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ARTICLE



The youngest egg of avian affinities from the Cretaceous of Patagonia

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ABSTRACT

We report the youngest fossil egg of avian affinities from the Cretaceous (Allen Formation, Campanian-Maastrichtian) of Patagonia, Argentina. The fossil consists in most of the internal cast of a single egg, preserving some eggshell fragments on one of its poles. Its axes are 4.5 cm and 3.06 cm. The eggshell surface is smooth, and its thickness average is 400 µm. The eggshell has two layers, with an ornithoid basic type and a ratite morphotype. The well-developed mammillary layer is 154 µm thick, with petal-shaped mammillae, the continuous layer is 251 µm thick. Shell microstructure is consistent with Laevisoolithidae, an ootaxon traditionally associated with enantiornithid birds. The shape of fibers of the testaceous membrane (TM) is preserved; these are flattened, with a thickness of 1.1 µm and a width of 4.8 µm each. The arrangement of the fibers of the TM is random, similar to that observed in extant reptiles. EDAX analysis reported that fibers are enriched in traces of Mg, Al, Si, P, F, and K, elements that are also present in both extant and fossil shell membrane. Cladistic analysis performed is consistent with the avian affinities established on the basis of macro, micro and ultrastructural characteristics.

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KEYWORDS

Eggshells; Río Negro; reproduction; Salitral Ojo de Agua locality; cladism

Introduction

The fossil record of avian eggs from the Late Cretaceous is relatively abundant and geographically extensive, with significant materials from China, Mongolia and Russia (Mikhailov 1991; Grellet-Tinner and Norell 2002; Kurochkin et al. 2011), and few examples from India, France and Romania (Dyke et al. 2012; Khosla and Sahni 1995; García 2000). South American avian eggs are scarce: only a nesting colony from Neuquén City and an isolated egg from Brazil (Schweitzer et al. 2002; Fernández et al. 2013; Marsola et al. 2014) have been documented. From Africa an avian egg has been documented from Morocco (Vianey-Liaud and Garcia 2003).

Herein, we present the youngest fossil record of an egg of avian affinities from the Cretaceous of Patagonia. The material comes from the Allen Formation (Campanian-Maastrichtian) and was collected in the Arriagada III site of the Salitral Ojo de Agua locality (northwest of the Río Negro province). It was associated with other fossil eggs (megaloolithids and arriagadoolithids), and bony remains of alvarezsaurid theropods (Salgado et al. 2007, 2009; Agnolin et al. 2012). We describe and classify the egg from Salitral Ojo de Agua in a parataxonomic scheme, as well as compare its eggshell features with other materials around the world (Mikhailov 1997; Schweitzer et al. 2002; Marsola et al. 2014). Because of the impossibility of associating this egg with a specific producer, we use phylogenetic analysis to provide a more accurate approach to understand the relationship of this material in a cladistics context (Tanaka et al. 2011, Vilá et al. 2017).

Materials and methods

The dimensions of the egg are 4.50 cm × 3.49 cm × 3.43 cm, and its volume is around 28 cm³ (Figure 1(a,b)). Measurements were taken with digital caliper Stainless, accurate to ± 0.02 mm. Eggshells were observed under a binocular lupe Nikon SMZ 645. SEM observations and EDAX analyses were performed at Centro Atómico Bariloche (Bariloche, Río Negro, Argentina) with SEM FEI Nano Nova 230. The material is housed in the Museo Provincial 'Carlos Ameghino' (Cipolletti, Río Negro, Argentina) with the collection number MPCA-Pv 600. Thin sections were performed following precise methodology for petrographic samples (Chinsamy and Raath 1992). Slides were observed under polarized light microscope Olympus BX51 model DP21 with crossed nicols. Egg volume was calculated mathematically using the volumetric formula for ellipsoids: (1) $V = 4/3\pi.a.b.c$ (a : length/2; b : width/2; c : width/2).

Geology

Salitral Ojo de Agua, north-central part of the Río Negro Province (Argentina), Arriagada III locality (39° 25' 55" S, 67° 17' 40" W) (Salgado et al. 2007), Allen Formation (Campanian-Maastrichtian). In the area of SOA and SST, Salgado et al. (2007) recognized two subunits for this formation. The lower one, the only present in SOA (we disagree with Agnolin et al. 2012, who interpreted the egg bearing-levels in SOA as the upper levels of the Allen Formation.), comprises fine-grained sandy deposits with subordinate muddy layers and thin evaporitic levels. The paleoenvironment is interpreted as a brackish lagoonal and supratidal environment, associated with aeolian sands (dunes) and

