



Eggshell association of the Late Maastrichtian (Late Cretaceous) at Blasi 2B fossil site: a scrambled of vertebrate diversity

M. Pérez-Pueyo¹, M. Moreno-Azanza^{1,2}, C. Núñez-Lahuerta^{1,2}, E. Puértolas-Pascual^{1,2}, B. Bádenas¹ & J. I. Canudo¹

¹ Grupo Aragosaurus-IUCA. Departamento de Ciencias de la Tierra, Facultad de Ciencias, Universidad de Zaragoza. c/Pedro Cerbuna 12, 50009 Zaragoza, Spain.

² Departamento de Ciências da Terra, Faculdade de Ciências e Tecnologia FCT, Universidade Nova de Lisboa, 2829-516 Caparica, Portugal.

Corresponding author:

M. Pérez-Pueyo
manuppueyo@unizar.es

Journal webpage:

<http://cienciasdaterra.novaidfct.pt/>

Copyright:

© 2021 M. Pérez-Pueyo *et al.* This is an open access article distributed under the terms and conditions of the [Creative Commons Attribution License \(CC BY\)](https://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

ISSN: 0254 - 055X

eISSN: 2183 - 4431

Abstract

Upper Cretaceous outcrops of the South-Central Pyrenees in north-eastern Spain show a rich palaeontological record of eggs and eggshells of vertebrates, in particular dinosaurs. The fossil site of Blasi 2B (Arén, Huesca) is added to the oological record of the Late Maastrichtian, with an association of at least five ootypes of dinosaur eggshells (one Spheroolithidae and four Prismooolithidae), two Krokoolithidae and one Testudoolithidae. Blasi 2B represents one of the most diverse Maastrichtian eggshell sites of the Southern Pyrenees, and remarks the presence of a diverse theropod dinosaur fauna during the Late Maastrichtian in the Ibero-Armorican Island, with at least 4 ootaxa recognised.

Keywords: South-Central Pyrenees, Tremp Fm, Chron C30n, Prismooolithidae, Spheroolithidae.

1. Introduction

The Upper Cretaceous outcrops of the South-Central Pyrenees (Tremp Basin, NE Spain) have yielded a rich record of fossil vertebrates, including amphibians, squamates, testudines, crocodylomorphs, pterosaurs and dinosaurs (Canudo *et al.*, 2016). Among dinosaurs, titanosaurian sauropods, rhabdodontids and hadrosaurid ornithopods, nodosaurid ankylosaurians and abelisaurid and maniraptoran theropods have been lately identified (Fondevilla *et al.*, 2019). From this record, eggshells and eggs remains stand out, being the most abundant those attributed to sauropod dinosaurs, represented by complete eggs and clutches (Vianey-Liaud & López-Martínez, 1997; Vila *et al.*, 2010). Besides, there are several sites with eggshells of theropods (Sellés *et al.*, 2014a), hadrosaurid ornithopods (Sellés *et al.*, 2014b) and putative ankylosaurs (Sellés & Galobart, 2016).

In this work, we present a new study about the oodiversity of the palaeontological site of Blasi 2B (referred as Blasi 2 in López-Martínez *et al.*, 2001), located north-western of the town of Arén (Huesca, NE Aragón). Blasi 2B occurs at the base of the informally called ‘Grey Unit’ of the Tremp Fm, which corresponds

to transitional and lagoonal deposits (Rosell *et al.*, 2001). Based on biostratigraphy (López-Martínez *et al.*, 2001) and magnetostratigraphy (Pereda-Suberbiola *et al.*, 2009), it has been dated as Late Maastrichtian, in particular within the upper part of magnetochron C30n. Blasi 2B corresponds to a 6.5 m-thick level of grey marls, directly overlaying the top of the Arén Fm, and is very rich and diverse in vertebrate microfossils, including bones and eggshells. The oodiversity of Blasi 2B was shallowly identified by López-Martínez *et al.* (1999; 2001), with the exception of Krokoolithidae eggshells (Moreno-Azanza *et al.*, 2013). Here, we present preliminary results of the study of the oodiversity and the Blasi 2 site, considering all the progresses made in the knowledge of palaeoology and palaeoological record of the Southern Pyrenees.

