Portugal, the nesting ground of the Late Jurassic

Moreno-Azanza, M.[1,2,3], Coimbra, R.[4], Guillaume, A.R.D.[1,2], Núñez-Lahuerta, C.[1,2,3,5], Puértolas-Pascual, E.[1,2], Rotatori, F.M. [2,3], Saleiro, A.[2,3], Sequero, C.[2,3,6], Tomás, C. [1,3] Ezquerro, L.[1,2,3,6]

1 Aragosaurus-IUCA, Recursos geológicos y Paleoambientes. Departamento de Ciencias de la Tierra, Facultad de Ciencias, Universidad de Zaragoza, Pedro Cerbuna 12, 50009 Zaragoza, Spain. david.geo.paleo@gmail.com dtorrome@gmail.com emedranoaguado@gmail.com
2 GeoBioTec, Departamento de Ciências da Terra, Faculdade de Ciências e Tecnologia, FCT, Universidade Nova de Lisboa, 2829-516 Caparica, Portugal. mmazanza@unizar.es eduardo.puertolas@gmail.com
3 Museu de Lourinhã, João Luís de Moura 95, 2530-158 Lourinhã, Portugal
4 GeoBioTec, Departamento de Geociencias, Universidade de Aveiro, Aveiro, Portugal
5 Departamento de Geología, Facultad de Ciencia y Tecnología, Universidad del País Vasco/Euskal Herriko Unibertsitatea UPV/EHU, Barrio Sarriena s/n, 48940 Leioa, Spain
6 Departamento de Geodinámica, Estratigrafía y Paleontología, Facultad de Ciencias Geológicas, Universidad Complutense de Madrid, C/ José Antonio Novais, 12, 28040, Madrid, Spain

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Introduction

Eggs and nests remain as relatively rare findings in the Pre-Cretaceous fossil record (Stein et al., 2019). Despite egg-laying amniotes appearing and diversifying long before the beginning of the Mesozoic, mineralized shelled eggs, those more susceptible of fossilization, appeared independently in the main clades of amniotes only at the end of the Triassic or beginning of the Jurassic (Norell et al., 2020). Earliest mineralized eggshells from dinosaurs are Sinemurian-Pliensbachian in age (Norell et al., 2020; Reisz et al., 2005), while the first testudines eggs date from the Bathonian (Buckman, 1860). Crocodylomorphs, despite having a huge Jurassic diversity and disparity, have a very scarce record of fossil eggs, with the first report on the Kimmeridgian (Russo et al., 2017). This poor record contrasts with the high abundance of Cretaceous localities with testudines, crocodylomorphs, pterosaur and dinosaur eggs that have been reported from all over the world (Carpenter, 1999 and references within). In this work we highlight the exception that proves the rule, the Jurassic coast of Portugal, where a handful of localities in the vicinities of Lourinhã and Leiria have provided an unrivaled record of eggshell fragments, eggs, clutches and embryos of testudines, crocodylomorphs and dinosaurs, dating from the Kimmeridgian to the earliest Tithonian.

Geological setting

The Lusitanian Basin is a large Mesozoic extensional structure at the western Iberian margin. The basin was formed as result of the extensional processes related to the North Atlantic opening, with four marked rift phases from the late Triassic to the early Cretaceous (Kullberg, 2000 and references within) In the central-western area, four depressions called Consolação, Bombarral-Alcobaça, Arruda and Turcifal sub-basins filled with syn-rift sedimentary successions of marine and continental deposits during the late Kimmeridgian, a shift from mixed marine environments (Consolação Fm., Abadia Fm. or Alcobaça Fm.) to more terrestrial (Lourinhã fm.) characterized all four sub-basins. These transitional environments have produced a plethora of vertebrate fossils, with an extensive record of osteological, ichnological and oological remains (Castanera et al., 2020; Mateus et al., 2017; Mocho et al., 2017).

Paleoological record

Testudines. Eggshells have a single report from the Jurassic of Portugal, being described by Kohring (1990) in the Guimarota Mine, from Leiria. Kohring described thin 150 μm shell fragments with aragonitic radial ultrastructure and a subtle compactituberculated ornamentation that he referred to the testudoid morphotype, using the morphotype as a parataxonomic rank. He then referred these eggshells to cryptodiran turtles, based on the fossil record of the Guimarota Mine. These eggshells have taller than wide aragonitic eggshell units, so are most likely attributable to Testudoolithidae, and the extremely thin eggshell probably is enough to erect a new ootaxon. Nevertheless, the materials studied by Kohring never returned to Portugal with the rest of the materials currently housed in the Museu Geológico de Lisboa and can be considered lost. Furthermore, the Guimarota Mine level KM11 of the Alcobaça formation is no longer accessible.

Crocodylomorphs. Portugal has the oldest record of crocodylomorph eggs, with the holotype of *Krokolithes dinophilus* having been described in the locality of Paimogo (Russo et al., 2017). These authors erected a new oospecies based on materials from the type locality and a series of other coeval localities in the Lourinhã formation. The diagnosis is based on a relatively large ellipsoidal egg with a relatively thin crocodyloid eggshell. This combination of features is diagnostic for the holotype egg, but difficult the attribution of most of the fragmentary referred material. In addition, the eggshells are largely recrystallized and the quality of the thin sections figured is not adequate.

