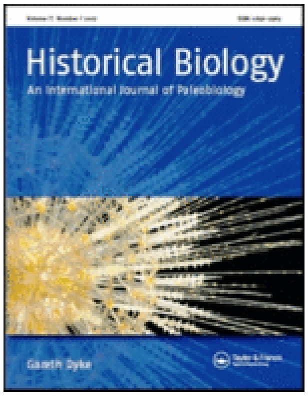

A new crocodylomorph related ootaxon from the late Maastrichtian of the Southern Pyrenees (Huesca, Spain)

Journal:	*Historical Biology*
Manuscript ID	GHBI-2022-0158.R1
Manuscript Type:	Original Article
Date Submitted by the Author:	n/a
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Keywords:	Crocodylomorpha, Krokolithidae, eggshell fragments, Tremp Basin, Late Cretaceous

A new crocodylomorph related ootaxon from the late Maastrichtian of the Southern Pyrenees (Huesca, Spain)

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Crocodylomorph eggs and eggshells are known as old as the Late Jurassic and are frequent components of most multiootaxic eggshell assemblages. Classified within the oofamily Krokolithidae, thei histo- and ultrastructures are conservative throughout geological time, characterized by inverted-trapezoid-shaped shell units that grow from highly spaced basal knobs and present a diagnostic tabular ultrastructure. Here we report 327 eggshell fragments from a new fossil site from the Maastrichtian of the Southern Pyrenees, Veracruz 1, and erect a new oogenus and oospecies, *Pachykrokolithus excavatum* oogen. et oosp. nov. characterized by crocodyloid morphotype and a prominent rugosocavate ornamentation. Eggshells from the slightly older locality of Blasi 2b, previously reported as aff. Krokolithidae, are also assigned to this new ootaxon. Different crocodylomorph taxa coexisted during the Late Cretaceous of the Tremp Basin, hindering the attribution of *Pachykrokolithus excavatum* oogen. et oosp. nov. to a single clade. Nevertheless, allodaposuchid eusuchians were dominant in this ecosystem, and are the most probable producers of *Pachykrokolithus excavatum* oogen. et oosp. nov. eggs.

Keywords: Crocodylomorpha, Krokolithidae, eggshell fragments, Tremp Basin, Late Cretaceous.

Introduction

Fossil crocodylomorphs are important components of most Mesozoic continental faunal assemblages, being significantly more diverse and disparate than their current representatives (Felice et al. 2021 and references within). Nevertheless, crocodylomorph eggs and eggshells are relatively scarce in the fossil record, especially when compared with dinosaurs (Carpenter and Alf 1994). Despite the osteological record of the clade Crocodylomorpha dates back to the Carnian, Late Triassic (Irmis et al. 2013), the oldest crocodylomorph eggshells known are almost 80 My younger, dating from the Kimmeridgian-Tithonian, Late Jurassic (Russo et al. 2017). First crocodylomorph eggshells had ultrastructure and histostructure very similar to that of their modern relatives, which remarkably remained constant through fossil record with few exceptions –e.g. *Mycomorphoolithus kohringii* Moreno-Azanza, Gasca and Canudo 2015, an eggshell with uncertain ootaxonomic affinities that has been postulated to be crocodylomorph related based in the extinction pattern observed in its shell units–. These conservative features are: 1) calcite composition; 2) tabular "book-like" ultrastructure, with remarkable horizontal cleavage of the calcite crystals; 3) subtriangular shell units; presence of basal knobs –subspherical microcrystalline agglomerates at the base of the shell units– that clearly differ from the eisospherites observed in other amniotes; and 4) shell unitis comprised by very few large crystals that comprise all the eggshell thickness, and laterally expand towards the external surface, showing blocky extinction pattern under cross-polarized light (Hirsch 1985; Mikhailov 1991; Kohring and Hirsch 1996; Mikhailov 1997; Moreno-Azanza et al. 2014).

The fossil record of Crocodylomorpha from the Tremp Formation (Southern Pyrenees, Spain) is rich and diverse and comprises both osteological and oological fossils (Pérez-Pueyo et al. 2021). Concerning the osteological record, five major clades have been recognized: Allodaposuchidae, Hylaeochampsidae, Crocodylia, Atoposauridae and Sebecosuchia (Puértolas-Pascual et al. 2016; Blanco et al. 2020; Sellés et al. 2020). The fossil record of Eusuchia (clade that includes all extant crocodylians and several extinct clades) recovered within the Tremp Basin corresponds to: postcranial bones, isolated teeth, cranial fragments and several skulls of allodaposuchids; isolated teeth and a mandible of hylaeochampsids; and few isolated teeth tentatively assigned to Crocodylia (Puértolas et al. 2011; Puértolas-Pascual et al. 2014; Blanco et al. 2014; Blanco et al. 2015; Puértolas-Pascual 2016; Blanco et al. 2020). Besides Eusuchia, only isolated teeth of atoposaurids, and scarce isolated teeth and a partial skeleton assigned to sebecosuchians have been recovered within the basin (Puértolas-Pascual et al. 2016; Blanco et al. 2020; Sellés et al. 2020).

Concerning the oological record of Crocodylomorpha, Moreno-Azanza *et al.* (2014) described thirteen eggshell fragments collected from the Blasi 2b microfossil site from the upper Maastrichtian part of the Tremp Formation. These eggshells where previously interpreted as presenting dinosaur spherulithic morphotype and attributed to aff. Megaloolithidae (López-Martínez et al. 1999; López Martínez 2003). However, Moreno-Azanza *et al.* (2014) reassigned them to Krokolithidae indet., based on a detailed analysis of their histo- and ultrastructure that revealed the presence of tabular ultrastructure, blocky extinction patterns and absence of true eisospherites. Due to the small sample size, these authors refrained to erect new ootaxa.

In this work, we describe hundreds of eggshells collected from the Maastrichtian part of the Tremp Formation, from the Veracruz 1 (VE1) fossil site. These eggshells are attributable to the oofamily Krokolithidae, and indistinguishable from the aff. Krokolithidae from Blasi 2b (BLA2B), although better preserved. This wider sample allows us to erect a new oogenus and oospecies of the oofamily Krokolithidae to include the eggshells from both localities, and compare them other Krokolithidae ootaxa and with *Stromatoolithus (Spheroolithus) europaeus*, a dinosaur ootaxon that is found in the same outcrops which, despite being ultrastructurally very different, can be easily misidentified in hand sample.

Geographical and geological setting

The fossil eggshells studied mostly come from the Veracruz 1 site, and in minor number, from Blasi 2b. Two additional eggshell fragments were also collected from 172-i/04/f site, and from a level close to the Areny 1. All these palaeontological sites were found in the Upper Cretaceous continental outcrops of the Southern Pyrenees (Ribargorza county, Huesca, NE Spain; Fig. 1A): Veracruz 1 site is close to the town of Biascas de Obarra (municipality of Beranuy), 172-i/04/f is located near the town of Serraduy (municipality of Isábena) and Blasi 2b and Areny 1 lay within the municipality of Arén.

In the Southern Pyrenees, there are a series of sedimentary domains developed during the Late Cretaceous to the Paleogene filled with marine to continental sediments (Muñoz 1992; Teixell 2004; Costa et al. 2010; Fondevilla et al. 2016), and all together conform the South-Pyrenean Basin. The materials described here come from the so-called Tremp Basin, whose sedimentary record widely crops out in the Tremp Syncline (Fig. 1A). The sedimentary unit including the fossil sites studied correspond to the Tremp Formation (Mey et al. 1968). It is a Maastrichtian-Paleocene transitional to continental unit, with an important record of Maastrichtian vertebrate fossils, including dinosaurs, pterosaurs, crocodylomorphs, testudines, squamates, amphibians and fishes, representing some of the last Mesozoic biological communities of vertebrates prior the K/Pg extinction event, being one of the few assemblages preserved in Europe for this age (Puértolas-Pascual 2016; Vila et al. 2016; Puértolas-Pascual et al. 2018; Fondevilla et al. 2019; Pérez-Pueyo et al. 2021). According to the stratigraphical proposal of Rosell et al. (2001), the Tremp Formation can be divided into four informal units, with the two lower units dated as Maastrichtian. These lower units are the ‘Grey Garumnian’, formed by mudstones, sandstones and limestones deposited in transitional and lagoonal environments (Eichenseer 1988; Riera et al. 2009; Oms et al. 2016), and the overlaying ‘Lower Red Garumnian’, dominated by multicoloured mudstones and intercalations of sandstones, representing fluvial and alluvial deposits with certain marine influence (Riera et al. 2009; Díez-Canseco et al. 2014).

Veracruz 1 fossil site is situated in the upper part of the 'Grey Garumnian' (Fig.1B, C). The eggshells appear in a 6.7–7 m-thick level of bioturbated grey marly mudstones with charcoal fragments, invertebrate shells –molluscs and crustaceans–, vertebrate bones, and eggshells which are more abundant at the top of the level. Several vertebrate clades have been identified, including osteichthyans, testudines, crocodylomorphs, hadrosaurid dinosaurs (Pérez-Pueyo et al. 2019) and, more recently, amphibians and theropod dinosaurs (Pérez-Pueyo 2022, obs. pers.). The 172-i/04/f fossil site is situated in the lower part of the 'Lower Red Garumnian' (Fig. 1C), not so far from Veracruz 1. This site has produced isolated bones of Hadrosauridae indet. and abundant crustacean fingers. A single eggshell fragment was recovered. Both sites have been dated within the magnetochron C29r (Puértolas-Pascual et al. 2018) (Fig.1C), thus laying within the last 400 kyr of the Maastrichtian.

Blasi 2b is situated in the lower part of the 'Grey Garumnian' (Fig. 1C) and has yielded abundant eggshell fragments (López-Martínez et al. 1999; López Martínez 2003; Moreno-Azanza et al. 2014) and numerous microvertebrate remains assigned to dinosaurs (López-Martínez et al. 2001; Torices et al. 2004; Pereda-Suberbiola et al. 2009; Cruzado-Caballero et al. 2013), crocodylomorphs (López-Martínez et al. 2001; Blanco et al. 2020); testudines (López-Martínez et al. 2001; Murelaga and Canudo 2005); amphibians, squamates (López-Martínez et al. 2001; Blain et al. 2010) and fishes (López-Martínez et al. 2001). One eggshell with crocodylomorph affinity was found in the 'Grey Garumnian' above the fossil tracksite of Areny 1 (Barco et al. 2001), in a similar stratigraphic position to Blasi 2b (Fig. 1C). Both sites (Blasi 2b and Areny 1) have been dated as late Maastrichtian (top of chron C30n; Fig.1C), by means of magnetostratigraphy (Pereda-Suberbiola et al. 2009).

Material and methods

Veracruz-1 site has yielded several hundreds of eggshell fragments, among other macro- and microfossils remains. Among these, 317 eggshells are included in this study, most of them big enough to be observed at naked eye and be picked up in situ during field surveys. No complete eggs have been recovered. Additionally, smaller fragments were recovered during microfossil sorting. Bulk rock samples were dried at room temperature and soaked in water with 5-10% hydrogen peroxide for ~24 hours. The resulting sediment was screen washed using 2-, 1- and 0.5-mm sieves.