2. Material and methodology

Over 2000 eggshell fragments have been recovered in the Blasi 2B site, after sieving over 5 tons of rock previously disaggregated with water and hydrogen peroxide. These eggshell samples were carefully examined under a stereomicroscope, and a subsample of 61 specimens was selected on the

basis of observed differences in eggshell thickness, shell unit shape and outer surface ornamentation. These fragments were photographed with secondary electrons with a JEOL JSM 6400 SEM. Measurements were taken using the software ImageJ. The material from Blasi 2B is housed at the palaeontological collection of the Museo de Ciencias Naturales de la Universidad de Zaragoza.

3. Results

We have identified 8 different ootaxa in the Blasi 2B site, including one Spheroolithidae, 4 Prismaticoolithidae, 2 Krokolithidae and 1 Testudoolithidae eggshells types.

Spheroolithidae eggshells have a mean thickness of 572 μm (N=4) and their outer surface shows a sagenotuberculate ornamentation (Fig.1A), with anastomosing ridges. In radial section, the shells show a prolatospherulitic morphotype (Fig. 1B), with radial calcitic ultrastructure. Shell units are partially fused towards the outer surface. No pores have been observed in the few thin sections available. We assign them tentatively to the taxon *Spheroolithus* aff. *europaeus* (Sellés *et al.*, 2014b) described in the nearby locality of Porrit-6, which share the morphotype and ornamentation pattern. We prefer to use open nomenclature since the fragments from Blasi 2B are significantly thinner than those of *Spheroolithus europaeus*. However, the few specimens available hinder further discussion.

The four prismaticoolithic ootypes identified have a prismatic structure, two of them show a distinctive dispersituberculate outer surface ornamentation with isolated domed tubercles (Fig. 1C). In radial section, two layers can be recognised (Fig. 1D): a mamillary layer, and a continuous layer, which can be subdivided in a squamatic zone and an external zone. Based on these features, we have interpreted them as belonging to the genus *Pseudogeckoolithus* (Vianey-Liaud & López-Martinez, 1997), in particular to *Pseudogeckoolithus* oosp. 1, which is thicker (mean 285 μm , N=30), and *Pseudogeckoolithus* oosp. 2, which is thinner (141 μm in average, N=2) and sometimes presents cratered tubercles (Fig. 1E). Vianey-Liaud & López-Martinez (1997) did not observe an external zone in *Pseudogeckoolithus*. Nevertheless, this has been recently reported in other *Pseudogeckoolithus* eggshell fragments from several localities of the Upper Cretaceous of Europe (Choi *et al.*, in press).

The other two prismaticoolithid eggshells present columnar-shaped shell units composed of mamillary and a continuous layer. No squamatic ultrastructure can be distinguished (Fig. 1F). Both show a smooth outer surface (Fig. 1G). These characters allow us to refer them to the oofamily Prismaticoolithidae. The poor preservation of the eggshells prevents further comparison, but both can be easily differentiated by their eggshell thickness (Prismaticoolithidae indet. 1 averages 572 μm (N=11) whereas Prismaticoolithidae indet. 2 averages 276 μm (N=9). Several Prismaticoolithidae ootaxa have been recognized in the Tremp Basin (Sellés *et al.*, 2014a). Prismaticoolithidae indet 1. and 2 differ from *Ageroolithus* eggshells both in the lack of the ratite morphotype and the squamatic ultrastructure. They also differ from *Sankofa pyrenaica* in lacking the distinct interlocking pattern in the middle part of the continuous layer. Finally, they can be easily differentiated from *Prismaticoolithus trempi* by the absence of dispersituberculate ornamentation with flattened nodes.

