

Revisiting Sabath's "Larger Avian Eggs" from the Gobi Cretaceous

Authors: Varricchio, David J., and Barta, Daniel E.

Source: Acta Palaeontologica Polonica, 60(1) : 11-25

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: <https://doi.org/10.4202/app.00085.2014>

The BioOne Digital Library (<https://bioone.org/>) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (<https://bioone.org/subscribe>), the BioOne Complete Archive (<https://bioone.org/archive>), and the BioOne eBooks program offerings ESA eBook Collection (<https://bioone.org/esa-ebooks>) and CSIRO Publishing BioSelect Collection (<https://bioone.org/csiro-ebooks>).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Revisiting Sabath's "Larger Avian Eggs" from the Gobi Cretaceous

DAVID J. VARRICCHIO and DANIEL E. BARTA



Varricchio, D.J. and Barta, D.E. 2015. Revisiting Sabath's "Larger Avian Eggs" from the Gobi Cretaceous. *Acta Palaeontologica Polonica* 60 (1): 11–25.

In 1991, Sabath described "larger avian eggs" from the Upper Cretaceous Barun Goyot and Djadokhta Formations of Mongolia. These were later included in the ootaxon *Gobioolithus major*. Here we recognize the larger avian eggs of Sabath as a distinct ootaxon, *Styloolithus sabathi*, oogen. et oosp. nov. These eggs differ from those of *Gobioolithus* in being larger (70 by 32 mm) and more elongate. Microscopically, the shell bears a third layer (possible external zone) thicker than the mammillary layer and nearly as thick as the second layer (possible squamatic zone); the continuous layer (including layers two and three) to mammillary layer thickness ratio is 3.1:1. Within the clutch, the tightly spaced eggs stand with their long axes steeply inclined. Adult remains are associated with two clutches, suggesting an incubation mode similar to that of troodontid maniraptorans, where adults sat atop largely buried eggs. *S. sabathi* provides evidence that relative egg size in Mesozoic non-ornithuromorph birds had increased markedly from the non-avian theropod condition in oviraptorids and troodontids, but had not yet reached the modern egg-adult proportions of Neornithes. Sediment-bound upright eggs appear common to Enantiornithes and more basal avians, suggesting that like non-avian theropods, these birds lacked chalazae, the chords of albumen allowing egg rotation in modern birds. Absence of this simple structure may have restricted these basal birds to ground nesting in areas with appropriate substrates and not permitted the type of nesting diversity found in Neornithes. Neornithes are the only Mesozoic clade of Dinosauria to nest completely free of sediment; this may have played a crucial role in their surviving the K-Pg mass extinction event.

Key words: Aves, Enantiornithes, ootaxa, birds, reproduction, eggs, Cretaceous, Mongolia.

David J. Varricchio [djv@montana.edu] and Daniel E. Barta [daniel.barta.paleo@gmail.com], Earth Sciences, Montana State University, Bozeman, MT 59717, USA.

Received 12 April 2014, accepted 10 June 2014, available online 26 June 2014.

Copyright © 2015 D.J. Varricchio and D.E. Barta. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

Sabath (1991) documented a diverse assemblage of eggs collected by the Polish-Mongolian Expeditions of 1963–1971 from multiple localities within the Gobi Desert, Mongolia. Among these eggs, he noted two potentially avian varieties (Fig. 1A, C). A smaller form came from the Khermeen Tsav I locality within the "Protoceratops horizon", correlative with the Campanian Barun Goyot Formation (Mikhailov et al. 1994; Jerzykiewicz 2000). These ellipsoid eggs measure on average 43 mm by 21 mm. At Khermeen Tsav, these eggs occur abundantly on several horizons representing repeat use of a nesting ground. Based on associated embryonic remains (Elzanowski 1981), Sabath (1991) tentatively assigned them to "*Gobipteryx minuta*". Recent description of additional Khermeen Tsav embryos recognized them as distinct from

Gobipteryx minuta, instead placing them in a new enantiornithine taxon, *Gobipipus reshetovi* (Kurochkin et al. 2013). The second avian egg of Sabath (1991), simply referred to as "larger avian eggs", derived from two localities, Khulsan of the Barun Goyot Formation and Bayn Dzak within the Djadokhta Formation. These eggs are much larger with a 70 mm length and a 32 mm maximum diameter and Sabath (1991) considered them to have an ornithoid microstructure strongly altered diagenetically. Specimens from Bayn Dzak include two partial clutches both with closely placed, sub-vertically oriented eggs and skeletal elements of adults lying atop. Sabath (1991) estimated egg conductance for both egg varieties. The small egg has a conductance value 8.3 times greater than that predicted for a modern avian egg of equivalent mass, whereas the larger avian eggs have a conductance just below the predicted value (Sabath 1991: fig. 9). But some ambiguity exists for these values. Original conductance

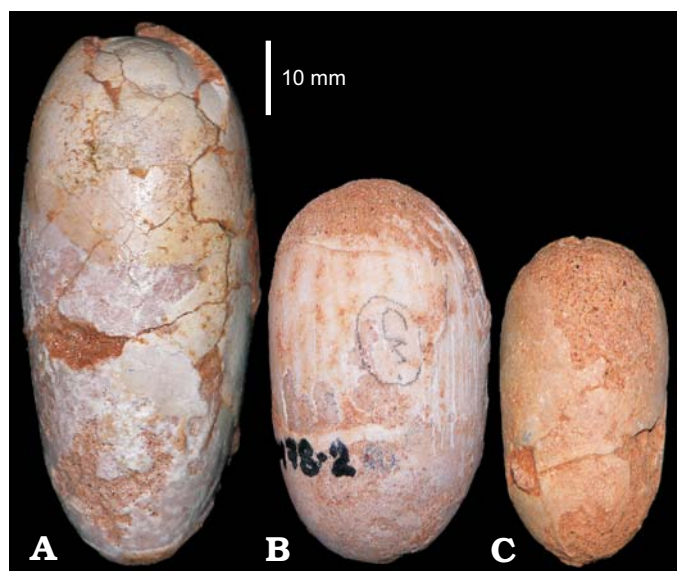


Fig. 1. Representative eggs for the three forms originally included in the oogenus *Gobioolithus* from the Late Cretaceous of Mongolia. **A.** The larger avian eggs of Sabath (1991), *Styloolithus sabathi* oogen. et oosp. nov. (ZPAL MgOv-II/25). **B.** *Gobioolithus major* Mikhailov, 1996a (PIN 4478-2). **C.** *Gobioolithus minor* Mikhailov, 1996a (ZPAL MgOv-III/10). The former classification included eggs such as ZPAL MgOv-II/25 representing the “larger avian eggs” of Sabath (1991) with Soviet collected specimens as *G. major*. Here we separate out the former based on size and shape as *S. sabathi*.

values for *Gobioolithus minor* are only 35% that of the values later determined by Deeming (2006). Unfortunately, the data for the larger avian eggs was left off the table summarizing his analysis, presumably in error (Sabath 1991: table 1). Nevertheless, even if these same discrepancies exist in the larger avian egg calculations of Sabath (1991), conductance values would still be much lower than *G. minor* and on par with those of modern birds.

Subsequent to Sabath (1991), the “*Gobipteryx* eggs” and these larger avian eggs continued to have an interrelated history. Mikhailov et al. (1994) linked these two egg varieties together with additional material collected by the Joint Soviet-Mongolian Paleontological and Geological Expeditions as “eggs of volant palaeognathous birds (*Gobipteryx*iformes)”. They considered these eggs to share a similar eggshell microstructure including a 2:1 spongy to mammillary layer ratio and angusticanalicate pores and recognized two informal groups: smaller “*Gobipteryx*” eggs (G1 group) for the Khermeen Tsav eggs of Sabath (1991) and additional Soviet-collected material from there, Khulsan, and Gilbert; and larger “*Gobipteryx*” eggs (G2 group) for the “larger avian eggs” of Sabath (1991) and somewhat smaller Soviet-collected specimens (Fig. 1B). Mikhailov et al. (1994) provided additional information on the Khermeen Tsav locality. G1 eggs occurred as isolated eggs “irregularly dispersed over the slopes in vertical or sub vertical positions” (Mikhailov et al. 1994: 108). Sabath (1991) considered the high conductance and good three-dimensional preservation of these eggs as indicative of underground burial, perhaps in a manner

similar to that of some modern megapodes like *Megapodius freycinet* (Mikhailov et al. 1994). Alternatively, Mikhailov et al. (1994) suggested the arrangement of G1 eggs may reflect flooding, subsequent floatation and displacement of the eggs, followed by the eggs settling into the sediment in an upright position as the flood waters receded.

Mikhailov (1996a) formally recognized the G1 and G2 groups as respectively, the ootaxa *Gobioolithus minor* and *Gobioolithus major* (Fig. 1). Although the formal systematic paleontology of the latter lists “Larger avian eggs: Sabath 1991” and has a size range inclusive of these big eggs, the description includes as the holotype and named material only six smaller and Soviet-collected eggs from Khulsan and Gilbert from the Barun Goyot Formation. Mikhailov (1996a, 1997b) considered the two *Gobioolithus* oospecies as identical in shape and microstructure, but differing in overall size and shell thickness. The two new oospecies comprised a new oofamily, the Gobioolithidae (Mikhailov 1996a).

To date, only a few Mesozoic eggs are clearly associated with avian skeletal material providing a taxonomic identification. Eggs with embryonic remains include *Gobioolithus minor* with *Gobipipus reshetovi* (Kurochkin et al. 2013), as well as unnamed eggs from the Late Cretaceous of Neuquén, Argentina (Schweitzer et al. 2002; Fernández et al. 2013), the Sebeş Formation of Romania (Dyke et al. 2012), and an isolated egg from the Khugenetslavkant locality, eastern Gobi Desert, Mongolia (Varricchio et al. in press). Additionally, the type specimen of *Nanantius valifanovi* occurred in association with in situ eggshell of *Subtiliolithus microtuberculatus* (Kurochkin 1996). All of these are now considered to belong to the Enantiornithes. The occurrence of possibly clutch-associated adults with the “larger avian eggs” differentiates them from all these examples. Additionally, their distinct clutch configuration differs from that of both *Gobioolithus minor*, the Soviet collected examples of *G. major*, and the Neuquén eggs (Fernández et al. 2013), suggesting potentially important reproductive differences. Consequently, we here revisit these larger avian eggs of Sabath (1991), providing additional description, photo documentation, and discussion of their taxonomic assignment and implications for reproductive behaviors. Because their inclusion in *G. major* groups them with a smaller egg form, potentially sharing more attributes with *G. minor*, we redefine *G. major* and also establish a new oogenus and oospecies for these “larger avian eggs”.

Institutional abbreviations.—MSU ES, Montana State University Earth Sciences, Bozeman, USA; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; ZPAL, Institute of Paleobiology of the Polish Academy of Sciences, Warsaw, Poland.

Other abbreviations.—C.I., consistency index; CL, continuous layer; EI, egg elongation index; EZ, external zone; ML, mammillary layer; R.I., retention index; SqZ, squamatic zone.

Systematic paleontology

Oofamily Gobioolithidae Mikhailov, 1996a

Oogenus *Gobioolithus* Mikhailov, 1996a

Type oospecies: *Gobioolithus minor* Mikhailov, 1996a; Upper Cretaceous, Khermeen Tsav locality.

