Faveoolithidae Zhao & Ding 1976     | <i>Parafaveoolithus</i> Zhang 2010   | <i>D. lishuiensis</i> Jin 2008   |
|                                |                                     |  | <i>D. pinglingensis</i> Zhao, Ye, Li, Zhao & Yan 1991                          |
|                                | Faveoolithidae Zhao & Ding 1976     | <i>Parafaveoolithus</i> Zhang 2010   | <i>D. pinglingensis</i> Zhao, Ye, Li, Zhao & Yan 1991                          |
|                                |                                     |  | <i>S. pinglingensis</i> Zhao, Ye, Li, Zhao & Yan 1991                          |
|                                | Megaloolithidae Zhao 1979           | <i>Megaloolithus</i> Mikhailov 1991  | <i>F. ningxiaensis</i> Zhao & Ding 1976  |
|                                |                                     |  | <i>F. zhangii</i> Jin 2008   |
|                                | Megaloolithidae Zhao 1979           | <i>Megaloolithus</i> Mikhailov 1991  | <i>P. macroporus</i> Zhang 2010  |
|                                |                                     |  | <i>P. microporus</i> Zhang 2010  |
| Megaloolithidae Zhao 1979      | <i>Megaloolithus</i> Mikhailov 1991 | <i>P. tiansicunensis</i> Zhang 2010  |  |
|                                |                                     | <i>P. xipingensis</i> Fang 1998  |  |
| Megaloolithidae Zhao 1979      | <i>Megaloolithus</i> Mikhailov 1991 | <i>C. dughii</i> Vianey-Liaud, Mallan, Buscail & Montgelard 1994                 |  |
|                                |                                     | <i>C. roussetensis</i> Vianey-Liaud, Mallan, Buscail & Montgelard 1994           |  |
| Megaloolithidae Zhao 1979      | <i>Megaloolithus</i> Mikhailov 1991 | <i>M. aureliensis</i> Vianey-Liaud, Mallan, Buscail & Montgelard 1994            |  |
|                                |                                     | <i>M. baghensis</i> Khosla & Sahni 1995  |  |
| Megaloolithidae Zhao 1979      | <i>Megaloolithus</i> Mikhailov 1991 | <i>M. balasinorensis</i> Mohabey 1998  |  |
|                                |                                     | <i>M. cylindricus</i> Khosla & Sahni 1995  |  |
| Megaloolithidae Zhao 1979      | <i>Megaloolithus</i> Mikhailov 1991 | <i>M. dholyaensis</i> Khosla & Sahni 1995  |  |
|                                |                                     | <i>M. dhoridungriensis</i> Mohabey 1998  |  |
| Megaloolithidae Zhao 1979      | <i>Megaloolithus</i> Mikhailov 1991 | <i>M. jabalpurensis</i> Khosla & Sahni 1995                                      |  |
|                                |                                     | <i>M. khenpurensis</i> Mohabey 1998  |  |
| Megaloolithidae Zhao 1979      | <i>Megaloolithus</i> Mikhailov 1991 | <i>M. mammillare</i> Vianey-Liaud, Mallan, Buscail & Montgelard 1994             |  |
|                                |                                     | <i>M. matleyi</i> Mohabey 1998   |  |
| Megaloolithidae Zhao 1979      | <i>Megaloolithus</i> Mikhailov 1991 | <i>M. megadermus</i> Mohabey 1998  |  |
|                                |                                     | <i>M. microtuberculata</i> Garcia & Vianey-Liaud 2001                            |  |
| Megaloolithidae Zhao 1979      | <i>Megaloolithus</i> Mikhailov 1991 | <i>M. mohabeyi</i> Khosla & Sahni 1995   |  |
|                                |                                     | <i>M. padiyalensis</i> Khosla & Sahni 1995                                       |  |
