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Historical Biology

An International Journal of Paleobiology

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/ghbi20

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To cite this article: Miguel Moreno-Azanza, Manuel Pérez-Pueyo, Eduardo Puértolas-Pascual, Carmen Núñez-Lahuerta, Octávio Mateus, Blanca Bauluz, Beatriz Bádenas & José Ignacio Canudo (2022): A new crocodylomorph related ootaxon from the late Maastrichtian of the Southern Pyrenees (Huesca, Spain), Historical Biology, DOI: 10.1080/08912963.2022.2098024

To link to this article: https://doi.org/10.1080/08912963.2022.2098024

Published online: 21 Jul 2022.

HISTORICAL BIOLOGY
https://doi.org/10.1080/08912963.2022.2098024

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

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ABSTRACT

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, characterised 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. characterised 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.

ARTICLE HISTORY
Received 26 May 2022
Accepted 29 June 2022

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 on the extinction pattern observed in its shell units–. These conservative features are as follows: (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-polarised light (Hirsch 1985; Mikhailov 1991, 1997; Kohring and Hirsch 1996; 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 recognised: 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; Blanco et al. 2014, 2015, 2020; Puértolas-Pascual et al. 2014; Puértolas-Pascual 2016). 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 13 eggshell fragments collected from the Blasi 2b microfossil site from the upper Maastrichtian part of the Tremp Formation. These eggshells were 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.

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Published online 21 Jul 2022

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; Figure 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.