Included oospecies: *Gobioolithus minor* Mikhailov, 1996a, *Gobioolithus major* Mikhailov, 1996a.

Diagnosis.—Small and slightly asymmetrical (with unequal poles) eggs with smooth surface and thin (0.1–0.4 mm) eggshell; egg elongation (EI) is 1.8–2.1. Eggshell is of ornithoid type with “normal” (~2:1) ratio between continuous (= spongy) and mammillary layers.

Stratigraphic and geographic range.—Upper Cretaceous, Barun Goyot and Djadokhta formations, Mongolia.

Gobioolithus major Mikhailov, 1996a

Fig. 1B.

Holotype: PIN 4478-1, complete egg.

Type locality: Khulsan locality, South Gobi Aimak, Mongolia.

Type horizon: Barun Goyot Formation, Upper Cretaceous.

Material.—Five complete eggs from localities Khulsan and Gilbert (PIN 3142-460, 4478-2, 4478-5, 4478-6, 4478-7).

Diagnosis.—Egg size 50–53.5 by 25–32 mm; eggshell thickness 0.2–0.4 mm.

Description.—*Gobioolithus major* is here redefined to include only the small sample of eggs collected by Soviet-Mongolian teams from Khulsan and Gilbert. These eggs show a limited size range averaging 52 mm long with a diameter of 29 mm (Fig. 2A). Average EI of the available specimens was 1.75, the lowest value among the *Gobioolithus* oospecies and the larger avian eggs of Sabath (1991), here recognized as *Styloolithus sabathi* oogen. et oosp. nov. (Fig. 2B). Although prior publications lack specific microstructural descriptions, photomicrographs, and details of the field occurrence for *G.*

major, Mikhailov (1996a, 1997b) confirms their similarity to the microstructure of *G. minor*.

Remarks.—Sediments within and surrounding the eggs consist of fine sand. Further, two small “hills” at the Khulsan locality preserved a distribution and orientation of the *G. major* eggs similar to that of the *G. minor* at Khermeen Tsav, suggesting the same breeding and nesting ecology in the two ootaxa (Konstantin Mikhailov personal communication). The PIN specimens show some lateral distortion as well as telescoping of shell parallel to the long axis, consistent with a sub vertical posture during burial.

Stratigraphic and geographic range.—Upper Cretaceous, Barun Goyot Formation, Mongolia.

Incertae sedis

Oogenus *Styloolithus* nov.

Figs. 1A, 3, 4A.

Etymology: From Greek *styl*, pillar or column, referring to the columnar arrangement of the elongate eggs within the clutch; *oo*, ova; and *lithos*, stone.

Type oospecies: *Styloolithus sabathi* nov., monotypic; see below.

Diagnosis.—As for type and only known oospecies.

Stratigraphic and geographic range.—As for the only oospecies.

Styloolithus sabathi nov.

Figs. 1A, 3, 4A.

Etymology: After Karol Sabath (1963–2007) in recognition of his initial description of these specimens and his stimulating contributions to the study of fossil eggs.

Holotype: ZPAL MgOv-II/7a–e, a clutch of at least four eggs associated with adult remains.

Type locality: Volcano locality, Bayn Dzak, South Gobi Aimak, Mongolia.

Type horizon: Djadokhta Formation, Upper Cretaceous.

Material.—ZPAL MgOv-I/19, MgOv-I/21a–c, and MgOv-

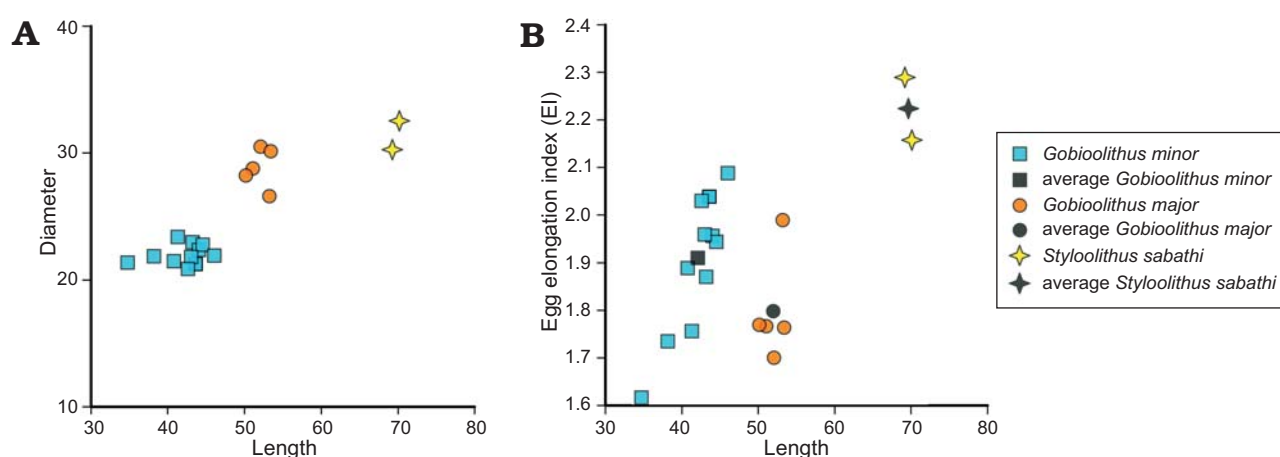


Fig. 2. Plots of diameter vs. length (A) and elongation index (EI) vs. length (B) for the three forms originally included in the oogenus *Gobioolithus*, showing good separation between the three varieties. *Gobioolithus minor* and *Styloolithus sabathi* oogen. et oosp. nov. data comes from ZPAL specimens, the data for *G. major* from PIN specimens. Much of the variation in EI appears to represent variability in the distortion of eggs, with some foreshortened along their long axis, whereas others exhibit modified diameters.

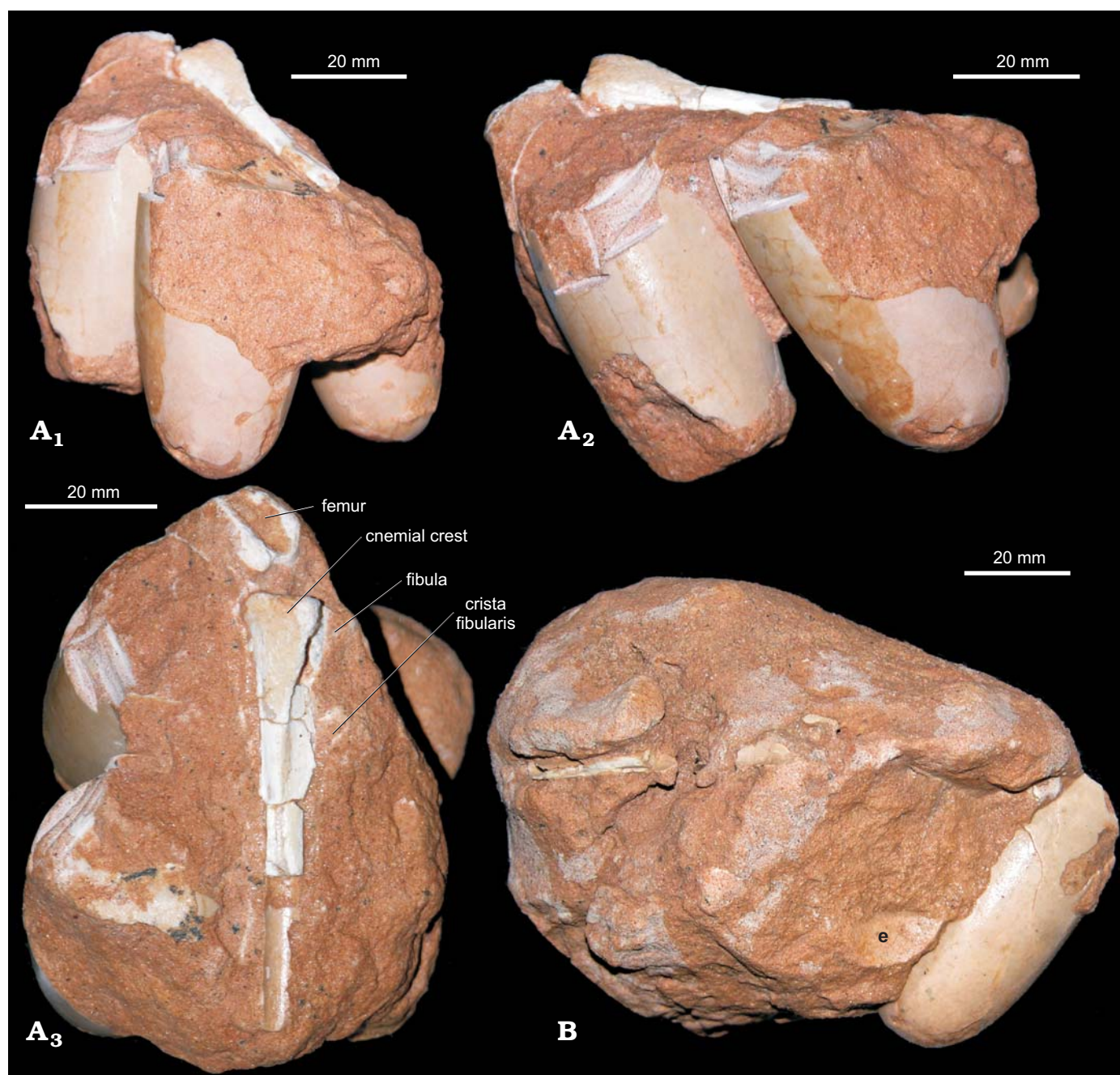


Fig. 3. Egg clutches for *Styloolithus sabathi* oogen. et oosp. nov. from the Upper Cretaceous Bayn Dzak locality. **A.** Type specimen, ZPAL MgOv-II/7a in dorso-oblique (A_1), lateral (A_2), and dorsal (A_3) views. A_1 and A_2 show three of the four eggs, whereas A_3 provides a view of the articulated distal femur and proximal tibia and fibula. The cnemial crest and crista fibularis are visible in this anteromedial view of the tibia. **B.** ZPAL MgOv-II/25, a second partial clutch with associated bone in lateral view showing one nearly intact egg and a small portion of a second (e). A poorly preserved tibia runs nearly horizontally just above and left of the egg.

I/25c–d, from Khulsan locality, South Gobi Aimak, Mongolia, Barun Goyot Formation, Upper Cretaceous; MgOv-II/6a–g and MgOv-II/25 from Bayn Dzak, South Gobi Aimak, Mongolia, Djadokhta Formation, Upper Cretaceous.

Diagnosis.—Differs from *Gobioolithus minor* and *G. major* by large size (70 × 32 mm), higher elongation index (2.0–2.3), and clutches consisting of likely more than four eggs, sub-vertically oriented and tightly spaced (Figs. 1–3). Potentially differs from *G. minor*, *G. major*, and all non-avi-

an theropod eggs by the presence of a third layer (possible external zone) thicker than its mammillary layer, and nearly as thick as its second layer (possible squamatic zone). Continuous layer (= second and third layers) to mammillary layer ratio is 3.1:1 rather than 2:1 (Fig. 4).