All 317 eggshell fragments were measured using a digital caliper, of which 25 were cleaned with an ultrasound bath for 15 min, dried and mounted and gold-coated for secondary electron imaging in a JEOL 3600 Scanning Electron Microscope housed at Servicios de Apoyo a la Investigación (SAI) of the University of Zaragoza. Six additional fragments where embedded in epoxy resin and cut into 20 µm thick thin sections, as standard 30 µm thin sections where too thick to observe certain crystallographic features of the eggshell. Thin section observations were performed with an Olympus BX53M petrographic microscope equipped with an Olympus DP27 digital camera, housed in the 'Instituto Universitario de Ciencias Ambientales' (IUCA) of the University of Zaragoza. All specimens were collected with permission under the regional and national Cultural Heritage law, and are currently housed in the Museo de Ciencias Naturales de la Universidad de Zaragoza (Canudo 2018). The new names published here are nomenclaturally available according to the requirements of the amended International Code of Zoological Nomenclature, including registration of the work in ZooBank (http://zoobank.org) with the following Life Science Identifier: urn:lsid:zoobank.org:pub:BA86B702-A1BB-4D7F-AF60-94E92A9E7207

Nomenclature follows Hirsch (1985) and Moreno-Azanza *et al.* (2014).

Systematic palaeontology

Oofamily Krokolithidae Kohring and Hirsch, 1996

Oogenus *Pachykrokolithus* oogen. nov.

urn:lsid:zoobank.org:act:70871E72-2C84-4347-8F8E-5C50F5B3E460

Diagnosis: as for the type and only oospecies

Etymology: Combined from the ancient Greek terms: “pachy” (meaning thick), “krokos” (from the combining form for the krokódilos meaning lizard), “oo” (from the combining form for ova, meaning egg), and “lithos” (meaning stone).

Oospecies *Pachykrokolithus excavatum* oogen. et oosp. nov.

urn:lsid:zoobank.org:act:503DE743-CE5C-4102-9A63-DEEEC34A5C9A

Etymology: From Latin “excavatum”=excavated, in reference to the prominent rugosocavate outer surface.

Type material: Holotype, a single eggshell fragment (MPZ 2022/268), gold coated for SEM. Paratype: 26 eggshell fragments gold coated, prepared for SEM (MPZ 2022/252 to MPZ 2022/277), 6 eggshell fragments prepared as thin sections (MPZ 2022/278 to MPZ 2022/283), and 284 unprepared eggshell fragments (MPZ 2022/286 to MPZ 2022/569).

Type locality and horizon: Veracruz 1 site, Biascas de Obarra, Ribagorza county (Huesca province, Spain). Tremp Formation, uppermost Maastrichtian (chron C29r).

Stratigraphy and geographical range: Lower Red Garumnian and Grey Garumnian units of Tremp Formation, Upper Maastrichtian, Ribagorza county (Huesca, NE Spain).

Additional sites, other than the type locality, include Blasi 2b site and an unnamed fossiliferous bed near Areny 1 site (top C30n), and 127-i/04/f (C29r).

Material: In addition to the type material, 13 eggshell fragments (MPZ 2013/20 to MPZ 2013/31) from the Blasi 2b locality, previously described by Moreno-Azanza *et al.* (2014); One eggshell fragment from 127-i/04/e (MPZ 2022/284); and one eggshell fragment found near Areny 1 site (MPZ 2022/285).

Synonimia

Dinosauroid-spherulitic type eggshell; López-Martínez, Canudo and Cuenca-Bescós 1999: 35-36.

Aff. Megaloolithidae; López-Martínez 2003: 136, pl. 1

Krokolithidae indet; Moreno-Azanza, Bauluz, Canudo, Puértolas-Pascual and Sellés 2014: 197, figs. 2, 3.

Spheroolithus aff. *europaeus*; Pérez-Pueyo, Gilabert, Moreno-Azanza, Puértolas-Pascual, Bádenas, Canudo 2019: 111

Diagnosis: Thick Krokolithidae eggshells (Mean thickness 814 µm, range 500-1100 µm), combining prominent rugosocavated ornamentation in the external surface and shell units packed together in the two outer thirds of the eggshell, with small pyramidal interstices between shell units in the inner third.

Figures 2, 4C-D

Description: Thick Krokolithidae eggshells with a mean thickness of 814 µm – N=317, SD= 0.08, range 500-1100 µm; Fig. 2A-D–. Eggshell units are taller than wider with width to height ratios ranging from 0.5 to 0.8, although some shell units can be as wide as tall. They are trapezoidal in shape, and are tightly packed (Fig. 2D), but for the inner third of the eggshell, where small pyramidal interstices are present between shell units –interstices being smaller than in other Krokolithidae eggshells. Occasionally there are some smaller shell units compressed between larger ones, partially filling these interstices.

The eggshell has three different layers: inner, middle and outer (Fig. 2A): 1) The inner layer comprised by microcrystalline basal knobs, which at high magnification has an irregular crystal arrangement (Fig. 2A), forming an irregular rosette-like arrangement of the basal plate and showing some vesiculation. These basal knobs act as nucleation centres for the shell units and are loosely spaced throughout the inner surface of the eggshell; 2) The middle layer is more compact than the inner layer and has the characteristic book-like tabular ultrastructure of the crocodylomorph eggshell (Fig. 2A). Vesicles are very scarce (Fig. 2A), and the massiveness of this layer results in some fragments showing conchoidal fractures when broken and prepared for examination; 3) The outer layer is also thick, representing more than half of the eggshell, and it is formed by large wedges with a marked cleavage following three directions, one parallel to the eggshell surface and two of them oblique to the eggshell surface (Fig. 2A). Vesicles are much more abundant in this layer. Some fragments have a fibrous ultrastructure, resulting from the abundant vesicles being aligned by the cleavage (Moreno-Azanza et al. 2014, figure 2A).

Pore channels are straight, very wide and funnel shaped (Fig. 2B), increasing their diameter towards the external and internal surfaces of the eggshell (Fig. 2E). They appear between shell units, and open to the interstices of the inner part of the eggshell, which are interconnected in a secondary horizontal pore system, as in other crocodylomorph eggshells.

In thin section, shell unit boundaries are clearly distinguished throughout most of the eggshell thickness, although some degree of fusion hinders their limits at the outer layer (Fig. 2C). Brownish-yellowish organic matter is present on the inner layer, the upper half of the middle layer and in the outer layer, whereas the lower half of the middle layer is white (Fig. 2C). Sinuous growth lines are present in the outer layer, parallel to the undulating outer surface(arrow in Fig. 2C). In cross-polarized light, the characteristic blocky extinction of the crocodylomorph eggshell can be observed (Fig. 2D). Each shell unit is formed by at least three extinction domains, shaped as irregular wedges, which comprise both the middle and outer layers of the eggshell. The microcrystalline nature of the basal knobs agrees with the lack of extinction pattern.

The external surface shows prominent rugosocavate ornamentation (sensu Marzola et al. 2015) (Fig. 2E, F). The surface is undulant, with bulges and depressions, which are subcircular to elliptical, and sometimes coalesce. The pore openings are subcircular and locate inside of some of these depressions. The general aspect of the surface ornamentation is thus similar to that observed in *Paleosuchus palpebrosus* eggshells (Marzola et al. 2015) but much more marked. Some circular dissolution pits can be observed (Fig 2E).

The inner surfaces have bulbous, irregular basal plate groups (Fig. 2G). They are randomly spaced, originating shell units of different sizes, depending on the available space between adjacent units. The contact between shell units is distinct and straight, with somewhat zigzagging profiles, giving the shell units a polygonal contour in inner view. Irregular polygonal gaps, somewhat elongated, locate in the junction points between three to five shell units, causing the secondary horizontal pore system (Fig. 2G).

Discussion

Comparison with other crocodylomorph related ootaxa

Well-preserved fragments of *Pachykrokolithus excavatum* oogen. et oosp. nov. have diagnostic features of the Krokolithidae oofamily, according to the emended diagnosis proposed by Jackson and Varricchio (2016), namely multi-layered eggshells with basal knobs and shell units with book-like tabular ultrastructure. Among the Krokolithidae, *Pachykrokolithus* oogen. nov. presents the thickest eggshells (Figure 3, Supplementary Table 1). Among Crocodylomorpha, the thickness of *Pachykrokolithus excavatum* oogen. et oosp. nov. is comparable to that of some eggshells of *Caiman latitrostris*, that have been reported to reach up to 850 μm in thickness (Schleich and Kästle 1988) although recent studies have shown that the eggshell thickness in this taxon highly varies within a single egg, as well as during incubation (Piazza et al. 2021).

Three valid oogenera are recognized within the oofamily Krokolithidae: *Krokolithes* Hirsch 1985; *Suchoolithus*, Russo, Mateus, Marzola and Balbino 2017; and *Neokrokolithes* Bravo, Sevilla and Barroso-Barcenilla 2019. In addition, *Bauruoolithus* Oliveira, Santucci, Andrade, Fuljaro, Basílio and Benton 2011, was originally described as a Krokolithidae, but was moved out of the oofamily by Jackson and Varricchio (2016) based on some features incompatible with Krokolithidae (e.g. lack of tabular book-like ultrastructure, absence of basal plate groups, and presence of sweeping extinction pattern), and even regard it as a nomen nudum due to the lack of appropriate illustration of the type specimens. Finally, *Mycomorphoolithus* Moreno-Azanza, Gasca and Canudo 2015 is classified as oofamily incertae sedis, but its affinity to Krokolithidae was stablished due to the presence of blocky extinction pattern and sub-trapezoidal shell units.

The comparison of *Pachykrokolithus excavatum* oogen. et oosp. nov. with the oogenera of the oofamily Krokolithidae supports its proposals as a new ootaxon. *Pachykrokolithus excavatum* oogen. et oosp. nov. is up to four times thicker than the Jurassic oogenus *Suchoolithus* and can be further differentiated in having taller than wider shell units and lacking the faint dispersituberculated ornamentation of *Suchoolithus* (Russo et al. 2017). *Neokrokoolithes* is much thinner than *Pachykrokolithus excavatum* oogen. et oosp. nov. and presents characteristic triangular nodes on the outer surface (Bravo et al. 2018) instead of the rugosocavate ornamentation of *Pachykrokolithus excavatum* oogen. et oosp. nov. *Krokolithes* eggshells are generally much thinner, usually 250 to 550 µm, and with a maximum thickness of 760 µm present in the unnamed Bridger Formation Eggshells described by Hirsch and Kohring (1992). In addition, the interstices between shell units are significantly larger in *Krokolithes* eggshells (Hirsch 1985; Kohring and Hirsch 1996), whereas in *Pachykrokolithus excavatum* oogen. et oosp. nov. they are restricted to the inner third of the eggshell.

The oogenus *Mycomorpholithus* from the Lower Cretaceous of Europe was originally described as having a smooth to wavy surface, '*…although extrinsic erosion of the numerous pore openings confers a reticulate appearance upon the outer surface*' (Moreno-Azanza et al. 2015). This oogenus was described prior to the definition of the rugosocavate ornamentation by Marzola *et al.* (2015), but its ornamentation is somewhat similar to the exaggerated rugosocavate ornamentation present in *Pachykrokolithus excavatum* oogen. et oosp. nov. The ornamentation of *Mycomorphoolithus* is highly related to the degree of development of the porosity – number and width of the pore channels–, which was postulated to increase during embryogenesis, reaching its maximum prior to hatch (Moreno-Azanza et al. 2015). A similar trend on the development of the porosity can be observed in *Pachykrokolithus excavatum* oogen. et oosp. nov., with some fragments having small circular pores in the bottom of the valleys excavated in the eggshell surface (Fig. 2E), to wider circular pores between large ridges, and finally a heavily ornamented eggshell surface with prominent ridges and multiple pores (Figure 2F). These similitudes reinforce the original interpretation of *Mycomorphoolithus* as a crocodylomorph eggshell. Nevertheless, *Pachykrokolithus excavatum* oogen. et oosp. nov. can be easily differentiated by the absence of anastomosing pores and mushroom-shaped of the shell units with larger interstices between shell units compared to *Mycomorphoolithus*.