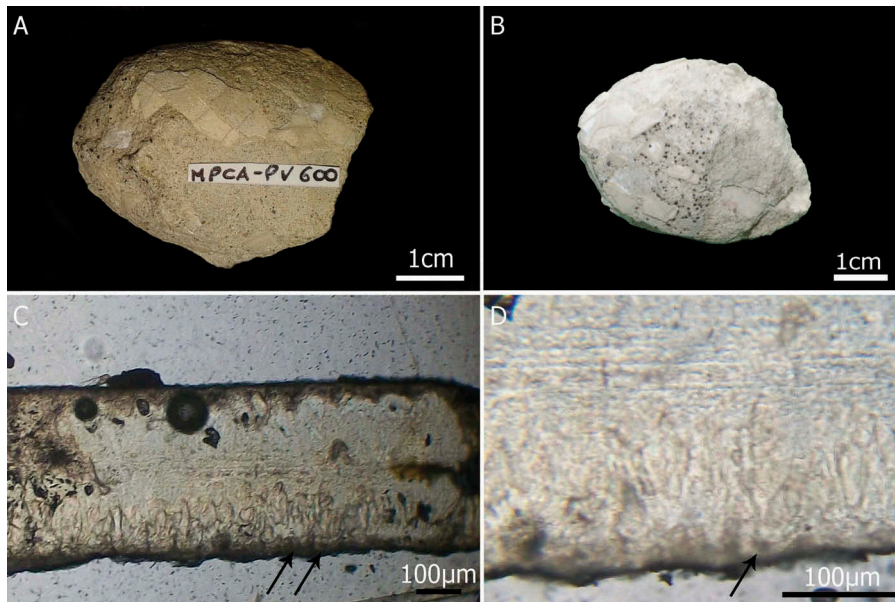


Figure 1. (a)-(b). Egg from Salitral Ojo de Agua in two views. (c). Radial view of a thin section with plain polarized light a two-layered eggshell. (d). Radial view of a details of the mammillary cone with a black round core in the base of the mammilla. Continuous layer shows horizontal growing lines.

deposits of ephemeral rivers. The abundant rhizoturbation, termite structures and caliches in the egg-bearing deposits indicate the existence of paleosols, developed presumably in a supratidal environment (Salgado et al. 2007).

Results

Oofamily Laevisoolithidae Mikhailov (1991)

Oogenus Tantumoolithus Oogen nov.

Type oospecies

Tantumoolithus lenis nov., monotypic; see below.

Etymology

From Latin Tantum, isolated, referring to the find of the eggs in the field; oo, ova; and lithos, stone.

Diagnosis

As for type and only known oospecies.

Stratigraphic and geographic range

As for the only oospecies.

Tantumoolithus lenis nov.

Figure 2, Figure 3.

Holotype

MPCA-Pv 600, uncomplete egg.

Type locality

Arriagada III locality, Río Negro province, Argentina.

Type horizon

Allen Formation, Upper Cretaceous.

Diagnosis

Small (4.50 cm × 3.49 cm × 3.43 cm, and its volume is around 28 cm³) and slightly asymmetrical (with unequal poles) eggs with smooth surface and thin (360-400 μm) eggshell (Figures 1(a,b) and 2(e)). Eggshell is of ornithoid basic type with (1.5:1) ratio between continuous and mammillary layers (Figures 1(c,d) and 2(a)). Base of the mammillae forming well-defined petaloid wedges, continuous layer with squamatic ultrastructure (Figures 2(b,c,d) and 3(a)). The limits between mammillas are straight, columnar (Figure 3(a)). The boundary between ML and CL is abrupt (ratite morphotype) (Figures 2(a) and 3(a)).

Stratigraphic and geographic range

Upper Cretaceous, Allen Formation, Río Negro, Argentina.

Description

The eggshell surface is smooth and the pore openings are rounded (Figures 1(a) and 2(e)). The eggshell thickness falls in this range 360,400 μm (Figures 1(c) and 2(a)). Two layers can be distinguished in the eggshell: 1) The mammillary layer with mammillas, which under SEM reveal a zone of radiating calcite crystallites (Figures 3(a), and 2) Continuous layer, which under SEM reveal a squamatic zone (encompassing squamatic ultrastructure) (Figure 2(d)). Mammillary layer is ca. 142 μm thick in average (Figure 2(a)). Calcite spherulites extend outward from the base of the mammillae forming well-defined petaloid wedges (Figure 2(b)). Each wedge shows rhombohedral calcitic crystals (Figure 3(a)). Mammillary layer was built up by closely packed mammillae (Figure 3(a)). The distance between each mammillary base is from 50 μm to more than 78 μm (Figure 2(a,b)). The organic core is spherical in shape (Figures 1(d) and 2(b)). Squamatic zone is well preserved (Figure 2(b,d)). The limit between the mammillary layer and continuous layers is abrupt (Figure 2(a,b)). The continuous layer is ca. 224 μm in average.

