

The controversial Les Labadous eggshells: A new and peculiar dromaeosaurid (Dinosauria: Theropoda) ootype from the Upper Cretaceous of Europe

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ABSTRACT

The fossil record of small-sized theropods in south-western Europe is scarce and fragmentary. In absence of more direct evidence, the oological record arises as an alternative source of information to infer biodiversity. In this regard, the controversial dinosaur eggshells from the Les Labadous locality in southern France are herein re-evaluated in the light of new material and current parataxonomic information. New data and analyses reveal a new eggshell type, *Montanoolithus labadousensis* oosp. nov., characterized by a unique combination of characters. Additionally, the phylogenetic analysis reinforces the placement of the new oospecies as the sister taxon of the North American *Montanoolithus strongorum*, refusing the previous attribution of the Les Labadous remains to Elongatoolithidae. The combination of microstructural and phylogenetic results suggests that *Montanoolithus labadousensis* was likely produced by a dromaeosaurine dromaeosaurid, a taxonomic attribution that is consistent with the biodiversity of small-sized theropods at the latest Cretaceous of south-western Europe.

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1. Introduction

In the latest Cretaceous, the Ibero-Armorican Island (the largest island in the European archipelago, corresponding to the present-day areas of Spain, France and Portugal) was home to a diverse dinosaur fauna composed of struthiosaurine nodosaurids, rhabdodontid iguanodontians, hadrosaurid and non-hadrosaurid hadrosauroids, and titanosaurian sauropods (Vila et al., 2016). Regarding theropods, the assemblage was mainly represented by taxa with Gondwanan and Laurasian affinities (Tortosa et al., 2014; Csiki-Sava et al., 2015) including middle to large-sized abelisaurid neoceratosaurs (i.e. *Arcovenator* Tortosa et al. 2014) and small-sized dromaeosaurids (Allain and Taquet 2000; Torices et al., 2013) and velociraptorines (Barroso-Barcenilla et al., 2009; Marmi et al., 2016). The theropod fossil record of the region is, however, very scarce, and limited to scattered and fragmentary skeletal elements (Le Loeuff and Buffetaut, 1998; Chanthasit and Buffetaut, 2009; Tortosa et al.,

2014). With the exception of *Pyropraptor* (Allain and Taquet, 2000) and some other few occurrences (Chanthasit and Buffetaut, 2009), most of the fossil remains of the Ibero-Armorican theropods correspond to isolated shed teeth (Torices et al., 2013).

Nevertheless, recent papers indicate that the oological remains arise as a substantial source of complementary information when assessing qualitative taxonomic diversity in absence of more direct evidence (Sellés et al., 2014; Tanaka et al., 2016; Zelenitsky et al., 2016). In this regard, the upper Cretaceous European theropod egg record is dominated by the oofamily Prismatoolithidae (Hirsch 1994), but other egg-groups such as Laevisoolithidae or Elongatoolithidae are suggested to be present at the region (Garcia et al., 1999; Garcia and Vianey-Liaud, 2001; Sellés et al., 2014).

Among all known theropod eggshells from the Late Cretaceous of south-western Europe, those from the lower Maastrichtian locality of Les Labadous (Rennes-le-Château, France; Fig. 1) are considered as one of the most controversial. Initially attributed to Cretaceous birds (Beetschen et al., 1977) and later to hadrosauroids (Beetschen, 1985), they are currently assigned to the oofamily ? Elongatoolithidae (Garcia, 1998; Garcia et al., 1999; Garcia and Vianey-Liaud, 2001). Given that elongatoolithid eggs are primarily known from Asia and North America (Mikhailov, 1997;

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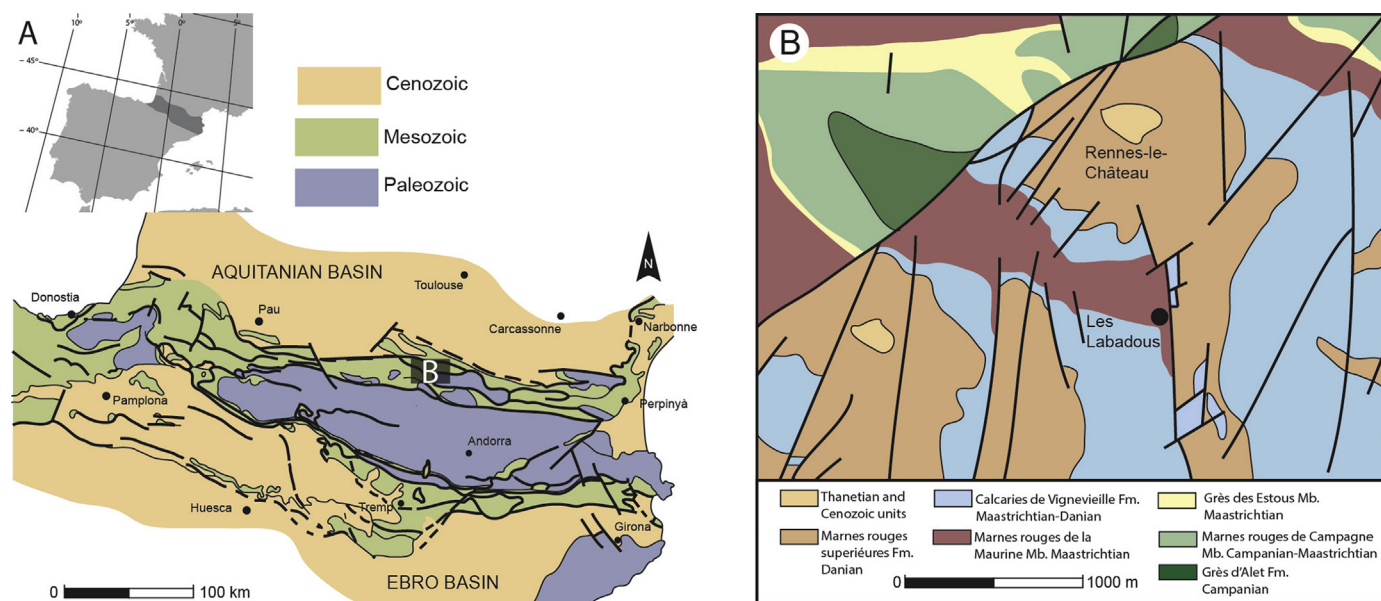