Russo et al. (2017) described a second ootaxon, *Suchoolithus portucalensis* based on a clutch of 13 small eggs from Cambelas (Torres Vedras). The diagnostic characters include a small ellipsoid egg with ornamented eggshell surfaces and shell units wider than taller. Authors also refer to a lack of interstices at the base of the shell units. Again, the thin sections provided difficult the identification of the described characters, but the unusual ornamentation on a crocodylomorph egg, coupled with the small egg size and unusually thin eggshell render this oogenus and oospecies easily diagnosable. In his PhD thesis, Castanhinha (2014) studied the same clutch and performed a propagation phase contrast X-ray synchrotron microtomography scan of one egg, stating the presence of a well-developed *in ovo* crocodylomorph embryo, confirming the crocodylomorph affinity of *Suchoolithus*.

In addition, Krokolithidae are the most abundant eggshells in the sampled microfossil vertebrate assemblages. These fragments are sub-millimetric, caramel colored, of thin eggshells (100 to 200 microns), smooth to slightly ornamented, and show typical crocodylomorph eggshell organization under the Scanning Electron Microscope (SEM). The lack of complete eggs hinders the identification of the diagnostic characters of *K. dinophilus*, but smooth or slightly undulated eggshells are much more frequent than those with dispersituberculated ornamentation, suggesting that *Krokolithes* is more abundant than *Suchoolithus* in these localities.

Dinosaurs. The first reports of dinosaur eggshells from Portugal date from the first years of the 1990's. Dantas et al. (1991, 1992) presented two meeting abstracts describing several localities in the vicinity of Lourinhã (Peralta, Paimogo and Valmitão beaches). In these outcrops the authors describe spherulithic eggshells that they tentatively assigned to Megaloolithidae, an oofamily associated with sauropod dinosaurs. In addition, they describe a dinosaur prismatic eggshell from Peralta that is described as very similar to the eggshells with obliquoprismatic morphotype from USA that later will be named *Preprismatoolithus coloradoensis* (Hirsch, 1994). It is noteworthy that Kohring (Kohring,

1993) describes spherulitic eggshells from the near beach of Porto Dinheiro (Porto "Pinheiro") that are similar to those described by Dantas et al (1991, 1992) in Peralta and Valmitão, which were collected between 1959 and 1982, but remained unidentified. Kohring (1993) agrees with the identification of the eggshells as spherulithic but proposes a more accurate Dendroolithidae (=Phaceloolithidae) affinity, an oofamily that has been related to both theropod and sauropod dinosaurs.

Since these first findings, several localities with dinosaur eggshells, eggs and clutches have been identified in the Jurassic coast of Portugal (e.g. Ribeiro et al., 2013a, b), but only eggshell ootaxa have been identified. The spherulithic eggshells have been reported in several additional localities, with the most spectacular specimen being a partial clutch with associated *Torvosaurus* embryonic material from Porto das Barcas (Araújo et al., 2013). Similar eggshell fragments are omnipresent in microfossil vertebrate assemblages, characterized by a spherulithic morphotype and sagenotuberculated ornamentation, although when heavily eroded they can be easily misidentified as megaloolithid eggshells. Another important occurrence is a sandstone block from Porto das Barcas containing two elongated partial eggs (Ribeiro et al., 2013). Concerning the prismatic eggshells, they are characterized by an oblicuoprismatic morphotype, with two layered eggshells with wide shell units and obliquocanaliculated pore system, probably belonging to an unnamed oospecies of *Preprismatoolithus*. The most significant specimen is the "Paimogo clutch" a taphonomic assemblage of over 80 eggs, some with embryos, formed by the washing of several dinosaur clutches (Ezquerro et al., 2024; Fernandes et al., 2021; MATEUS, 1997). Additional important specimens include the Peralta nest, a collection of over 60 complete to collapsed eggs collected in four jackets in one of the outcrops originally described by (Dantas et al., 1992) currently under study. Finally, in 2019, a large jacket containing two to three small, seemingly individualized but in close proximity clutches was excavated in the beach of Canhiçal by our team and is currently under study. This vast collection of eggshells allowed establishing a faster and less destructive sampling protocol for geochemical analysis, ultimately providing more reliable paleoenvironmental reconstructions (Coimbra et al., 2023)

Meaningful absences. It is noteworthy that, despite sauropods being the most ubiquitous dinosaur fossils in the Lourinhã Fm, no sauropod eggshells or eggs have been identified in Portugal. Ongoing research on the eggshell of early-diverging sauropodomorphs suggests that their eggshell is poorly mineralized, regarded as soft by some authors (Norell et al., 2021). Jurassic and Early Cretaceous sauropod eggshells are significantly thinner than their late Jurassic equivalents. The lack of sauropod eggshell in the Lourinhã Fm. represents evidence of ecological behavior of Jurassic sauropod nesting elsewhere, far from the alluvial flats, or it is caused by a taphonomic bias. The lack of ornithischian eggshells predating the Cretaceous is a global enigma that it is also observed in the Jurassic of Portugal.

Conclusion

In the last 40 years, the Jurassic coast of Portugal has produced the second oldest Testudines' eggshells, the two oldest instances of Crocodylomorpha eggshells, the oldest crocodylomorph embryos, and two of the oldest theropod embryos, together with several clutches of crocodylomorphs and dinosaurs. Nowadays, it remains as an unrivaled window to Amniotes' reproduction during the final millions of years of the Jurassic.

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