

Fig. 4. Variations in outer surface ornamentation of prismaticoolithid theropod eggshell *Trigonoolithus amoae* 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  $\mu\text{m}$ .

Localized orange luminescent deposits within an eggshell have been interpreted as a replacement of degraded organic matter by  $\text{Mn}^{2+}$  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 amoae* 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



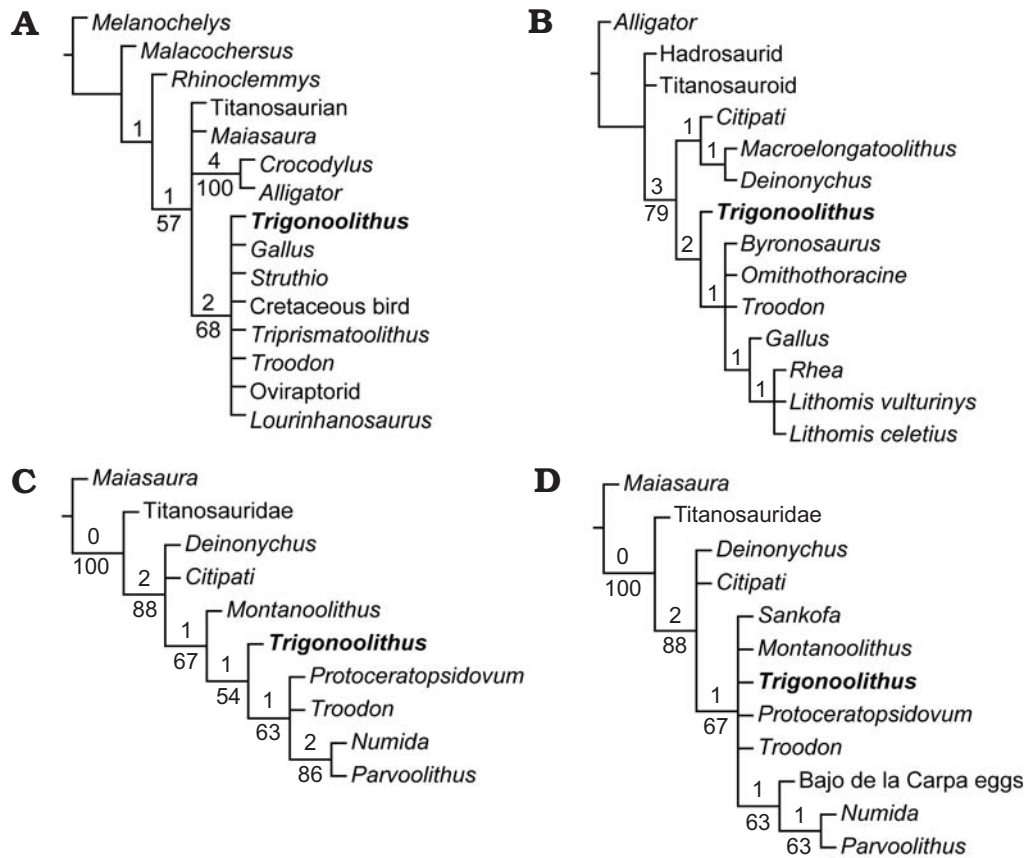


Fig. 5. Strict consensus trees showing the hypothesized phylogenetic position of *Trigonoolithus amoe* oogen. et oosp. nov. from La Cantalera 1 site, Early Barremian. **A.** Matrix of Varricchio and Jackson (2004). Strict consensus of six equally parsimonious trees of 38 steps was recovered (C.I. 0.737;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

**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 Prismatoolithidae 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.