| Megaloolithidae Zhao 1979      | <i>Megaloolithus</i> Mikhailov 1991 | <i>M. petralta</i> Vianey-Liaud, Mallan, Buscail & Montgelard 1994               |  |
|                                |                                     | <i>M. phensaniensis</i> Mohabey 1998   |  |
| Megaloolithidae Zhao 1979      | <i>Megaloolithus</i> Mikhailov 1991 | <i>M. problematica</i> Mohabey 1998  |  |
|                                |                                     | <i>M. rahiolensis</i> Mohabey 1998   |  |
| Megaloolithidae Zhao 1979      | <i>Megaloolithus</i> Mikhailov 1991 | <i>M. siruguei</i> Vianey-Liaud, Mallan, Buscail & Montgelard 1994               |  |
|                                |                                     | <i>M. trempii</i> Vianey-Liaud, Mallan, Buscail & Montgelard 1994                |  |
| Megaloolithidae Zhao 1979      | <i>Megaloolithus</i> Mikhailov 1991 | <i>M. walpurensis</i> Khosla & Sahni 1995  |  |
|                                |                                     | <i>S. erbeni</i> Mones 1980  |  |
| Ovaloolithidae Mikhailov 1991  | <i>Ovaloolithus</i> Zhao 1979       | <i>O. chinkangkouensis</i> (Zhao & Jiang 1974)                                   |  |
|                                |                                     | <i>O. dinormithoides</i> Mikhailov 1994  |  |
|                                |                                     | <i>O. huangtulingensis</i> Yu 1998   |  |
|                                |                                     | <i>O. laminadermus</i> (Zhao & Jiang 1974)                                       |  |
|                                |                                     | <i>O. mixtistriatus</i> Zhao 1979  |  |
|                                |                                     | <i>O. monoistriatus</i> Zhao 1979  |  |
|                                |                                     | <i>O. tenuisus</i> Bray 1999   |  |
|                                |                                     | <i>O. tristriatus</i> Zhao 1979  |  |
|                                |                                     | <i>O. turpanensis</i> Zhang & Wang 2010  |  |
|                                |                                     | <i>O. utahensis</i> Bray 1999  |  |
| <i>O. weiqiaoensis</i> Yu 1998 |                                     |  |  |



|   |   |  |   |  |
|---|---|--|---|--|
|   |   | <i>Boletuoolithus</i> Bray 1998  | <i>B. carlylensis</i> Bray 1998   |  |
|   |   | <i>Guegoolithus</i> Moreno-Azanza, Canudo & Gasca 2014                       | <i>G. turoloensis</i> Moreno-Azanza, Canudo & Gasca 2014  |  |
|   |   | <i>Paraspheroolithus</i> Zhao 1979   | <i>P. sanwangbacunensis</i> Fang 2005<br><i>P. shizuiwanensis</i> Fang, Lu, Jiang & Lang 2008<br><i>P. yanchengensis</i> Xiaosi 1998  |  |
|   |   | <i>Placoolithus</i> Zhao 1979  | <i>P. taohensis</i> Zhao 1979<br><i>P. tiantaiensis</i> Jin 2008  |  |
|   |   | <i>Shixingoolithus</i> Zhao et al. 1991                                      | <i>S. erbeni</i> Zhao, Ye, Li, Zhao & Yan. 1991   |  |
|   | Spheroolithidae Zhao 1979                                     | <i>Spheroolithus</i> Zhao 1979 (= " <i>Oolithes spheroides</i> " Young 1954) | <i>S. albertensis</i> Zelenitsky and Hills 1997<br><i>S. choteauensis</i> Jackson & Varrichio 2010<br><i>S. changchiungtingensis</i> (Zhao & Jiang 1974)<br><i>S. europaeus</i> Sellés, Vila & Galobart 2014<br><i>S.</i> (= <i>Paraspheroolithus irenensis</i> (Zhao & Jiang 1974)<br><i>S. jincunensis</i> Fang, Lu, Jiang & Yang 2003<br><i>S. maiauroides</i> Mikhailov 1994<br><i>S. megadermus</i> (Young 1959)<br><i>S. tenuicorticus</i> Mikhailov 1994<br><i>S. zhangoucaensis</i> Fang 2000 |  |