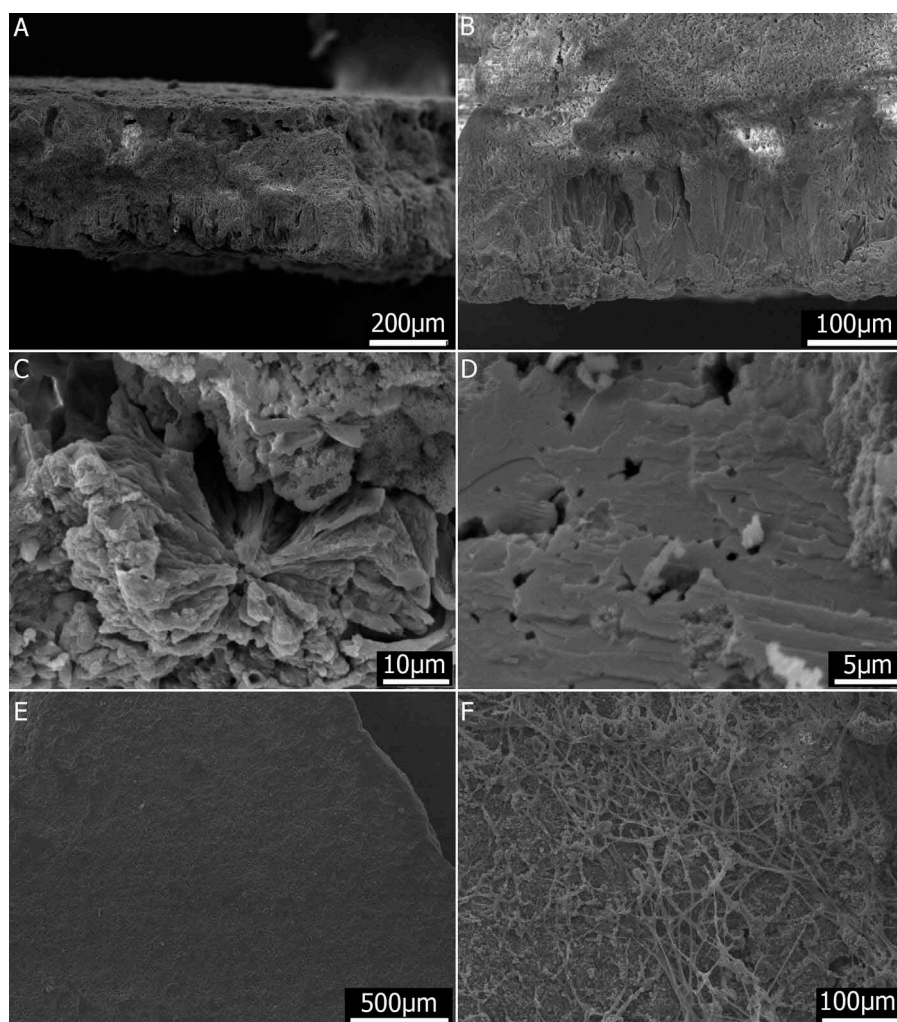


Figure 2. SEM. (a). Radial view of the complete thickness, we observed a two layered eggshell. (b). Detail of the abrupt limit of the Mammillary layer and continuous layer. Mammillary layer has mammillary cones with its core preserved, the calcium grow up around the core building a petaloid structure. Wedges have rombohedral calcium crystals and Continuous layer reveals under high magnification a Squamatic Zone with squamatic texture. (c). Inner view, detail of the base of the mammilla. (d). Radial view, detail of squamatic zone, with squamatic texture, where can be seen tiny holes. (e). Upper view, smooth external surface. (f). Inner view, detail of the disposition of fibers from the testaceous membrane which have been preserved.

The eggshell reveals an ornithoid basic type, a ratite morphotype, and an angusticanaliculated pore system, with a strong developed mammillary layer $\frac{1}{2}$ to $\frac{1}{3}$ of the complete thickness. Squamatic zone present tiny holes at high magnification within the squamatic zone, which ranges in size between $0.3 \mu\text{m}$ and $1.5 \mu\text{m}$ (Figure 2(d)). Eggshell thin sections were analyzed under plain polarized light, where each mammilla show a core in the base rounded by calcite crystals growing around them (base of the mammilla), and continuous layer shows horizontal growing lines (Figure 1(b,c)). Thin sections reveal that continuous layer appears as a compact layer with fine horizontal lines, which would reflect the pattern of deposition of the calcium (Figures 1(b) and 2(c)).

Discussion

The egg described in this work was associated to partial eggs and numerous eggshells of the oofamily Arriagadoolithidae (Agnolin et al. 2012). The egg *Tantumoolithus lenis* clearly does not belong to this oofamily for the following reasons. 1) Arriagadoolithid eggs have a diameter of ca. 70 mm (? maximum width) and unknown

length, while *T. lenis* has a shorter diameter $4.5 \text{ cm} \times 3.49 \text{ cm} \times 3.43 \text{ cm}$. 2) Arriagadoolithid eggshells have three layers (mammillary, prismatic and external layer) of distinct calcite texture, whereas *T. lenis* eggshell presents only two layers (mammillary layer and continue layer). 3) The average value of the eggshell thickness in Arriagadoolithus is 1mm, while *T. lenis* is thinner $400 \mu\text{m}$. 4) Three different types of ornamental patterns were observed in Arriagadoolithus eggs, while *T. lenis* has a smooth surface. Finally, 5) Arriagadoolithus eggs present a prismatic layer, while the *T. lenis* has a continuous layer with squamatic texture, without any evidence of prisms. For all these reasons, we consider that *T. lenis* does not fit with this Rionegran oofamily.

