

Unusual theropod eggshells from the Early Cretaceous Blesa Formation of the Iberian Range, Spain

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Trigonoolithus amoae oogen. et oosp. nov. is described on the basis of abundant eggshell fragments from the La Cantalera 1 site in the Early Cretaceous (early Barremian) Blesa Formation, Teruel Province, northern Spain. The surface ornamentation, the most diagnostic feature of the new oogenus, consists of closely spaced sub-triangular or rounded protuberances that have not previously been reported in any other ootaxon. The eggshells present three distinct layers, with a gradual transition between prismatic and mammillary layers, and a poorly developed external layer with progressive prismatic to external layer transition, a combination of characters that allows them to be assigned to Prismatoolithidae. Phylogenetic analyses based on oological characters place *Trigonoolithus* at the base of Prismatoolithidae.

Key words: Dinosauria, Theropoda, Prismatoolithidae, parataxonomy, dinosaur eggshells, Barremian, Cretaceous, Blesa Formation, Teruel Province, Spain.

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Introduction

Primatoolithidae eggs and eggshells have been recovered from Asia, Europe and North America (Mikhailov 1997), and this oofamily extends from the Late Jurassic (Hirsch 1994; Mateus et al. 1997) to the latest Cretaceous (Vianey-Liaud and López-Martínez 1997). However, these eggshells are especially abundant in Late Cretaceous localities (Zelenitsky and Hills 1996; Vianey-Liaud and López-Martínez 1997; Varricchio et al. 2002), whereas the record in the Early Cretaceous is sparse and restricted to the Iberian Peninsula (Canudo et al. 2010).

Although first thought to have been laid by hypsilophodontid dinosaurs (Horner and Weishampel 1988) or even basal ceratopsians (Mikhailov 1994), the reinterpretation of a clutch of eggs with embryos previously assigned to *Orodromeus makelai* (Horner and Weishampel 1988) and *Primatoolithus levis* eggshells as *Troodon formosus* embryos has confirmed the theropod origin of this type of eggshell (Horner and Weishampel 1996; Varricchio et al. 2002; Zelenitsky et al. 2002). In addition, eggs with a prismatic structure and embryonic material assigned to the theropod *Lourinhanosaurus*, which has recently been identified as a basal coelurosaurian (Carrano et al. 2012), have been reported in the Late Juras-

sic of Portugal (Mateus et al. 1997). The eggshell structure resembles material assigned to the Prismatoolithidae oogenus *Preprimatoolithus* from the Late Jurassic of Colorado, which is the type genus of Prismatoolithidae (Zelenitsky and Hills 1996). Finally, Prismatoolithidae is strongly related to some avian eggshells (Zelenitsky et al. 2002), with incipient states of the most characteristic avian eggshell feature, the squamatic structure, having been unambiguously reported in Upper Cretaceous Prismatoolithidae eggs from North America (Zelenitsky et al. 2002; Jackson and Varricchio 2010) and Spain (López-Martínez and Vicens 2012).

Such a substantial amount of taxonomic information, with primitive and derived taxa based on skeletal remains associated with the same oofamily, has provided an unrivalled sample to test the viability of the cladistic approach to egg classification. Several analyses have been carried out (Varricchio and Jackson 2004; Grellet-Tinner and Makovicky 2006; Zelenitsky and Thierrien 2008a, b), all yielding similar information: Prismatoolithidae + avian eggs is a monophyletic clade, sister to, or closely related to, oviraptorid and/or dromaeosaurian eggs, with some Prismatoolithidae eggs being more closely related to dromaeosaurians than to other Prismatoolithidae eggs (e.g., *Lourinhanosaurus* forming a polytomy with oviraptorid eggs in Varricchio and Jackson 2004). This incongruence with the phylogenetic hypothesis

based on skeletal characters—according to which dromaeosaurians are more closely related to troodontids than to oviraptorids and all these groups are more derived than *Lourinhanosaurus*—is the most important issue for this approach (Zelenitsky and Thierrien 2008a).

In this paper we report a new oogenus and oospecies within the oofamily Prismatoolithidae from the Early Cretaceous La Cantalera 1 site in Teruel Province, Spain, and assess its phylogenetic relationship to previously described ootaxa.

Institutional abbreviations.—MPZ, Museo Paleontológico de la Universidad de Zaragoza, Zaragoza, Spain.

Geological and palaeontological setting

The Iberian basin of northeast Spain is an intracratonic basin that developed during Mesozoic extension (Salas et al. 2001). An Early Cretaceous stage of rifting resulted in the formation of several subsiding basins across the Iberian Peninsula. The La Cantalera site is located in the Oliete subbasin, within the large Cretaceous Maestrazgo basin (Salas et al. 2001). The La Cantalera site consists of outcrops of Early Cretaceous clay deposits (“Wealden facies”) of the lower Blesa Formation. This lithostratigraphic unit has a complex evolution in the area around the locality of Josa, where a small, isolated basin developed, including a lower part with alluvial to lacustrine sedimentary deposits, followed by an upper part with two episodes that record coastal and lagoonal deposition (Canudo et al. 2010). Laterally, these grey clays yield abundant Jurassic clasts and invertebrate marine fossils reworked from the nearby palaeorelief. Aurell et al. (2004) showed that the palaeorelief surrounding the small, isolated basin resulted from the Jurassic uplift of marly limestone rocks along a set of N-S to NE-SW trending normal faults (Fig. 1)

The locality of La Cantalera is dated as early Barremian, within the *Triquetra* Subzone by *Atopochara trivolis triquetra* (Riveline et al. 1996; Canudo et al. 2012). This locality has been interpreted as an ephemeral lake or pond within an alluvial setting associated with small alluvial fans (Aurell et al. 2004). La Cantalera includes a microvertebrate accumulation consisting mainly of teeth and isolated postcranial remains, although eggshells are also present. In the sense of Eberth and Currie (2005), La Cantalera is a vertebrate microfossil assemblage (i.e., a concentration of small, multitaxic vertebrate remains dominated by elements that are less than 5 cm in maximum dimension). These vertebrate remains include partially articulated remains and disarticulated vertebrate debris. The latter formed as an attritional deposit through progressive accumulation on a poorly drained floodplain (Canudo et al. 2010). Within this low-energy depositional setting, preservational patterns differ and the faunal assemblage includes both autochthonous and parautochthonous elements. The locality has yielded thousands of skeletal remains from at least 31