|   | Youngoolithidae Zhang 2010                                    | <i>Youngoolithus</i> Zhao 1979   | <i>Y. xiaguanensis</i> Zhao 1979  |  |
| Prismatic (dinosauroid)                     | Prismatoolithidae Hirsch 1994                                 | <i>Preprismatoolithus</i> Zelenitsky & Hills 1996                            | <i>P. coloradensis</i> (Hirsch 1994)  |  |
|   |   | <i>Prismatoolithus</i> Zhao & Li 1993  | <i>P. caboti</i> Garcia, Feist, Cabot, Valentin & Viane-Liaud 2000<br><i>P. gebiensis</i> Zhao & Li 1993<br><i>P. hanshuiensis</i> Zhou 1998<br><i>P. heyuanensis</i> Lü 2006<br><i>P. hirschi</i> Jackson & Varrichio 2010<br><i>P. hukouensis</i> Zhao 1999<br><i>P. jenseni</i> Bray 1999<br><i>P. levis</i> Zelenitsky & Hills 1996<br><i>P. matellensis</i> Vianey-Liaud & Crochet 1993<br><i>P. tenuis</i> Vianey-Liaud & Crochet 1993<br><i>P. tremptii</i> Sellés, Vila & Galobart 2014       |  |
|   |   | <i>Protoceratopsidovum</i> Mikhailov 1994                                    | <i>P. fluxuosum</i> Mikhailov 1994<br><i>P. minimum</i> Mikhailov 1994<br><i>P. sincerum</i> Mikhailov 1994   |  |
|   |   | <i>Sankofa</i> López-Martínez & Vicens 2012                                  | <i>S. pyrenaica</i> López-Martínez & Vicens 2012  |  |
|   |   | <i>Spheruprismatoolithus</i> Bray 1999                                       | <i>S. condensus</i> Bray 1999   |  |
|   |   | <i>Trigonooolithus</i> Moreno-Azanza, Canudo & Gasca 2013                    | <i>T. amoae</i> Moreno-Azanza, Canudo & Gasca 2013  |  |
|   |   | Incertae sedis   | <i>Pseudogeooolithus</i> Vianey-Liaud & López-Martínez 1997   | <i>P. nodosus</i> Viane-Liaud & López-Martínez 1997                                      |
| Ornithoid                                   | Elongatoolithidae Zhao 1975                                   | <i>Continuoolithus</i> Zelenitsky, Hills & Currie 1996                       | <i>C. canadensis</i> Zelenitsky, Hills & Currie 1996  |  |
|   |   | <i>Ellipsooolithus</i> Mohabey 1998  | <i>E. khedaensis</i> Mohabey 1998   |  |
|   |   | <i>Elongatoolithus</i> Zhao 1975   | <i>E. andrewsi</i> Zhao 1975<br><i>E. chichenshanensis</i> Fang, Lu, Jiang & Yang 2003<br><i>E. elongatus</i> (Young 1954)<br><i>E. excellens</i> Mikhailov 1994<br><i>E. frustrabilis</i> Mikhailov 1994<br><i>E. lajiaensis</i> Fang, Lu, Jiang & Wang 2003<br><i>E. magnus</i> Mikhailov 1994<br><i>E. sigillarius</i> Mikhailov 1994<br><i>E. subitectorius</i> Mikhailov 1994<br><i>E. taipinghuensis</i> Yu 1998  |  |
|   |   | <i>Heishanoolithus</i> Zhao & Zhao 1999                                      | -   |  |
|   |   | <i>Macroelongatoolithus</i> Li, Yin & Liu 1995                               | <i>M. carlylei</i> (Jensen 1970)<br><i>M. sixiaensis</i> Li, Yin & Liu 1995<br><i>M. zhang</i> Fang et al. 2000   |  |
|   |   | <i>Macrooolithus</i> Zhao 1975   | <i>M. mutabilis</i> Mikhailov 1994<br><i>M. rugustus</i> (Young 1965)<br><i>M. turoloensis</i> Sanjuán, Canudo & Cuenca-Bescós 2000<br><i>M. yaotunensis</i> Zhao 1975  |  |
|   |   | <i>Nanhsiungoolithus</i> Zhao 1975   | <i>N. chuetienensis</i> Zhao 1975   |  |
|   |   | <i>Paraelongatoolithus</i> Wang, Wang, Zhao & Jiang 2010                     | <i>P. reticulatus</i> Wang, Wang, Zhao & Jiang 2010   |  |
|   |   | <i>Porituberooolithus</i> Zelenitsky, Hills & Currie 1996                    | <i>P. warnensis</i> Zelenitsky, Hills & Currie 1996   |  |
|   |   | <i>Spongiooolithus</i> Bray 1999   | <i>S. hirschi</i> Bray 1999   |  |