T. lenis shows some differences with the eggs of the oofamily Elongatoolithidae. The elongatoolithids eggs from China are elongate and relatively large (9.8–11 cm long, 6.5–8 cm wide) (Zhao 1975), in turn, *T. lenis*, although elongate, is smaller than those ($4.5 \text{ cm} \times 3.49 \text{ cm} \times 3.43$).

Tantumoolithus lenis has two layers, as the Elongatoolithidae eggs described by Zhao (1975) and the Laevisoolithidae described by Mikhailov (1997, p. 66). *Tantumoolithus lenis* is smaller and has thinner eggshell than those eggs described by

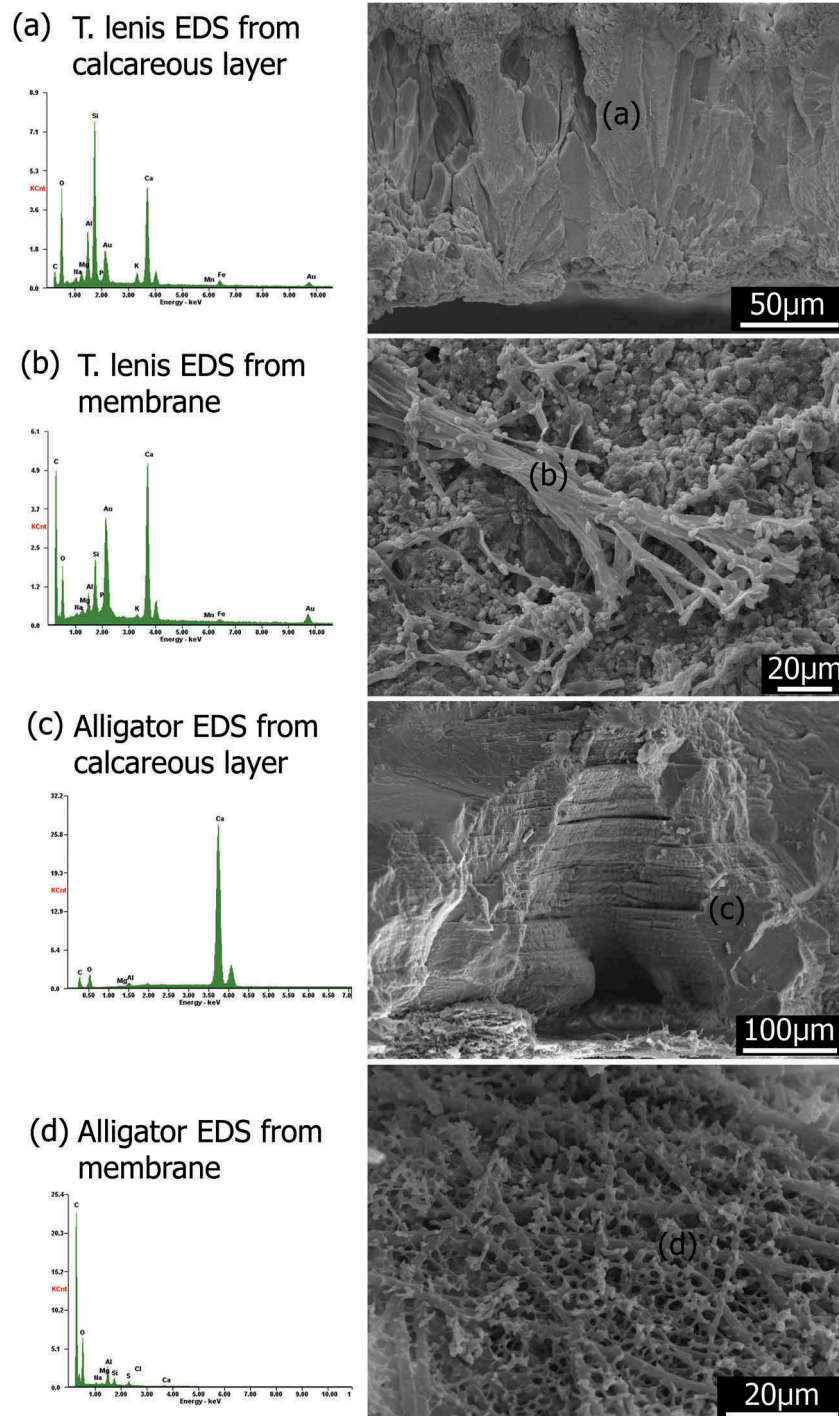


Figure 3. Edax analysis of calcareous eggshell and testaceous membrane of SOA egg and *Caiman latirostris* eggs. (a), (b) and (c) in pictures mark the points where EDAX analyses were performed. (a).EDAX of the calcareous eggshell MPCA-Pv 600. (b). EDAX of the fibers of the testaceous membrane of MPCA-Pv 600. (c). EDAX of the calcareous eggshell of *Caiman latirostris*. (d). EDAX of the testaceous membrane of *Caiman latirostris*.