Description.—The largest intact piece for ZPAL MgOv-II/7 includes four partial eggs standing with their long axes nearly parallel in well-sorted fine sandstone and adjacent to one another. Immediately above them is an articulated hind limb

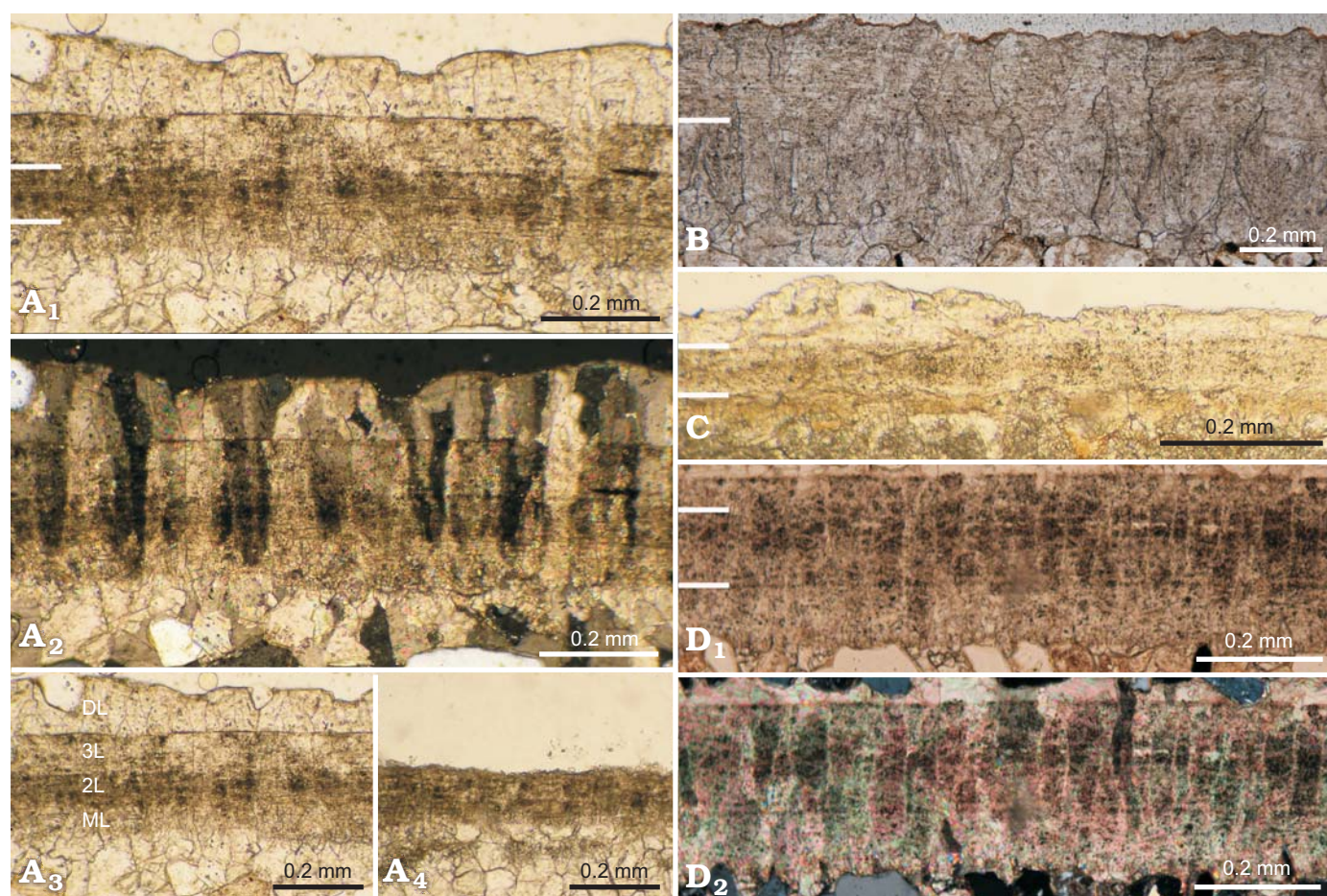


Fig. 4. Petrographic thin sections of avian and non-avian theropod eggshells from the Upper Cretaceous. **A.** *Styloolithus sabathi* oogen. et oosp. nov. (ZPAL MgOv-II-6); horizontal lines at the left side of A_1 mark, from bottom to top, the boundaries between the mammillary, second (possible squamatic zone), and third (possible external zone) layers. A_2 , same as A_1 , but in polarized light. A_3 , thin section 9-6 highlighting the same three structural layers as in A_1 , including the mammillary layer (ML), second layer (2L), and third layer (3L). DL represents the outer diagenetic layer. A_4 , thin section 9-5, showing properly proportioned ML and 2L, but a loss of the 3L. **B.** *Protoceratopsidovum sincerum* Mikhailov, 1994 (PIN 3143/121), horizontal line at left marks the boundary between the mammillary layer and palisade layer. **C.** *Gobiolithus minor* Mikhailov, 1996a (ZPAL MgOv-III/11b), horizontal lines at left mark, from bottom to top, the boundaries between the mammillary layer, squamatic zone, and an outer recrystallized zone, possibly representing either diagenetic overgrowth or an altered biological external zone. **D.** Neuquén enantiornithine eggshell MSU ES 177 (Schweitzer et al. 2002: fig. 1), horizontal lines at left in D_1 mark, from bottom to top, the boundaries between the mammillary layer, squamatic zone, and external zone. D_2 , same as D_1 , but in polarized light. Images in plane (A_1 , A_3 , A_4 , B, C, D_1) and polarized (A_2 , D_2) light.

with distal femur, and proximal tibia and fibula. Assuming the bones were flat lying puts all four eggs steeply inclined with plunges of 45–70°. All trend in nearly the same direction. The eggs are elongate and smooth. Three well-preserved eggs retain complete eggshell circumferences over their lowermost 60–70%. Weathering has reduced the fourth egg to one partial side. All four eggs appear to have broken upper ends. One egg has a larger than 1.5 cm piece of displaced eggshell lying across its broken upper end. A second retains a portion of eggshell wrapping over to form the blunt end but matrix overlies other portions of the cross-section. Matrix covers the broken upper ends of the other eggs as well.

Two eggs still have their bottoms intact, but egg dimensions are still difficult to assess on these matrix bound eggs, and better proportions come from other specimens. Preserved lengths are 55 and 59 mm. Estimated original length was likely around 70 mm. One egg provides a max-

imum available diameter of 29 mm, but is clearly partially distorted. Normal maximum diameter likely exceeded 30 mm. Associated with the matrix-bound eggs are four additional egg bottoms. The uniform and asymmetric orientation of the matrix-bound eggs suggests that if the eggs within the clutch were arranged symmetrically, then at least four eggs would be needed to complete the clutch. Hence, these isolated eggs likely belong to the clutch and the minimum number of eggs was eight. These pieces demonstrate that the eggs should have a circular cross-section, but that this is often distorted due to lithostatic compaction. One egg has matrix covering the upper broken end. This distorted specimen has a length of 52 mm to the break, and a maximum diameter of 35 mm with a 30 mm perpendicular diameter. Consequently, the original estimate of 70 by 32 mm is likely accurate (Sabath 1991).

Three bones lie in articulation across the upper portions

of the four eggs. In their current state of preservation and preparation, the femur and fibula provide only few details. The poorly preserved distal femur consists of a shaft fragment eroded to expose the large medullary cavity that expands slightly distally for the development of the condyles. Maximum diameter is 8.4 mm. The preserved portion of the tibia measures over 40 mm, and with the impression of its diaphysis, 63 mm. However, these are likely far short of the actual length of the original element. The mediolateral width at the proximal end is 9.7 mm, and at the level of the crista fibularis, 8.1 mm. The mediolateral and anteroposterior diameters of the distal most shaft are 5.7 mm and 3.5 mm. Proximally, the cnemial crest appears robust despite portions of its anteriormost projection being broken off. The cnemial crest angles anterolaterally. Distally the crest thins rapidly and disappears into the shaft by about 29 mm down the shaft. The crista fibularis is thin anteroposteriorly but projects as far as the lateral margin of the proximal end. The medial margin of the tibia is slightly concave until a point equivalent to the end of the cnemial crest. The shaft is anteroposteriorly compressed with a just slightly convex anterior aspect, and more convex posterior one. Portions of the anterior aspect of the fibula are damaged, however some morphology remains visible. Proximally, the fibula has a rounded, mediolaterally compressed articulation. The shaft arcs medially and expands only to taper rapidly and end at the level of the proximal crista fibularis.

These elements provide a few features likely relevant to the taxonomic identification: the size and breadth of the crista fibularis, the arc of the proximal tibia, and the relatively short and unfinished condition of the fibula. *Nanantius valifanovi* (Kurochkin 1996: fig. 10), now likely *Gobipteryx minuta* (Chiappe et al. 2001), exhibits all of these features. However these elements in ZPAL MgOv-II/7 are nearly twice the linear dimensions, have a more prominent cnemial crest, and appear to lack the nutrient foramen on the *Nanantius* tibia.

Three other bone fragments were collected with this specimen, but their relationship to the eggs is unclear. These include a shaft cross-section (2.7 by 4.2 mm), the end of a compressed element, and a relatively large (18 by 23 mm) flattish fragment, which seems too robust to correspond with the leg elements.

ZPAL MgOV-II/25 represents a second Bayn Dzak specimen that preserves bone in association with eggs. The specimen consists of a sandstone block with one near complete egg and a small impression of a second. Above these, as in ZPAL MgOV-II/7, lie one or perhaps two skeletal elements. However, these elements have sustained substantial recent erosion. The good egg has a similar shape and surface texture to those of the type specimen, being elongate and smooth. The incomplete egg is 57 mm from its intact narrow pole to the upper broken edge, marked by a broken and displaced fragment. The diameter is 28.6 mm. Adjacent to this egg is a small patch where eggshell once sat. It is unclear if this represents a remnant of an entire egg or simply a displaced fragment. Sabath (1991) considered there to be a third pos-

sible egg, but this was not apparent in the current condition of the specimen. Assuming the limb bone was horizontal, the intact egg would have a plunge of 45°.

The bone sits 15 mm above the egg and consists merely of a shaft fragment and an impression of bone separated by a gap of 11 mm. The trend is consistent with the two parts representing a single element as indicated by Sabath (1991: pl. 16: 2). The represented length of the element would be 52 mm, likely something far short of the element's true length. Because the cross-section changes from more triangular to transversely expanded, the bone likely represents a tibia. Shaft dimensions are 3.6 by 5.0 mm and more distally 2.3 by 5.1 mm.

Another egg, curated under this same specimen number, ZPAL MgOv-II/25, is particularly complete, providing a good view of the egg size and shape. The egg is clearly asymmetric with both narrow and blunt ends and with the maximum diameter closer to the blunt end. This egg measures 69.1 by 30.3 mm. With the previous eggs, this provides an estimate of the elongation index for *S. sabathi* of on average 2.2.

ZPAL MgOv-II/6 consists of a collection of eggs from the Ruins at Bayn Dzak. Likely only some of these eggs belong to *S. sabathi*. Among the ZPAL MgOv-II/6 eggs is a complete but distorted egg with a length of 71.1 mm and an average diameter of 25.5 mm. However, externally this and the other eggs have irregular boundaries showing crushing, lateral shifting and bulging related to telescoped portions of the eggs. Broken portions reveal that internally these eggs are largely filled with crystals and open spaces in contrast to the earlier described specimens.