Besides eggshells referable to dinosaurs, Krokolithidae eggshells are also present in the Blasi 2B assemblage. They are characterized by a crocodyloid morphotype, with trapezoidal-shape shell units that broaden towards the outer surface (Fig. 1H). Externally, the eggshells have wavy outer surfaces, with circular depressions. The two ootypes differ in their thickness: *Krokolithes* sp. 1 (370 μm , N=3) and *Krokolithes* sp. 2 (276 μm , N=1). Finally, a single eggshell fragment with testudoid morphotype has been identified. It is badly preserved but can be ascribed to Testudoolithidae on the basis of its toughly packaged subcylindrical shell units with radial ultrastructure.

4. Discussion and conclusions

Blasi 2B shows a highly diverse assemblage of eggshells, with at least 7 ootaxa. *Spheroolithus* aff. *europaeus* was probably laid by hadrosaurid dinosaurs; whereas the four ootaxa here attributed to Prismaticoolithidae would correspond to theropod dinosaurs. *Pseudogeckoolithus* eggshells had in the past an uncertain attribution (see Vianey-Liaud & López-Martinez, 1997; Sellés, 2012), but recent research (Choi *et al.*, in press) has postulated that they belong to maniraptoran theropods. The other two prismaticoolithid ootaxa are not so well-preserved and their assignation to a particular taxon is difficult, as Prismaticoolithidae-like eggshells have been identified

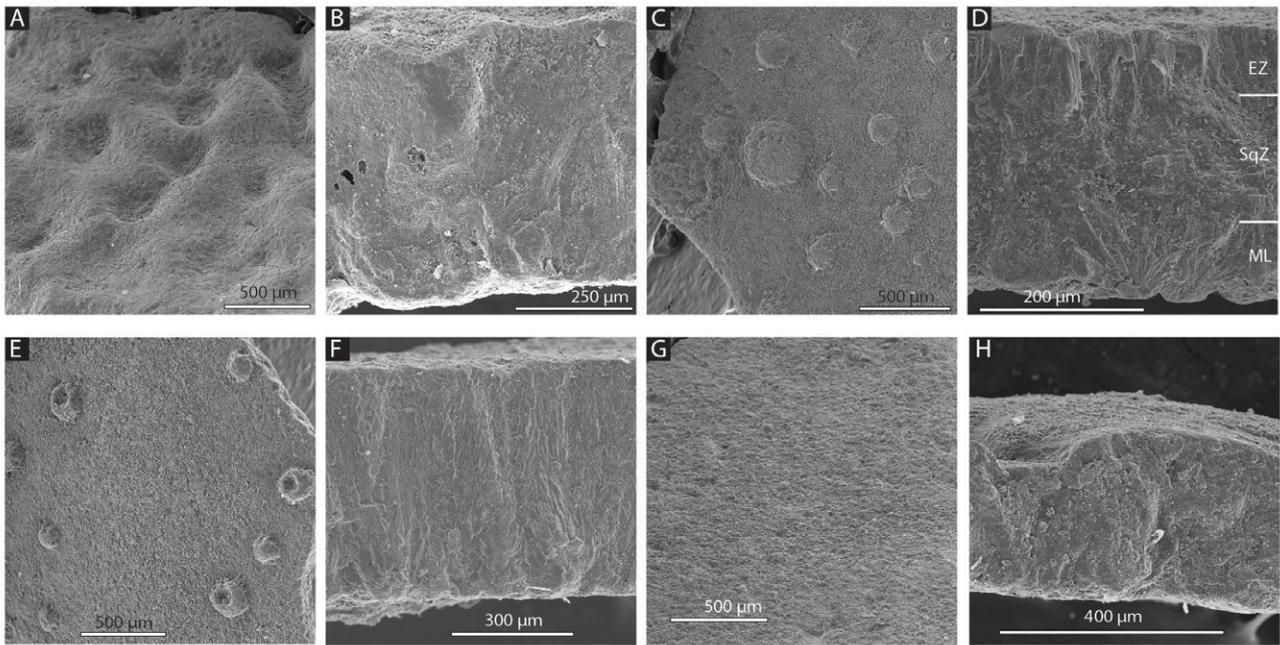


Fig. 1. -SEM images of the vertebrate eggshells from Blasi 2B site (Huesca, Aragón): A- Outer surface and B- radial section of *Spheroolithus* aff. *europaeus* eggshell; C- Outer surface and D- radial section of *Pseudogeckolithus* sp. 1 eggshell; E- Outer surface of *Pseugeckolithus* sp. 2 eggshell; F- Radial section G- and outer surface of Prismaoolithidae indet. 1; H- Radial section of *Krokolithes* sp. 2. Abbreviations: EZ: external zone, ML: mammillary layer, SqZ: squamatic zone.