## References

- Amo Sanjuan, O., Canudo, J.I., and Cuenca-Bescós, G. 2000. First record of Elongatoolithidae eggshell fragment from the Lower Barremian of Europe (Cuesta Corrales 2, Galve Basin, Teruel, Spain). In: A.M. Bravo and T. Reyes (eds.), *First International Symposium on Dinosaur Eggs and Babies*, 7–13. Imprenta Provincial de la Diputació de Lleida, Lleida.
- Agolín, F.L., Powell, J.E., Novas, F.E., and Kundrát, M. 2012. New alvarezsaurid (Dinosauria, Theropoda) from uppermost Cretaceous of north-western Patagonia with associated eggs. *Cretaceous Research* 35: 33–56.
- Aurell, M., Bádenas, B., Canudo, J.I., and Ruiz-Omeñaca, J.I. 2004. Evolución tectosedimentaria de la Fm. Blesa (Cretácico Inferior) en el entorno del yacimiento de vertebrados de la Cantalera (Josa, Teruel). *Geogaceta* 35: 11–13.
- Bray, E.S. 1999. Eggs and eggshells from the Upper Cretaceous North Horn Formation, central Utah. In: D.D. Gillette (ed.), *Vertebrate Paleontology in Utah*. *Utah Geological Survey* 99-1: 361–375.
- Buscalioni, A.D., Fregenal, M.A., Bravo, A., Poyato-Ariza, F.J., Sanchíz, B., Báez, A.M., Cambra Moo, O., Martín Closas, C., Evans, S.E., and Marugán Lobón, J. 2008. The vertebrate assemblage of Buenache de la Sierra (Upper Barremian of Serranía de Cuenca, Spain) with insights into its taphonomy and palaeoecology. *Cretaceous Research* 29: 687–710.
- Canudo, J.I., Gasca, J.M., Aurell, M., Badiola, A., Blain, H.-A., Cruzado-Caballero, P., Gómez-Fernández, D., Moreno-Azanza, M., Parrilla, J., Rabal-Garcés, R., and Ruiz-Omeñaca, J.I. 2010. La Cantalera: an exceptional window onto the vertebrate biodiversity of the Hauterivian–Barremian transition in the Iberian Peninsula. *Journal of Iberian Geology* 36: 295–324.
- Canudo, J.I., Gasca, J.M., Moreno, M., and Aurell, M. 2012. New information about the stratigraphic position and age of the sauropod *Aragosaurus ischiaticus* from the Early Cretaceous of the Iberian Peninsula. *Geological Magazine* 149: 252–263.
- Carrano, M.T., Benson, R.B.J., and Sampson, S.D. 2012. The phylogeny of Tetanurae (Dinosauria: Theropoda). *Journal of Systematic Palaeontology* 10: 211–300.