Other specimens consist of only partial eggs. For example, ZPAL MgOv-I/19 consists of a box of 26 egg halves or smaller parts collected in 1970 from Khulsan. Thirteen of these consist of the narrow pole and varying amounts of the egg. A few represent cross-sections, and others simply assorted egg fragments. One ornamented piece clearly does not belong. Three egg fragments contain abundant small shell fragments nested within each other in the bottom of the egg, in a rosette-like pattern. A fourth egg bottom has a nearly intact bottom, but its upper portion consists of small highly fractured shell. The accumulation of shells within the egg bottoms is consistent with an upright egg orientation. Potentially, as eggs were exposed subaerially in the Cretaceous, erosion and breakage of the eggshell could lead to the build up of fragments in the egg bottom.

As noted by Sabath (1991), the eggshell is poorly preserved. Typically, eggshell catalogued under ZPAL MgOv-II/6 measures 0.25 mm thick and displays three possible structural layers. We were unable to examine the ultrastructure of these layers with scanning electron microscopy (SEM); thus, interpretations of *Styloolithus sabathi* eggshell must remain tentative at this time. Because of this uncertainty, our use of the terms "second layer" and "third layer" in the following eggshell description should not be treated as necessarily equivalent to the avian and non-avian theropod eggshell terms "squamous zone" and "external zone",

respectively. However, we provide comparisons of these internal divisions within *S. sabathi* eggshell to the squamatic zone and external zone of better-known eggshells and suggest their possible homology. Mikhailov (1997a) defines the continuous layer of avian and non-avian theropod eggshell to consist of both the squamatic zone and external zone. Our use of "continuous layer" to refer to *Styloolithus* eggshell in the Eggshell comparisons section below is for ease of comparison with previous measurements of this layer only, and refers to the combined thickness of the second and third layers, our uncertainty about the ultrastructure of which is described above and in the following paragraphs. We interpret a fourth layer as diagenetic overgrowth (Fig. 4A).

The innermost layer is rather thin, averaging 0.06 mm. Though nucleation sites are not clearly preserved, the few remaining altered mammillary cones are spaced, on average, 0.08 mm apart, as measured center-to-center from radial thin sections. Faint radiating crystal structures arising from the knob-shaped mammillae may be present as in *Gobioolithus minor* (Mikhailov 1991: pl. 35: 2a, b, 3), though the diagenetic alteration and lack of SEM images for these specimens do not allow for more definite confirmation of this observation. Future examination of the eggshell with cathodoluminescence and SEM could clarify the extent of alteration and other features of *S. sabathi* eggshell described below.

The transition between the first and second layers is fairly gradual and is marked by the first appearance of dark-colored horizontal banding that increases in density throughout the 0.10 mm thick second layer. The prismatic shell units are clearly visible in the second layer under polarized light, but largely hidden in plain light where the strong horizontal banding predominates. The second layer exhibits dark-colored, dense horizontal lines in thin section that may represent the lamellar arrangement (Dennis et al. 1996) of the organic matrix of squamatic ultrastructure. The second layer also appears similar to that of a Cretaceous avian egg from the Neuquén locality of Argentina (Fig. 4C, D) where SEM examination confirms the presence of the squamatic ultrastructure in this layer (Schweitzer et al. 2002: fig. 1). Squamatic ultrastructure is commonly found to varying degrees of development in the squamatic zone of the continuous layer of derived maniraptoran and avian eggshells (Zelenitsky et al. 2002). Despite the above evidence suggesting the presence of squamatic ultrastructure in the second layer of *S. sabathi* eggshell, we note that SEM is necessary to confirm the presence of the individual scale-shaped grains of calcite that characterize squamatic ultrastructure (Mikhailov 1991). As the term "squamatic zone" properly refers to the second layer of eggshell for which squamatic ultrastructure has been observed (Mikhailov 1991; 1997a), we use the term "second layer" in the absence of SEM observation of squamatic ultrastructure in *Styloolithus sabathi* eggshell.

The third structural layer has an average thickness of 0.09 mm and is separated from the underlying layers by an abrupt transition, visible primarily as a color difference between the darker second layer and the more translucent third layer.

The position of this transition varies slightly among adjacent shell units. The margins of a potential pore are visible through the entire thickness of layers one through three (Fig. 4A). We interpret the third layer as an external zone, sensu Mikhailov (1991), despite its great relative thickness, based on its similar appearance to the external zone of some avian eggshells as viewed in thin sections (Jackson et al. 2010: fig. 3A, B; 2013: fig. 3D, E). The eggshells figured in Jackson et al. (2010, 2013) share a darker continuous layer that abruptly transitions to a lighter-colored overlying external zone. Mikhailov (1991) notes that such translucence and a lesser amount of organic content compared to the continuous layer is characteristic of the external zone. The observed lack of horizontal banding and continuation of the columnar extinction pattern through the third layer of *Styloolithus sabathi* eggshell in thin section concurs with descriptions of extant avian external zones (Dennis et al. 1996; Fraser et al. 1999), thus demonstrating their probable homology, though SEM is needed to test this. Previous authors (Zelenitsky et al. 2002; Varricchio and Jackson 2004a; Jackson et al. 2010) often refer to the external zone in theropod and avian eggshell as an "external layer", but Mikhailov (1997b) suggests that the external zone can be treated as a separate structural layer only when better demarcated from the squamatic zone, as in paleognaths and members of the Galloanserae. We note that all of these authors, regardless of terminology, refer to the same general structure, one that is likely homologous among derived maniraptorans and birds, but absent in oviraptorosaurs (Elongatoolithidae), for example (Zelenitsky et al. 2002; Varricchio and Jackson 2004a).

The absence of a third layer in some thin sections catalogued under ZPAL Mg-Ov-II/6 is likely a taphonomic phenomenon (Fig. 4A). In these specimens the thickness of the remaining eggshell corresponds to the combined thickness of the mammillary and second layers in complete specimens. Further, they exhibit an outer surface with an irregular texture and some loose calcite grains that appear to have separated from the outer surface of the exposed second layer. Given that the external zone of fossil eggshells is often found partially separated from the underlying squamatic zone, it has been inferred that a plane of weakness likely exists between the squamatic and external zones in theropod and avian eggshell (Jackson and Varricchio 2010; Jackson et al. 2013). We have observed a similar separation in modern goose eggshell (uncatalogued MSU ES specimen). These examples highlight the potential for errors in interpreting an external zone as absent in taphonomically altered fossil eggshell (Zelenitsky et al. 2002; Jackson and Varricchio 2010).

An outermost fourth layer is separated by a clearly demarcated line from the remainder of the eggshell and displays a continuation of the columnar extinction pattern of the shell units throughout its thickness. Many of the crystals are deflected at a slight angle at the boundary between the third and fourth layers, and some display a blockier morphology with irregular boundaries.

Evidence in favor of a diagenetic origin for the fourth

layer includes the abrupt transition with the third layer at its base, its inconsistent thickness, its relative lack of dark-colored, presumably organic matter compared to all of the underlying layers, and the occasionally irregular shape of some of its crystals compared to the underlying columns (Fig. 4A). Though the fourth layer exhibits crystallographic continuity with the third layer, diagenetic calcite can grow in structural continuity with biogenic calcite (Grellet-Tinner et al. 2010).

Eggshell comparisons.—Microstructure, egg size, and elongation index distinguish *Styloolithus sabathi* from all avian and non-avian theropod eggs from the Cretaceous (Table 1). *Styloolithus sabathi* differs from the Mongolian elongatoolithid oögenera *Macroolithus* and *Elongatoolithus* by its smaller egg size, lack of surface ornamentation, possible presence of an external zone, and clutches with subvertically oriented eggs. Though they share a similar elongation index and asymmetrical shape, *S. sabathi* differs from all members of the Mongolian prismatoolithid oögenus *Protoceratopsidovum* Mikhailov, 1994, by its smaller egg size, thinner eggshell, and possible presence of an external zone. It further differs from *Protoceratopsidovum fluxuosum* by its lack of surface ornamentation. *S. sabathi* has a greater continuous layer (CL): mammillary layer (ML) thickness ratio than *Protoceratopsidovum sincerum* (PIN 614-58/1, PIN 3143/121; Fig. 4B), and *Protoceratopsidovum minimum* (PIN uncatalogued).

Styloolithus sabathi differs from eggs referred to the Mongolian troodontid *Byronosaurus jaffei*, and the Mongolian oöspecies *Oblongoolithus glaber*, *Laevioolithus sochavai*, and *Subtiliolithus microtuberculatus* through possessing a greater CL: ML ratio, lesser eggshell thickness, and possible presence of an external zone (Table 1). *Styloolithus sabathi* also lacks the small tubercles sometimes present on the surface of *S. microtuberculatus* eggshell (Mikhailov 1991). *S. sabathi* shares the presence of a possible external zone with *Parvoolithus tortuosus* and unnamed eggs containing enantiornithine embryos from the Late Cretaceous of Mongolia (Zelenitsky 2004; Balanoff et al. 2008; Varricchio et al. in press) and Argentina (Schweitzer et al. 2002; Fernández et al. 2013), as well as a small unnamed egg from the Campanian Bayn Dzak locality, Mongolia (Grellet-Tinner and Norell 2002). *S. sabathi* differs from all of these eggs by having a larger CL: ML ratio, greater eggshell thickness (except for the Argentine eggshell, which has a nearly equal thickness), and larger egg size.

Differences between *Styloolithus sabathi* and the two *Gobioolithus* oöspecies include larger egg size, a greater elongation index, greater CL: ML thickness ratio, and the possible presence of an external zone. *S. sabathi* additionally possesses thicker eggshell than *G. minor* (Table 1, Fig. 4C).

Styloolithus sabathi has smaller eggs, a greater CL: ML ratio, and a lesser eggshell thickness than the North American troodontid *Troodon formosus* (oöspecies *Prismatoolithus levis*). The external zone of *Troodon* also does not always appear more translucent compared to the prismatic layer in thin section (Jackson et al. 2010), as is potentially the case for *S.*

sabathi, some Eocene avian eggs (Kohring and Hirsch 1996; Jackson et al. 2013) and extant avian (Kohring and Hirsch 1996; Jackson et al. 2010) eggshells. In one *T. formosus* thin section (Jackson et al. 2010: fig. 2F), a transition from a darker to a lighter portion of the prismatic layer seen about two-thirds of the way towards the exterior eggshell surface does not correspond to the boundary between the prismatic layer and external zone as confirmed by SEM imaging (Jackson et al. 2010: fig. 2D). This may suggest that the possible external zone in *S. sabathi* is not as thick as inferred from color transitions in thin section alone. Nevertheless, correspondence between color transitions in thin section and the position of the external zone in SEM is found for other *Troodon* eggshell (though defined by a transition from a lighter prismatic layer to a darker external zone, opposite of the avian examples below) (Varricchio et al. 2002) and the eggshell of fossil and extant birds (Kohring and Hirsch 1996; Jackson et al. 2010, 2013). However, the effects of differing thin section thickness and potential diagenetic alteration of eggshell should temper assertions about the thickness of eggshell structural zones or layers inferred solely on the basis of color transitions.