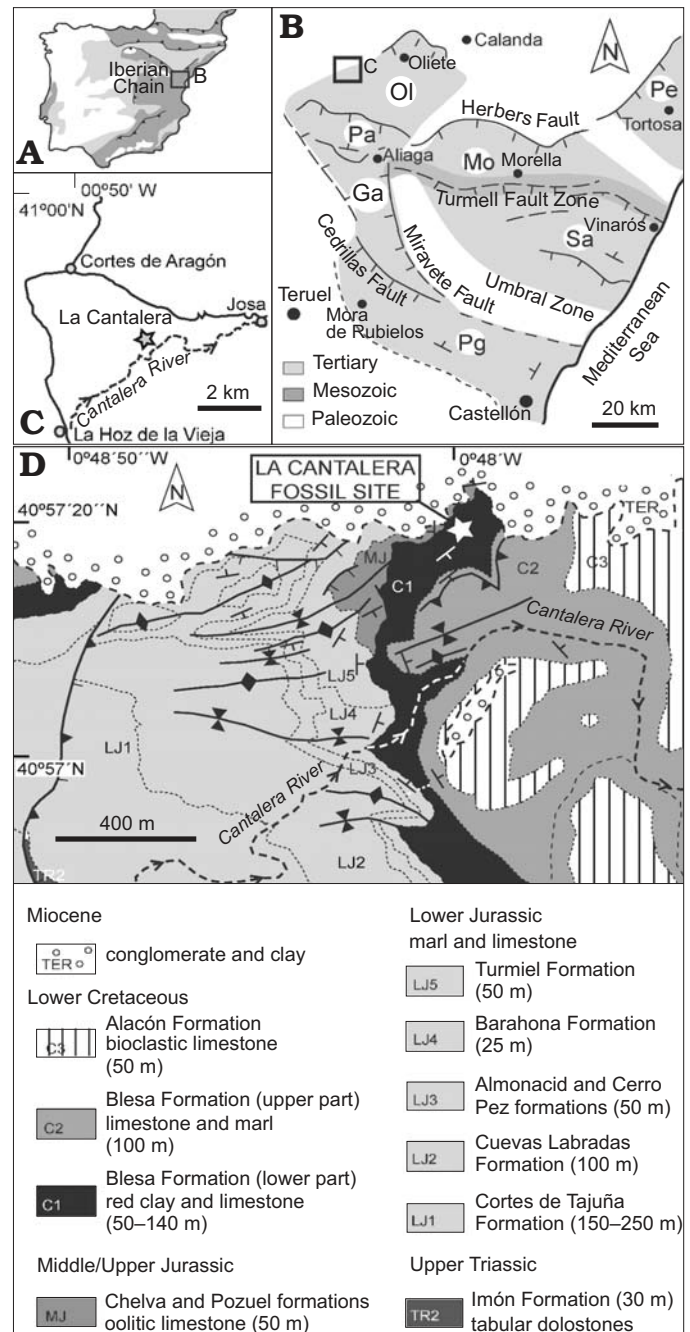


Fig. 1. Geographical and geological location of the site of La Cantalera 1 (early Barremian, Teruel, Spain), modified from Canudo et al. (2010). **A.** Simplified geological map of the Iberian Peninsula. **B.** Palaeogeographic subbasins (Ol, Oliete; Pa, Las Parras; Ga, Galve; Mo, Morella; Pe, Perelló; Sa, Salzedella; Pg, Peñagolosa) within the Maestrazgo Basin and active faults during Early Cretaceous sedimentation, modified from Salas et al. (2001). **C.** Detailed location of the La Cantalera site near the village of Josa, Teruel. **D.** Geological map of the La Cantalera area with the local geological units.

taxa (Canudo et al. 2010) and no less than 8 different ootaxa (Moreno-Azanza et al. 2009a). The faunal assemblage of La Cantalera consists almost exclusively of terrestrial and amphibious taxa that lived nearby (Canudo et al. 2010). Because there is no indication of significant transport, the faunal as-

semblage can be regarded as a time-averaged sample of the source community (sensu Rogers and Brady 2010), specifically the La Cantalera wetland ecosystem.

Even though research on the vertebrate palaeontology of the Early Cretaceous of Spain has mainly focused on skeletal remains, eggshell fragments are among the most abundant fossils in the microsites of the Iberian Range (Köhring 1990; Buscalioni et al. 2008; Amo-Sanjuan et al. 2000; Moreno-Azanza 2009a, b), and they are present in high diversity. These are unlikely to represent egg debris from a single nesting area; nevertheless, they are probably a representative sample of the taxa nesting in the ecosystem (Moreno-Azanza et al. 2009a). Although eggshell fragments have been described in the Iberian Range since the early 1990s, it is noteworthy that no complete eggs, nests, or clutches are reported to date, and only one oospecies has been erected: *Macroolithus turolensis* Amo-Sanjuan, Canudo, and Cuenca-Bescós, 2000, from the early Barremian of Teruel Province.

Material and methods

The eggshell fragments were collected by washing and sifting the sediment recovered during several field campaigns from 1997–2000. Over three tons of sediment from the La Cantalera locality were processed, resulting in the recovery of over 3000 eggshells, 347 of which are included in this study.

The sediments were processed using 2% hydrogen peroxide and sieves of 2, 1, and 0.5 mm mesh. The eggshell fragments were sorted under a binocular microscope. Twenty-two eggshell fragments were prepared as tangential and radial sections, and studied under an Olympus BX 41 petrographic microscope. Twenty-five fragments were mounted, gold-coated and viewed with a JEOL 6400 SEM at the University of Zaragoza. In addition, cathodoluminescence (CL) analyses were performed with a Nikon Eclipse 50i POL optical microscope coupled with a cathodoluminescence system (model CL8200 Mk5-1) at the Institut Català d'Arqueologia Clàssica (ICAC; Tarragona, Spain).

The nomenclature follows Mikhailov (1997). Accordingly, tabular ultrastructure refers to the regular transverse striation of homogeneous calcite within the crystals that form the eggshell, as present in crocodylian and avian eggshells. On the other hand, tabular crystals refer to the habit of the calcite crystals that radiate out of the organic cores in the mammillary layer and form the prismatic and external layers of the eggshell.

Systematic palaeontology

Oofamily Prismatoolithidae Hirsch, 1994

Type oogenus: *Preprismatoolithus* Hirsch, 1994; Morrison Formation, upper part of Salt Wash Member (Upper Jurassic); Young locality, Delta County, Colorado, USA.

Emended diagnosis.—Eggshells with at least two layers: a lower mammillary layer with radial-tabular ultrastructure and an upper prismatic layer with prisms with tabular ultrastructure. Transition between mammillary and prismatic layer is gradual. A third external layer with tabular ultrastructure may be present. Angusticanalicate or obliquicanalicate pore system; outer surface smooth, undulating or sculptured. Eggshell thickness 300–1220 μm ; eggs elongate, ovoidal- or ellipsoidal-shaped; EL (elongation index): ratio of the long diameter of an egg to its short diameter = 1.8–2.7.

Oogenus *Trigonoolithus* nov.

Type species: *Trigonoolithus amoae* oogen. et oosp. nov., see below.