|   |   | <i>Trachoolithus</i> Mikhailov 1994  | <i>T. faticannus</i> Mikhailov 1994   |  |
|   |   | <i>Undulatooolithus</i> Wang, Zhao, Wang, Li & Zou 2013                      | <i>U. pengi</i> Wang, Zhao, Wang, Li & Zou 2013   |  |
|   |   | Oblongoolithidae Mikhailov 1996  | <i>Oblongoolithus</i> Mikhailov 1996  | <i>O. glaber</i> Mikhailov 1996  |
|   |   | Laevisoolithidae Mikhailov 1991  | <i>Laevisoolithus</i> Mikhailov 1991  | <i>L. sochavai</i> Mikhailov 1991  |
|   |   |  | <i>Subtiloolithus</i> Mikhailov 1991  | <i>S. kachchhensis</i> Khosla & Sahni 1995<br><i>S. microtuberculatus</i> Mikhailov 1991 |
| Medioolithidae Kohring & Hirsch 1996        | <i>Medioolithus</i> Kohring & Hirsch 1996                     | <i>M. getseltalensis</i> Kohring & Hirsch 1996                               |   |  |
| Montanoolithidae Zelenitsky & Therrien 2008 | <i>Montanoolithus</i> Zelenitsky & Therrien 2008              | <i>M. strongorum</i> Zelenitsky & Therrien 2008                              |   |  |
| Incertae sedis                              | <i>Ageroolithus</i> Vianey-Liaud & López-Martínez 1997        | <i>A. fontlongensis</i> Vianey-Liaud & López-Martínez 1997                   |   |  |
|   | <i>Dispersinuberooolithus</i> Zelenitsky, Hills & Currie 1996 | <i>D. exilis</i> Zelenitsky, Hills & Currie 1996                             |   |  |
|   | <i>Tristraguoolithus</i> Zelenitsky, Hills & Currie 1996      | <i>T. craciodes</i> Zelenitsky, Hills & Currie 1996                          |   |  |



## A2. Fossil Crocodylomorpha eggs

Table 2: Fossil Crocodylomorpha eggs

| References                         | L (mm)  | W (mm)  | ST ( $\mu$ m) | EI        | Age, stratigraphy and locality  |
|------------------------------------|---------|---------|---------------|-----------|---|
| Patnaik & Schleich, 1993           | 64      | 54      | 190-660       | 1,19      | Pliocene, Upper Siwaliks, Saketi Fossil Park, India   |
| Panadés I Blas & Patnaik, 2009     | 84      | 64-54   | 180-760       | 1,31-1,56 | Upper Miocene, Chinji Formation, Uchhri, Pakistan   |
| Kohring, 1992                      | -       | -       | 300           | -         | Lower Miocene, Lower Freshwater Molasse, Ulm, Germany   |
| Kohring & Hirsch, 1996             | 53      | 30      | -             | 1,77      | Middle Eocene, Geiseltal, Germany   |
|                                    | 52      | 25      | 300-450       | 2,08      |   |
|                                    | 60      | 35      | 350-450       | 1,71      |   |
|                                    | 40      | 19      | 290-360       | 2,11      |   |
|                                    | 35      | 30      | 300           | 1,17      |   |
|                                    | 44      | 44      | 360-450       | 1,00      |   |
| Hirsch, 1985                       | 56 (50) | 36 (30) | 250-450       | 1,67      | Eocene, DeBeque Formation, Colorado, USA  |
| Hirsch & Kohring, 1992             | 65-68   | 44      | 600-700       | 1,48-1,55 | Middle Eocene, Bridger Formation, Wyoming, USA  |
| Singh <i>et al.</i> , 1998         | -       | -       | 350           | -         | Latest Cretaceous, Intertrappean Beds, Malabar Hill, India  |
| Prasad <i>et al.</i> , 2015        | -       | -       | 420-480       | -         | Latest Cretaceous, Intertrappean Beds, Kislapuri, India   |
| Srivastava <i>et al.</i> , 2015    | 68      | 44      | 430-470       | 1,54      | Late Maastrichtian, Lameta Formation, Lameta Ghat, India  |