The presence of an external zone in Cretaceous Mongolian avian eggs remains controversial, and questions whether or not the possible presence of an external zone in *Styloolithus sabathi* is unique among these eggs. Despite his earlier (1991) assignment of *Gobioolithus* eggshell to the “neognathous morphotype”, Mikhailov (1997b, 2014) considered an external zone to be absent in *Gobioolithus minor* eggshell, and Mikhailov (2014) proposed all third layers reported from similar eggs (e.g., those in Grellet-Tinner and Norell 2002; Balanoff et al. 2008) to be diagenetic in origin. If Mikhailov’s (1997b, 2014) assertions are correct, the lack of an external zone in *G. minor* (and presumably *G. major*) represents a major difference with *Styloolithus sabathi*. However, reexamination of an SEM image (Mikhailov 1991: pl. 35: 1) of *G. minor* microstructure suggests an alternative hypothesis. If the diagenetically altered upper third of the eggshell is considered to be a recrystallized external zone, then the ratios between the three layers would be similar to those observed for *S. sabathi*. Additionally, a possible third layer can be observed in some *G. minor* thin sections (Fig. 4C). Similar to the possible third layer in the SEM image, this layer varies greatly in thickness and exhibits blocky crystal morphology. While both of these traits can be indicative of recrystallization, the possibility remains that what is observed is an altered external zone. Mikhailov (2014) noted that well-preserved examples of *G. minor* lack the “explicit presence” of an external zone, though given the apparent ease with which this zone can separate from the remainder of the eggshell, this may not constitute definitive evidence against the presence of an external zone in *G. minor*. We consider the presence or absence of an external zone in *G. minor* eggshell an open question, awaiting the application of analytical techniques such as those utilized by Jackson et al. (2010) to assess the presence of an external zone in *Troodon formosus* eggshell.

Table 1. Comparison of Upper Cretaceous elongate eggs from Mongolia and other theropod and avian eggs with *Styloolithus sabathi* oogen. et oosp. nov. All eggs are from Mongolian localities except for the Argentinian egg described by Schweitzer et al. (2002) and *Troodon* eggs from Montana, USA. EI, elongation index, SqU, squamatic ultrastructure.

Ootaxon	Age and formation	Egg size (mm)	Egg shape EI	Surface ornamentation present?	Predominant [total] shell thickness range	Second layer + external zone: first layer thickness ratio	SqU present in second layer?	External zone present?	Reference
<i>Macroolithus</i>	various, see reference	>170 (long)	slightly asymmetrical? 2.0–2.4	yes	[0.8–2.5]	2:1–3:1	yes	no	Mikhailov 1994
<i>Elongatoolithus</i>	various, see reference	90–170 (long)	slightly asymmetrical? 2.0–2.4	yes	[0.7–1.6]	2:1–3:1	yes	no	Mikhailov 1994
<i>Troodon formosus</i> (<i>Prismatoolithus levis</i>)	Campanian Two Medicine and Judith River formations	120–160 × 30–70	asymmetrical 2.0	no	0.78–1.2	2.1:1	yes	yes	Varricchio et al. 2002; Zelenitsky et al. 2002; Jackson et al. 2010
<i>Byronosaurus jaffei</i> (troodontid) eggs	Campanian Djadokhta Formation	?, only partial eggs are known	asymmetrical	no	0.43–0.47	1.7:1–1.9:1	?	no	Grellet-Tinner 2005
<i>Protoceratopsidovum fluuosum</i>	Campanian Djadokhta and Barun Goyot formations	130–150 × 50–57	? 2.3–3.0	yes	0.6–0.7 [0.3–1.4]	?	no?	no	Mikhailov 1994, 2014
<i>Protoceratopsidovum sincerum</i>	Campanian Djadokhta and Barun Goyot formations	110–120 × 40–50	asymmetrical 2.3–2.5	no	0.6–0.7, [0.3–1.2]	1:1	no?	no	Mikhailov 1994 2014; Zelenitsky and Therrien 2008; DB personal observation
<i>Protoceratopsidovum minimum</i>	Campanian Djadokhta and Barun Goyot formations	100–?110 × 40–?50	asymmetrical 2–2.75	no	0.3–0.7	2.6:1	no?	no	Mikhailov 1994, 2014; DB personal observation
<i>Oblongoolithus glaber</i>	Campanian? Barun Goyot Formation	Short diameter <40	known only from partial eggs.	no	0.3–0.7	0.5:1–1.5:1	yes	no	Mikhailov 1996b, 1997
<i>Laevisoolithus sochavai</i>	?Campanian–Maastichtian Nemegt Formation	<70 (long)	?	no	<1.0	1.3:1	yes	no	Mikhailov 1991
<i>Subtiliolithus microtuberculatus</i>	?Campanian–Maastichtian? Nemegt Formation	?	known only from eggshell fragments	yes	0.3–0.4	1:2–1:3	yes	no	Mikhailov 1991
<i>Parvoolithus tortuosus</i>	Campanian? Barun Goyot Formation	40 × 25	asymmetrical 1.6	no	up to 0.1	2:1	yes	yes	Mikhailov 1996b; Zelenitsky 2004
<i>Gobioolithus major</i>	Campanian Barun Goyot Formation	50–53.5 × 25–32	asymmetrical 1.8–2.0	no	0.2–0.4	2:1	yes	?	Mikhailov 1996a; this paper
<i>Gobioolithus minor</i>	Campanian Barun Goyot Formation	30–46 × 20–24	asymmetrical 1.8–2.0	no	0.1–0.2	2:1	yes	?	Mikhailov 1996a
Unnamed egg	Campanian Bayn Dzak locality	25.8 × 15.9	? 1.6	no	0.17	1:1.25	yes?	yes?	Grellet-Tinner and Norell 2002; Mikhailov 2014
Egg containing enantiornithine embryo	Late Cretaceous Khugenetslavkant locality	47.5 × 22.3	symmetrical? 2.1	yes?	0.18	2:1	yes	yes?	Balanoff et al. 2008; Mikhailov 2014; Varricchio et al. (in press)
Egg containing enantiornithine embryo	Campanian Bajo de la Carpa Formation, Argentina	45 × 27	asymmetrical 1.7	no	0.26	1.9:1	yes	yes	Schweitzer et al. 2002; Fernández et al. 2013
<i>Styloolithus sabathi</i>	Campanian Djadokhta and Barun Goyot formations	70 × 32	asymmetrical 2.0–2.3	no	0.25	3.1:1	yes?	yes?	this paper

Interestingly, Zelenitsky (2004) described an external zone for *Parvooolithus tortuosus* Mikhailov 1996b, a possible avian egg (Zelenitsky and Therrien 2008) from Mongolia that is nearly identical in size to both *Gobiooolithus minor* and an egg with a possible external zone described by Balanoff et al. (2008). Though Mikhailov (1996b) considered *Parvooolithus* as incertae sedis on the basis of diagenetically altered material, Zelenitsky (2004) examined better preserved eggshell of the oogenus and identified a typical non-avian or avian theropod division of structural layers and zones (mammillary layer, squamatic and external zones). The avian identity of *P. tortuosus* is posited based on the results of a cladistic analysis of oological characters (Zelenitsky and Therrien 2008). An external zone is also known for a probable enantiornithine egg from Neuquén, Argentina (Schweitzer et al. 2002; Fig. 4D). Thus, Mongolian avian eggshells other than *Stylooolithus sabathi* may also possess an external zone, necessitating use of additional diagnostic characters to identify *S. sabathi* in the absence of whole eggs.

Though *Stylooolithus sabathi* shares vertically inclined, asymmetrical eggs and some microstructural features with some prismatoolithid eggs (including columnar prisms and, with *Prismatoolithus levis*, a possible external zone), its overall egg size and shell thickness are less than that of any known prismatoolithids. Furthermore, its prismatic columns are more consistently obscured under plane-polarized light than those of *Prismatoolithus levis* and the *Protoceratopsidovum* oospecies. Additionally, the presence of a possible external zone thicker than the mammillary layer and nearly as thick as the second layer is not observed in prismatoolithids and other non-avian theropod eggs. Similarly thick external zones are known, however, for some members of the extant avian orders Procellariiformes (Procellariidae, Pelecanoididae, Hydrobatidae), Ciconiiformes (Ardeidae, Cochleariidae, Ciconiidae), Falconiformes (Falconidae), Gruiformes (Eurypygae), Charadriiformes (Charadrii), and Cuculiformes (Cuculinae) (Mikhailov 1997a). When *Stylooolithus sabathi* is plotted on the EZ/SqZ vs. eggshell thickness graphs of Mikhailov (1997a), it plots above most of the regression lines for the various extant avian groups, showing that its EZ/SqZ ratio is at the upper range for that of living birds. The CL:ML ratio of *S. sabathi* plots within the range of extant avian taxa on the same graphs.

Stratigraphic and geographic range.—Khulsan locality, South Gobi Aimak, Mongolia, Barun Goyot Formation, Upper Cretaceous; Volcano and Ruins localities, Bayn Dzak, Mongolia, Djadokhta Formation, Upper Cretaceous.

Phylogenetic analyses

Stylooolithus sabathi was incorporated into three recent cladistic analyses of oological characters (Jin et al. 2010; Tanaka et al. 2011; López-Martínez and Vicens 2012) in order to assess its phylogenetic affinities.

For the 19 characters in the Jin et al. (2010) data matrix, *Stylooolithus sabathi* was coded as follows: 1100?1111?111??0122. No other parameters of the original analysis were modified. The heuristic search produced 261 equally parsimonious trees of length 43, a C.I. of 0.71 (excluding the uninformative Character 10), and an R.I. of 0.84. *S. sabathi* was recovered on the majority-rule consensus tree as part of a polytomy with *Gallus gallus*, eggs of *Lourinhanosaurus*, and a clade of avian and non-avian maniraptorans (Fig. 5A). The remainder of the topology did not vary from that of the original analysis (Jin et al. 2010: fig. 4). Coding characters 8, 9, 11, 12, and 13 as “?” to reflect uncertainty about the structure of the second and third layers of *S. sabathi* also placed it as an indeterminate theropod egg on the 50% majority-rule consensus tree.

Stylooolithus sabathi was coded for the 16 characters in the Tanaka et al. (2011) data matrix as follows: 322?1?021011?????. Differing from the original analysis, we used a heuristic search in PAUP* 4.0 (Swofford 2003), instead of version 3.1.1. We also used the default ACCTRAN optimization, as Tanaka et al. (2011) did not specify the type of optimization used. The analysis produced 299 equally parsimonious trees of length 31, a C.I. of 0.87, and an R.I. of 0.97. We were unable to reproduce the exact topology of the original strict consensus tree (Tanaka et al. 2011: fig. 5), but all consensus trees recovered share a broadly similar topology with the original. In the strict consensus tree *S. sabathi* falls out in a polytomy with other theropod ootaxa, but is recovered as the sister ootaxon to *Gobiooolithus minor* in the 50% majority-rule consensus tree (Fig. 5B). Coding characters 5, 8, and 9 as “?” to reflect uncertainty about the clutch arrangement and structure of the second and third layers of *S. sabathi* placed it in an unresolved position relative to both prismatoolithids and avian eggs on the 50% majority-rule consensus tree.