Etymology: From the ancient Greek *trigonos*, triangle, in reference to the shape of the protuberances that ornament the outer surface of most fragments, and Greek *oo*, from the combining form for *ova*, egg, and *lithos*, stone.

Diagnosis.—As for the type and only known oospecies.

Geographic and stratigraphic range.—As for the type oospecies.

Trigonoolithus amoae oosp. nov.

Figs. 2–4.

2009 Prismatoolithidae indet.; Moreno-Azanza et al. 2009a: 151A.

2010 Prismatoolithidae indet.; Canudo et al. 2010: 218–219, fig. 6.4.

2013 Prismatoolithidae indet.; Moreno-Azanza et al. 2013: 22, figs. 1c, d, 2d, 3c, d.

Etymology: After the late Olga Amo-Sanjuan, pioneer in the study of the Lower Cretaceous eggshell in the Iberian Range and sadly deceased.

Holotype: MPZ 2012/737, an eggshell fragment.

Type locality: La Cantalera 1 site, near the village of Josa, Teruel Province, Spain.

Type horizon: Lower Cretaceous (early Barremian), Blesa Formation.

Material.—25 eggshell fragments gold-coated and mounted for SEM, numbered MPZ 2012/728 to MPZ 2012/736, MPZ 2012/738 to MPZ 2012/745, MPZ 2012/765 to MPZ 2012/767, and MPZ 2012/843 to MPZ 2012/846; 22 eggshell fragments prepared in radial thin sections, numbered MPZ 2012/847 to MPZ 2012/868; 300 additional eggshell fragments numbered MPZ 2012/428 to MPZ 2012/727. All from type locality.

Diagnosis.—Prismatoolithidae eggshell with three different layers, with gradual transition between mammillary and prismatic layer and between prismatic and external layer, and angusticanalicate pore system. Outer surface strongly sculptured with ornamentation made up of well-formed triangle-shaped and/or rounded unconnected protuberances. Eggshell thickness 330–1040 μm (mean 672 μm , standard deviation 106.46 μm).

Description.—Eggshell thickness ranges between 330–1040 μm including ornamentation ($n = 300$). The eggshell exhibits a strongly sculptured outer surface, with numerous independent protuberances with sections that vary from round to isosceles triangles (Figs. 2A, 4A, D). A few eggshells present

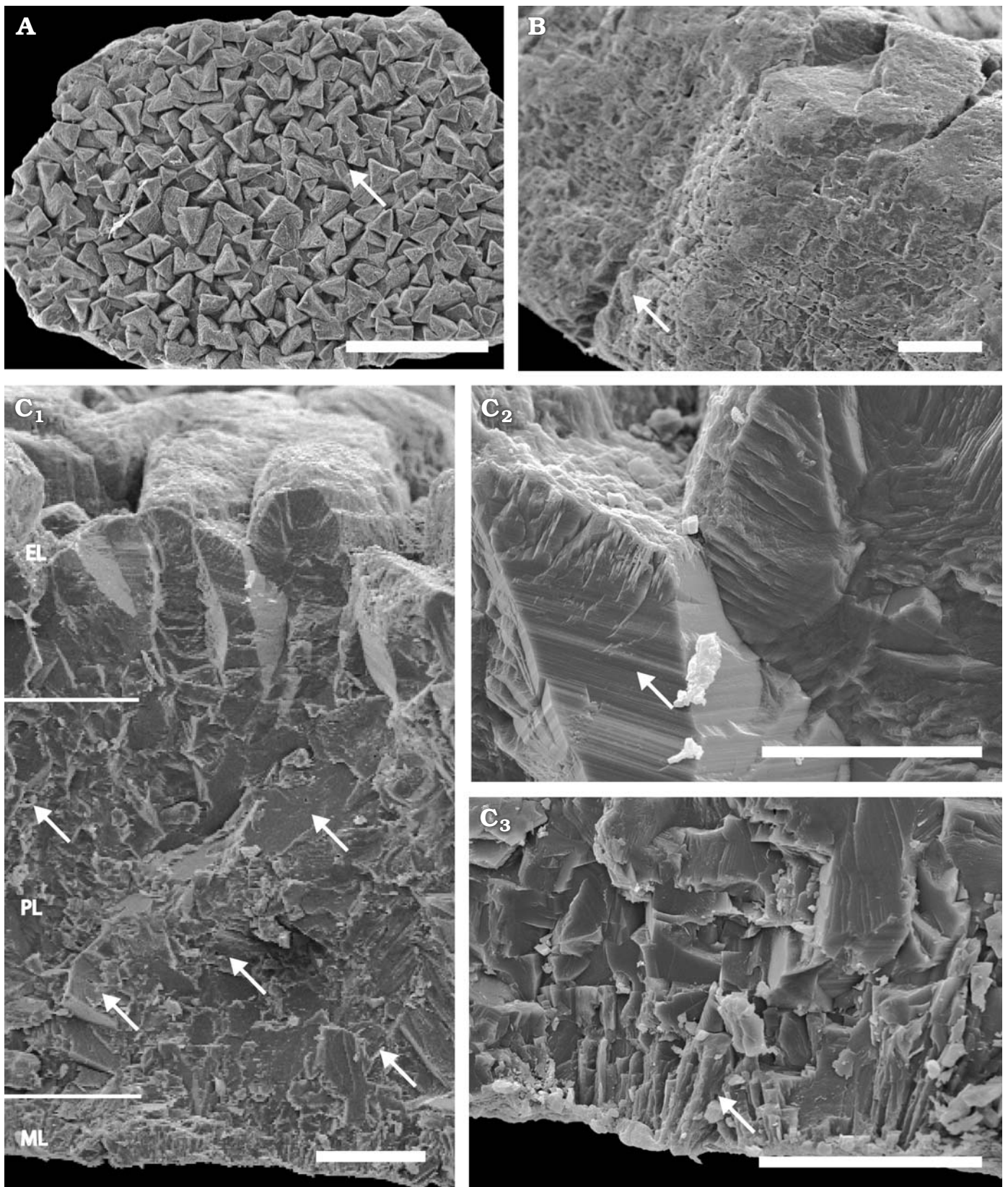


Fig. 2. Pristatoolithid eggshell *Trigonoolithus amoae* oogen. et oosp. nov. from La Cantalera 1 site, Early Barremian. **A.** MPZ 2012/740, external surface with ornamentation consisting of tightly packed sub-triangular protuberances. Arrow points to sub-circular pore opening. **B.** MPZ 2012/846, outer shell surface is at the top of the image. Radial section shows a straight pore (arrow) characteristic of angusticanaliculate pore system. **C.** MPZ 2012/737, holotype, radial section showing mammillary layer (ML), prismatic layer (PL) and external layer (EL) (C). White lines show approximate position of gradual transition between layers. Arrows point to vesicles that are present in the mammillary and prismatic layer, but absent in the external layer. Detail →

Table 1. Comparison of eggshell thickness of Prismatoolithidae and closely related ootaxa.