Finally, Hirsch and Quinn (1990) describe a single 1100 µm-thick eggshell fragment from the Two Medicine Formation (Campanian, Late Cretaceous), as a putative crocodile eggshell, a determination supported by other authors (Jackson and Varricchio 2010). This eggshell fragment is poorly preserved, but presents large shell units arranged in wedges, which would support its crocodylomorph affinity. Nevertheless, in radial cross section it has a rhombohedral fracture (Hirsch and Quinn 1990 figure 13C), which suggests the eggshell is recrystallized, and a overlaying granular layer with remains of sedimentary grains embedded that hinders any further comparison.

Similitudes with the dinosaurian ootaxa Stromatoolithus (Spheroolithus) europaeus

The oospecies *Spheroolithus europaeus* Sellés, Vila and Galobart 2014 was described from Porrit-6 site in the upper Maastrichtian outcrops of the Tremp Formation in the village of El Pont d'Orrit (Lleida, Spain), which locates 17 km to the east of Veracruz 1 site and 5 km to the east of Blasi 2b site (Fig. 1A, C). Porrit-6 is located in the lower part of the 'Grey Garumnian', having a roughly equivalent stratigraphic position to

Blasi 2b, within the upper part of chron C30n (Fig. 1C). Since the original description of this oospecies, Zhou et al. (2021) have proposed that it belongs to the oogenus *Stromatoolithus*, based on its straight pore canals and fine ornamentation. It is important to note that this attribution was based on the original description and without direct examination of the type material by Zhou et al. (2021). To acknowledge this taxonomic proposal but to avoid confusion if this assignation is disregarded after future revision, we chose to refer to this ootaxon as *Stromatoolithus (Spheroolithus) europaeus* Sellés et al. 2014). *Stromatoolithus (Spheroolithus) europaeus* has a slightly thicker eggshell than *Pachykrokolithus excavatum* oogen. et oosp. nov. (Fig. 4). It has a well-defined prolatospherulithic morphotype with highly fused shell units with radial calcite structure, and is characterized by sagenotuberculate ornamentation comprising fine irregular ridges, and two types of pore openings, one elliptical and large and another circular and small (Sellés et al. 2014).

The similar thickness and ornamented outer of *Pachykrokolithus excavatum* oogen. *et* oosp. nov. and *Stromatoolithus (Spheroolithus) europaeus*, causes that weathered specimens of can be easily misidentified during sample picking, and even with low magnification SEM pictures. Furthermore, the ultrastructure of both ootaxa may be obliterated by minimal recrystallization, making it even more difficult to properly identify and differentiate them. Nevertheless, thin sections are unequivocal to differentiate both oospecies (Fig. 4 B, D), as *Stromatoolithus (Spheroolithus) europaeus* has slender shell units, marked growth lines throughout the shell thickness and sweeping extinction, whereas *Pachykrokolithus excavatum* oogen. *et* oosp. nov. has wider shell units, with faint grown lines restricted to the upper part of the eggshell, and blocky extinction. This emphasizes the importance of thin sections in the study of fossil eggs together with Scanning Electron Microscope imaging, two complementary techniques required for a proper diagnosis of ootaxa.

Taxonomic affinities of Pachykrokolithus excavatum oogen. et oosp. nov.

The lack of embryonic remains or gravid females associated with eggs in Veracruz 1 site hinders the precise identification of the egg laying taxon that produced *Pachykrokolithus excavatum* oogen. *et* oosp. nov. eggshells. Nevertheless, the crocodylomorph affinities of this ootaxon can be discussed by reviewing the diverse crocodylomorph osteological record of the Tremp Formation to search for putative egg layers.

Allodaposuchidae (basal eusuchians closely related with the crown group Crocodylia) is the most abundant crocodylomorph clade in the Tremp Basin. Indeed, their recovered fossils consist of the most reliably taxonomically identified and well-studied crocodylomorph remains of the whole Basin. During the last decade, four skulls assigned to four different species, *Arenysuchus gascabadiolorum* Puértolas, Canudo and Cruzado-Caballero, 2011, *Agaresuchus subjuniperus* (Puértolas-Pascual, Canudo and Moreno-Azanza, 2014), *Allodaposuchus palustris* Blanco, Puértolas Pascual, Marmi, Vila and Sellés, 2014 and *Allodaposuchus hulki* Blanco, Fortuny, Vicente, Luján, García-Marçà and Sellés, 2015, have been found within the Maastrichtian of the Tremp Basin. Besides, dozens of isolated generalist conical teeth and several fragmentary cranial remains assigned to Allodaposuchidae indet. have also been recovered, including teeth found in Veracruz 1 and Blasi 2b (Blanco et al. 2020; Puértolas-Pascual et al. 2016). Interestingly, the holotype of *A. subjuniperus* (C29r, latest Maastrichtian, Huesca, Spain) was geographically recovered only 800 m from Veracruz 1 and 300 m from 127-i/04/f (Fig. 1A); and the holotype of *A. gascabadiolorum* (C30n–C29r, late Maastrichtian, Huesca, Spain) was located 100 m from Blasi 2b and 3 km from Areny 1

(Fig. 1A). Therefore, both taxa were recovered in the same geographic area and very close stratigraphic levels to the sites where eggshells of *Pachykrokolithus excavatum* oogen. et oosp. nov. specimens have been recovered (Fig. 1C).

Regarding Hylaeochampsidae (another clade of basal eusuchians closely related with Allodaposuchidae and crown group Crocodylia), only remains assigned to cf. *Acynodon* have been identified within the Tremp Formation (Blanco et al. 2020; Puértolas-Pascual et al. 2016). The most important fossil of this taxon is an almost complete small mandible from Els Nerets (C31r, early Maastrichtian, Lleida, Spain) assigned to *Acynodon* sp. (Blanco et al. 2020). The rest of the remains recovered in the Tremp Formation consist of isolated teeth assigned to cf. *Acynodon*. Although very scarce, they are distributed throughout the basin (including Blasi 2b) and throughout the Maastrichtian (from C31r to C29r) (Blanco et al., 2020; Puértolas-Pascual et al., 2016).

The presence of the crown group Crocodylia within the Tremp basin is less reliable as only 3 isolated teeth assigned to cf. *Thoracosaurus* have been found. However, more complete remains, such as a skull, have been found in the Maastrichtian of France (Laurent et al. 2000). Therefore, its presence in the Tremp Basin is possible and the assignment as a producer of *Pachykrokolithus excavatum* oogen. et oosp. nov. cannot be completely ruled out.

Besides eusuchians, other crocodylomorphs recovered within the basin are Atoposauridae. Although two species have been described in other Maastrichtian localities of Europe, *Aprosuchus ghirai* Venczel and Codrea, 2019 and *Sabresuchus* (= *Theriosuchus*) *sympiestodon* (Martin, Rabi and Csiki, 2010), both from the Haţeg Basin (Romania), only a few isolated teeth assigned to Atoposauridae indet. have been found in the Maastrichtian of the Tremp basin (Puértolas-Pascual et al. 2016; Blanco et al. 2020).

The rarest clade corresponds to Sebecosuchia. Of this clade, isolated teeth assigned to cf. *Doratodon* have been recovered from several sites of the Tremp basin with ages ranging from C30r to C29r (Blanco et al. 2020). However, no teeth of this type have been recovered from nearby sites where eggshells of *Pachykrokolithus excavatum* oogen. et oosp. nov. have been found. On the other hand, The Sebecidae *Ogresuchus furatus* Sellés, Blanco, Vila, Marmi, López-Soriano, Llácer, Frigola, Canals and Galobart, 2020, from the early Maastrichtian (C32n-C31r) of the Tremp basin (Coll de Nargó, Lleida, Spain), have been recently described (Sellés et al., 2020). No other material assigned to *Ogresuchus* has been identified at other locations of the Tremp Basin.

Considering the high abundance of the osteological fossil remains of Eusuchia within the Tremp basin and their geographical/stratigraphical proximity to the sites where *Pachykrokolithus excavatum* oogen. et oosp. nov. has been found, the most likely producers are the basal eusuchians Allodaposuchidae or, although less probable, Hylaeochampsidae.

Concluding remarks

Pachykrokolithus excavatum oogen. et oosp. nov. is a new oogenus and oospecies of the oofamily Krokolithidae, which has been identified in four localities of the Maastrichtian (Late Cretaceous) of the southern Pyrenees. Its ornamented external surface, unusual thickness for a crocodile eggshell and large shell units have led to several misidentifications as a dinosaurian (*Megaloolithus* and *Spheroolithus*) eggshell, but the combination of a rugosocavate ornamentation, presence of basal knobs tabular book-like ultrastructure, and blocky extinction pattern confirm its belonging to Krokolithidae. These emphasizes the importance of combining thin section analysis and high magnification Scanning Electron Microscope Images in the study of fossil eggshells.

Among the putative egg layers, allodaposuchid crocodylomorphs are the most likely producers of *Pachykrokolithus excavatum* oogen. et oosp. nov. eggs.

Acknowledgments

This research is supported by the PLEC2021-008203 project, funded by MCIN/AEI/10.13039/501100011033 and by the European Union "NextGenerationEU"/PRTR", the Spanish Ministry of Science and Innovation (project PID2021-122612OB-I00) and by the Government of Aragón-FEDER 2014–2020 *Construyendo Europa desde Aragón* (Group E18: *Aragosaurus: Recursos Geológicos y Paleoambientales*) and Fundação para a Ciência e a Tecnologia (grant number PTDC/CTA-PAL/31656/2017 and research unit UIDB/04035/2020; GeoBioTec). Authors would like to acknowledge the use of Servicio General de Apoyo a la Investigación-SAI, Universidad de Zaragoza. MMA and EPP funded by Ministerio de Universidades and Unión Europea-NextGenerationEU "Requalification of Spanish university system for 2021-2023". MPP is supported by the Spanish Ministry of Education, Culture and Sport (Grant Number FPU 16/03064). CNL is the recipient of a Juan de la Cierva-Formación contract (FJC2020-044561-I), supported by the MCIN and co-financed by the NextGenerationEU/PRTR. We thank the contribution of the two anonymous reviewers and the editor, Dr. Gareth Dyke.

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The authors report there are no competing interests to declare.

Figure 1. Geographic and geological context of the paleontological sites with crocodylomorph sites of the Southern Pyrenees. A. Geological map of the Southern Pyrenees, focused on the Tremp Syncline and its Upper Cretaceous-Paleogene outcrops (modified from López-Martínez and Vicens, 2012). B. Stratigraphic log of the upper Maastrichtian Tremp Formation from the Beranuy outcrops. Color of rocks are indicated. Key: I. Parallel lamination II. Low-angle cross-bedding III. Planar cross-bedding. IV. Inclined heterolithic cross-bedding V. Flaser, wavy and lenticular bedding VI. Ripples VII. Quartz pebbles. VIII. Mud pebbles IX. Bioturbation X. Root marks-mottling XI. Plant remains XII. Undifferentiated bioclasts XIII. Bivalves XIV. Gastropods XV. Decapods XVI. Vertebrate bones XVII. Eggshells XVIII. Dinosaur tracks. C. Chronostratigraphic framework of the Western Tremp Syncline (magnetostratigraphic data after Pereda-Suberbiola et al., (2009); Canudo et al., (2016); Puértolas-Pascual et al., (2018), with the stratigraphic position of the sites studied in this paper. AM3: Amor 3: type locality of *Agaresuchus subjuniperus,* AR1: Areny-1, BLA2B: Blasi 2B, El: Elias: type locality of *Arenysuchus gascabadiolorum* PO6: Porrit-6, VE1: Veracruz 1.