Mikhailov (1996, Mikhailov 1997), assigned to the oofamily Elongatoolithidae. On the other hand, the eggshell of *T. lenis* has a smooth surface, whereas elongatoolithids have an ornamented external surface.

Tantumoolithus lenis differs from the Mongolian elongatoolithid oogenera *Macroolithus* and *Elongatoolithus* by its lesser egg size, smooth external surface, and thinner eggshells (Table 1).

Prismatoolithidae eggshells reveals a prismatic morphotype, which differs from *T. lenis* which has a ratite morphotype, the condition of this oofamily in having eggshells with smooth surface and finely linearituberulated ornamentation, angusticanalculated pore system and, elongated and slightly asymmetrical eggs. Though they share the presence of squamatic ultrastructure in the second layer and the absent of an external zone. *T. lenis* differs from all members of the Mongolian prismatoolithid oogenus *Protoceratopsidovum* Mikhailov (1994), by its smaller

Table 1. Comparison of Upper Cretaceous elongate eggs from Mongolia and other theropod and avian eggs with *Tantumoolithus lenis* oogen. oosp. nov. El, elongation index, SqU, squamatic ultrastructure. Modified from Varricchio and Barta (2015).

Ootaxa	Age and Formation	Egg size in mm	Egg shape El	Surface ornamentation present?	Shell thickness range	Second layer + External Zone: Mammillary layer	SqU present in the second layer?	External Zone present?	Reference
<i>Macroolithus</i>	various, see reference	>170 long	slightly asymmetrical?	yes	[0.8–2.5]	2:1–3:1	yes	no	Mikhailov 1994
<i>Elongatoolithus</i>	various, see reference	90–170 long	slightly asymmetrical?	yes	[0.7–1.6]	2:1–3:1	yes	no	Mikhailov 1994
<i>Troodon formosus</i>	Campanian Two Medicine and Judith River	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; Zelenitsky et al. 2010; Jackson et al. 2010
<i>Prismatoolithus levis</i>	Campanian Djadokhta Formation	?, only partial egg are known	asymmetrical	no	0.43–0.47	1.7:1–1.9:1	?	no	Grellet-Tinner 2005
<i>Byronosaurus jaffei</i> (troodontid) egg	Campanian Djadokhta and Baru Goyot Formation	130–150 × 50–57	? 2.3–3.0	yes	0.6–0.7	?	?no	no	Mikhailov 1994
<i>Protoceratopsidovum fluxuosum</i>	Campanian Djadokhta and Baru Goyot Formation	110–120 × 40–50	asymmetrical 2.3–2.5	no	[0.3–1.4] 0.6–0.7	1:0:1	?no	no	Mikhailov 1994; Zelenitsky and Terrien 2008; DB personal
<i>Protoceratopsidovum sincerum</i>	Campanian Djadokhta and Baru Goyot Formation	100–?110 × 40–?50	asymmetrical 2–2.75	no	0.3–0.7	2.6:1	no?	no	Mikhailov 1994; DB personal
<i>Protoceratopsidovum minimum</i>	Campanian? Baru 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>Oblongoolithus glaber</i>	?Campanian-Maastrichtian Nemegt Formation	<70 (long)	?	no	<1.0	1.3:1	yes	no	Mikhailov 1991
<i>Laevioolithus sochavai</i>	?Campanian – Maastrichtian? Nemegt Formation	?	known only from eggshell fragments	yes	0.3–0.4	1.2–1:3	yes	no	Mikhailov 1991
<i>Microtuberculatus</i>	Campanian? Baru Goyot Formation	40 × 25	asymmetrical 1.6	no	up to 0.1	2:0:1	yes	yes	Mikhailov 1996b; Zelenitsky 2004
<i>Parvoolithus tortuosus</i>	Campanian Baru Goyot Formation	50–53.5 × 25–32	asymmetrical 1.8–2.0	no	0.2–0.4	2:0:1	yes	?	Mikhailov 1996a; Varricchio and Barta 2015
<i>Gobioolithus major</i>	Campanian Baru Goyot Formation	30–46 × 20–24	asymmetrical 1.8–2.0	no	0.1–0.2	2:0:1	yes	?	Mikhailov 1996a
<i>Gobioolithus minor</i>	Campanian Baru Goyot Formation	25.8 × 15.9	? 1.6	no	0.17	1:1.25	yes?	yes?	Grellet-Tinner and Norell 2002;
Unnamed egg	Late Cretaceous Khugenetslavkant locality	47.5 × 22.3	symmetrical? 2.1	yes?	0.18	2:0:1	yes	yes?	Balanoff et al. 2008;
Egg containing enantiornithine embryo	Campanian Bajo de la Carpa Formation, Argentina	45 × 27	asymmetrical 1.7	no	0.26	1.9:1	yes	yes	Schwetzer et al. 2002; Fernández et al. 2013
Egg containing enantiornithine embryo	Campanian Djadokhta and Baru Goyot Formation	70 × 32	asymmetrical 2.0–2.3	no	0.25	3:1:1	yes	yes	Varricchio and Barta 2015
<i>Styloolithus sabathi</i>	Campanian-Maastrichtian, Allen Formation, Rio Negro, Argentina	45 × 34.9 × 34.3	asymmetrical 1.2	no	0.36–0.40	1.5:1	yes	no	This paper