in many theropod groups, including allosauroids, maniraptoran and avian theropods. Furthermore, López-Martínez *et al.*, (1999, 2001), recognised six types of prismaoolithid eggshells in Blasi 2B, based on thin section analysis, three of which are not presented in our sample. Further research is needed to precise the number of putative theropod taxa. Nevertheless, the eggshell record in Blasi 2B points to a high diversity of theropods during the Late Maastrichtian, as reported by previous works (Sellés *et al.*, 2014a). This is concordant with the Theropoda record in the Ibero-Armorican island during the Late Maastrichtian (Torices *et al.*, 2015; Fondevilla *et al.*, 2019), with dromaeosaurids and abelisaurids (cf. *Arcovenator*) recognised specially by dental remains.

Crocodylomorphs are represented in the Southern Pyrenees by four species described and named therein, but according to fossil teeth and other fragmentary cranial remains there would be up to ten taxa (Blanco *et al.*, in press). Although the diversity of clades is wide, basal eusuchians belonging to Allodaposuchidae and Hylaeochampsidae predominate. Within Blasi 2B, teeth from allodaposuchids, aff. *Acynodon* and an indeterminate mesoeucrocodylian have been recovered. However, the assignment of the Blasi 2B eggshells to a concrete genus or family is, for the moment, impossible. It is interesting to note that none of the ootypes match in thickness with *Krokolithes* oosp. eggshells (~0,75 mm) described

by Moreno-Azanza *et al.* (2013), not present in our sample, probably pointing to the presence of three different *Krokolithes* oosps. Further Testudooolithidae eggshells are needed to confirm that their presence is not anecdotal in the Blasi 2B assemblage.

The preliminary analysis of the Blasi 2B eggshell assemblage shows a high eggshell diversity, with between eight and eleven ootaxa. Nevertheless, some of the ootaxa are represented by few specimens, possibly representing an intraoespecific variation that would be detected if the sample size is increased. Even when the oodiversity is underestimated, Blasi 2 is one of the most diverse oological sites of the Maastrichtian of the Tremp Basin.

Acknowledgments

This research forms part of the project CGL2017-85038-P and is subsidized by the Spanish Ministry of Science and Innovation, the European Regional Development Fund, the Government of Aragón (Grupo Aragosaurus: Recursos geológicos y Paleoambientes) the Fundação para a Ciência e a Tecnologia project PTDC/CTA-PAL/31656/2017 and the GeoBioTec (UIDB/04035/2020). M.P-P is supported by the Spanish Ministry of Education, Culture and Sport (Grant Number FPU 16/03064). M.M-A, C.N-L and E.P-P are supported by the Fundação para a Ciência e a Tecnologia, Portugal (Grant numbers SFRH/BPD/113130/2015, SFRH/BPD/116759/2016, PTDC/CTA-PAL/31656/2017). We are grateful to Xavier Pereda-Suberbiola and Bernat Vila for their valuable comments on the original version of the manuscript. The authors would like to thank the use of the 'Servicio General de Apoyo a la Investigación'-SAI, Universidad de Zaragoza.