| Moreno-Azanza <i>et al.</i> , 2013 | -       | -       | 750           | -         | Late Maastrichtian, La Posa Formation, Arén, Spain  |
| Kerourio, 1987                     | -       | -       | 640           | -         | Early Maastrichtian, Aix-en-Provence, France  |
| Ribeiro <i>et al.</i> , 2006       | 45-50   | 35-30   | 240-360       | 1,28-1,67 | Campanian-Maastrichtian, Araçatuba Formation, , Brazil  |
| Oliveira <i>et al.</i> , 2011      | 58-65   | 32-36   | 150-250       | 1,81      | Campanian-Maastrichtian, Adamantina Formation, Jales, Brazil  |
| Garcia, 2000                       | -       | -       | 290           | -         | Middle-Late Campanian, La Neuve, Aix-en-Provence, France  |
| Novas <i>et al.</i> , 2009         | 30      | 16      | 200           | 1,88      | Turonian-Santonian, Cajones Formation, Santa Cruz de La Sierra, Bolivia                               |
| Rogers, 2001                       | 49      | 28      | 600-700       | 1,75      | Early Albian, Glen Rose Formation, Texas, USA   |
| Ribeiro <i>et al.</i> , 2011       | 43      | 29      | 100           | 1,48      | Aptian, Crato Member, Santana Formation, Brazil   |
| Buscalioni <i>et al.</i> , 2008    | -       | -       | 250           | -         | Upper Barremian, La Huérgina Limestone Formation, Cuenca, Spain                                       |
| Kohring, 1990                      | -       | -       | 300-700       | -         | Early Barremian, Galve, Spain   |
| Moreno-Azanza, 2014                | -       | -       | 520           | -         | Early Barremian, Blesa, El Castelar & Mirambel Formations, La Cantalera, Spain                        |
| Canudo <i>et al.</i> , 2010        | -       | -       | 300           | -         | Late Hauterivian-Early Barremian, lower Blesa Formation, La Cantalera, Spain                          |
| Ensom, 1997                        | -       | -       | 150-400       | -         | Berriasian, top of the Cherty Freshwater Member of the Lulworth Formation, Dorset, UK                 |
| Antunes <i>et al.</i> , 1998       | 70      | 40      | 200-350       | 1,75      | Late Kimmeridgian, Praia Amoreira-Porto Novo, Lourinhã Formation, Paimogo, Portugal                   |
| This study                         | 42      | 26      | 163           | 1,62      | Tithonian, Assenta Member, Lourinhã Formation, Cambelas, Portugal                                     |
|                                    | -       | -       | 239 (253)     | -         | Late Kimmeridgian-earliest Tithonian, Praia Azul Member, Lourinhã Formation, Peralta, Portugal        |
|                                    | -       | -       | 200 (220)     | -         | Late Kimmeridgian-earliest Tithonian, Praia Azul Member, Lourinhã Formation, Casal Rola, Portugal     |
|                                    | -       | -       | 172 (243)     | -         | Late Kimmeridgian, top of the Praia Amoreira-Porto Novo Member, Lourinhã Formation, Paimogo, Portugal |
|                                    | 70      | 40      | 248 (392)     | 1,75      | Late Kimmeridgian, base of the Praia Azul Member, Lourinhã Formation, Paimogo, Portugal               |



### A3. Egg and body size parameters in extant Crocodylomorpha

**Table 3: Egg and body size parameters for 23 extant species of Crocodylomorpha.** After Thorbjarnarsson, 1996, and Marzola et al., 2014, and references therein. Note: the data for *Crocodylus suchus* is not available since only recently (2011) has this species been considered as distinct from *Crocodylus niloticus*, and, therefore, only the data for the latter is considered.