Figure 2. *Pachykrokolithus excavatum* oogen. et oosp. nov. from the Upper late Maastrichtian Veracruz 1 site (Tremp Formation) A). Scanning Electron Microscope secondary electron images (A, B, E-F) and thin section microphotographs (C, D). A, MPZ-2022/268 holotype eggshell fragment in radial section, showing a three-layered eggshell and trapezoidal shell units. The inner layer (IL) has a rosette-like structure, with basal knobs. The middle layer (ML) has book-like tabular ultrastructure (BLTU) and sparse vesiculation (Ve). The thicker outer layer (OL) represents more than half of the eggshell thickness, has more vesicles (Ve) and shows marked cleavage (CLV). B, MPZ- 2022/277 eggshell fragment in radial section, showing a funnel shaped pore channel (PC) and a basal knob (BK). C, MPZ 2022/282 eggshell fragment thin section under parallel-polarized light, showing the brownish colour of the basal knobs (BK) of the inner layer (IN) and the outer layer (OL), compared with a much clearer medium layer (ML) due to the different distribution of organic matter. Note the sinuous growth lines (GL) parallel to the eggshell surface. D, MPZ 2022/282 eggshell fragment in radial section under cross-polarized light, showing the blocky extinction, with extinction domains expanding in lateral development in the outer layer. E, MPZ 2022/251 eggshell

fragment outer surface, having a prominent rugosocavate ornamentation with bulges and depressions, with subcircular pore openings within the depressions (PO), and incipient dissolution pits (DP). F, MPZ 2022/252 eggshell fragment outer surface, with even more marked rugosocavate ornamentation, with some of the bulges coalescing into ridges. G, MPZ/2022/265 eggshell fragment inner surface with irregular, randomly spaced basal plate groups. Irregular polygonal gaps locate in the junction points between shell units, resulting in the interstices that connect with pore openings.

Figure 3. Box and whiskers plot comapring the maximun eggshell thickness of moderm taxa, fossil ootaxa, and the measured thickness of *Pachykrokolithus excavatum* oogen. et oosp. nov., with boxes reporesenting the two medium percentiles with inclusive medians. Note that *Pachykrokolithus excavatum* oogen. et oosp. nov., is thicker than most other crocodylomorph related eggshells.

Figure 4. Comparison between *Stromatoolithus (Spheroolithus) europaeus* (A, B) and *Pachykrokolithus excavatum* oogen. et oosp. nov. (C, D). A, IPS-64162, *Stromatoolithus (Spheroolithus) europaeus* Scanning Electron Microscope secondary electron image of the outer surface composed of fine ridges. B, IPS-58973g, *Stromatoolithus (Spheroolithus) europaeus* thin section microphotograph, showing fused spherulitic shell units, with tightly packed growth lines and swapping extinction. C, MPZ 2022/251, *Pachykrokolithus excavatum* oogen. et oosp. nov. Scanning Electron Microscope secondary electron image of the outer surface showing prominent rugosocavate ornamentation, with pore openings. D, MPZ 2022/278, *Pachykrokolithus excavatum* oogen. et oosp. nov. thin section microphotograph showing a slightly thinner eggshell with wide trapezoidal shell units and growth lines limited to the outer layer. Extinction pattern is blocky.

A new crocodylomorph related ootaxon from the late Maastrichtian of the Southern Pyrenees (Huesca, Spain)

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A new crocodylomorph related ootaxon from the late Maastrichtian of the Southern Pyrenees (Huesca, Spain)

Crocodylomorph eggs and eggshells are known as old as the Late Jurassic and are frequent components of most multiootaxic eggshell assemblages. Classified within the oofamily Krokolithidae, thei histo- and ~~ultrastructurwes~~ultrastructures are conservative throughout geological time, characterized by inverted-trapezoid-shaped shell units that grow from highly spaced basal knobs and present a diagnostic tabular ultrastructure. Here we report 327 eggshell fragments from a new fossil site from the Maastrichtian of the Southern Pyrenees, Veracruz 1, and erect a new oogenus and oospecies, *Pachykrokolithus excavatum* oogen. et oosp. nov. characterized by crocodyloid morphotype and a prominent rugosocavate ornamentation. Eggshells from the slightly older locality of Blasi 2b, previously reported as aff. Krokolithidae, are also assigned to this new ootaxon. Different crocodylomorph taxa coexisted during the Late Cretaceous of the Tremp Basin, hindering the attribution of *Pachykrokolithus excavatum* oogen. et oosp. nov. to a single clade. Nevertheless, allodaposuchid eusuchians were dominant in this ecosystem, and are the most probable producers of *Pachykrokolithus excavatum* oogen. et oosp. nov. eggs.

Keywords: Crocodylomorpha, Krokolithidae, eggshell fragments, Tremp Basin, Late Cretaceous.

Introduction

Fossil crocodylomorphs are important components of most Mesozoic continental faunal assemblages, being significantly more diverse and disparate than their current representatives (Felice et al. 2021 and references within). Nevertheless, crocodylomorph eggs and eggshells are relatively scarce in the fossil record, especially when compared with dinosaurs (Carpenter and Alf 1994). Despite the osteological record of the clade Crocodylomorpha dates back to the Carnian, Late Triassic (Irmis et al. 2013), the oldest crocodylomorph eggshells known are almost 80 My younger, dating from the Kimmeridgian-Tithonian, Late Jurassic (Russo et al. 2017). First crocodylomorph eggshells had ultrastructure and histostructure very similar to that of their modern relatives, which remarkably remained constant through fossil record with few exceptions –e.g. *Mycomorphoolithus kohringii* Moreno-Azanza, Gasca and Canudo 2015, an eggshell with uncertain ootaxonomic affinities that has been postulated to be crocodylomorph related based in the extinction pattern observed in its shell units–. These conservative features are: 1) calcite composition; 2) tabular “book-like” ultrastructure, with remarkable horizontal cleavage of the calcite crystals; 3) subtriangular shell units; presence of basal knobs –subspherical microcrystalline agglomerates at the base of the shell units– that clearly differ from the eisospherites observed in other amniotes; and 4) shell unitis comprised by~~,~~ very few large crystals that comprise all the eggshell thickness, and laterally expand towards the external surface, showing blocky extinction pattern under cross-polarized light (Hirsch 1985; Mikhailov 1991; Kohring and Hirsch 1996; Mikhailov 1997; Moreno-Azanza et al. 2014).

The fossil record of Crocodylomorpha from the Tremp Formation (Southern Pyrenees, Spain) is rich and diverse and comprises both osteological and oological fossils (Pérez-Pueyo et al. 2021). Concerning the osteological record, five major clades have been recognized: Allodaposuchidae, Hylaeochampsidae, Crocodylia, Atoposauridae and Sebecosuchia (Puértolas-Pascual et al. 2016; Blanco et al. 2020; Sellés et al. 2020). The fossil record of Eusuchia (clade that includes all extant crocodylians and several extinct clades) recovered within the Tremp Basin corresponds to: postcranial bones, isolated teeth, cranial fragments and several skulls of allodaposuchids; isolated teeth and a mandible of hylaeochampsids; and few isolated teeth tentatively assigned to Crocodylia (Puértolas et al. 2011; Puértolas-Pascual et al. 2014; Blanco et al. 2014; Blanco et al. 2015; Puértolas-Pascual 2016; Blanco et al. 2020). Besides Eusuchia, only isolated teeth of atoposaurids, and scarce isolated teeth and a partial skeleton assigned to sebecosuchians have been recovered within the basin (Puértolas-Pascual et al. 2016; Blanco et al. 2020; Sellés et al. 2020).

Concerning the oological record of Crocodylomorpha, Moreno-Azanza *et al.* (2014) described thirteen eggshell fragments collected from the Blasi 2b microfossil site from the upper Maastrichtian part of the Tremp Formation. These eggshells where previously interpreted as presenting dinosaur spherulithic morphotype and attributed to aff. Megaloolithidae (López-Martínez et al. 1999; López Martínez 2003). However, Moreno-Azanza *et al.* (2014) reassigned them to Krokolithidae indet., based on a detailed analysis of their histo- and ultrastructure that revealed the presence of tabular ultrastructure, blocky extinction patterns and absence of true eisospherites. Due to the small sample size, these authors refrained to erect new ootaxa.

In this work, we describe hundreds of eggshells collected from the Maastrichtian part of the Tremp Formation, from the Veracruz 1 (VE1) fossil site. These eggshells are attributable to the oofamily Krokolithidae, and indistinguishable from the aff. Krokolithidae from Blasi 2b (BLA2B), although better preserved. This wider sample allows us to erect a new oogenus and oospecies of the oofamily Krokolithidae to include the eggshells from both localities, and compare them other Krokolithidae ootaxa and with *Stromatoolithus (Spheroolithus) europaeus*, a dinosaur ootaxon that is found in the same outcrops which, despite being ultrastructurally very different, can be easily misidentified in hand sample.

Geographical and geological setting

The fossil eggshells studied mostly come from the Veracruz 1 site, and in minor number, from Blasi 2b. Two additional eggshell fragments were also collected from 172-i/04/f site, and from a level close to the Areny 1. All these palaeontological sites were found in the Upper Cretaceous continental outcrops of the Southern Pyrenees (Ribargorza county, Huesca, NE Spain; Fig. 1A): Veracruz 1 site is close to the town of Biascas de Obarra (municipality of Beranuy), 172-i/04/f is located near the town of Serraduy (municipality of Isábena) and Blasi 2b and Areny 1 lay within the municipality of Arén.

In the Southern Pyrenees, there are a series of sedimentary domains developed during the Late Cretaceous to the Paleogene filled with marine to continental sediments (Muñoz 1992; Teixell 2004; Costa et al. 2010; Fondevilla et al. 2016), and all together conform the South-Pyrenean Basin. The materials described here come from the so-called Tremp Basin, whose sedimentary record widely crops out in the Tremp Syncline (Fig. 1A). The sedimentary unit including the fossil sites studied correspond to the Tremp Formation (Mey et al. 1968). It is a Maastrichtian-Paleocene transitional to continental unit, with an important record of Maastrichtian vertebrate fossils, including dinosaurs, pterosaurs, crocodylomorphs, testudines, squamates, amphibians and fishes, representing some of the last Mesozoic biological communities of vertebrates prior the K/Pg extinction event, being one of the few assemblages preserved in Europe for this age (Puértolas-Pascual 2016; Vila et al. 2016; Puértolas-Pascual et al. 2018; Fondevilla et al. 2019; Pérez-Pueyo et al. 2021). According to the stratigraphical proposal of Rosell et al. (2001), the Tremp Formation can be divided into four informal units, with the two lower units dated as Maastrichtian. These lower units are the 'Grey Garumnian', formed by mudstones, sandstones and limestones deposited in transitional and lagoonal environments (Eichenseer 1988; Riera et al. 2009; Oms et al. 2016), and the overlaying 'Lower Red Garumnian', dominated by multicoloured mudstones and intercalations of sandstones, representing fluvial and alluvial deposits with certain marine influence (Riera et al. 2009; Díez-Canseco et al. 2014).

Veracruz 1 fossil site is situated in the upper part of the 'Grey Garumnian' (Fig.1B, C). The eggshells appear in a 6.7–7 m-thick level of bioturbated grey marly mudstones with charcoal fragments, invertebrate shells –molluscs and crustaceans–, vertebrate bones, and eggshells which are more abundant at the top of the level. Several vertebrate clades have been identified, including osteichthyans, testudines, crocodylomorphs, hadrosaurid dinosaurs (Pérez-Pueyo et al. 2019) and, more recently, amphibians and theropod dinosaurs (Pérez-Pueyo 2022, obs. pers.). The 172-i/04/f fossil site is situated in the lower part of the 'Lower Red Garumnian' (Fig. 1C), not so far from Veracruz 1. This site has produced isolated bones of Hadrosauridae indet. and abundant crustacean fingers. A single eggshell fragment was recovered. Both sites have been dated within the magnetochron C29r (Puértolas-Pascual et al. 2018) (Fig.1C), thus laying within the last 400 kyr of the Maastrichtian.