For the 12 characters in the data matrix of López-Martínez and Vicens (2012), *Stylooolithus sabathi* was assigned the following character states: 111131?2???2. The states for Character 12 for *Citipati* and *Deinonychus* were both changed from “1” to “2,” to better reflect the presence of well-developed squamatic structure in both of these egg types (Norell et al. 1994; Grellet-Tinner and Makovicky 2006; Mikhailov 2014). Our branch-and-bound search produced 27 trees of length 19, with a C.I. of 0.94 (excluding uninformative Characters 7 and 11), and an R.I. of 0.96. The topology of the strict consensus tree (Fig. 5C) was unaltered, excepting the placement of *S. sabathi* in a polytomy with the Bajo de la Carpa probable enantiornithine egg (Schweitzer et al. 2002) and the clade containing *Parvooolithus* and *Numida*, the guineafowl. Coding characters 6 and 12 as “?” to reflect uncertainty about the structure of the second and third layers of *S. sabathi* placed *S. sabathi* and the Bajo de la Carpa avian egg in a polytomy with *Troodon*, *Protoceratopsidovum*, *Sankofa*, and the *Parvooolithus*–*Numida* clade on the strict consensus tree.

Taken together, the results of these analyses suggest an avian identity for *Stylooolithus sabathi*, supporting the results of our qualitative comparisons. An avian identity for *S. sabathi* is supported by possession of a suite of traits shared

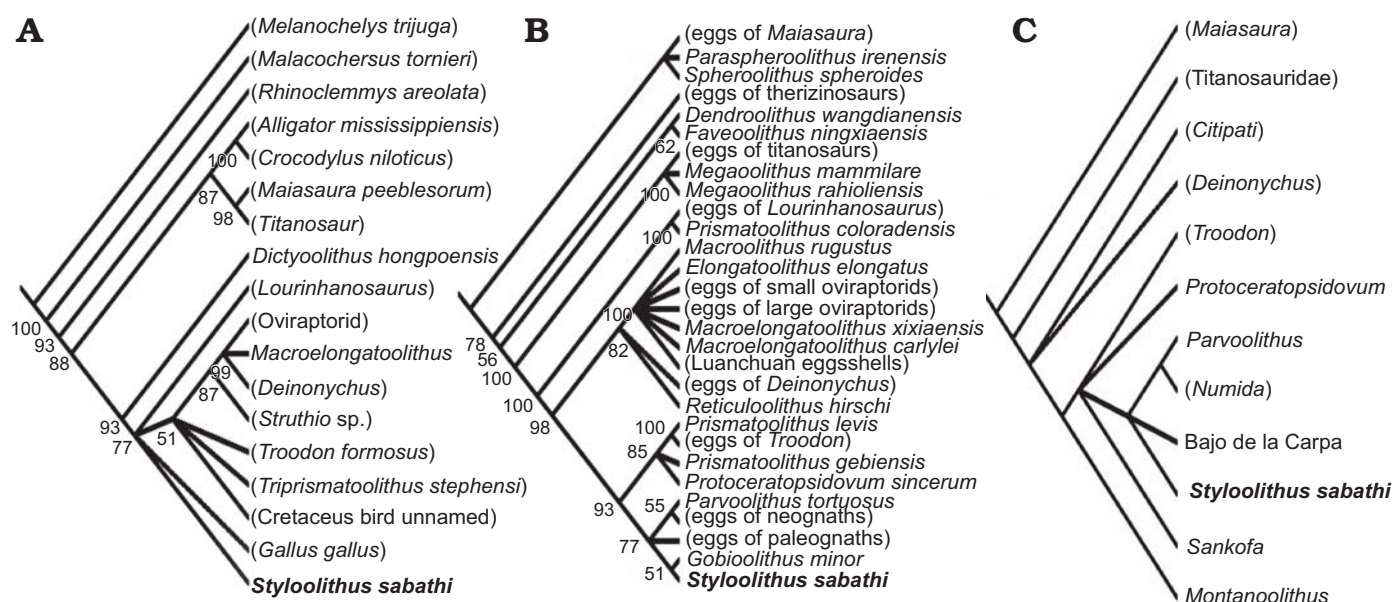


Fig. 5. Phylogenetic placement of *Styloolithus sabathi* oogen. et oosp. nov. resulting from cladistic analyses. Data matrix from Jin et al. (2010) (A), Tanaka et al. (2011) (B), López-Martínez and Vicens (2012) (C). Note to distinguish egg parataxonomic names from taxonomic names, the latter are placed within parentheses. A and B represent majority rule consensus trees with values below each node representing the percentages of all most parsimonious trees in which each clade was recovered. C is the strict consensus tree. Placement favors an avian assignment for *Styloolithus sabathi* oogen. et oosp. nov.

with some or all of the avian eggs included in each of the three analyses. None of these features are unique to Mesozoic avian eggs, but no non-avian theropod possesses the complete suite. The traits include (i) well-defined squamatic structure (Jin et al. 2010; Tanaka et al. 2011; López-Martínez and Vicens 2012) with visible prism boundaries (Jin et al. 2010); (ii) presence of an external zone (Tanaka et al. 2011); (iii) indiscrete shell units (Tanaka et al. 2011); (iv) sub vertical orientation of egg long axes (Tanaka et al. 2011); (v) asymmetrical, elongate eggs (Tanaka et al. 2011); and (vi) open, single-layered clutch (Jin et al. 2010). Utilizing the uncertain codings described above, this list of shared characters is reduced to features iii through vi, all of which may also be found among non-avian theropod eggs. However, even with the highest degree of uncertainty in character coding, *S. sabathi* does not group with non-avian theropod eggs to the exclusion of avian eggs in any of the three analyses; rather, *Styloolithus* either occupies a polytomy that includes both avian eggs and non-avian theropod eggs (Jin et al. [2010]; López-Martínez and Vicens [2012] analyses) or is unresolved relative to both of these groups (Tanaka et al. [2011] analysis).

If *Styloolithus* proves to possess well-defined squamatic ultrastructure, it would then display a combination of characters from the three analyses not found in any non-avian theropod eggs. Additionally, the great relative thickness of the external zone to the squamatic zone, a feature not assessed cladistically, is also absent from non-avian theropods. Imai et al. (2014) also list three features that, in combination, are not found in non-avian theropod eggs, but are present in some avian eggs. These are (i) three structural layers, (ii) thin eggshell (much less than 1.0 mm), and (iii) an unornamented eggshell surface. *S. sabathi* exhibits (ii) and (iii), and likely

possesses (i), though this statement and our cladistic results are dependent upon interpretation of the third layer of *S. sabathi* eggshell as a true external zone. If this proves not to be the case upon future examination with SEM, the phylogenetic placement of *S. sabathi* in these analyses may be altered.

Discussion

Including the *Styloolithus sabathi* specimens within *Gobioolithus major* as formerly suggested gave the false impression that there was a gradient of size and shape among these specimens. Our observations (Figs. 1, 2) found discrete end-members. *Styloolithus sabathi* differs from the *Gobioolithus* oospecies in being larger, more elongate (i.e., a greater EI), and having a greater CL: ML ratio. The clutch arrangement of tightly spaced, steeply inclined eggs represents a distinct pattern, as *G. minor* eggs are reported only to occur separately (Mikhailov et al. 1994). Although Mikhailov et al. (1994) suggested that the distribution of *G. minor* eggs possibly reflected taphonomic processes, the large difference in conductance values (Sabath 1991) between *S. sabathi* and *G. minor* further supports a different incubation mode for these ootaxa. We consider *S. sabathi* as sufficiently distinct from *Gobioolithus* to fall outside the oofamily Gobioolithidae and currently consider it incertae sedis.

Sabath (1991) considered the associated bones of both MgOv-II/7 and MgOv-II/25 as of the right size to fit “into the expected size range of parents (probably a bird)”. As to the avian identification, the skeletal elements in MgOv-II/7 provide only a few characters, with the truncated fibula being the only exclusively avian feature (O'Connor et al. 2011).

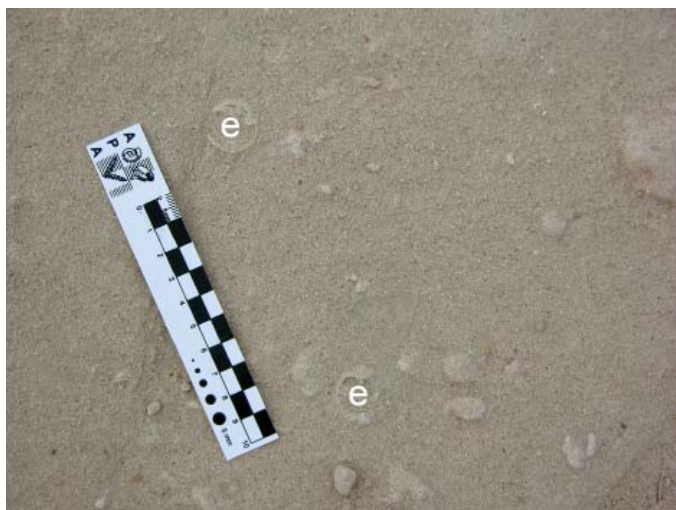


Fig. 6. Plan view of bedding plane from the enantiornithine nesting locality of Fernández et al. (2013) located on the campus of the Universidad Nacional del Comahue, North of Neuquén city, Argentina within the Bajo de la Carpa Formation (Río Colorado Subgroup, Neuquén Group, Middle-Upper Santonian). Erosion is just exposing the blunt, upper end of two eggs (e). The vertical orientation and scattered distribution of eggs characterizes this site (Fernández et al. 2013).

The size and breadth of the crista fibularis and the concave medial aspect of the proximal tibia also occur in the enantiornithine *Gobipteryx minuta* (*Nanantius valifanovi*) (Kurochkin 1996). If avian, then the single cnemial crest would exclude the individual from Ornithuromorpha. Thus, the best identification would be as a non-ornithuromorph bird, and possibly an enantiornithine with a somewhat close relationship to *Gobipteryx minuta*. Although clearly all past workers considered them to have all the necessary attributes of avian eggs (Sabath 1991; Mikhailov et al. 1994; Mikhailov 1996a, 1997b), the eggshell provides no single definitive feature that would necessarily distinguish these eggs as clearly avian versus non-avian theropod. If this avian identification proves wrong, then the most likely alternative identification is a troodontid (see below). Nevertheless, phylogenetic analysis tentatively favors an avian identification (Fig. 5).

Sabath's (1991) qualitative assessment of the adult to egg proportions can be quantitatively evaluated using various allometric equations not formerly available. If avian, then the allometric equation of Campbell and Marcus (1992) for least shaft circumference of the tibiotarsus provides a means of estimating the mass of the presumed adult. Campbell and Marcus (1992) found that in the vast majority of modern birds, the least shaft circumference occurs in the distal one-third of the shaft length. Consequently, the measurement for only ZPAL MgOv-II/25 provides a reasonable estimate. However, due to the incomplete nature of the elements in both ZPAL MgOv-II/7 and ZPAL MgOv-II/25, the actual minimal value may not be preserved. The shaft circumference for ZPAL MgOv-II/25 predicts an adult mass of 1700 g. The equation of Blueweiss et al. (1978: table 1) and this mass predict an egg of 79.9 g. The estimated mass of *S. sabathi* eggs assuming an avian density of 1.06 g/cm³ is 39.5g or 49% of the

predicted value and concurs with the qualitative assessment of Sabath (1991).