- Eberth, D.A. and Currie, P.J. 2005. Vertebrate taphonomy and taphonomic modes. In: P.J. Currie and E.B. Koppelhus (eds.), *Dinosaur Provincial Park. A Spectacular Ancient Ecosystem Revealed*, 453–477. Indiana University Press, Bloomington.
- García, G., Feist, M., Cabot, A., Valentin, X., and Vianey-Liaud, M. 2000. Les oeufs de dinosaures du Crétacé supérieur du bassin de Villeveyrac-Mèze (Hérault, France): description d'une nouvelle oospèce de *Prismatoolithus*. *Bulletin de la Société Géologique de France* 171: 283–289.
- Goloboff, P., Farris, J.C., and Nixon, K.C. 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24: 774–786.
- Grellet-Tinner, G. and Makovicky, P. 2006. A possible egg of the dromaeosaur *Deinonychus antirrhopus*: phylogenetic and biological implications. *Canadian Journal of Earth Sciences* 43: 705–719.
- Hirsch, K.F. 1994. Upper Jurassic eggshells from the Wertern interior of North America. In: K. Carpenter, J. Horner, and K.F. Hirsch (eds.), *Dinosaur Eggs and Babies*, 137–150. Cambridge University Press, Cambridge.
- Horner, J.R. and Weishampel, D.B. 1988. A comparative embryological study of two ornithischian dinosaurs. *Nature* 332: 256–257.
- Horner, J.R. and Weishampel, D.B. 1996. A comparative embryological study of two ornithischian dinosaurs—a correction. *Nature* 383: 103.
- Jackson, F.D. and Varricchio, D.J. 2010. Fossil eggs and eggshell from the lowermost Two Medicine Formation of western Montana, Sevenmile Hill locality. *Journal of Vertebrate Paleontology* 30: 1142–1156.
- Jackson, F.D., Horner, J.R., and Varricchio, D.J. 2010. A study of a *Troodon* egg containing embryonic remains using epifluorescence microscopy and other techniques. *Cretaceous Research* 31: 255–262.
- Jin, X., Jackson, F.D., Varricchio, D.J., Azuma, Y., and He, T. 2010. The first *Dictyoolithus* egg clutches from the Lishui basin, Zhejiang Province, China. *Journal of Vertebrate Paleontology* 30: 188–195.
- Kohring, R. 1990. Fossile Reptil-Eierschalen (Chelonina, Crocodilia, Dinosauria) aus dem unterem Barremium von Galve (Provinz Teruel, SE Spanien). *Paläontologische Zeitschrift* 64: 392–344.
- Liesa, C.L., Soria, A.R., Meléndez, N., and Meléndez, A. 2006. Extensional fault control on the sedimentation patterns in a continental rift basin: El Castellar Formation, Galve sub-basin, Spain. *Journal of the Geological Society, London* 163: 487–498.
- López-Martínez, N. and Vicens, E. 2012. A new peculiar dinosaur egg, *Sankofa pyrenaica* oogen. nov. oosp. nov. from the Upper Cretaceous coastal deposits of the Aren Formation, South-Central Pyrenees, Lleida, Catalonia, Spain. *Palaeontology* 55: 325–339.
- Magalhães Ribeiro, C.M. 1999. Utilização de catodoluminescência em cascas de ovos de dinossauros. *Ameghiniana, Resúmenes* 36, 4: 15R.
- Mateus, I., Mateus, H., Antunes, M.T., Mateus, O., Taquet, P., Ribeiro, V., and Manuppella, G. 1997. Couvée, oeufs et embryons d'un dinosaure théropode du Jurassique supérieur de Lourinha (Portugal). *Comptes Rendus de l'Académie des Sciences de Paris* 325: 71–78.
- Mikhailov, K.E. 1994. Theropod and protoceratopsian dinosaur eggs from the Cretaceous of Mongolia and Kazakhstan. *Paleontological Journal* 28: 101–120.
- Mikhailov, K.E. 1997. Fossil and Recent eggshell in amniotic vertebrates; fine structure, comparative morphology and classification. *Special Papers in Palaeontology* 56: 1–80.
- Moreno-Azanza, M., Gasca, J.M., and Canudo, J.I. 2009a. A high-diversity eggshell locality from the Hauterivian–Barremian transition of the Iberia Peninsula. *Journal of Vertebrate Paleontology* 29 (Supplement to No. 3): 151A.
- Moreno-Azanza, M., Gasca, J.M., and Canudo, J.I. 2009b. New data on the Valanginian–Hauterivian reptile ootaxa of the Iberian Range (NE of Spain). *Tribute to Charles Darwin to Bernissart Iguanodonts: New perspectives on Vertebrate Evolution and Early Cretaceous Ecosystems, Programme, Abstracts and Field Trips Guidebook*, 72. Brussels.