egg size, thinner eggshell, different elongation index, the absence of external ornamentation, *T. lenis* share with this group the absence of external zone. It further differs from *Protoceratopsidovum fluxuosum* by the presence of external ornamentation. In the other hand all prismatoolithus Mongolian oospecies do not have squamatic ultrastructure in the second layer (Table 1). *T. lenis* share with *Pismatoolithus levis* the lack of ornamentation, and the squamatic texture in the second layer (Mikhailov 1994) and differs from it oospecies in that *P. levis* have thicker eggshells, CL:ML with a bigger ratio and in possessing external zone.

T. lenis differs from eggs referred to the Mongolian troodontid *Byronosaurus jaffei*, in its thickness range were *B. jaffei* have a greater CL:ML ratio.

Differences between *T. lenis* and the two *Gobioolithus* oospecies include larger egg size, a different elongation index were *Gobioolithus* eggs have a high index, then the CL:ML ratio is bigger than the ratio shown in *T. lenis*. *Gobioolithus minor* have thinner eggshells (Table 1).

Tantumoolithus lenis fits better with the eggs described from the oofamily Laevisoolithidae, where the eggs are 7 cm long and 3.5–4 cm wide (Zhao 1975; Mikhailov 1991). Eggshells of Laevisoolithidae oofamily are thinner than 1 mm, and the mammillary layer is $\frac{1}{2}$ to $\frac{2}{3}$ of the shell thickness (Mikhailov 1997, p. 66): these characteristics are also observed in *Tantumoolithus lenis*. In the other hand the Mongolian oospecies *Oblongoolithus glaber*, *Laevisoolithus sochavai*, and *Subtiliolithus microtuberculatus* have similar range of size of egg, eggshell thickness, similar CL:ML ratio, all of them do not have external zone, and have squamatic ultrastructure in their second layer, finally from all these three oospecies lack external ornamentation, except *Subtiliolithus microtuberculatus* (Mikhailov 1991) (Table 1).

Parvoolithus tortuosus and unnamed eggs containing enantiornithine embryos from the Late Cretaceous of Mongolia (Zelenitsky 2004; Balanoff et al. 2008) 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) have squamatic texture in the second layer and lack the external ornamentation except the egg containing enantiornithine embryo from Late Cretaceous Khugenetslavkant locality which probably have had ornamentation (Table 1). In the other hand *T. lenis* have similar egg size than all this eggs except of the unnamed egg from Bayn Dzak locality which is smaller; finally all this eggs differs in having external zone (Table 1).

Tantumoolithus lenis is more voluminous than those from Neuquén, which are attributed to enantiornithines based on embryo evidence (Schweitzer et al. 2002; Fernández et al. 2013). On the other hand, the Neuquenian eggs reveal an external zone in their eggshell, as other eggs described from Valle do Río (Brazil), Peixe Formation (Turonian-to-Maastrichtian) (Marsola et al. 2014).

In sum, *T. lenis* is referred to the Laevisoolithidae oofamily, a conclusion further supported by its eggshell thickness, which fits in the range of this oofamily, its smooth surface, volume, and shell characteristics. Thus, the Salitral Ojo de Agua egg is tentatively attributed to enantiornithid birds

(Schweitzer et al. 2002; Fernández et al. 2013; Marsola et al. 2014). Cladistics analysis confirms this hypothesis (See Figure 4).

The egg described in this work is the youngest egg of avian affinities from the Cretaceous of Patagonia. In fact, the eggs from Neuquén attributed to enantiornithine birds (Schweitzer et al. 2002; Fernández et al. 2013) were collected from rocks of Santonian age, while the Allen Formation, from which the material herein described comes from, is Campanian-Maastrichtian in age, that is, ten to fifteen million years younger.