Varricchio et al. (1997) note that one important difference between reproduction in modern birds and non-avian theropods like oviraptorids and troodontids was an increase in relative egg mass, i.e. the egg to adult body mass ratio. Whereas these non-avian theropods clearly show an increase in relative egg mass compared to other non-avian dinosaurs, they have eggs only approximately 27–39% the predicted value for a modern avian (Table 2; Varricchio and Jackson 2004b). The numbers for *S. sabathi* and two definitive enantiornithines show a significant increase over these values, but the total egg output between non-avian maniraptorans producing two eggs at a time via monautochronic ovulation and these basal avians differs only slightly. This suggests that basal avians in losing the function of the right ovary and oviduct (Zheng et al. 2013) had increased their relative egg size without significantly increasing their egg output per laying interval. Nevertheless, a large gap still remains in relative egg size between Enantiornithes and modern Neornithes.

Both the Neuquén locality of Argentina and the Khermeen Tsav locality of Mongolia preserve an abundance of enantiornithine eggs scattered but in upright positions, potentially representing the incubation mode of these taxa (Mikhailov et al. 1994; Fernández et al. 2013; Kurochkin et al. 2013; Fig. 6). *S. sabathi* is thus important in exhibiting a different clutch configuration, with multiple, tightly arranged eggs, a pattern quite similar to that of *Prismatoolithus* eggs and troodontids (Sabath 1991; Mikhailov 1997b; Varricchio et al. 1997, 2013). Additionally, these two groups share low conductance values and clutch-associated adults (Varricchio et al. 1997, 2013; Erickson et al. 2007; Grellet-Tinner 2006). Potentially these features could be used to assign *S. sabathi* to the troodontids, but we feel that currently this is supported neither by the skeletal features nor the eggshell microstructure. One might question the gaps between bone and eggshell as well as the tops of these eggs as discounting the adult as brooding. However, these features likely result from post-mortem crushing. Wilson et al. (2014) demonstrate that it is the upper portions of eggs that get most disturbed during burial and compaction. Burial eventually leads to cracks forming in the eggs, sediment rains in and fills the bottom portion of the egg. This sediment fill serves to maintain the original egg shape. Depending on how completely the egg is infilled, the upper portion is variably preserved, but commonly exhibits more fracturing, smaller eggshell pieces, and greater distortion from the original shape. The similarity in nesting in comparison to troodontids suggests that this incubation mode carried over or was independently evolved in parallel among basal birds. The sediment planted arrangement of eggs in *S. sabathi*, *G. minor*, and the Neuquén enantiornithine likely precluded the possibility of egg rotation as in modern birds. In crocodilians and other reptiles, rotation of eggs during early development terminates the embryos (Deeming 1991). Thus the eggs of non-avian maniraptoran theropods as well as basal birds including enantiornithines

Table 2. Relative egg size in avian and non-avian maniraptoran theropods. *Machairasaurus*, *Nemegtomaia*, *Neuquenornis*, and the Romanian bird values based on descriptions in Dong and Currie (1996), Fanti et al. (2012), Schweitzer et al. (2002), Chiappe and Calvo (1994), and Dyke et al. (2012). *Citipati*, *Byronosaurus*, and *Troodon* estimates based on examination of specimens IGM 100/1004, IGM 100/1003, and MOR 748 and 553. Adult masses calculated from the femur equation of Anderson et al. (1985) for non-avian dinosaurs and scaling equations for various elements in Campbell and Marcus (1992) and Field et al. (2013) for the avian taxa. Egg volumes were calculated from greatest length and diameter using the equation in Hoyt (1979) except that of *Troodon* (Varricchio et al. 2013). Predicted egg weight refers to the weight of an egg predicted from adult mass using an allometric equation based on modern birds (Blueweiss et al. 1978). The percentages in parentheses for the non-avian maniraptorans represent the total egg production as hypothesized for the laying of two eggs at a time through monoautochronic ovulation. All weights are in grams and volume in cubic centimeters.

Taxon or ootaxon	Adult weight (g)	Egg volume (cm ³)	Egg weight (g)	Predicted egg weight (g)	Observed: predicted egg weight
<i>Citipati</i>	74 800	534	566	1470	39% (77%)
cf. <i>Machairasaurus</i>	39 300	231	245	897	27% (55%)
<i>Nemegtomaia</i>	40 100	231	245	911	27% (54%)
<i>Byronosaurus</i>	22 500	178	189	584	32% (65%)
<i>Troodon</i>	51 400	296.4	314.2	1100	29% (57%)
<i>Styloolithus</i>	1 700	37.3	39.5	79.9	49%
<i>Neuquenornis</i>	379	17.9	19.0	25.1	75%
Romanian bird	293	13.0	13.8	20.6	67%

appear to lack chalazae, the chords of albumen present in birds that allow the embryo to maintain an upright position during egg rotation (Terres 1995). The absence of this simple feature may have had a profound effect on non-ornithomorph birds by restricting their nesting localities to areas with substrates that would permit the planting of eggs. Recent paleontologic discoveries demonstrated that some non-avian maniraptoran theropods shared a similar respiratory system, brain, feathered integument and even small body size with Neornithes (Prum 1999; Larsson et al. 2000; O'Connor and Claessens 2005; Turner et al. 2007). Consequently, the presence of chalazae may represent an important difference of Neornithes, the only Mesozoic clade of Dinosauria to nest completely free of sediment and the only clade to survive the K–Pg mass extinction event.

Sabath (1991: 181) considered that these two specimens, ZPAL MgOV-II/7 and ZPAL MgOV-II/25, “if not accidental, could be interpreted as an evidence for very intensive parental care, with even lethal consequences to the parent protecting the nest”. This represented the first interpretation of a clutch-associated adult as evidence of parental care. The years following Sabath (1991) would reveal a number of clutch-associated adults within non-avian theropods closely related to birds, including three oviraptorids, *Citipati*, *Nemegtomaia*, and cf. *Machairasaurus* (Norell et al. 1995; Dong and Currie 1996; Fanti et al. 2012) and two troodontids, *Troodon* and an unnamed Mongolian form (Varricchio et al. 1997; Erickson et al. 2007). Also, eggs are assigned to the dromaeosaur *Deinonychus* based upon their preservation appressed to the exterior of adult gastralia (Grellet-Tinner and Makovicky 2006). All of these non-avian theropods are considered to have engaged in some form of parental care, which appears to have carried over into Mesozoic birds. In 2008, Varricchio et al. suggested that the large size of clutches in these theropods was most consistent with paternal or male only care. In a subsequent analysis using a strictly avian data set, Birchard et al. (2013) found insufficient evidence

to distinguish paternal from maternal. Assuming a clutch of eight eggs as in ZPAL MgOV-II/7 provides a clutch mass of 317 g. Using the adult mass for ZPAL MgOV-II/25, this clutch mass represents 104% of the predicted value and provides no insight into the mode of parental care.

Conclusions

- Egg size, shape and microstructure clearly distinguish *Styloolithus sabathi* from the *Gobioolithus* oospecies. Clutch arrangement likely further represents an additional difference.
- The clutch-associated bones likely represent an enantiornithine bird and are suitably sized to represent the parent.
- *Styloolithus sabathi* provides evidence that relative egg size had increased markedly from the non-avian theropod condition in oviraptorids and troodontids, but had not yet reached the modern egg-adult proportions.
- *Styloolithus sabathi* eggs were arranged upright into a tight clutch configuration akin to that of troodontids. The tight arrangement of multiple eggs differs from other possible incubation modes found in *G. minor* and the Neuquén enantiornithine. This suggests that some enantiornithines engaged in an incubation mode carried over or evolved in parallel with troodontids, where adults sat atop largely buried eggs.
- Sediment-bound upright eggs appear common to basal birds including Enantiornithes, suggesting that as in non-avian theropods (Varricchio et al. 1997), these birds lack chalazae, the chords of albumen allowing egg rotation in modern birds. Absence of this simple structure may have restricted Enantiornithes to ground nesting in areas with appropriate substrates and not permitted the type of nesting diversity found in Neornithes. Neornithes are the only Mesozoic clade of Dinosauria to nest completely free of sediment and the only clade to survive the K–Pg mass

extinction event. Possession of chalazae may have potentially afforded Neornithes two advantages. First, they could take advantage of a variety of sediment-free nesting environments such as in trees, on rock ledges, in caves or cavities. Second, Neornithes would be able to adjust their eggs during incubation in times of environmental perturbation.

Acknowledgements

We thank the Paleontological Institute, Russian Academy of Sciences, Moscow and the Institute of Paleobiology of the Polish Academy of Sciences, Warsaw for access to their excellent specimens with special thanks to Konstantin Mikhailov (PIN) for his openness with specimens and information and Adam Halamski (ZPAL) for logistics support and patience in our bill paying. Also, Cyprian Kulicki (ZPAL) provided assistance with microscopy. Frankie Jackson (Montana State University, Bozeman, USA) provided helpful discussion and assistance with thin sections used for comparison. We also thank Daniel Lawver (Montana State University, Bozeman, USA) for conversations about avian eggshell. This research was supported by NSF grant #0847777 (EAR) to DJV. We thank Konstantin Mikhailov and Darla Zelenitsky (Department of Geoscience, University of Calgary, Canada) for reviews that improved the final manuscript.