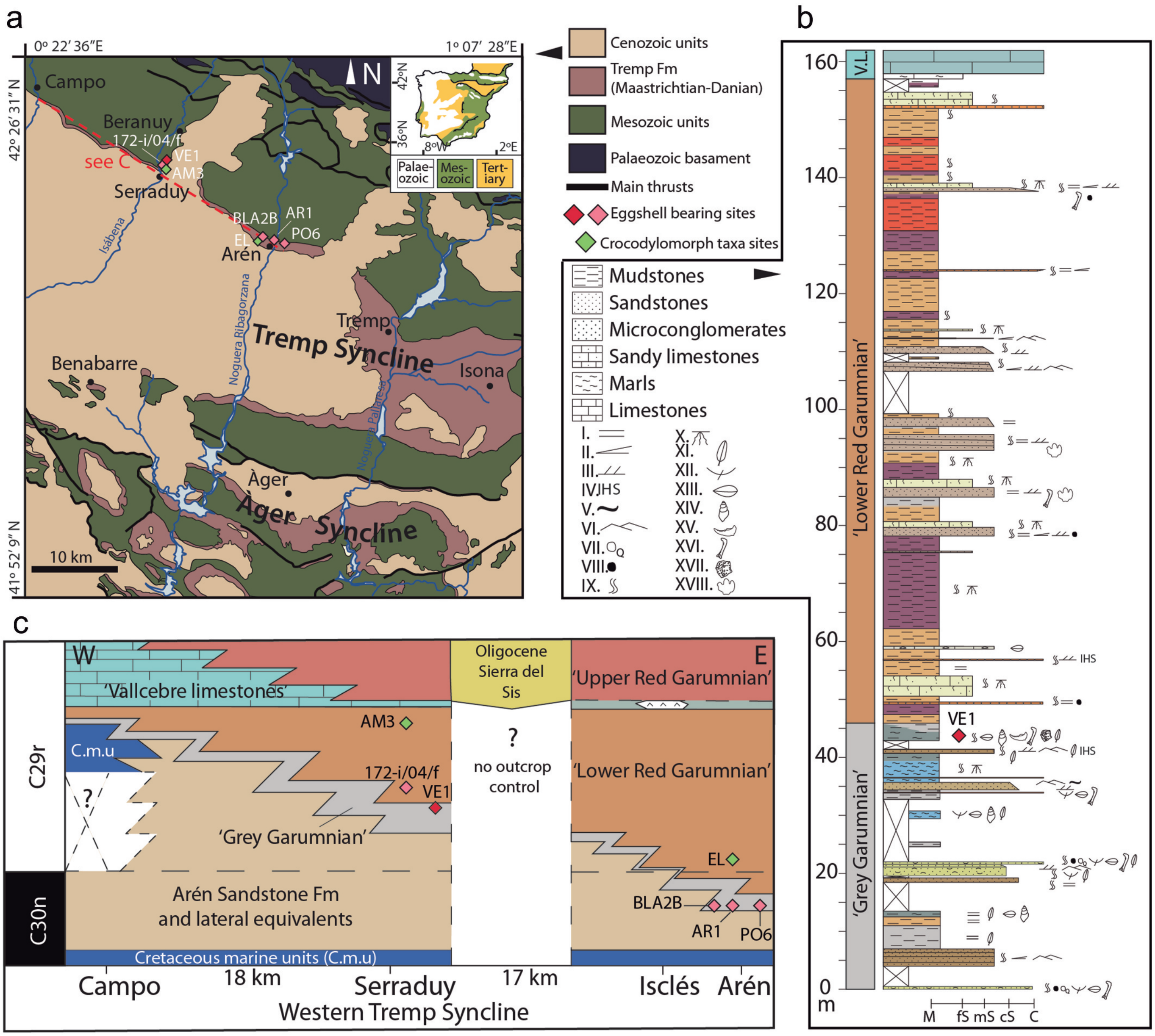

Figure 1. Geographic and geological context of the palaeontological sites with crocodylomorph sites of the Southern Pyrenees. a. Geological map of the Southern Pyrenees, focused on the Tremp Syncline and its Upper Cretaceous-Palaeogene outcrops (modified from López-Martínez and Vicens, 2012). b. Stratigraphic log of the upper Maastrichtian Tremp Formation from the Beranuy outcrops. Colour 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. (Lopez-Martinez 2012)

In the Southern Pyrenees, there are a series of sedimentary domains developed during the Late Cretaceous to the Palaeogene 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 (Figure 1a). The sedimentary unit including the fossil sites studied correspond to the Tremp Formation (Mey et al. 1968). It is a Maastrichtian-Palaeocene 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' (Figure 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' (Figure 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) (Figure 1c), thus laying within the last 400 kyr of the Maastrichtian.

Blasi 2b is situated in the lower part of the 'Grey Garumnian' (Figure 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 (Figure 1c). Both sites (Blasi 2b and Areny 1) have been dated as late Maastrichtian (top of chron C30n; Figure 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 h. 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 were 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 et al. 1999, pp. 35–36.

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

Krokolithidae indet; Moreno-Azanza et al. 2014, p. 197, (Figures 2, 3).

Spheroolithus aff. *europaeus*; Pérez-Pueyo, Gilabert, Moreno-Azanza, Puértolas-Pascual, Bádenas, Canudo 2019, p. 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; Figure 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 (Figure 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 (Figure 2a): (1) The inner layer is comprised of microcrystalline basal knobs, which at high magnification has an irregular crystal arrangement (Figure 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 (Figure 2a). Vesicles are very scarce (Figure 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 (Figure 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 (Figure 2b), increasing their diameter towards the external and internal surfaces of the eggshell (Figure 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 (Figure 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 (Figure 2c). Sinuous growth lines are present in the outer layer, parallel to the undulating outer surface (arrow in Figure 2c). In cross-polarised light, the characteristic blocky extinction of the crocodylomorph eggshell can be observed (Figure 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) (Figure 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 (Figure 2e).