Testaceous membrane

A series of fibers with a random arrangement were observed under SEM, which would have formed part of the testaceous membrane. The preservation of this structure is unusual, and requires extraordinary conditions of preservation. The fibers are flattened, with a thickness of 1.1 μm and a width of 4.8 μm each (Figure 3(f)). The fibers structure is similar in morphology and topography to the shell membrane of living crocodiles, which displays a random arrangement (Figure 3(d)). In this way, some authors have described several remnants of eggshell membrane in dinosaur eggs as permineralized fibers (Kohring 1999; Varricchio et al. 2002; Grellet-Tinner 2005). EDAX analysis reported that the fibers of *Tantumoolithus lenis* are enriched in traces of Mg, Al, Si, P, F, and K (Figure 3(c,d)). The analysis also showed a notable peak of carbon, evident with respect to the peaks of calcium, oxygen and aluminum (Figure 3(b,d)).

At this point it is unclear, however, if the higher relative contents of carbon detected in the permineralized fibers from the shell membrane of *Tantumoolithus lenis* represent organic residues of the original shell membrane, or if they are derived from bacteria that facilitated fossilization of the membrane fibers (Folk and Lynch 2001). As we did not find such high concentrations of carbon in other parts of the eggshell equally exposed to prospective contamination by recent organic carbon, we assume that the high carbon fraction is consistent with an organic preservation. We also consider that the allotment of carbon could refer to an accumulation and permineralization of a secondary organic carbon after fossilization of the eggshell, but the excellent preservation of the *Tantumoolithus lenis* fibers allow us to assume that it is an original permineralized testaceous fiber. In future studies we will perform immunohistoessay to determinate if some protein have been preserve.

Cladistic analysis

A cladistic analysis was performed using the data matrix of Vilá et al. (2017) which includes 36 taxa and 16 characters. We added to the Vilá et al.'s matrix two ootaxa: MPCA-Pv 600 and Enantiornithes eggs from the Neuquén City (MUCPv-350). The matrix and the character list are provided in Appendix sections.

The analysis was carried out using TNT (Goloboff et al. 2008). A heuristic tree search was performed consisting in 1000 replicates of Wagner trees (with random addition sequence of taxa)

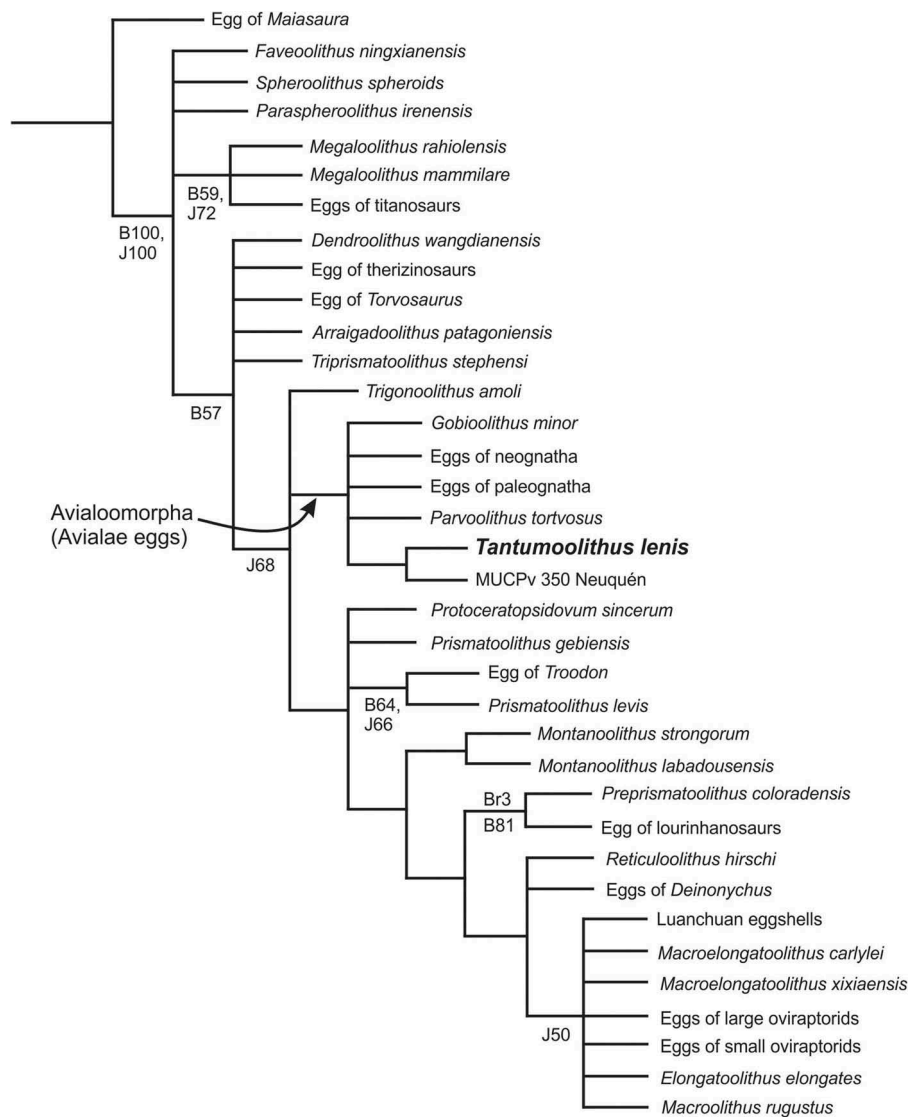


Figure 4. Strict consensus of 126 MPT. B, Bootstrap, Br, Bremer, J, Jackknife values.

followed by branch swapping (TBR: saving 10 trees per replicate). 126 most parsimonious trees of 46 steps were retrieved (CI: 0.587; RI: 0.877).