Ootaxa	Thickness			Outer surface ornamentation	Reference
	Min	Max	Mean		
Prismatoolithidae					
<i>Preprismatoolithus coloradoensis</i>	700	1000	—	smooth	Hirsch 1994
<i>Prismatoolithus</i> oospp.	300	1220	—		Zhao and Li 1993
<i>Prismatoolithus matellensis</i>	1060	1220	—	smooth	Vianey-Liaud and Crochet 1993
<i>Prismatoolithus tenuis</i>	300	600	—	smooth	Vianey-Liaud and Crochet 1993
<i>Prismatoolithus levis</i>	700	1000	—	smooth	Zelenitsky and Hills 1996
<i>Prismatoolithus gebiensis</i>	700	900	—	smooth	Zhao and Li 1993
<i>Prismatoolithus hanshuiensis</i>	1000	1200	—		Zhou et al. 1998
<i>Prismatoolithus jenseni</i>	830	1160	910–1100	smooth	Bray 1999
<i>Prismatoolithus hirschi</i>	500	561	—	smooth	Jackson and Varricchio 2010
<i>Prismatoolithus caboti</i>	500	600	—	disperse protuberances	Garcia et al. 2000
<i>Prismatoolithus heyuanensis</i>	—	—	520	smooth	Lu et al. 2006
<i>Protoceratopsidovum</i> oospp.		300	1400		Mikhailov 1994
<i>Protoceratopsidovum sincerum</i>	300	1200	—	smooth	Mikhailov 1994
<i>Protoceratopsidovum minimum</i>	300	700	—	smooth	Mikhailov 1994
<i>Protoceratopsidovum fluxuosum</i>	600	1400	—	fine ridges	Mikhailov 1994
<i>Spheruprismatoolithus</i> oosp.	500	900	—	ridges and nodes	Bray 1999
<i>Sankofa pirenaica</i>	190	340	270	smooth	López-Martínez and Vicens 2012
<i>Trigonoolithus amoae</i>	330	1040	—	triangular and/or rounded protuberances	this work
Arriagadoolithidae					
<i>Arriagadoolithus patagoniensis</i>	900	1200	1000	low nodes, isolated node-like ridges, and low long interconnected ridges	Agnolin et al. 2012
<i>Triprismatoolithus stephensi</i>	525	850	—	evenly distributed tubercles	Jackson and Varricchio 2010

both morphologies in the same fragment. Protuberances range from 80–300 μm , with a density of 30 protuberances per mm^2 .

The straight pore canals are sparse and occur around the ornamentation; pore openings are circular, with an average diameter of 10 μm . The pore system, therefore, is angusticanalicate (Fig. 2B).

The columns are narrow and their boundaries faint, with a height to width ratio of 4:1. The eggshells have three distinct structural layers, with a gradual transition between mammillary and prismatic layers and between prismatic and external layers (Fig. 2C). The prismatic layer to mammillary layer thickness ratio ranges from 3:1 to 4:1, and the prismatic layer to external layer ratio varies from 2:1 to 3:1. Mammillary, prismatic and external layers exhibit tabular ultrastructure (Fig. 2D). In the mammillary layer, crystals radiate outward from the organic cores (Fig. 2D₂) until they reach their neighbours from adjacent mammillae (see Moreno-Azanza et al. 2013, for a full description of this process). Crystals sub-parallel to the direction of eggshell growth survive to form the prismatic and external layers. Crystals in the prismatic layer show a poorly developed squamatic structure, with few vesicles (Fig. 2C). Prisms in the third structural layer are wider than those of the prismatic layer,

of the triangular ornamentation (C₂), where compact calcite structure can be seen. Vesicles are absent. Arrow points to tabular structure. Detail of the mammillary layer (C₃), showing tabular crystals and gradual transition between mammillary layer and prismatic layer. Scale bars: A, 1000 μm ; B, 200 μm ; C₁, 100 μm ; C₂, C₃, 50 μm .

with more defined crystals and identifiable, calcite crystal faces and boundaries (Fig. 2D).

Radial thin sections greater than 30 μm in thickness show faint growth lines in the lower half of the eggshell, namely in the mammillary and lower part of the prismatic layers (Fig. 3A). Column boundaries are visible in the mammillary layer, but indistinguishable in the prismatic layer under a light microscope (Fig. 3B₁). The inner shell surface exhibits tightly packed mammillae, with more than 40 mammillae per mm^2 . The mammillae display radiating tabular crystals, and are strongly cratered in most specimens and completely eroded in others (Figs. 2E, 3B₁). Only a few eggshell fragments exhibit an eisospherite, and in these the central core appears eroded.

Remarks.—The presence of the prismatic structure, with a gradual transition between the mammillary and prismatic layers, represents a synapomorphy of the Prismatoolithidae and a character shared with most modern and fossil neognath bird eggs (López-Martínez and Vicens 2012). In addition, *Trigonoolithus amoae* has a similar eggshell thickness to other Prismatoolithidae eggs (Table 1).

Prismatoolithidae includes five oogenera: *Preprismatoolithus* Hirsch, 1994; *Prismatoolithus* Zhao and Li, 1993; *Protoceratopsidovum* Mikhailov, 1994; *Spheruprismatoolithus* Bray, 1999; and *Sankofa* López-Martínez and Vicens, 2012.

Trigonoolithus shares its angustiprismatic morphotype and angusticanalicate pore system with *Sankofa*, *Prisma-*