| Extant crocodylians               | L (mm)   | W (mm)    | ST ( $\mu\text{m}$ ) | EI        | EM (g) | V ( $\text{cm}^3$ ) | BM (kg) | BL (cm) |
|-----------------------------------|----------|-----------|----------------------|-----------|--------|---------------------|---------|---------|
| <i>Alligator mississippiensis</i> | 68,2-76  | 41,1-44,8 | 510-530              | 1,65-1,58 | 76,6   | 69,3                | 47,8    | 227     |
| <i>Alligator sinensis</i>         | 68       | 34        | 300-380              | 2,00      | 48,2   | 41,1                | 14,6    | 151     |
| <i>Paleosuchus palpebrosus</i>    | 62-71,5  | 39-42     | 410                  | 1,59-1,70 | 68,6   | 56,7                | 5,9     | 108     |
| <i>Paleosuchus trigonatus</i>     | -        | -         | -                    | -         | 67,2   | -                   | 7,5     | 125     |
| <i>Caiman crocodylus</i>          | 65       | 40        |                      | 1,63      | 62,9   | 54,4                | 10,9    | 143     |
| <i>Caiman yacare</i>              | -        | -         | -                    | -         | 63,0   | 62,8                | 18,5    | 140     |
| <i>Caiman latirostris</i>         | 63-66    | 40,9-46   | 360-850              | 1,54-1,43 | 76,2   | 64,1                | 14,6    | 161     |
| <i>Melanosuchus niger</i>         | 67,7     | 39,8      | -                    | 1,70      | 143,6  | -                   | 82      | 280     |
| <i>Crocodylus acutus</i>          | 77-77,8  | 48-48,9   | 400-520              | 1,60-1,59 | 112,8  | 95,1                | 76,7    | 266     |
| <i>Crocodylus intermedius</i>     | -        | -         | -                    | -         | 110,4  | -                   | 107,9   | 299     |
| <i>Crocodylus johnstoni</i>       | 58-66    | 40-45     | 400                  | 1,45-1,47 | 69,7   | 59,5                | 19,5    | 188     |
| <i>Crocodylus mindorensis</i>     | 69,3     | 37,3      | 430                  | 1,86      | 73,6   | -                   | 36,9    | 178     |
| <i>Crocodylus moreletti</i>       | -        | -         | -                    | -         | 79,5   | -                   | 31,7    | 203     |
| <i>Crocodylus niloticus</i>       | 74-79,2  | 43-51     | 530-580              | 1,72-1,55 | 107,1  | 94                  | 94,2    | 281     |
| <i>Crocodylus novaeguinae</i>     | 76       | 43        | -                    | 1,77      | 88,5   | 73,5                | 39,9    | 208     |
| <i>Crocodylus palustris</i>       | 75       | 46        | -                    | 1,63      | 99,5   | 83,1                | 42,7    | 232     |
| <i>Crocodylus porosus</i>         | 77-81    | 50-52     | 530-600              | 1,54-1,56 | 109,2  | 109,1               | 78,7    | 270     |
| <i>Crocodylus rhombifer</i>       | -        | -         | -                    | -         | 104,3  | -                   | 57,5    | 219     |
| <i>Crocodylus siamensis</i>       | 76       | 51        | -                    | 1,49      | 106,9  | 103,5               | 42,5    | 232     |
| <i>Mecistops cataphractus</i>     | -        | -         | -                    | -         | 146    | -                   | 50,5    | 232     |
| <i>Osteolaemus tetraspis</i>      | 63       | 37        | -                    | 1,70      | 55     | 45,1                | 18,8    | 131     |
| <i>Tomistoma schlegelii</i>       | 90-101,6 | 55-63,5   | -                    | 1,64-1,60 | 139,9  | 148,81              | 119     | 305     |
| <i>Gavialis gangeticus</i>        | 82       | 56        | 300-590              | 1,46      | 161,4  | 134,6               | 147     | 341     |