Blasi 2b is situated in the lower part of the 'Grey Garumnian' (Fig. 1C) and has yielded abundant eggshell fragments (López-Martínez et al. 1999; López Martínez 2003; Moreno-Azanza et al. 2014) and numerous ~~microvertebrates~~microvertebrate remains assigned to dinosaurs (López-Martínez et al. 2001; Torices et al. 2004; Pereda-Suberbiola et al. 2009; Cruzado-Caballero et al. 2013), crocodylomorphs (López-Martínez et al. 2001; Blanco et al. 2020); testudines (López-Martínez et al. 2001; Murelaga and Canudo 2005); amphibians, squamates (López-Martínez et al. 2001; Blain et al. 2010) and fishes (López-Martínez et al. 2001). One eggshell with crocodylomorph affinity was found in the 'Grey Garumnian' above the fossil tracksite of Areny 1 (Barco et al. 2001), in a similar stratigraphic position to Blasi 2b (Fig. 1C).

Both sites (Blasi 2b and Areny 1) have been dated as late Maastrichtian (top of chron C30n; Fig.1C), by means of magnetostratigraphy (Pereda-Suberbiola et al. 2009).

Material and methods

Veracruz-1 site has yielded several hundreds of eggshell fragments, among other macro- and microfossils remains. Among these, 317 eggshells are included in this study, most of them big enough to be observed at naked eye and be picked up in situ during field surveys. No complete eggs have been recovered. Additionally, smaller fragments were recovered during microfossil sorting. Bulk rock samples were dried at room temperature and soaked in water with 5-10% hydrogen peroxide for ~24 hours. The resulting sediment was screen washed using 2-, 1- and 0.5-mm sieves.

All 317 eggshell fragments were measured using a digital caliper, of which 25 were cleaned with an ultrasound bath for 15 min, dried and mounted and gold-coated for secondary electron imaging in a JEOL 3600 Scanning Electron Microscope housed at Servicios de Apoyo a la Investigación (SAI) of the University of Zaragoza. Six additional fragments where embedded in epoxy resin and cut into 20 µm thick thin sections, as standard 30 µm thin sections where too thick to observe certain crystallographic features of the eggshell. Thin section observations were performed with an Olympus BX53M petrographic microscope equipped with an Olympus DP27 digital camera, housed in the 'Instituto Universitario de Ciencias Ambientales' (IUCA) of the University of Zaragoza. All specimens were collected with permission under the regional and national Cultural Heritage law, and are currently housed in the Museo de Ciencias Naturales de la Universidad de Zaragoza (Canudo 2018). The new names published here are nomenclaturally available according to the requirements of the amended International Code of Zoological Nomenclature, including registration of the work in ZooBank (http://zoobank.org) with the following Life Science Identifier: urn:lsid:zoobank.org:pub:BA86B702-A1BB-4D7F-AF60-94E92A9E7207

Nomenclature follows Hirsch (1985) and Moreno-Azanza *et al.* (2014).

Systematic palaeontology

Oofamily Krokolithidae Kohring and Hirsch, 1996

Oogenus *Pachykrokolithus* oogen. nov.

urn:lsid:zoobank.org:act:70871E72-2C84-4347-8F8E-5C50F5B3E460

Diagnosis: as for the type and only oospecies

Etymology: Combined from the ancient Greek terms: “pachy” (meaning thick), “krokos” (from the combining form for the krokódilos meaning lizard), “oo” (from the combining form for ova, meaning egg), and “lithos” (meaning stone).

Oospecies *Pachykrokolithus excavatum* oogen. et oosp. nov.

urn:lsid:zoobank.org:act:503DE743-CE5C-4102-9A63-DEEEC34A5C9A

Etymology: From Latin “excavatum”=excavated, in reference to the prominent rugosocavate outer surface.

Type material: Holotype, a single eggshell fragment (MPZ 2022/268), gold coated for SEM. Paratype: 26 eggshell fragments gold coated, prepared for SEM (MPZ 2022/252 to MPZ 2022/277), 6 eggshell fragments prepared as thin sections (MPZ 2022/278 to MPZ 2022/283), and 284 unprepared eggshell fragments (MPZ 2022/286 to MPZ 2022/569).

Type locality and horizon: Veracruz 1 site, Biascas de Obarra, Ribagorza county (Huesca province, Spain). Tremp Formation, uppermost Maastrichtian (chron C29r).

Stratigraphy and geographical range: Lower Red Garumnian and Grey Garumnian units of Tremp Formation, Upper Maastrichtian, Ribagorza county (Huesca, NE Spain).

Additional sites, other than the type locality, include Blasi 2b site and an unnamed fossiliferous bed near Areny 1 site (top C30n), and 127-i/04/f (C29r).

Material: In addition to the type material, 13 eggshell fragments (MPZ 2013/20 to MPZ 2013/31) from the Blasi 2b locality, previously described by Moreno-Azanza *et al.* (2014); ~~1~~One eggshell fragment from 127-i/04/e (MPZ 2022/284); and ~~1~~one eggshell fragment found near Areny 1 site (MPZ 2022/285).

Synonimia

Dinosauroid-spherulitic type eggshell; López-Martínez, Canudo and Cuenca-Bescós 1999: 35-36.

Aff. Megaloolithidae; López-Martínez 2003: 136, pl. 1

Krokolithidae indet; Moreno-Azanza, Bauluz, Canudo, Puértolas-Pascual and Sellés 2014: 197, figs. 2, 3.

Spheroolithus aff. *europaeus*; Pérez-Pueyo, Gilabert, Moreno-Azanza, Puértolas-Pascual, Bádenas, Canudo 2019: 111

Diagnosis: Thick Krokolithidae eggshells (Mean thickness 814 µm, range 500-1100 µm~~) with~~), combining prominent rugosocavated ornamentation in the external surface~~.~~ ~~Shell~~ and shell units packed together in the two outer thirds of the eggshell, with small pyramidal interstices between shell units in the inner third.

Figures 2, 4C-D

Description: Thick Krokolithidae eggshells with a mean thickness of 814 µm – N=317, SD= 0.08, range 500-1100 µm; Fig. 2A-D–. Eggshell units are taller than wider with width to height ratios ranging from 0.5 to 0.8, although some shell units can be as wide as tall. They are trapezoidal in shape, and are tightly packed (Fig. 2D), but for the inner third of the eggshell, where small pyramidal interstices are present between shell units –interstices being smaller than in other Krokolithidae eggshells. Occasionally there are some smaller shell units compressed between larger ones, partially filling these interstices.

The eggshell has three different layers: inner, middle and outer (Fig. 2A): 1) The inner layer comprised by microcrystalline basal knobs, which at high magnification has an irregular crystal arrangement (Fig. 2A), forming an irregular rosette-like arrangement of the basal plate and showing some vesiculation. These basal knobs act as nucleation centres for the shell units and are loosely spaced throughout the inner surface of the eggshell; 2) The middle layer is more compact than the inner layer and has the characteristic book-like tabular ultrastructure of the crocodylomorph eggshell (Fig. 2A). Vesicles are very scarce (Fig. 2A), and the massiveness of this layer results in some fragments showing conchoidal fractures when broken and prepared for examination; 3) The outer layer is also thick, representing more than half of the eggshell, and it is formed by large wedges with a marked cleavage following three directions, one parallel to the eggshell surface and two of them oblique to the eggshell surface (Fig. 2A). Vesicles are much more abundant in this layer. Some fragments have a fibrous ultrastructure, resulting from the abundant vesicles being aligned by the cleavage (Moreno-Azanza et al. 2014, figure 2A).

Pore channels are straight, very wide and funnel shaped (Fig. 2B), increasing their diameter towards the external and internal surfaces of the eggshell (Fig. 2E). They appear between shell units, and open to the interstices of the inner part of the eggshell, which are interconnected in a secondary horizontal pore system, as in other crocodylomorph eggshells.

In thin section, shell unit boundaries are clearly distinguished throughout most of the eggshell thickness, although some degree of fusion hinders their limits at the outer layer (Fig. 2C). Brownish-yellowish organic matter is present on the inner layer, the upper half of the middle layer and in the outer layer, whereas the lower half of the middle layer is white (Fig. 2C). Sinuous growth lines are present in the outer layer, parallel to the undulating outer surface(arrow in Fig. 2C). In cross-polarized light, the characteristic blocky extinction of the crocodylomorph eggshell can be observed (Fig. 2D). Each shell unit is formed by at least three extinction domains, shaped as irregular wedges, which comprise both the middle and outer layers of the eggshell. The microcrystalline nature of the basal knobs agrees with the lack of extinction pattern.

The external surface shows prominent rugosocavate ornamentation (sensu Marzola et al. 2015) (Fig. 2E, F). The surface is undulant, with bulges and depressions, which are subcircular to elliptical, and sometimes coalesce. The pore openings are subcircular and locate inside of some of these depressions. The general aspect of the surface ornamentation is thus similar to that observed in *Paleosuchus palpebrosus* eggshells (Marzola et al. 2015) but much more marked. Some circular dissolution pits can be observed (Fig 2E).

The inner surfaces have bulbous, irregular basal plate groups (Fig. 2G). They are randomly spaced, originating shell units of different sizes, depending on the available space between adjacent units. The contact between shell units is distinct and straight, with somewhat zigzagging profiles, giving the shell units a polygonal contour in inner view. Irregular polygonal gaps, somewhat elongated, locate in the junction points between three to five shell units, causing the secondary horizontal pore system (Fig. 2G).

Discussion

Comparison with other crocodylomorph related ootaxa

Well-preserved fragments of *Pachykrokolithus excavatum* oogen. et oosp. nov. have diagnostic features of the Krokolithidae oofamily, according to the emended diagnosis proposed by Jackson and Varricchio (2016), namely multi-layered eggshells with basal knobs and shell units with book-like tabular ultrastructure. Among the Krokolithidae, *Pachykrokolithus* oogen. nov. presents the thickest eggshells (Figure 3, Supplementary Table 1). Among Crocodylomorpha, the thickness of *Pachykrokolithus excavatum* oogen. et oosp. nov. is comparable to that of some eggshells of *Caiman latitrostris*, that have been reported to reach up to 850 µm in thickness (Schleich and Kästle 1988) although recent studies have shown that the eggshell thickness in this taxon highly varies within a single egg, as well as during incubation (Piazza et al. 2021).

Three valid oogenera are recognized within the oofamily Krokolithidae: *Krokolithes* Hirsch 1985; *Suchoolithus*, Russo, Mateus, Marzola and Balbino 2017; and *Neokrokolithes* Bravo, Sevilla and Barroso-Barcenilla 2019. In addition, *Bauruoolithus* Oliveira, Santucci, Andrade, Fuljaro, Basílio and Benton 2011, was originally described as a Krokolithidae, but was moved out of the oofamily by Jackson and Varricchio (2016) based on some features incompatible with Krokolithidae (e.g. lack of tabular book-like ultrastructure, absence of basal plate groups, and presence of sweeping extinction pattern), and even regard it as a nomen nudum due to the lack of appropriate illustration of the type specimens. Finally, *Mycomorphoolithus* Moreno-Azanza, Gasca and Canudo 2015 is classified as oofamily incertae sedis, but its affinity to Krokolithidae was stablished due to the presence of blocky extinction pattern and sub-trapezoidal shell units.