References

- Anderson, J.F., Hall-Martin, A., and Russell, D.A. 1985. Long-bone circumference ad weight in mammals, birds, and dinosaurs. *Journal Zoology* 207: 53–61.
- Balanoff, A.M., Norell, M.A., Grellet-Tinner, G., and Lewin, M. R. 2008. Digital preparation of a probable neoceratopsian preserved within an egg, with comments on microstructural anatomy of ornithischian eggshells. *Naturwissenschaften* 95: 493–500.
- Birchard, G.F., Ruta, M., and Deeming, D.C. 2013. Evolution of parental incubation behaviour in dinosaurs cannot be inferred from clutch mass in birds. *Biology Letters* 9:2 0130036.
- Blueweiss, L., Fox, H., Kudzma, V., Nakashima, D., Peters, R., and Sams, S. 1978. Relationships between body size and some life history parameters. *Oecologia* 37: 257–272.
- Campbell, K.E. and Marcus, L. 1992. The relationships of hindlimb bone dimensions to body weight in birds. *Natural History Museum of Los Angeles County Science Series* 36: 395–412.
- Chiappe, L.M. and Calvo, J.O. 1994. *Neuquenornis volans*, a new Upper Cretaceous bird (Enantiornithes: Avisauridae) from Patagonia, Argentina. *Journal of Vertebrate Paleontology* 14: 230–246.
- Chiappe, L.M., Norell, M., and Clark, J. 2001. A new skull of *Gobipteryx minuta* (Aves: Enantiornithes) from the Cretaceous of the Gobi Desert. *American Museum Novitates* 3346: 1–15.
- Deeming, D.C. 1991. Egg incubation: its effects on embryonic development in birds and reptiles. In: D.C. Deeming and M.W.J. Ferguson (eds.), *Egg Incubation*, 307–323. Cambridge University Press, Cambridge.
- Deeming, D.C. 2006. Ultrastructural and functional morphology of eggshells supports the idea that dinosaur eggs were incubated buried in a substrate. *Paleontology* 49: 171–185.
- Dennis, J.E., Xiao, S.-Q., Agarwal, M., Fink, D.J., Heuer, A.H., and Caplan, A.I. 1996. Microstructure of matrix and mineral components of eggshells from white leghorn chickens (*Gallus gallus*). *Journal of Morphology* 228: 287–306.
- Dong, Z.-M. and Currie, P.J. 1996. On the discovery of an oviraptorid skeleton on a nest of eggs at Bayan Mandahu, Inner Mongolia, People's Republic of China. *Canadian Journal of Earth Sciences* 33: 631–636.
- Dyke, G., Vremir, M., Kaiser, G., and Naish, D. 2012. A drowned Mesozoic bird breeding colony from the Late Cretaceous of Transylvania. *Naturwissenschaften* 99: 435–442.
- Elzanowski, A. 1981. Embryonic bird skeletons from the Late Cretaceous of Mongolia. *Palaeontologia Polonica* 42: 147–179.
- Erickson, G.M., Rogers, K.C., Varricchio, D.J., Norell, M.A., and Xu, X. 2007. Growth patterns in brooding dinosaurs reveals the timing of sexual maturity in non-avian dinosaurs and genesis of the avian condition. *Biology Letters* 3: 558–561.
- Fanti F., Currie, P.J., and Badamgarav, D. 2012. New specimens of *Nemegtomaia* from the Baruungoyot and Nemegt Formations (Late Cretaceous) of Mongolia. *PLoS ONE* 7 (2): e31330.
- Fernández, M.S., García, R.A., Fiorelli, L., Scolaro, A., Salvador, R.B., Co-taro, C.N., Kaiser, G.W., and Dyke, G.J. 2013. A large accumulation of avian eggs from the Late Cretaceous of Patagonia (Argentina) reveals a novel nesting strategy in Mesozoic birds. *PLoS ONE* 8 (4): e61030.
- Field, D.J., Lynner, C., Brown, C., and Darroch, S.A.F. 2013. Skeletal correlates for body mass estimation in modern and fossil flying birds. *PLoS ONE* 8 (11): e82000.
- Fraser, A., Bain, M., and Solomon, S. 1999. Transmission electron microscopy of the vertical crystal layer and cuticle of the eggshell of the domestic fowl. *British Poultry Science* 40: 626–631.
- Grellet-Tinner, G. 2005. *A Phylogenetic Analysis of Oological Characters: a Case Study of Saurischian Dinosaur Relationships and Avian Evolution*. Unpublished PhD dissertation. University of Southern California, Los Angeles.
- Grellet-Tinner, G. 2006. Oology and the evolution of thermophysiology in saurischian dinosaurs: homeotherm and endotherm deinonychosaurians? *Papéis Avulsos de Zoologia* 46: 1–10.
- 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.
- Grellet-Tinner, G. and Norell, M.A. 2002. An avian egg from the Campanian of Bayn Dzak, Mongolia. *Journal of Vertebrate Paleontology* 22: 719–721.
- Grellet-Tinner, G., Corsetti, F., and Buscalioni, A. 2010. The importance of microscopic examinations of eggshells: Discrimination of bioalteration and diagenetic overprints from biological features. *Journal of Iberian Geology* 36: 181–192.
- Hoyt, D.F. 1979. Practical methods of estimating volume and fresh weight of bird eggs. *The Auk* 96: 73–77.
- Imai, T., Azuma, Y., and Jackson, F.D. 2014. Oldest known avian eggshell from the Lower Cretaceous (Upper Barremian) Kitadani Formation, Katsuyama City, Fukui, Japan. In: *Abstracts of International Symposium on Asian Dinosaurs in Fukui 2014*, 26–28. Fukui Prefectural Dinosaur Museum, Fukui.
- 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., 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.
- Jackson, F.D., Varricchio, D.J., and Corsini, J.A. 2013. Avian eggs from the Eocene Willwood and Chadron formations of Wyoming and Nebraska. *Journal of Vertebrate Paleontology* 33: 1190–1201.
- Jerzykiewicz, T. 2000. Lithostratigraphy and sedimentary settings of the Cretaceous dinosaur beds of Mongolia. In: M.J. Benton, M.A. Shishkin, D.M. Unwin, and E.N. Kurochkin (eds.), *The Age of Dinosaurs in Russia and Mongolia*, 279–296. Cambridge University Press, Cambridge.
- 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. and Hirsch, K.F. 1996. Crocodilian and avian eggshells from the Middle Eocene of the Geiseltal, Eastern Germany. *Journal of Vertebrate Paleontology* 167–180.

- Kurochkin, E.N. 1996. A new large enantiornithid from the Late Cretaceous of Mongolia. *Proceedings Zoological Institute, Russian Academy of Sciences* 277: 130–141.
- Kurochkin, E.N., Chatterjee, S., and Mikhailov, K. 2013. An embryonic enantiornithine bird and associated eggs from the Cretaceous of Mongolia. *Paleontological Journal* 47: 1252–1269.
- Larsson, H.C.E., Sereno, P.C., and Wilson, J.A. 2000. Forebrain enlargement among nonavian theropod dinosaurs. *Journal of Vertebrate Paleontology* 20: 615–618.
- 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.
- Mikhailov, K.E. 1991. Classification of fossil eggshells of amniotic vertebrates. *Acta Palaeontologica Polonica* 36: 193–238.
- Mikhailov, K. 1994. Theropod and protoceratopsian dinosaur eggs from the Cretaceous of Mongolia and Kazakhstan. *Paleontological Journal* 28: 101–120.
- Mikhailov, K.E. 1996a. Bird eggs in the Upper Cretaceous of Mongolia. *Paleontological Journal* 30: 114–116.
- Mikhailov, K.E. 1996b. New genera fossil eggs from the Upper Cretaceous of Mongolia. *Paleontological Journal* 30: 122–124.
- Mikhailov, K.E. 1997a. Avian eggshells: an atlas of scanning electron micrographs. *British Ornithologists' Club Occasional Publication* 3: 1–88.
- Mikhailov, K.E. 1997b. Fossil and recent eggshell in amniotic vertebrates: fine structure, comparative morphology and classification. *Special Papers in Palaeontology* 56: 1–80.
- Mikhailov, K.E. 2014. Eggshell structure, parataxonomy and phylogenetic analysis: some notes on articles published from 2002 to 2011. *Historical Biology* 26: 144–154.
- Mikhailov, K.E., Sabath, K., and Kurzanov, S. 1994. Eggs and nests from the Cretaceous of Mongolia. In: K. Carpenter, K.F. Hirsch, and J.R. Horner (eds.), *Dinosaur Eggs and Babies*, 88–115. Cambridge University Press, Cambridge.
- Norell, M.A., Clark, J.M., Chiappe, L.M., and Dashzeveg, D. 1995. A nesting dinosaur. *Nature* 378: 774–776.
- Norell, M.A., Clark, J.M., Dashzeveg, D., Barsbold, R., Chiappe, L.M., Davidson, A.R., McKenna, M.C., Perle, A., and Novacek, M.J. 1994. A theropod dinosaur embryo and the affinities of the Flaming Cliffs dinosaur eggs. *Science* 266: 779–782.
- O'Connor, P. and Claessens, L. 2005. Basic avian pulmonary design and flow-through ventilation in non-avian theropod dinosaurs. *Nature* 436: 253–256.
- O'Connor, J., Chiappe, L.M., and Bell, A. 2011. Pre-modern birds: avian divergences in the Mesozoic. In: G. Dyke and G. Kaiser (eds.), *Living Dinosaurs: The Evolutionary History of Modern Birds*, 39–114. John Wiley and Sons, New York.
- Prum, R.O. 1999. Development and evolutionary origin of feathers. *Journal Experimental Zoology* 285: 291–306.
- Sabath, K. 1991. Upper Cretaceous amniotic eggs from the Gobi Desert. *Acta Palaeontologica Polonica* 36: 151–192.
- 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.
- Swofford, D.L. 2003. *PAUP*: Phylogenetic Analysis Using Parsimony (* and Other Methods), Version 4.0 b10*. Sinauer Associates, Sunderland.
- Tanaka, K., Lü, J., Kobayashi, Y., Zelenitsky, D.K., Xu, L., Jia, S., Qin, S., and Tang, M. 2011. Description and phylogenetic position of dinosaur eggshells from the Luanchuan area of western Henan Province, China. *Acta Geologica Sinica* 85: 66–74.
- Terres, J.K. 1995. *The Audubon Society Encyclopedia of North American Birds*. 1109 pp. Wings Books, New York.
- Turner, A.H., Pol, D., Clarke, J.A., Erickson, G.M., Norell, M.A. 2007. A basal dromaeosaurid and size evolution preceding avian flight. *Science* 317: 1378–1381.
- Varricchio, D.J. and Jackson, F.D. 2004a. A phylogenetic assessment of prismatic dinosaur eggs from the Cretaceous Two Medicine Formation of Montana. *Journal of Vertebrate Paleontology* 24: 931–937.
- Varricchio, D.J. and Jackson, F.D. 2004b. Two eggs sunny-side up: reproductive physiology in the dinosaur *Troodon formosus*. In: P.J. Currie, E.B. Koppelhus, M.A. Shugar, and J.L. Wright (eds.), *Feathered Dragons: Studies on the Transition from Dinosaur to Birds*, 215–233. Indiana University Press, Bloomington.
- Varricchio, D.J., Balanoff, A.M., and Norell, M.A. (in press). Reidentification of avian embryonic remains from the Cretaceous of Mongolia. *PLoS ONE*.
- Varricchio, D.J., Horner, J.R., and Jackson, F. 2002. Embryos and eggs for the Cretaceous theropod *Troodon formosus*. *Journal of Vertebrate Paleontology* 22: 564–576.
- Varricchio, D.J., Jackson, F., Borkowski, J., and Horner, J.R. 1997. Nest and egg clutches of the dinosaur *Troodon formosus* and the evolution of avian reproductive traits. *Nature* 385: 247–250.
- Varricchio, D.J., Jackson, F.D., Jackson, R.A., and Zelenitsky, D.K. 2013. Porosity and water vapor conductance of two *Troodon formosus* eggs: an assessment of incubation strategy in a maniraptoran dinosaur. *Paleobiology* 39: 278–296.
- Varricchio, D.J., Moore, J.R., Erickson, G.M., Norell, M.A., Jackson, F.D., and Borkowski, J.J. 2008. Avian paternal care had dinosaur origin. *Science* 322: 1826–1828.
- Wilson, H.M., Heck, C.T., Varricchio, D.J., Jackson, F.D., and Jin, X. 2014. Evaluating deformation in *Spheroolithus* dinosaur eggs from Zhejiang, China. *Historical Biology* 26: 173–182.
- Zelenitsky, D.K. 2004. *Description and Phylogenetic Implications of Extant and Fossil Oologic Remains*. 383 pp. Unpublished Ph.D. Dissertation, University of Calgary, Calgary, Canada.
- Zelenitsky, D.K. and Therrien, F. 2008. Phylogenetic analysis of reproductive traits of maniraptoran theropods and its implications for egg parataxonomy. *Palaeontology* 51: 807–816.
- Zelenitsky, D.K., Modesto, S., and Currie, P.J. 2002. Bird-like characteristics of troodontid theropod eggshell. *Cretaceous Research* 23: 297–305.
- Zheng, X., O'Connor, J., Huchzermeyer, F., Wang, X., Wang, Y., Wang, M., and Zhou, Z. 2013. Preservation of ovarian follicles reveals early evolution of avian reproductive behaviour. *Nature* 495: 507–511.