

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

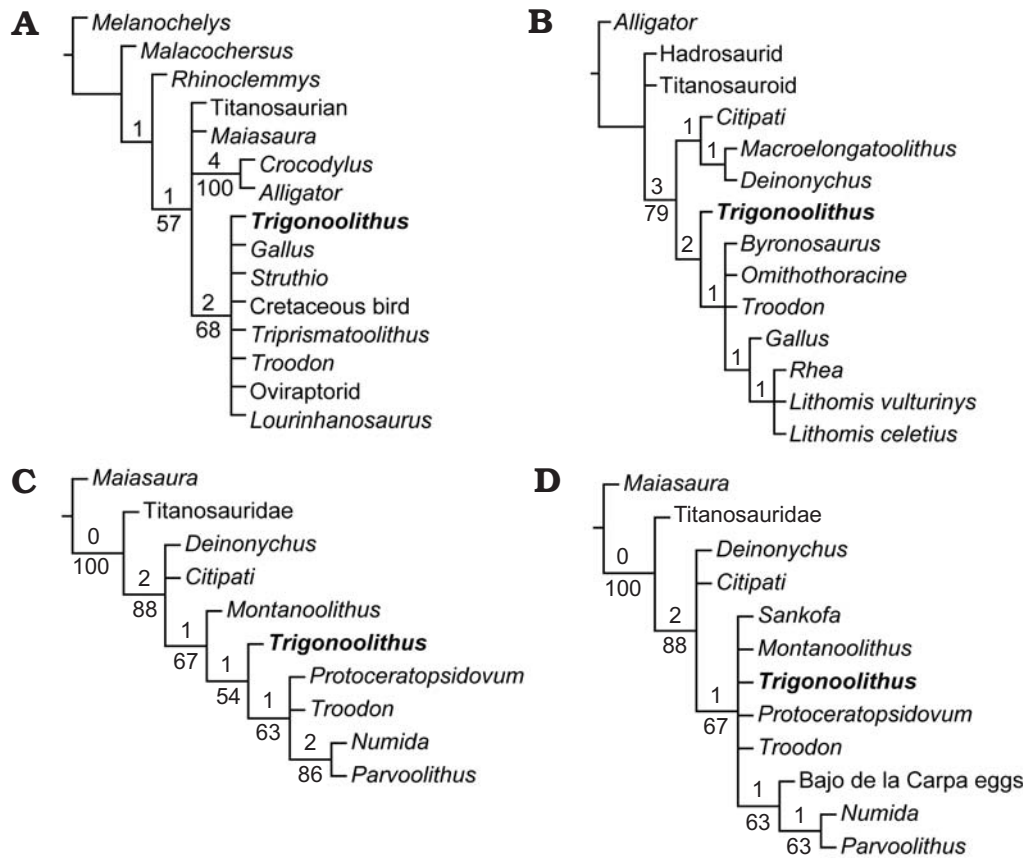


Fig. 5. Strict consensus trees showing the hypothesized phylogenetic position of *Trigonoolithus amoe* oogen. et oosp. nov. from La Cantalera 1 site, Early Barremian. **A.** Matrix of Varricchio and Jackson (2004). Strict consensus of six equally parsimonious trees of 38 steps was recovered (C.I. 0.737; 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 Prismaoolithidae 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 “Prismaoolithidae+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: Elongaloolithidae, including *Citipati*, *Macroelongaloolithus*, and *Deinonychus* eggs, and Prismaoolithidae+avian eggs. The oogenus *Trigonoolithus* is placed as the sister taxon of all other Prismaoolithidae 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 Prismaoolithidae only in the presence of outer surface ornamentation. All the more derived Prismaoolithidae 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 Prismaoolithidae+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-elongaloolithid theropod ootaxon. The presence of ornamentation on the external surface places *Trigonoolithus* as the basalmost member of Prismaoolithidae.

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 Prismaoolithidae 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.

Acknowledgements

Hernando Royo Plumed (Institut Català d'Arqueologia Clàssica, Tarragona, Spain) took the cathodoluminescence images. Cristina Gallejo (Servicio de Apoyo a la Investigación, Universidad de Zaragoza, Spain) took the SEM images. Rupert Glasgow (Zaragoza, Spain) edited the text in English. Darla Zelenitsky (University of Calgary, Canada), Leonardo Salgado (Universidad de Río Negro, Argentina) and Frankie Jackson Montana State University, Bozeman, USA) reviewed and helped improve the paper substantially. We thank our editor, Michael Benton (University of Bristol, UK) for his comments and suggestions. This paper forms part of the project CGL2010-16447 and is subsidized by the Spanish Ministerio de Economía y Competitividad, the European Regional Development Fund, and the Government of Aragón, European Social Fund (“Grupos Consolidados” and “Dirección General de Patrimonio Cultural”). MMA is supported by a FPI grant (BES-2008-005538) from the Ministerio de Economía y Competitividad, JMG. is supported by a FPI grant (B064/08B) from the Government of Aragón. The authors acknowledge the use of the Servicio General de Apoyo a la Investigación-SAI, Universidad de Zaragoza, Spain.

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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??0?

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