The comparison of *Pachykrokolithus excavatum* oogen. et oosp. nov. with the oogenera of the oofamily Krokolithidae supports its proposals as a new ootaxon. *Pachykrokolithus excavatum* oogen. et oosp. nov. is up to four times thicker than the Jurassic oogenus *Suchoolithus* and can be further differentiated in having taller than wider shell units and lacking the faint dispersituberculated ornamentation of *Suchoolithus* (Russo et al. 2017). *Neokrokoolithes* is much thinner than *Pachykrokolithus excavatum* oogen. et oosp. nov. and presents characteristic triangular nodes on the outer surface (Bravo et al. 2018) instead of the rugosocavate ornamentation of *Pachykrokolithus excavatum* oogen. et oosp. nov. *Krokolithes* eggshells are generally much thinner, usually 250 to 550 μm, and with a maximum thickness of 760 μm present in the unnamed Bridger Formation Eggshells described by Hirsch and Kohring (1992). In addition, the interstices between shell units are significantly larger in *Krokolithes* eggshells (Hirsch 1985; Kohring and Hirsch 1996), whereas in *Pachykrokolithus excavatum* oogen. et oosp. nov. they are restricted to the inner third of the eggshell.

The oogenus *Mycomorpholithus* from the Lower Cretaceous of Europe was originally described as having a smooth to wavy surface, '*...although extrinsic erosion of the numerous pore openings confers a reticulate appearance upon the outer surface*' (Moreno-Azanza et al. 2015). This oogenus was described prior to the definition of the rugosocavate ornamentation by Marzola *et al.* (2015), but its ornamentation is somewhat similar to the exaggerated rugosocavate ornamentation present in *Pachykrokolithus excavatum* oogen. et oosp. nov. The ornamentation of *Mycomorphoolithus* is highly related to the degree of development of the porosity – number and width of the pore channels–, which was postulated to increase during embryogenesis, reaching its maximum prior to hatch (Moreno-Azanza et al. 2015). A similar trend on the development of the porosity can be observed in *Pachykrokolithus excavatum* oogen. et oosp. nov., with some fragments having small circular pores in the bottom of the valleys excavated in the eggshell surface (Fig. 2E), to wider circular pores between large ridges, and finally a heavily ornamented eggshell surface with prominent ridges and multiple pores (Figure 2F). These similitudes reinforce the original interpretation of *Mycomorphoolithus* as a crocodylomorph eggshell. Nevertheless, *Pachykrokolithus excavatum* oogen. et oosp. nov. can be easily differentiated by the absence of anastomosing pores and mushroom-shaped of the shell units with larger interstices between shell units compared to *Mycomorphoolithus*.

Finally, Hirsch and Quinn (1990) describe a single 1100 µm-thick eggshell fragment from the Two Medicine Formation (Campanian, Late Cretaceous), as a putative crocodile eggshell, a determination supported by other authors (Jackson and Varricchio 2010). This eggshell fragment is poorly preserved, but presents large shell units arranged in wedges, which would support its crocodylomorph affinity. Nevertheless, in radial cross section it has a rhombohedral fracture (Hirsch and Quinn 1990 figure 13C), which suggests the eggshell is recrystallized, and a overlaying granular layer with remains of sedimentary grains embedded that hinders any further comparison.

Similitudes with the dinosaurian ootaxa Stromatoolithus (Spheroolithus) europaeus

The oospecies *Spheroolithus europaeus* Sellés, Vila and Galobart 2014 was described from Porrit-6 site in the upper Maastrichtian outcrops of the Tremp Formation in the village of El Pont d'Orrit (Lleida, Spain), which locates 17 km to the east of Veracruz 1 site and 5 km to the east of Blasi 2b site (Fig. 1A, C). Porrit-6 is located in the lower part of the 'Grey Garumnian', having a roughly equivalent stratigraphic position to

Blasi 2b, within the upper part of chron C30n (Fig. 1C). ~~*Spheroolithus*~~Since the original description of this oospecies, Zhou et al. (2021) have proposed that it belongs to the oogenus *Stromatoolithus*, based on its straight pore canals and fine ornamentation. It is important to note that this attribution was based on the original description and without direct examination of the type material by Zhou et al. (2021). To acknowledge this taxonomic proposal but to avoid confusion if this assignation is disregarded after future revision, we chose to refer to this ootaxon as *Stromatoolithus (Spheroolithus) europaeus* Sellés et al. 2014). *Stromatoolithus (Spheroolithus) europaeus* has a slightly thicker eggshell than *Pachykrokolithus excavatum* oogen. et oosp. nov. (Fig. 4). It has a well-defined prolatospherulithic morphotype with highly fused shell units with radial calcite structure, and is characterized by sagenotuberculate ornamentation comprising fine irregular ridges, and two types of pore openings, one elliptical and large and another circular and small (Sellés et al. 2014).

The similar thickness and ornamented outer of *Pachykrokolithus excavatum* oogen. *et* oosp. nov. and *Stromatoolithus (Spheroolithus) europaeus*, causes that weathered specimens of can be easily misidentified during sample picking, and even with low magnification SEM pictures. Furthermore, the ultrastructure of both ootaxa may be obliterated by minimal recrystallization, making it even more difficult to properly identify and differentiate them. Nevertheless, thin sections are unequivocal to differentiate both oospecies (Fig. 4 B, D), as *Stromatoolithus (Spheroolithus) europaeus* has slender shell units, marked growth lines throughout the shell thickness and sweeping extinction, whereas *Pachykrokolithus excavatum* oogen. *et* oosp. nov. has wider shell units, with faint grown lines restricted to the upper part of the eggshell, and blocky extinction. This emphasizes the importance of thin sections in the study of fossil eggs together with Scanning Electron Microscope imaging, two complementary techniques required for a proper diagnosis of ootaxa.

Taxonomic affinities of Pachykrokolithus excavatum oogen. et oosp. nov.

The lack of embryonic remains or gravid females associated with eggs in Veracruz 1 site hinders the precise identification of the egg laying taxon that produced *Pachykrokolithus excavatum* oogen. *et* oosp. nov. eggshells. Nevertheless, the crocodylomorph affinities of this ootaxon can be discussed by reviewing the diverse crocodylomorph osteological record of the Tremp Formation to search for putative egg layers.

Allodaposuchidae (basal eusuchians closely related with the crown group Crocodylia) is the most abundant crocodylomorph clade in the Tremp Basin. Indeed, their recovered fossils consist of the most reliably taxonomically identified and well-studied crocodylomorph remains of the whole Basin. During the last decade, four skulls assigned to four different species, *Arenysuchus gascabadiolorum* Puértolas, Canudo and Cruzado-Caballero, 2011, *Agaresuchus subjuniperus* (Puértolas-Pascual, Canudo and Moreno-Azanza, 2014), *Allodaposuchus palustris* Blanco, Puértolas Pascual, Marmi, Vila and Sellés, 2014 and *Allodaposuchus hulki* Blanco, Fortuny, Vicente, Luján, García-Marçà and Sellés, 2015, have been found within the Maastrichtian of the Tremp Basin. Besides, dozens of isolated generalist conical teeth and several fragmentary cranial remains assigned to Allodaposuchidae indet. have also been recovered, including teeth found in Veracruz 1 and Blasi 2b (Blanco et al. 2020; Puértolas-Pascual et al. 2016). Interestingly, the holotype of *A. subjuniperus* (C29r, latest Maastrichtian, Huesca, Spain) was geographically recovered only 800 m from Veracruz 1 and 300 m from 127-i/04/f (Fig. 1A); and the holotype of *A. gascabadiolorum* (C30n–C29r, late Maastrichtian, Huesca, Spain) was located 100 m from Blasi 2b and 3 km from Areny 1

(Fig. 1A). Therefore, both taxa were recovered in the same geographic area and very close stratigraphic levels to the sites where eggshells of *Pachykrokolithus excavatum* oogen. et oosp. nov. specimens have been recovered (Fig. 1C).

Regarding Hylaeochampsidae (another clade of basal eusuchians closely related with Allodaposuchidae and crown group Crocodylia), only remains assigned to cf. *Acynodon* have been identified within the Tremp Formation (Blanco et al. 2020; Puértolas-Pascual et al. 2016). The most important fossil of this taxon is an almost complete small mandible from Els Nerets (C31r, early Maastrichtian, Lleida, Spain) assigned to *Acynodon* sp. (Blanco et al. 2020). The rest of the remains recovered in the Tremp Formation consist of isolated teeth assigned to cf. *Acynodon*. Although very scarce, they are distributed throughout the basin (including Blasi 2b) and throughout the Maastrichtian (from C31r to C29r) (Blanco et al., 2020; Puértolas-Pascual et al., 2016).

The presence of the crown group Crocodylia within the Tremp basin is less reliable as only 3 isolated teeth assigned to cf. *Thoracosaurus* have been found. However, more complete remains, such as a skull, have been found in the Maastrichtian of France (Laurent et al. 2000). Therefore, its presence in the Tremp Basin is possible and the assignment as a producer of *Pachykrokolithus excavatum* oogen. et oosp. nov. cannot be completely ruled out.

Besides eusuchians, other crocodylomorphs recovered within the basin are Atoposauridae. Although two species have been described in other Maastrichtian localities of Europe, *Aprosuchus ghirai* Venczel and Codrea, 2019 and *Sabresuchus* (= *Theriosuchus*) *sympiestodon* (Martin, Rabi and Csiki, 2010), both from the Haţeg Basin (Romania), only a few isolated teeth assigned to Atoposauridae indet. have been found in the Maastrichtian of the Tremp basin (Puértolas-Pascual et al. 2016; Blanco et al. 2020).

The rarest clade corresponds to Sebecosuchia. Of this clade, isolated teeth assigned to cf. *Doratodon* have been recovered from several sites of the Tremp basin with ages ranging from C30r to C29r (Blanco et al. 2020). However, no teeth of this type have been recovered from nearby sites where eggshells of *Pachykrokolithus excavatum* oogen. et oosp. nov. have been found. On the other hand, The Sebecidae *Ogresuchus furatus* Sellés, Blanco, Vila, Marmi, López-Soriano, Llácer, Frigola, Canals and Galobart, 2020, from the early Maastrichtian (C32n-C31r) of the Tremp basin (Coll de Nargó, Lleida, Spain), have been recently described (Sellés et al., 2020). No other material assigned to *Ogresuchus* has been identified at other locations of the Tremp Basin.

Considering the high abundance of the osteological fossil remains of Eusuchia within the Tremp basin and their geographical/stratigraphical proximity to the sites where *Pachykrokolithus excavatum* oogen. et oosp. nov. has been found, the most likely producers are the basal eusuchians Allodaposuchidae or, although less probable, Hylaeochampsidae.

Concluding remarks

Pachykrokolithus excavatum oogen. et oosp. nov. is a new oogenus and oospecies of the oofamily Krokolithidae, which has been identified in four localities of the Maastrichtian (Late Cretaceous) of the southern Pyrenees. Its ornamented external surface, unusual thickness for a crocodile eggshell and large shell units have led to several misidentifications as a dinosaurian (*Megaloolithus* and *Spheroolithus*) eggshell, but the combination of a rugosocavate ornamentation, presence of basal knobs tabular book-like ultrastructure, and blocky extinction pattern confirm its belonging to Krokolithidae. These emphasizes the importance of combining thin section analysis and high magnification Scanning Electron Microscope Images in the study of fossil eggshells.

Among the putative egg layers, allodaposuchid crocodylomorphs are the most likely producers of *Pachykrokolithus excavatum* oogen. et oosp. nov. eggs.