References

- Blanco A., Puértolas-Pascual E., Marmi J., Moncunill-Solé B., Llácer S. & Rössner G. E. (In press) - Late Cretaceous (Maastrichtian) crocodyliforms from north-eastern Iberia: a first attempt to explain the crocodyliform diversity based on tooth qualitative traits. *Zool. J. Linn. Soc-Lond.* zlz106.
- Canudo J.I., Oms O., Vila B., Galobart À., Fondevilla V., Puértolas-Pascual E., Sellés A. G., Cruzado-Caballero P., Dinarès-Turell J., Vicens E., Castanera D., Company J., Burrell L., Estrada R., Marmi J. & Blanco A. (2016) - The upper Maastrichtian dinosaur fossil record from the southern Pyrenees and its contribution to the topic of the Cretaceous–Palaeogene mass extinction event. *Cretac. Res.* 57, 540–551.
- Choi S., Moreno-Azanza M., Csiki-Sava Z., Prondvai E. & Lee Y. (In press) - Comparative crystallography suggests maniraptoran theropod affinities for latest Cretaceous European ‘Geckoid’ eggshell. *Pap. in Palaeontol.* doi.org/10.1002/spp2.1294
- Fondevilla V., Riera V., Vila B., Dinarès-Turell J., Vicens E., Gaete R., Oms O. & Galobart À. (2019) - Chronostratigraphic synthesis of the latest Cretaceous dinosaur turnover in south-western Europe. *Earth-Sci. Rev.* 191, 168–189.
- López-Martínez N., Canudo J. I. & Cuenca G. (1999) - Latest Cretaceous eggshells from Arén (Southern Pyrenees, Spain). In: *First International Symposium on Dinosaur Eggs and Babies*, Isona i Conca Dellà, Spain, 35–36.
- López-Martínez N., Canudo J. I., Ardévol L., Pereda-Suberbiola X., Orue-Etxebarria X., Cuenca-Bescós G., Ruiz-Omeñaca J. I., Murelaga X. & Feist M. (2001) - New dinosaur localities near the Cretaceous/Tertiary boundary (Arén south central Pyrenees, Spain). *Cretac. Res.* 22, 41–61.
- Moreno-Azanza M., Bauluz B., Canudo J. I., Puértolas-Pascual E. & Sellés A. G. (2013) - A re-evaluation of aff. *Megaloolithidae* eggshell fragments from the uppermost Cretaceous of the Pyrenees and implications for crocodylomorph eggshell structure. *Hist. Biol.* 26, 195–205.
- Pereda-Suberbiola X., Canudo J. I., Cruzado-Caballero P., Barco J. L., López-Martínez N. & Ruiz-Omeñaca J. I. (2009) - The last hadrosaurid dinosaurs of Europe: a new lambeosaurine from the uppermost Cretaceous of Arén (Huesca, Spain). *C.R. Palevol* 8, 559–572.
- Rosell J., Linares R. & Llombart C. (2001) - El “Garumniense” prepirenaico. *Revista de la Sociedad Geológica de España* 14, 47–56.
- Sellés A. G. (2012) - *Oological record of dinosaurs in South-Central Pyrenees (SW Europe): Parataxonomy, diversity and biostratigraphical implications*. PhD Thesis, Universitat de Barcelona, 237 p.
- Sellés A. G., Vila B. & Galobart À. (2014a) - Diversity of theropod ootaxa and its implications for the latest Cretaceous dinosaur turnover in southwestern Europe. *Cretac. Res.* 49, 45–54.
- Sellés A. G., Vila B. & Galobart À. (2014b) - *Spheroolithus europaeus*, oosp. nov. (late Maastrichtian, Catalonia), the youngest oological record of hadrosauroids in Eurasia. *J. Vertebr. Paleontol.* 34, 725–729.
- Sellés A. G. & Galobart À. (2016) - Reassessing the endemic European Upper Cretaceous dinosaur egg *Cairanoolithus*. *Hist. Biol.* 28(5), 583–596.
- Torices A., Currie P. J., Canudo J. I. & Pereda-Suberbiola X. (2015) - Theropod dinosaurs from the Upper Cretaceous of the South Pyrenees Basin of Spain. *Acta Palaeontol. Pol.* 60(3), 611–626.
- Vianey-Liaud M. & López-Martínez N. (1997) - Late Cretaceous dinosaur eggshells from the Tremp Basin, southern Pyrenees, Lleida, Spain. *J. Paleontol.* 71, 1157–1171.
- Vila B., Jackson F. D., Fortuny J., Sellés A. G. & Galobart À. (2010) - 3-D modelling of megaloolithid clutches: insights about nest construction and dinosaur behaviour. *PLoS ONE* 5, e10362.