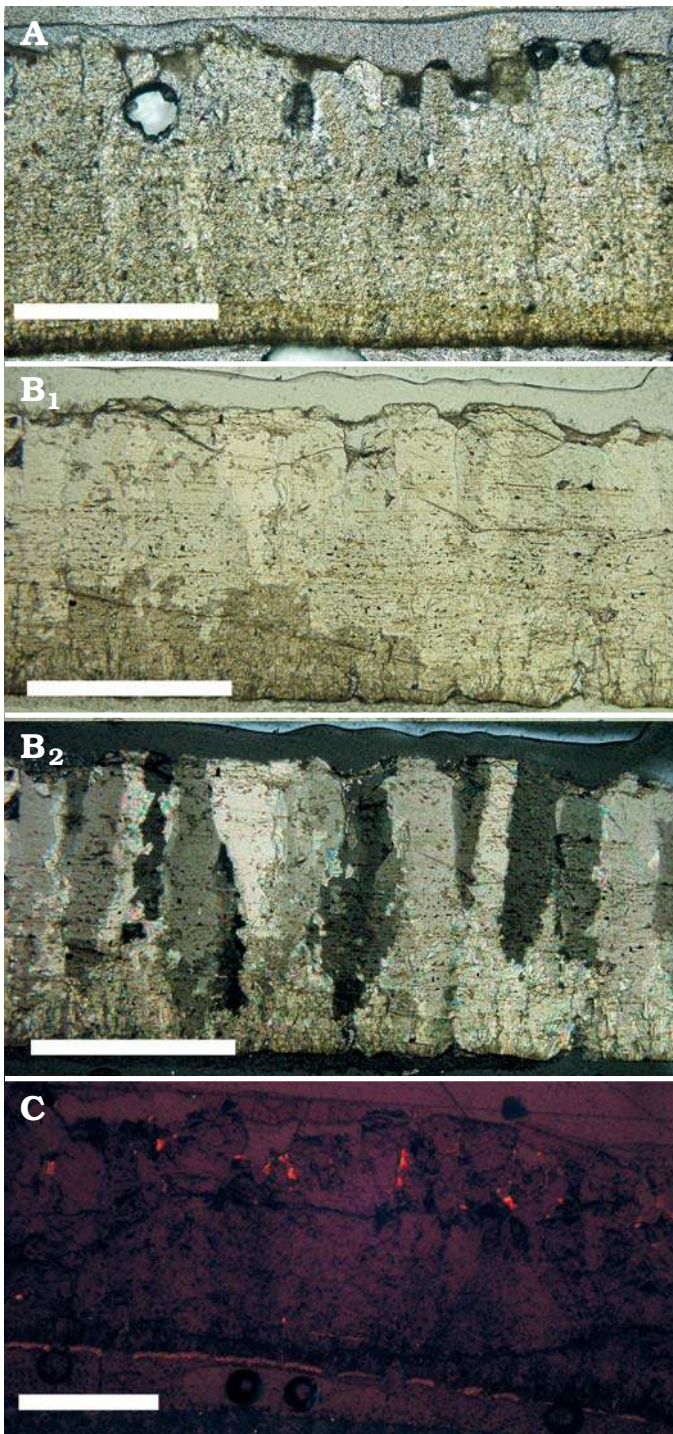


Fig. 3. Thin-sections of primateoolithid theropod eggshell *Trigonoolithus amoae* oogen. et oosp. nov. from La Cantalera 1 site, Early Barremian. A. MPZ 2012/856, light microphotograph. B. MPZ 2012/862, light microphotograph (B₁), microphotograph showing eggshell under cross-polars (B₂). C. MPZ2012/850, cathodoluminescence image showing dark blue luminescence except for some orange tones in the mammillary layer, probably due to the high amount of organic matter in this area. Scale bars 500 μ m.

toolithus, and *Protoceratopsidovum*, unlike *Preprimateoolithus*, which has oblique pore canals that cross columns. *Protoceratopsidovum* eggs have a smooth surface or fine linearituberculate ornamentation, whereas *Primateoolithus*

oospecies have a smooth to finely sculptured surface (Zelensky and Hills 1996). Only a single oospecies, *Primateoolithus caboti* Garcia, Feist, Cabot, Valentin, and Vianey-Liaud, 2000 from the Upper Cretaceous of France, shares with *Trigonoolithus* a well-developed ornamentation. However, the *P. caboti* shell is thinner and presents dispersituberculate ornamentation with spherical nodes up to four times larger than those present in *Trigonoolithus*.

Bray (1999) described the oogenus *Spheruprimateoolithus* as a Primateoolithidae eggshell with outer surface ornamentation. The ornamentation of this ootaxon is described as sculptured, with nodes that coalesce to form ridges on the outer shell surface, resulting in a dominant ramotuberculate to dispersituberculate ornamentation (Bray 1999: fig. 3), as opposed to the individualized protuberances that are present in *Trigonoolithus*. Also, *Spheruprimateoolithus* exhibits a lower prismatic layer to mammillary layer ratio (1:1) and a combination of angusticanalicate and rimocanalicate pores that are not present in *Trigonoolithus*. *Spheruprimateoolithus* presents widely spaced nucleation sites, and shell units that flare towards the outer surface of the eggshell and have a sweeping extinction pattern. Indeed, the inclusion of *Spheruprimateoolithus* in Primateoolithidae has been questioned by Jackson and Varricchio (2010), who point out that the described features of the structure of this ootaxon are not compatible with prismatic theropod eggs.

The oogenus *Sankofa* displays a smooth surface and a lower eggshell thickness. In addition, *Trigonoolithus* does not show the characteristic jagged central structure in the palisade layer (sensu López-Martínez and Vicens 2012).

Triprimateoolithus stephensi eggs from the Upper Cretaceous Two Medicine Formation of Montana display a prismatic structure, but were not assigned to the oofamily Primateoolithidae by Jackson and Varricchio (2010) due to the presence of well-developed ornamentation and the abrupt contact between the second and third structural layers. Recently, Agnolin et al. (2012) defined a new oofamily, Arriagadoolithidae, and *Arriagadoolithus*, a similar three-layered eggshell found in the Upper Cretaceous of Patagonia. *Trigonoolithus* differs from Arriagadoolithidae in displaying a gradual transition between the second and third structural layers.

Geographic and stratigraphic range.—Early Barremian of the Iberian Range. Blesa (Oliete subbasin), El Castellar (Galve subbasin) and Mirambel Formations (Morella subbasin).

Taphonomic analysis

Trigonoolithus amoae eggshells show very low luminescence, which is dark blue in all the eggshells except the lower part of the mammillae, where it is dark brownish to orange (Fig. 3C). The luminescence at the base of the mammillae has been found in other fossil eggshells (Grellet-Tinner and Makovicky 2006: figs. 3E, F, 4F; Jackson et al. 2010: fig. 2c).