Bootstrap, Bremer and Jackknife support values were calculated (only Bremer support values greater than 2 and Bootstrap support and Jackknife values greater than 50% are indicated in the Figure 4). The support for the branches is low, with only one node having Bremer support values higher than 2 and a few nodes having Bootstrap and Jackknife values higher than 50% (Figure 4).

The strict consensus tree resolved *Tantumoolithus lenis* as nested in the ooclade Avialoomorpha (Figure 4), which are attributed to Avialae (defined as 'living birds and all maniraptorans closer to them than to *Deinonychus*', Padian 2004). MPCA-Pv 600 shares with other avialoomorphs by squamatic structure of well-defined squamatic zone (character list 8). In turn, *Tantumoolithus lenis* and MUCPv-350 are united by the absent of pore lip around pore opening (character list 13).

Thus, the cladistic analysis is consistent with the assignation of MPCA-Pv 600 to a theropod of avian affinities (possibly an

enanthiornithine bird), based on micro and ultrastructural characteristics.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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Appendix 1

Character list taken from Tanaka et al. (2011) which is based on Zelenitsky (2004).

- 1-Predominant ornamentation: reticulate (0), shagreen (1), nodose (2), smooth (3), linear ridges (4).
- 2-Egg symmetry and shape: spherical (0), symmetrical elongate (1) or asymmetrical elongate (2).
- 3-Egg long axis orientation: absent (0), subhorizontal (1) or subvertical (2)
- 4- Clutch arrangement: ring without central opening (0), unarranged cluster (1), ring with central opening (2) or circular cluster (3)
- 5-Egg pairing: paired (0) or unpaired (1).
- 6- First layer or base of shell units: acicular (0) or wedge-like (1)
7. Undulating boundary: absent (0) or present (1).
8. Squamatic structure of squamatic zone: absent (0), ill-defined (1) or well-defined (2).
- 9-External zone: absent (0) or present (1)
- 10-Shell units: indiscrete (0), discrete and fan-shaped (1) or discrete and columnar (2).
- 11-Shell units primarily: acicular (spherulitic) (0) or non-spherulitic (1).
- 12-Shell porosity: porous (0) or non-porous (1)
- 13-Pore lip around pore opening: present (0) or absent (1)
- 14-Pore opening in clusters: absent (0) or present (1)
- 15-Pore canals: non-tubular (0) or tubular (1)
- 16-Pore system: irregular canals (0), multiple branching canals (1), straight with perpendicular orientation (2) or straight with oblique orientation (3)

Appendix 2

Matrix

Egg of *Maiasaura* 000?0000000000
Paraspheroolithus irenensis 0000?0000000000
Spheroolithus spheroids 0000?0000000000
Faveoolithus ningxianensis 1001?00000000001

Egg of titanosaurs 2001?00001000012
Megaloolithus mammilare 2001?00001000012
Megaloolithus raholiensis 2001?00001000012
Egg of Lourinhanosaurs 311?100100101013
Preprismatoolithus coloradensis 3112000100101013
Macroolithus rugustus 4112011100110012
Elongatoolithus elongates 4112011100110012
Egg of small oviraptorids 4112011100110012
Egg of large oviraptorids 411?11100110012
Macroelongatoolithus xixiaensis 4112011100110012
Macroelongatoolithus carlylei 4???11100110012
Eggs of Deinonychus 4???10100110012
Reticuloolithus hirschi 4112010100110012
Prismatoolithus levis 3223010102110112
Egg of Troodon 3223010102110112
Prismatoolithus gebiensis 3223010102110012
Protoceratopsidovum sincerum 3223010102110012
Parvoolithus tortvosus 32??110212110012
Eggs of paleognatha 3113110210110012
Eggs of neognatha 4213110212110012
Gobioolithus minor 322?1102?0110012
Luanchuan eggshells 4???11100110012
Montanoolithus labadousensis 0???10102110012
Trigonoolithus amoei 2???10112110012
Montanoolithus strongorum 0212010102110012
Triprismatoolithus stephensi 1???10112110003
Arrigadoolithus patagoniensis 1???10112110003
Egg of Torvosaurus 100311000211?01
Egg of therizinosaurus 1003110?02110001
Dendroolithus wangdianensis 1,003110?02110001
MUCPv-350 Neuquen 322111?21211101?
Tantumoolithus lenis SOA 32???11202111012