



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: Elongatoolithidae, including *Citipati*, *Macroelongatoolithus*, 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-elongatoolithid 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.

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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