The inner surfaces have bulbous, irregular basal plate groups (Figure 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 and five shell units, causing the secondary horizontal pore system (Figure 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 recognised within the oofamily Krokolithidae: *Krokolithes* Hirsch 1985; *Suchoolithus*, Russo, Mateus, Marzola and Balbino 2017; and *Neokrokolithes* Bravo, Sevilla and Barroso-Barcenilla 2018. 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

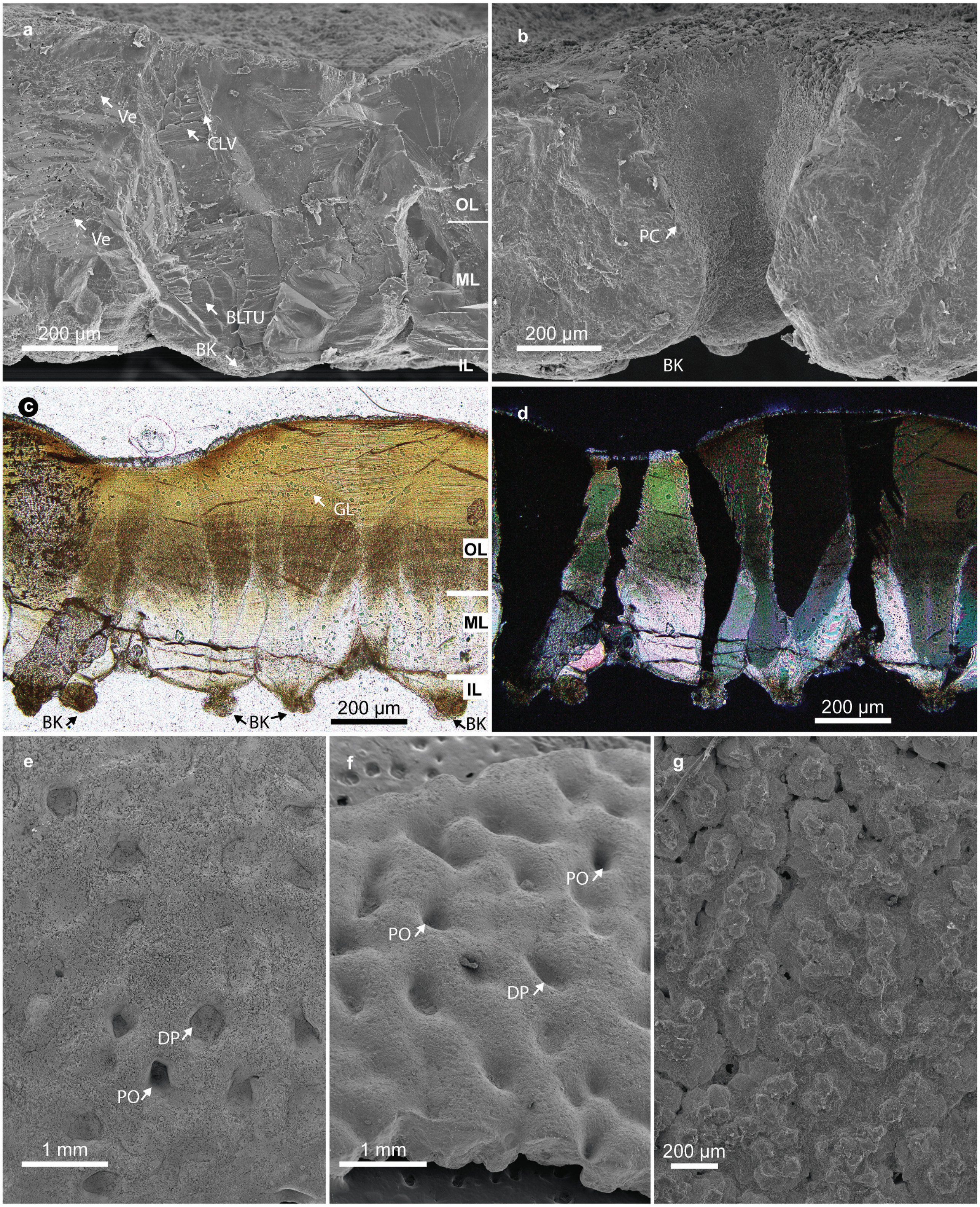

Figure 2. *Pachykrokolithus excavatum* oogen. et oosp. nov. from the Upper late Maastrichtian Veracruz 1 site (Tremp Formation) a). Scanning Electron Microscope secondary electron images (a, b, e–f) and thin section microphotographs (c, d). A, MPZ-2022/268 holotype eggshell fragment in radial section, 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-polarised 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-polarised 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.