Acknowledgments

This research is supported by the PLEC2021-008203 project, funded by MCIN/AEI/10.13039/501100011033 and by the European Union “NextGenerationEU”/PRTR”, the Spanish Ministry of Science and Innovation (project ~~CGL2017-85038-P~~PID2021-122612OB-I00) and by the Government of Aragón-FEDER 2014–2020 *Construyendo Europa desde Aragón* (Group E18: *Aragosaurus: Recursos Geológicos y Paleoambientales*) and Fundação para a Ciência e a Tecnologia (grant number PTDC/CTA-PAL/31656/2017 and research unit UIDB/04035/2020; GeoBioTec). Authors would like to acknowledge the use of Servicio General de Apoyo a la Investigación-SAI, Universidad de Zaragoza. MMA and EPP funded by Ministerio de Universidades and Unión Europea-NextGenerationEU “Requalification of Spanish university system for 2021-2023”. MPP is supported by the Spanish Ministry of Education, Culture and Sport (Grant Number FPU 16/03064). CNL is the recipient of a Juan de la Cierva-Formación contract (FJC2020-044561-I), supported by the MCIN and co-financed by the NextGenerationEU/PRTR. ~~Rupert Glasgow proofread the text. REVIEWERS AND EDITOR~~We thank the contribution of the two anonymous reviewers and the editor, Dr. Gareth Dyke.

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The authors report there are no competing interests to declare.

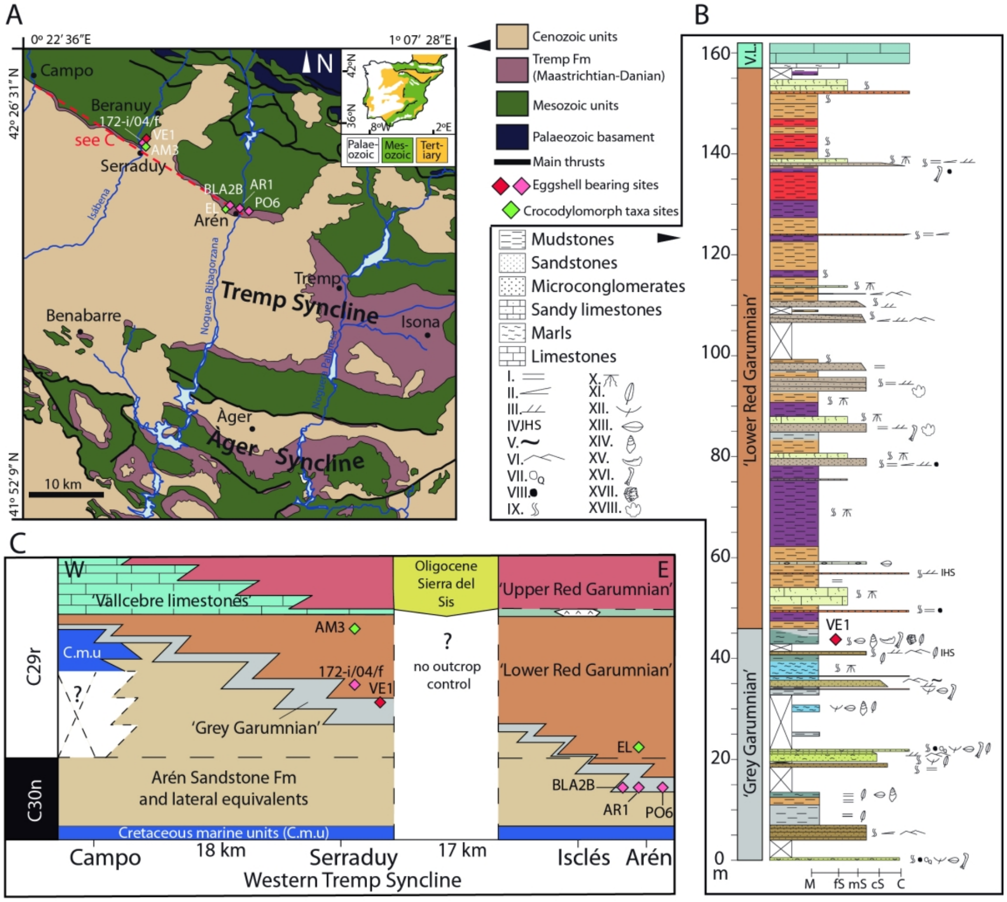
Figure 1. Geographic and geological context of the paleontological sites with crocodylomorph sites of the Southern Pyrenees. A. Geological map of the Southern Pyrenees, focused on the Tremp Syncline and its Upper Cretaceous-Paleogene outcrops (modified from López-Martínez and Vicens, 2012). B. Stratigraphic log of the upper Maastrichtian Tremp Formation from the Beranuy outcrops. Color of rocks are indicated. Key: I. Parallel lamination II. Low-angle cross-bedding III. Planar cross-bedding. IV. Inclined heterolithic cross-bedding V. Flaser, wavy and lenticular bedding VI. Ripples VII. Quartz pebbles. VIII. Mud pebbles IX. Bioturbation X. Root marks-mottling XI. Plant remains XII. Undifferentiated bioclasts XIII. Bivalves XIV. Gastropods XV. Decapods XVI. Vertebrate bones XVII. Eggshells XVIII. Dinosaur tracks. C. Chronostratigraphic framework of the Western Tremp Syncline (magnetostratigraphic data after Pereda-Suberbiola et al., (2009); Canudo et al., (2016); Puértolas-Pascual et al., (2018), with the stratigraphic position of the sites studied in this paper. AM3: Amor 3: type locality of *Agaresuchus subjuniperus,* AR1: Areny-1, BLA2B: Blasi 2B, El: Elias: type locality of *Arenysuchus gascabadiolorum* PO6: Porrit-6, VE1: Veracruz 1.

Figure 2. *Pachykrokolithus excavatum* oogen. et oosp. nov. from the Upper late Maastrichtian Veracruz 1 site (Tremp Formation) A). Scanning Electron Microscope secondary electron images (A, B, E-F) and thin section microphotographs (C, D). A, MPZ-2022/268 holotype eggshell fragment in radial section, showing a three-layered eggshell and trapezoidal shell units. The inner layer (IL) has a rosette-like structure, with basal knobs. The middle layer (ML) has book-like tabular ultrastructure (BLTU) and sparse vesiculation (Ve). The thicker outer layer (OL) represents more than half of the eggshell thickness, has more vesicles (Ve) and shows marked cleavage (CLV). B, MPZ- 2022/277 eggshell fragment in radial section, showing a funnel shaped pore channel (PC) and a basal knob (BK). C, MPZ 2022/282 eggshell fragment thin section under parallel-polarized light, showing the brownish colour of the basal knobs (BK) of the inner layer (IN) and the outer layer (OL), compared with a much clearer medium layer (ML) due to the different distribution of organic matter. Note the sinuous growth lines (GL) parallel to the eggshell surface. D, MPZ 2022/282 eggshell fragment in radial section under cross-polarized light, showing the blocky extinction, with extinction domains expanding in lateral development in the outer layer. E, MPZ 2022/251 eggshell

fragment outer surface, having a prominent rugosocavate ornamentation with bulges and depressions, with subcircular pore openings within the depressions (PO), and incipient dissolution pits (DP). F, MPZ 2022/252 eggshell fragment outer surface, with even more marked rugosocavate ornamentation, with some of the bulges coalescing into ridges. G, MPZ/2022/~~XXX~~265 eggshell fragment inner surface with irregular, randomly spaced basal plate groups. Irregular polygonal gaps locate in the junction points between shell units, resulting in the interstices that connect with pore openings.

Figure 3. Box and whiskers plot comapring the maximun eggshell thickness of moderm taxa, fossil ootaxa, and the measured thickness of *Pachykrokolithus excavatum* oogen. et oosp. nov., with boxes reporesenting the two medium percentiles with inclusive medians. Note that *Pachykrokolithus excavatum* oogen. et oosp. nov., is thicker than most other crocodylomorph related eggshells.

Figure 4. Comparison between *Stromatoolithus (Spheroolithus) europaeus* (A, B) and *Pachykrokolithus excavatum* oogen. et oosp. nov. (C, D). A, IPS-64162, *Stromatoolithus (Spheroolithus) europaeus* Scanning Electron Microscope secondary electron image of the outer surface composed of fine ridges. B, IPS-58973g, *Stromatoolithus (Spheroolithus) europaeus* thin section microphotograph, showing fused spherulitic shell units, with tightly packed growth lines and swapping extinction. C, MPZ 2022/251, *Pachykrokolithus excavatum* oogen. et oosp. nov. Scanning Electron Microscope secondary electron image of the outer surface showing prominent rugosocavate ornamentation, with pore openings. D, MPZ 2022/278, *Pachykrokolithus excavatum* oogen. et oosp. nov. thin section microphotograph showing a slightly thinner eggshell with wide trapezoidal shell units and growth lines limited to the outer layer. Extinction pattern is blocky.



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177x159mm (300 x 300 DPI)