Fig. 1. Geo-location of the Les Labadous site. (A) Geological map of the Pyrenees showing the distribution of Mesozoic outcrops. (B) Detailed geological map of the Rennes-le-Château area, modified from [Fondevilla et al. \(2016\)](#).

[Carpenter, 1999](#)), and taxonomically attributed to oviraptorid theropods on the base of embryonic and skeletal evidence ([Norell et al., 2001](#); [Cheng et al., 2008](#); [Weishampel et al., 2008](#); [Wang et al., 2016](#)), the occurrence of this eggshell type in Europe deserves further review and discussion. Therefore, here we describe, re-evaluate and discuss the dinosaurian oological remains from the Les Labadous locality, and its implication in the theropod dinosaur assemblage of south-western Europe.

2. Geological setting

The Les Labadous locality is situated south of the village of Rennes-le-Château in the Upper Aude Valley (Aude Department, France). The eggshell-bearing site was discovered by one of the authors (J-C.B) in 1971, about 250 m west of Les Labadous farm. Stratigraphically, the eggshell-bearing level (F6 after [Beetschen, 1985](#)) falls within the upper strata of the continental Marnes rouges de la Maurine (Red Marls of Maurine) Formation, few metres below the conglomerate beds of the Poudingue Fleuri (Fleuri Conglomerate) Member. A recent study by [Fondevilla et al. \(2016\)](#) indicates that the latter member falls within the upper part of the C31r magnetostratigraphic chron. Hence, the locality is correlated with a late early Maastrichtian age.

3. Material and methods

A total of 54 *in situ* eggshell fragments were originally recovered by one of the authors (J-C.B) in 1971 from a single point in the Les Labadous locality. The material studied in the present paper consists of 15 eggshell fragments (IPS-96481 to IPS-96490), housed in the Institut Català de Paleontologia Miquel Crusafont. A preliminary identification, photographic documentation and measurements were performed on all the available material by using a Leica® MZ 16A binocular microscope and analysed with Leica® Application Suite software. Seven uncoated eggshell fragments (IPS-96482 to IPS-96488) were studied using the Zeiss EVO® MA10 environmental scanning electronic microscope (ESEM) housed in the Microscopy Service of the Universitat Autònoma de Barcelona. Two of the eggshell fragments (IPS-96481 and IPS-96482) were prepared as standard petrographic thin sections (30 µm) and analysed with a

Leica® DM 2500P polarized light microscope under 20× and 50× magnification. We also examined additional eggshell material (10 eggshell fragments) from the original material collected in 1971 by J.C. Beetschen and currently housed at the Université de Montpellier. The nomenclature, terminology and parataxonomic classification of the dinosaur fossil eggs and eggshells follows [Mikhailov \(1997\)](#).

In order to explore the phylogenetic position and the taxonomic affinity of the Les Labadous eggshells, we took the extensive theropod eggs data matrix provided by [Tanaka et al. \(2011\)](#). With the aim to achieve even a deeper analysis of the phylogenetic relationships through the theropod lineage, we add five additional egg-taxa to the data matrix: *Trigonoolithus* ([Moreno-Azanza et al., 2014](#)), *Montanoolithus* ([Zelenitsky and Therrien, 2008](#)), *Arragadoolithus* ([Agnolin et al., 2012](#)), *Triprismatoolithus* ([Jackson and Varricchio, 2010](#)), and the egg of *Torvosaurus* ([Araújo et al., 2013](#); [Ribeiro et al., 2014](#)). The ootaxon *Dendroolithus* and the egg of therizinosaur were also recoded based on the characters from the literature ([Jin et al., 2010](#); [Kobayashi et al., 2013](#); [Supplementary Appendix 1](#)).

An equally weighted parsimony analysis was carried out using TNT v.1.1 ([Goloboff et al., 2008](#)). A traditional heuristic tree search was performed starting from 1000 replicates of Wagner trees (using random addition sequence of taxa) followed by tree bisection-reconstruction (TBR) branch swapping (holding 10 trees per replicate). To test the support of the phylogenetic hypotheses, Bremer support and bootstrap decay index (absolute frequencies based on 10,000 replicates) values were also performed in TNT 1.1 software.

4. Systematic palaeontology

Montanoolithidae Zelenitsky and Therrien 2008
Montanoolithus Zelenitsky and Therrien 2008
Montanoolithus labadousensis oosp. nov.

Etymology. From Les Labadous (Aude Department, France), the farm located near the site where the fossils were found.

Holotype. 1 eggshell fragment (IPS-96485).

Referred specimens. Fourteen eggshell fragments (IPS-96481, IPS-96482, IPS-96483, IPS-96484, IPS-96486 to IPS-96490), including two new thin sections (IPS-96481b and IPS-96482c).

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