- Moreno-Azanza, M., Mariani, E., Bauluz, B., and Canudo, J.I. 2013. Growth mechanisms in dinosaur eggshells: an insight from electron backscatter diffraction. *Journal of Vertebrate Paleontology* 33:121–130.
- Norell, M. A., Clark, J.M., Demberelyin, D., Rinchen, B., Chiappe, L.M., Davidson, A.R., McKenna, M.C., Altangerel, P., and Novacek, M.J. 1994. A theropod dinosaur embryo and the affinities of the Flaming Cliffs dinosaur eggs. *Science* 266: 779–782.
- Riveline, J., Berger, J.P., Feist, M., Martín-Closas, C., Schudack, M., and Soulié-Marsche, I. 1996. European Mesozoic–Cenozoic charophyte biozonation. *Bulletin de la Société géologique de France* 167: 453–468.
- Rogers, R. and Brady, M. 2010. Origins of microfossil bonebeds: insights from the Upper Cretaceous Judith River Formation of north-central Montana. *Paleobiology* 36: 80–112.
- Salas, R., Guimera, J., Más, R., Martín-Closas, C., Meléndez, A., and Alonso, A. 2001. Evolution of the Mesozoic central Iberian Rift System and its Cainozoic inversion (Iberian Chain). *Mémoires du Muséum Nationale de l'Histoire Naturelle* 186: 145–185.
- Sato, T., Cheng, Y.-N., Wu, X.-C., Zelenitsky, D.K., and Hsiao, H.-F. 2005. A pair of shelled eggs inside a female dinosaur. *Science* 308: 375.
- Schweitzer, M.H., Jackson, F.D., Chiappe, L.M., Schmitt, J.G., Calvo, J.O., and Rubilar, D.E. 2002. Late Cretaceous avian eggs with embryos from Argentina. *Journal of Vertebrate Paleontology* 22: 191–195.
- Tyler, C. 1964. *Wilhelm von Nathusius 1821–1899. On Avian Egg Shells* [translated and edited version of his work]. 104 pp. The University of Reading, Reading.
- Varricchio, D.J. and Jackson, F.D. 2004. A phylogenetic assessment of prismatic dinosaur eggs from the Cretaceous Two Medicine Formation of Montana. *Journal of Vertebrate Paleontology* 24: 931–937.
- Vianey-Liaud, M. and López-Martínez, N. 1997. Late Cretaceous dinosaur eggshells from the Tremp basin, southern Pyrenees, Lleida, Spain. *Journal of Paleontology* 71: 1157–1171.
- Vincent, F. 2010. *Detection and Imaging of in Ovo Fossil Embryos by Synchrotron Microtomography: Study of the Enigmatic Embryos from Phu Phok (Lower Cretaceous, Thailand)*. Unpublished Ph.D. thesis, European Synchrotron Radiation Facility, Grenoble.
- Wright, V.P. and Platt, N.H. 1995. Seasonal wetland carbonate sequences and dynamic catenas: a re-appraisal of palustrine limestones. *Sedimentary Geology* 99: 65–71.
- Zelenitsky, D.K., Modesto, S.P., and Currie, P.J. 2002. Bird-like characteristics of troodontid theropod eggshell. *Cretaceous Research* 23: 297–305.
- Zelenitsky, D.K. and Therrien, F. 2008a. Phylogenetic analysis of reproductive traits of maniraptoran theropods and its implications for egg parataxonomy. *Palaeontology* 51: 807–816.
- Zelenitsky, D.K. and Therrien, F. 2008b. Unique maniraptoran egg clutch from the Upper Cretaceous Two Medicine Formation of Montana reveals theropod nesting behaviour. *Palaeontology* 51: 1253–1259.

# Appendix 1

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

Varricchio and Jackson (2004)	layer in <i>Troodon</i> eggshell has been considered confirmed (see Jackson et al. 2010).
Characters 1 and 11 were ordered, as suggested by Zelenitsky and Therrien (2008a).	
<i>Trigonoolithus</i> 3121202100???	<i>Troodon</i> 2112012021120010010
	<i>Trigonoolithus</i> ??????1211100??000
Grellet-Tinner and Makovicky (2006)	Zelenitsky and Therrien (2008a, b) and López-Martinez and Vicens (2012)
Phu Phok eggs not included (see text for discussion). Characters 9 and 14 have been recoded for <i>Troodon</i> , as the presence of a third	<i>Trigonoolithus</i> ?0??31??1?11