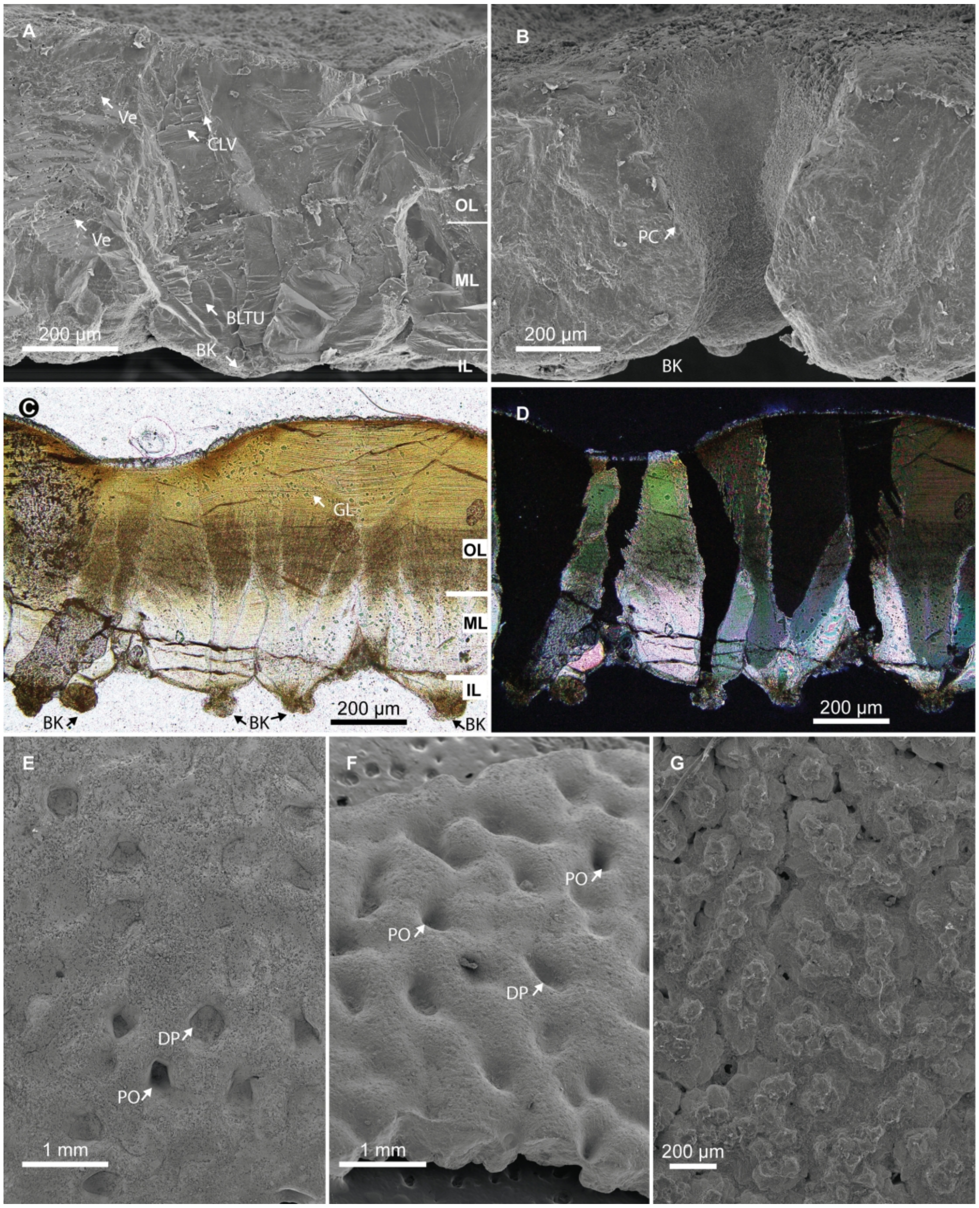

Figure 2. Pachykrokolithus excavatum oogen. et oosp. nov. from the Upper late Maastrichtian Veracruz 1 site (Tremp Formation) A). Scanning Electron Microscope secondary electron images (A, B, E-F) and thin section microphotographs (C, D). A, MPZ-2022/268 holotype eggshell fragment in radial section, showing a three-layered eggshell and trapezoidal shell units. The inner layer (IL) has a rosette-like structure, with basal knobs. The middle layer (ML) has book-like tabular ultrastructure (BLTU) and sparse vesiculation (Ve). The thicker outer layer (OL) represents more than half of the eggshell thickness, has more vesicles (Ve) and shows marked cleavage (CLV). B, MPZ- 2022/277 eggshell fragment in radial section, showing a funnel shaped pore channel (PC) and a basal knob (BK). C, MPZ 2022/282 eggshell fragment thin section under parallel-polarized light, showing the brownish colour of the basal knobs (BK) of the inner layer (IN) and the outer layer (OL), compared with a much clearer medium layer (ML) due to the different distribution of organic matter. Note the sinuous growth lines (GL) parallel to the eggshell surface. D, MPZ 2022/282 eggshell fragment in radial section under cross-polarized light, showing the blocky extinction, with extinction domains expanding in lateral development in the outer layer. E, MPZ 2022/251 eggshell fragment outer surface, having a prominent rugosocavate ornamentation with bulges and depressions, with subcircular pore

openings within the depressions (PO), and incipient dissolution pits (DP). F, MPZ 2022/252 eggshell fragment outer surface, with even more marked rugosocavate ornamentation, with some of the bulges coalescing into ridges. G, MPZ/2022/265 eggshell fragment inner surface with irregular, randomly spaced basal plate groups. Irregular polygonal gaps locate in the junction points between shell units, resulting in the interstices that connect with pore openings.

183x225mm (300 x 300 DPI)

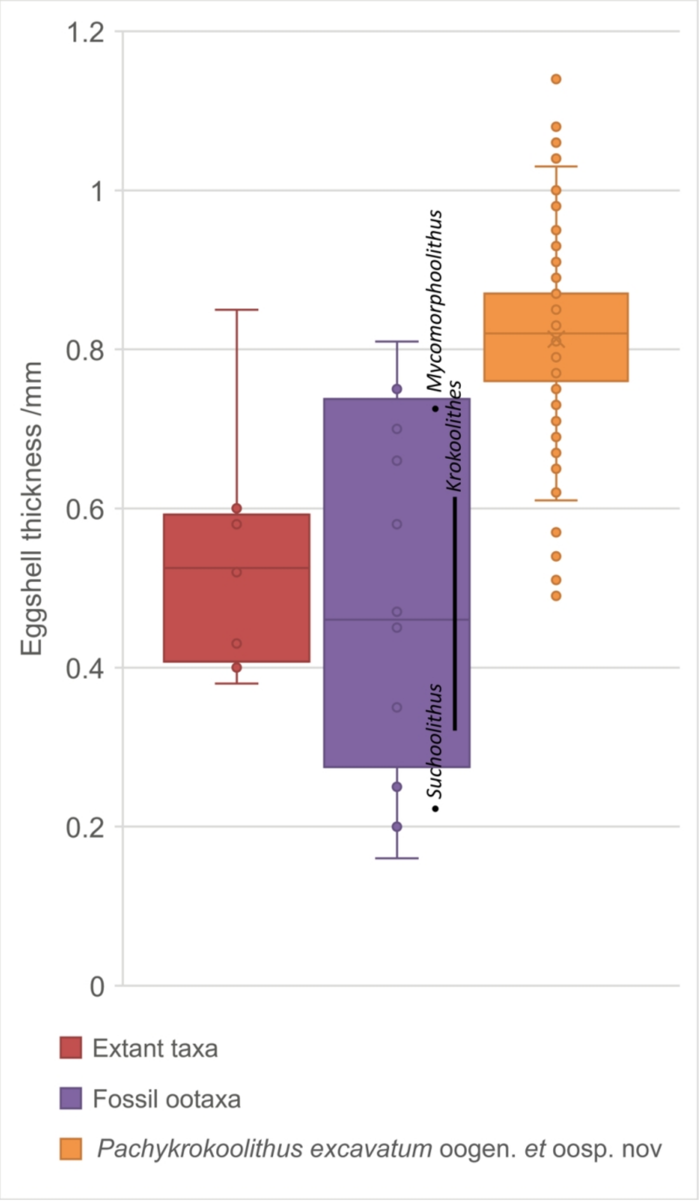

Figure 3. Box and whiskers plot comapring the maximun eggshell thickness of moderm taxa, fossil ootaxa, and the measured thickness of Pachykrokolithus excavatum oogen. et oosp. nov., with boxes reporesenting the two medium percentiles with inclusive medians. Note that Pachykrokolithus excavatum oogen. et oosp. nov., is thicker than most other crocodylomorph related eggshells.

87x150mm (300 x 300 DPI)

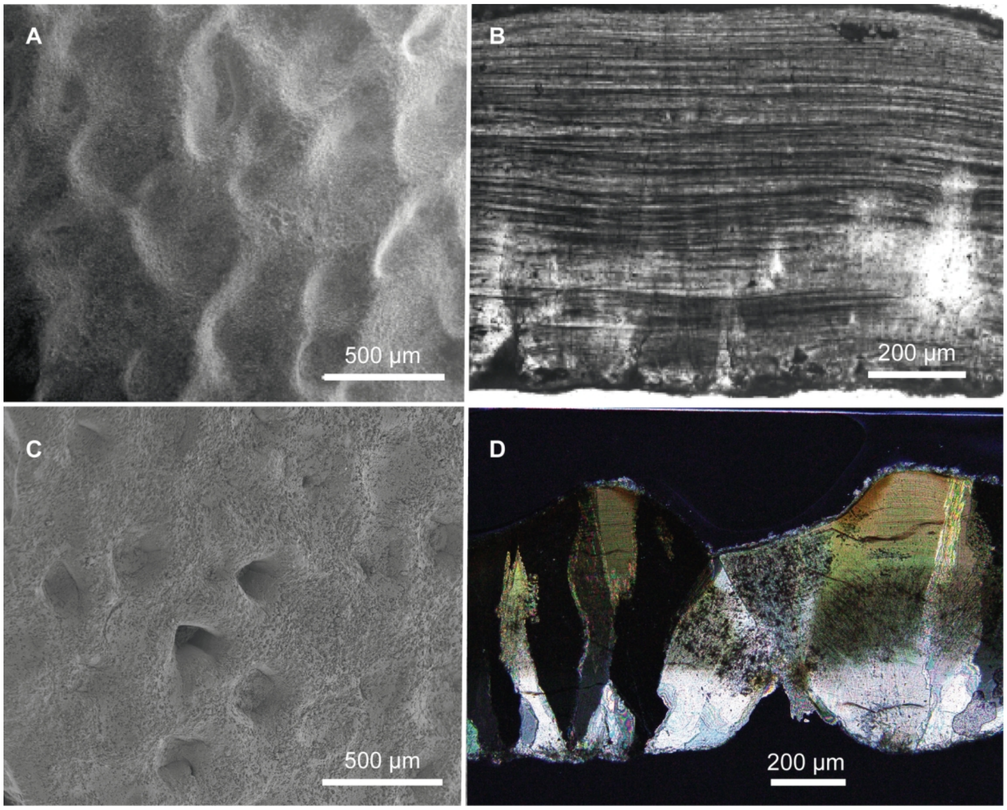

Figure 4. Comparison between Stromatoolithus (Spheroolithus) europaeus (A, B) and Pachykrokolithus excavatum oogen. et oosp. nov. (C, D). A, IPS-64162, Stromatoolithus (Spheroolithus) europaeus Scanning Electron Microscope secondary electron image of the outer surface composed of fine ridges. B, IPS-58973g, Stromatoolithus (Spheroolithus) europaeus thin section microphotograph, showing fused spherulitic shell units, with tightly packed growth lines and swapping extinction. C, MPZ 2022/251, Pachykrokolithus excavatum oogen. et oosp. nov. Scanning Electron Microscope secondary electron image of the outer surface showing prominent rugosocavate ornamentation, with pore openings. D, MPZ 2022/278, Pachykrokolithus excavatum oogen. et oosp. nov. thin section microphotograph showing a slightly thinner eggshell with wide trapezoidal shell units and growth lines limited to the outer layer. Extinction pattern is blocky.

154x123mm (300 x 300 DPI)

Supplementary table 1. Maximum eggshell thickness for modern taxa and fossil ootaxa.

Taxa or ootaxa	Maximum eggshell thickness in mm	References
Extant taxa		
Alligator mississippiensis	0.53	Deeming and Ferguson, 1990 Hirsch and Kohring, 1992 Marzola et al., 2015
Alligator sinensis	0.38	Wink and Elsey, 1994
Caiman latirostris	0.85	Schlëich and Kästle, 1988
Paleosuchus palpebrosus	0.41	Marzola et al., 2015
Crocodylus acutus	0.52	Schmidt and Schönwetter, 1943 Hirsch and Kohring, 1992
Crocodylus johnstoni	0.4	Deeming and Ferguson, 1990 Hirsch and Kohring, 1992
Crocodylus mindorensis	0.43	Marzola et al., 2015
Crocodylus niloticus	0.58	Schmidt and Schönwetter, 1943 Deeming and Ferguson, 1990
Crocodylus porosus	0.6	Schmidt and Schönwetter, 1943
Gavialis gangeticus	0.59	Ferguson, 1985
		Schleich, H.H. et al., 1994
Fossil eggshells and ootaxa		
Krokolithes dinophilus Late Jurassic Portugal	0.76	Russo et al., 2017
Suchoolithus portucalensis Late Jurassic Portugal	0.16	Russo et al.. 2017
Neokrokoolithus trigonalis Early Cretaceous Spain	0.2	Bravo et al., 2018
Mycomorphoolithus kohringi Early Cretaceous Spain	0.81	Moreno-Azanza et al., 2015
Early Cretaceous Glen Rose Fm USA	0.7	Rogers, 2001
Late Cretaceous Argentina	0.75	Frenguelli, 1951
Late Cretaceous Morocco	0.45	Garcia et al., 2003
Late Cretaceous-Malabar Hill section India	0.35	Singh et al., 1998
Late Cretaceous Lameta Fm India	0.47	Srivastava et al., 2015
Late Cretaceous Bolivia	0.2	Novas et al., 2009
Late Cretaceous Araçacatuba Fm Brazil	0.36	Ribeiro et al., 2006
Late Cretaceous Adamantina Fm Brazil	0.25	Oliveira et al., 2011
Eocene Bridger Fm USA	0.76	Hirsch and Kohring, 1992

Eocene De Beque Fm USA	0.58	Hirsch, 1985
Eocene Germany	0.45	Kohring and Hirsch, 1996
Pliocene India	0.66	Patnaik and Schleich, 1993

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