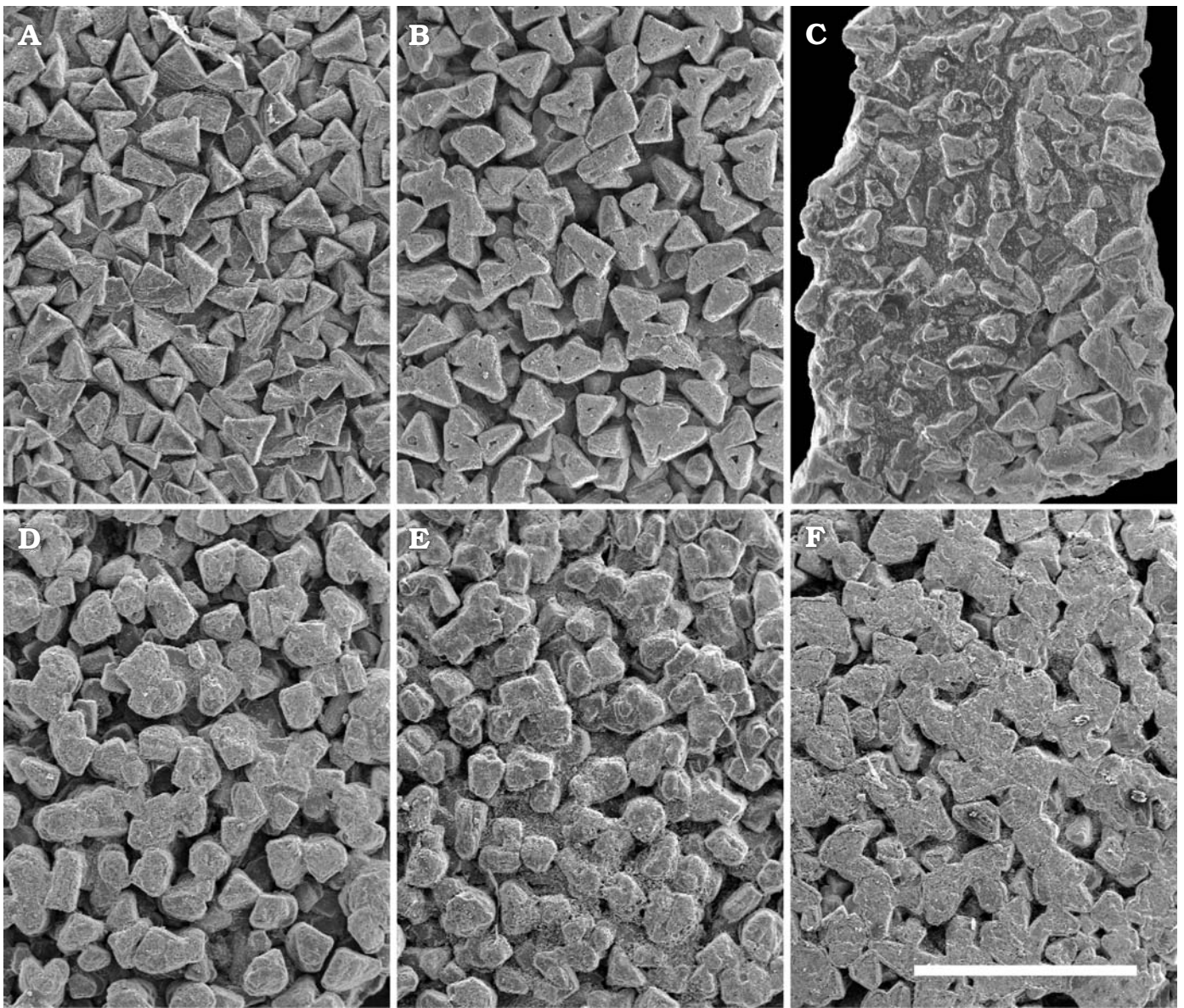


Fig. 4. Variations in outer surface ornamentation of primateoolithid theropod eggshell *Trigonoolithus amoe* oogen. et oosp. nov. from La Cantalera 1 site, Early Barremian. Eggshells showing triangular (A–C) and rounded ornamentation (D–F). Pristine eggshells showing well-preserved ornamentation (A, D). Lightly eroded eggshells showing degradation (B, E). Eroded eggshells showing coalescence of triangles (C, F). A. MPZ 2012/740. B. MPZ 2012/742. C. MPZ 2012/743. D. MPZ 2012/731. E. MPZ 2012/729. F. MPZ 2012/728. Scale bar 1000 μm .

Localized orange luminescent deposits within an eggshell have been interpreted as a replacement of degraded organic matter by Mn^{2+} during diagenesis. Jackson et al. (2010) suggested this scenario for the luminescence of the third layer of the *Troodon* eggshell. The eggshell considered by these authors shows the same luminescence in the mammillae as in the third layer, so an analogous origin of the luminescence is plausible. Notably, no luminescence is present in the ornamentation of *Trigonoolithus*; therefore, its triangular shape cannot result from recrystallization. The unusual shape of the ornamentation of *Trigonoolithus* eggshells is unique among ootaxa. However, triangular sections are common in calcite crystals of inorganic origin and organic carbonate minerals, and triangular structures have been described from tangen-

tial thin-sections in the prismatic layers of avian eggshell (von Nathusius 1821–1899 in Tyler 1964: 17). The triangular crystal shape is an expression of the ternary axis of the calcite and the organic control of the growth of the faces perpendicular to the (0001) axis of the crystals.

The presence of *Trigonoolithus amoe* eggshell fragments with both rounded and triangular ornamentation in the same locality is puzzling. Once recrystallization is rejected as an explanation, three hypotheses can be suggested to explain the origin of the differences in ornamentation.

Variations in shape within the same egg are frequent in other theropod eggs, and elongate eggs usually show different ornamentation in the pole area and equator (see for example Mikhailov 1994, 1997). As no complete *Trigonoolithus*

amoae eggs are known, no direct evidence exists to support any of the hypotheses. Nevertheless, fragments with both kinds of ornamentation are extremely rare. This contrasts with eggs that exhibit the transitional ornamentation (Elongatoolithidae), in which ornamentation varies according to its position on the egg. The possibility of a very short transition area between the two ornamentation patterns cannot be rejected.

Alternatively, taphonomic erosion of the nodes due to mechanical abrasion with transport, or more probably early diagenetic dissolution, may account for this variation. Against this hypothesis is the fact that triangular ornamentation is present in both well-preserved eggshells and weathered fragments (Fig. 4). As noted above, the La Cantalera 1 site has a complex taphonomical history. Autochthonous, well-preserved fossils that occur in anatomical position are mixed with parautochthonous remains that were washed in from the surrounding floodplain (Canudo et al. 2010). In addition, hydromorphic palaeosols at the La Cantalera 1 site occur in horizons or patches that are characterized by variable coloration and represent palustrine deposition. Hydromorphic soils likely produced a corrosive early burial environment (Wright and Platt 1995). In this context, eggshells exposed to different taphonomic processes have accumulated in the same locality influenced by the local palaeohydrology (i.e., fluctuations in an ephemeral water body and in the phreatic zone). Fig. 4 illustrates two sequences of degradation for eggshells with sub-triangular ornamentation (Fig. 4A–C) and rounded nodes (Fig. 4D–F). These include eggshells with well-preserved (Fig. 4A, C), smoothed (Fig. 4B, D) and coalescent ornamentation (Fig. 4E, F). The presence of pristine eggshells with triangular and rounded nodes, and the different paths observed in the degradation of both eggshells rules out the hypothesis of taphonomical modifications in the shape of the nodes.