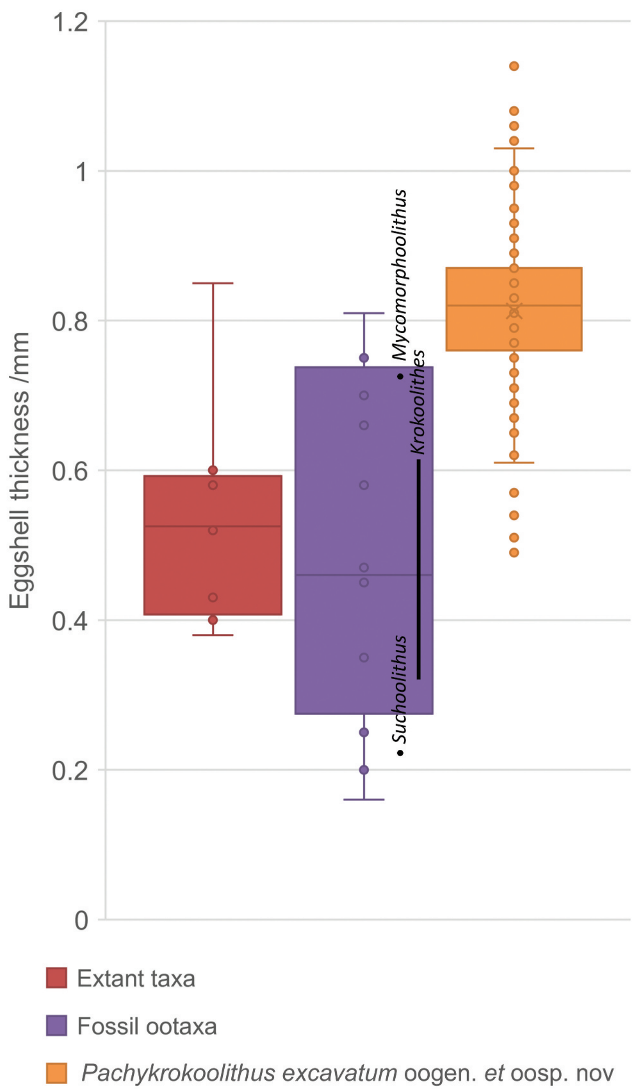

Figure 3. Box and whiskers plot comapring the maximun eggshell thickness of moderm taxa, fossil ootaxa, and the measured thickness of *Pachykrokolithus excavatum* oogen. et oosp. nov., with boxes representing the two medium percentiles with inclusive medians. Note that *Pachykrokolithus excavatum* oogen.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

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 250–550 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 (Figure 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 shape 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 recrystallised, 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 (Figure 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 (Figure 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. (Figure 4). It has a well-defined prolatospherulithic morphotype with highly fused shell units with radial calcite structure and is

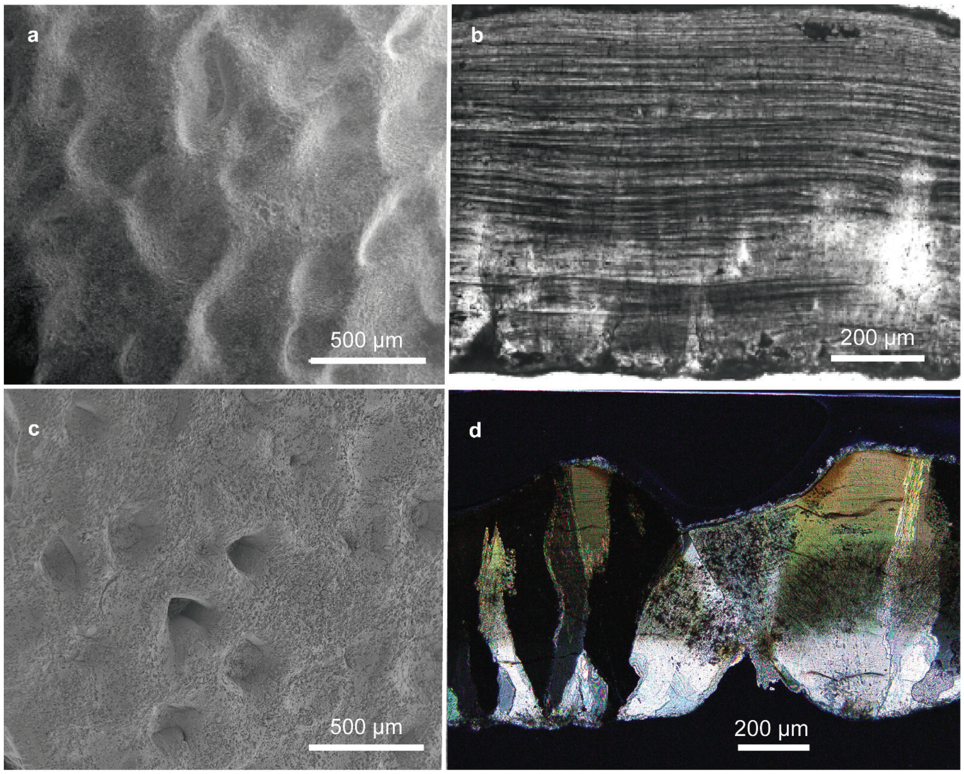

Figure 4. Comparison between *Stromatoolithus* (*Spheroolithus*) *europaeus* (a, b) and *Pachykrokolithus excavatum* oogen. et oosp. nov. (c, d). A, IPS-64162, *Stromatoolithus* (*Spheroolithus*) *europaeus* Scanning Electron Microscope secondary electron image of the outer surface composed of fine ridges. B, IPS-58973 g, *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.

characterised 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 surface 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 images. Furthermore, the ultrastructure of both ootaxa may be obliterated by minimal recrystallisation, making it even more difficult to properly identify and differentiate them. Nevertheless, thin sections are unequivocal to differentiate both oospecies (Figure 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 emphasises 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 to 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 (Puértolas-Pascual et al. 2016; Blanco et al. 2020). 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 (Figure 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 (Figure 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 (Figure 1c).

Regarding Hylaeochampsidae (another clade of basal eusuchians closely related to Allodaposuchidae and crown group Crocodylia), only remains assigned to cf. *Acynodon* have been identified within the Tremp Formation (Puértolas-Pascual et al. 2016; Blanco et al. 2020). 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) (Puértolas-Pascual et al. 2016; Blanco et al. 2020).

The presence of the crown group Crocodylia within the Tremp basin is less reliable as only three 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 emphasise 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.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This work was supported by the Fundação para a Ciencia e a Tecnologia [PTDC/CTA-PAL/31656/2017,UIDB/04035/2020]; Gobierno de Aragón [Group E18: Aragosaurus: Recursos Geológicos y Pal]; Ministerio de Educacion, Cultura y Deporte [FPU 16/03064]; Ministerio de Universidades Unión Europea-NextGenerationEU [Maria Zambrano. Requalification of Spanish univers]; Ministerio de Universidades (by Unión Europea-NextGenerationEU) [Maria Zambrano. Requalification of Spanish univers]; MCIN/AEI/10.13039/501100011033 and by the European Union 'NextGenerationEU'/PRTR", [FJC2020-044561-I,PLEC2021-008203]; Spanish Ministry of Science and Innovation [CGL2017-85038-P; MCIN/AEI/10.13039/501100011033 and by the European Union "NextGenerationEU"/PRTR",MCIN/AEI/10.13039/501100011033 and by the European Union "NextGenerationEU"/PRTR", [FJC2020-044561-I,PLEC2021-008203].

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