Finally, triangular ornamented fragments and sub-rounded ornamented fragments may be considered to represent two different oospecies that differ in ornamentation. *Trigonoolithus* eggshells have been recovered from several other localities in the Iberian Range, including in Teruel Province the Colladico Blanco site in the El Castellar Formation (early Barremian) near the village of Galve and several microsites of the Mirambel Formation (early Barremian). Eggshells with both rounded and triangular ornamentation are identified from all localities. As both eggshells appear together in all the localities studied, we chose not to split the eggshells into two different oospecies on the basis of differences of ornamentation.

Taking all the above into account, we consider the hypothesis of variation in the ornamentation of *Trigonoolithus* within the same egg to be the most parsimonious. The low number of eggshell fragments with both ornamentation patterns may be due to an abrupt transition between the two ornamentations.

Phylogenetic analysis

Four cladistic analyses were carried out using the software TNT v1.1 (Goloboff et al. 2008) to assess the phylogenetic position of *Trigonoolithus amoae* oogen. et oosp. nov. These included character matrices proposed by Varricchio and Jackson (2004), Grellet-Tinner and Makovicky (2006) and Zelenitsky and Therrien (2008a, b). Also, López-Martínez and Vicens (2012) have published a new analysis of Prismatoolithidae using the matrix of Zelenitsky and Therrien (2008a, b) and adding the new oogenus *Sankofa* and the Patagonian eggs of the Bajo de la Carpa Formation (Schweitzer et al. 2002). This matrix was also considered as an independent analysis. For each resulting matrix, the tree-space was searched using a heuristic search algorithm with tree-bisection-reconnection (TBR) branch swapping and 1,000 random addition replicates, retaining 10 trees in each replication. All characters were equally weighted. Bremer supports and bootstrap frequencies (1,000 bootstrap replicates) were used to assess the robustness of the nodes.

All searches produced similar results. Strict consensus trees for the four analyses are shown in Fig. 5.

Varricchio and Jackson (2004) (Fig. 5A).—Characters 1 and 11 were ordered, as suggested by Jin et al. (2010).

Results.—Six equally parsimonious trees of 38 steps were recovered, and the strict consensus is shown in Fig. 5A. The inclusion of *Trigonoolithus* results in a significant deterioration of the resolution of the consensus. Even the Adams consensus (not shown) is less resolved than that previously published. All chelonian eggs are recovered as successive outgroups of the archosaurian clade. Within archosaur eggs, the four major groups represented (crocodilians, ornithischians, sauropods, and theropods) form a polytomy. Likewise, all theropod eggs are recovered in a polytomy. Attempts to increase the resolution of the tree, either by safely pruning taxa or by generating a reduced consensus, fail to improve the results. Nevertheless, the inclusion of *Trigonoolithus* within the clade Prismatoolithidae+avian eggs is strongly supported.

Grellet-Tinner and Makovicky (2006) (Fig. 5B).—In addition to the inclusion of *Trigonoolithus*, several changes were made to this dataset. First, Vincent (2010) has shown that the Phu Phok theropod eggs included in the original analysis contained anguimorph lizard embryos. Therefore, the description of the eggshell structure requires detailed revision before these eggs are included in future analyses. Furthermore, Grellet-Tinner and Makovicky (2006) coded the absence of a third layer in *Troodon formosus* eggs. However, this condition is controversial, and different interpretations have been published (Jackson et al. 2010). If *Troodon* eggshell is coded as having two layers, the result is similar to that shown in Fig. 5B. However, *Troodon* and *Byronosaurus* form a clade that is in polytomy with ornithoracine and avian eggshell. If *Troodon* is coded as having

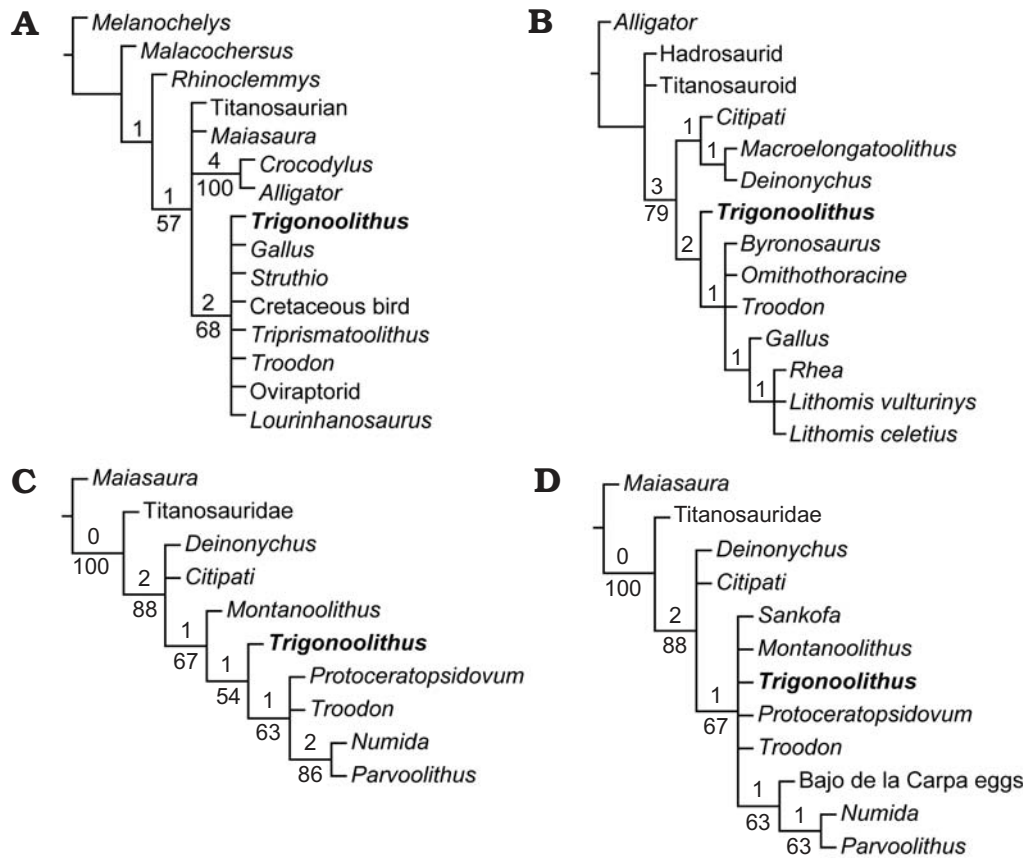


Fig. 5. Strict consensus trees showing the hypothesized phylogenetic position of *Trigonoolithus amoe* oogen. et oosp. nov. from La Cantalera 1 site, Early Barremian. **A**. Matrix of Varricchio and Jackson (2004). Strict consensus of six equally parsimonious trees of 38 steps was recovered (C.I. 0.737; R.I. 0.853; R.C. 0.629). **B**. Matrix of Grellet-Tinner and Makovicky (2006). Strict consensus tree of three equally most parsimonious trees of 36 steps (C.I. 0.750; R.I. 0.852; R.C. 0.639). **C**. Matrix of Zelenitsky and Therrien (2008b). Most parsimonious tree of 18 steps (C.I. 1.000; R.I. 1.000; R.C.1.000). **D**. López-Martínez and Vicens (2012) version of the dataset: a new analysis of Primateoolithidae using the matrix of Zelenitsky and Therrien (2008) and adding the new oogenus *Sankofa* and the Patagonian eggs of Bajo de la Carpa (Schweitzer et al. 2002). Strict consensus of seven equally parsimonious trees of 19 steps (C.I. 0.947; R.I. 0.958; R.C. 0.907). All trees show *Trigonoolithus* placed in polytomy or at the base of the “Primateoolithidae+avian eggs” clade.

three layers, the troodontid clade collapses, as shown in Fig. 5B. Furthermore, if both *Byronosaurus* and *Troodon* are coded as having three layers, the result does not differ from the one shown in Fig. 5B. To date there is no published description of the eggshell of *Byronosaurus* eggs besides the character codes given in Grellet-Tinner and Makovicky (2006). Taking this into account, we have chosen the second hypothesis as we think that the presence of a third layer has been strongly confirmed in *Troodon* eggs (Jackson et al. 2010), but we have no additional information concerning *Byronosaurus*.

Results.—Three equally most parsimonious trees of 36 steps were recovered (Fig. 5B). In this analysis *Alligator* eggs appear as outgroup to all dinosaurian eggs. Sauropod, ornithopod and theropod eggs form a polytomy. Within theropod eggs, two clades are recovered: Elongatoolithidae, including *Citipati*, *Macroelongatoolithus*, and *Deinonychus* eggs, and Primateoolithidae+avian eggs. The oogenus *Trigonoolithus* is placed as the sister taxon of all other Primateoolithidae eggs included in this analysis, sharing the presence of three structural layers—possibly reversed in *Byronosaurus*—and the gradual transition between the first and second structur-

al layers. *Trigonoolithus* differs from more derived Primateoolithidae only in the presence of outer surface ornamentation. All the more derived Primateoolithidae form a polytomy with the Neornithes clade.

Zelenitsky and Therrien (2008a, b) (Fig. 5C).—No changes besides the inclusion of *Trigonoolithus* were made.

Results.—One most parsimonious tree of 18 steps was recovered (Fig. 5C). *Trigonoolithus* is placed as basal to Primateoolithidae+avian eggs, on the basis of the presence of a third structural layer, a character state not present in *Montanoolithus*. The latter is regarded as the most basal non-elongatoolithid theropod ootaxon. The presence of ornamentation on the external surface places *Trigonoolithus* as the basalmost member of Primateoolithidae.

López-Martínez and Vicens (2012) (Fig. 5D).—No changes besides the inclusion of *Trigonoolithus* were made.

Results.—The inclusion of *Trigonoolithus* in this dataset produces seven equally parsimonious trees of 19 steps (Fig. 5D), and results in the collapse of all Primateoolithidae oogenera

in a polytomy with *Montanolithus* and avian eggs, this node being supported by the presence of three structural layers.

Because only eggshell fragments rather than entire eggs were studied, only a few characters could be coded for *Trigonoolithus* in each matrix: Varricchio and Jackson (2004), 73% of characters coded; Grellet-Tinner and Makovicky (2006), 53% of characters coded; Zelenitsky and Therrien (2008a, b), 50% of characters coded; López-Martínez and Vicens (2012), 50% of characters coded. Thus the results of the analyses should be treated with caution.

Parataxonomic remarks and taxonomic affinity

The position of *Trigonoolithus* as basal to all other Prismatoolithidae eggs considered—or at least in close relation with the basal forms of this oofamily—is stable in all the analyses reported above. As no formal phylogenetic definition has been provided for the clade Prismatoolithidae (Zelenitsky and Therrien 2008a), the inclusion of *Trigonoolithus* within this clade/oofamily or in a monotypic oofamily sister to Prismatoolithidae + Aves is arbitrary. Nevertheless, given the lack of more complete material, we have chosen not to erect a new oofamily.

Eggs with a prismatic structure have been assigned to troodontid dinosaurs on the basis of embryonic remains found inside eggs (Horner and Weishampel 1996; Varricchio et al. 2002). The oospecies *Prismatoolithus levis* has been assigned to *Troodon formosus* (Varricchio et al. 2002), and two-layered prismatic eggs have also been assigned to *Byronosaurus jaffei* (Grellet-Tinner and Makovicky, 2006). Nevertheless, cladistic analyses including oological characters show that this oofamily may include other more basal non-avian theropods, e.g., the basal coelurosaur *Lourinhanosaurus*. Furthermore, eggs of oviraptorids and *Deinonychus* have been assigned to the Elongaloolithidae oofamily, on the basis of embryonic remains and the association of an egg with adult skeletal remains, respectively (Norell et al. 1994; Grellet-Tinner and Makovicky 2006; Sato et al. 2005). Thus, we consider that *Trigonoolithus* was laid by a non-dromaeosaurian, non-oviraptorid coelurosaur theropod dinosaur, more derived than *Lourinhanosaurus* but less derived than troodontids.

Ten types of theropod teeth have been reported from La Cantalera (Canudo et al. 2010). Two of these correspond to the basal tetanurans Baryonychinae indet. and Carcharodontosauridae indet. Seven other morphotypes correspond to Maniraptoriformes, including dromaeosaurians, Velociraptorinae indet. and undetermined maniraptorans. Given the phylogenetic assumptions outlined above and the latest skeleton—based theropod phylogeny (Carrano et al. 2012), Baryonychinae indet. and Carcharodontosauridae indet. are more basal than the hypothetical egg-layer of *Trigonoolithus*. Moreover, Dromaeosaurinae indet. can a priori be

related with elongaloolithid eggs. Only Maniraptora indet. and aff. *Paronychodon* sp. fit the phylogenetic status of the hypothetical egg-layer. These are the most plausible candidates for having produced the *Trigonoolithus* eggs.

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Appendix 1

Additions and changes to the data matrices used in the phylogenetic analyses.

Varricchio and Jackson (2004)

Characters 1 and 11 were ordered, as suggested by Zelenitsky and Therrien (2008a).

Trigonoolithus 3121202100???

layer in *Troodon* eggshell has been considered confirmed (see Jackson et al. 2010).

Troodon 2112012021120010010

Trigonoolithus ??????1211100??000

Grellet-Tinner and Makovicky (2006)

Phu Phok eggs not included (see text for discussion). Characters 9 and 14 have been recoded for *Troodon*, as the presence of a third

Zelenitsky and Therrien (2008a, b) and López-Martinez and Vicens (2012)

Trigonoolithus ?0??31??1?11