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The first complete fossil avian egg from the Quaternary of South America

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ABSTRACT

In this contribution we report a fossil avian egg with an exceptional preservation. This material was recovered from sediments assigned to the Late Pleistocene-Early Holocene of Uruguay and it could be included as one of the few Cenozoic cases of complete preservation of fossil avian eggs. The micro and macrostructural analysis of the egg and its eggshell allow us to assign it to Family Tinamidae.

1. Introduction

Fossil eggs and clutches are better known in Mesozoic than Cenozoic units, assigned mostly to dinosaur eggs (for a revision of fossil eggs record see Carpenter et al., 1994; Mikhailov, 1997; Hechenleitner et al., 2015, Deeming and Ruta, 2015). The fossil record during Pleistocene and Holocene includes several eggshell fragments and embryos of Elephant birds (Aepyornithidae) from Madagascar (Balanoff and Rowe, 2007; Angst et al., 2015), Mihirungs (Dromornhithidae) from Australia (Miller et al., 1999; Angst et al., 2015; Grellet-Tinner et al., 2016) and Moas from New Zealand (Anderson, 1989; Gill, 2006; Huynen et al., 2010). In addition, there are reports of eggshell fragments of sea birds from the Pleistocene of Bermuda (e.g. Olson and Hearty, 2003, 2013). It is remarkable the intact condition of the *Fratercula dowi* eggs from the Late Pleistocene of California (Guthrie et al., 2000) and a near intact penguin egg from the Holocene of New Zealand (Ksepka, 2011).

In South America is usual to find Rheidae eggshells in archaeological sites (Apolinaire and Turnes, 2008). There are records of eggshells assigned to *Rhea pennata* from the Holocene of Argentina (Medina et al., 2011a; 2011b, 2019 and references therein), and eggshells of *Rhea americana* from the Late Holocene of Uruguay (e.g. Brum, 2009).

Tinamous have a scant South American fossil record represented by fragmentary bone remains spanning the last 17 million years (Tonni, 1977; Tambussi and Tonni, 1985; Tambussi, 1987, 1989; Chiappe, 1991; Tambussi et al., 1993; Tambussi and Noriega, 1996; Bertelli and Chiappe, 2005; Cenizo et al., 2012). All Cenozoic records are limited to Argentina and only Pleistocene remains are also known from Peru and Brazil (Brodkorb, 1963; Campbell, 1979). The most Quaternary tinamous have been assigned to living species with the exception of *Nothura paludosa* Mercerat (1897) and an unnamed species of *Nothura*, both from the Pleistocene of Argentina (Mercerat, 1897; Picasso and Degrange, 2009).

In this contribution we report an exceptionally well preserved fossil egg assigned to a tinamid bird, which represent the first record of a fossil avian egg from Uruguay and the first complete fossil avian egg from the Quaternary of South America.

Technical abbreviations- **PLM:** Polarized light microscopy; **SEM:** Scanning electron microscopy; **TLM:** Thermal lens microscopy.

Institutional abbreviations- **MIM:** Museo del Indio y la Megafauna, Cerros Azules, Maldonado-Uruguay.

2. Geological settings

The egg was collected in pelitic sediments, brown in color, with silty clay and silt, clay deposits, and gravel. More precisely, the fossil was recovered in a level with high concentration of calcium carbonate concretions which correspond to a fluvial deposit with the formation of temporary-seasonality lagoons (Fig. 1). These sediments have been assigned to the Late Pleistocene-Early Holocene and included in the Dolores Formation (Goso, 1972), which has been interpreted as having been deposited under more arid climatic conditions than the present, during the last glacial maximum (Ubilla and Perea, 1999; Martínez and Ubilla, 2004, Ubilla and Martínez, 2016). The outcrops of this unit are present in great part of the southern Uruguayan territory (Panario and Gutierez, 1999; Martínez and Ubilla, 2004; Ubilla and Martínez, 2016). Its fossil record includes a great diversity of land mammals like *Galea*

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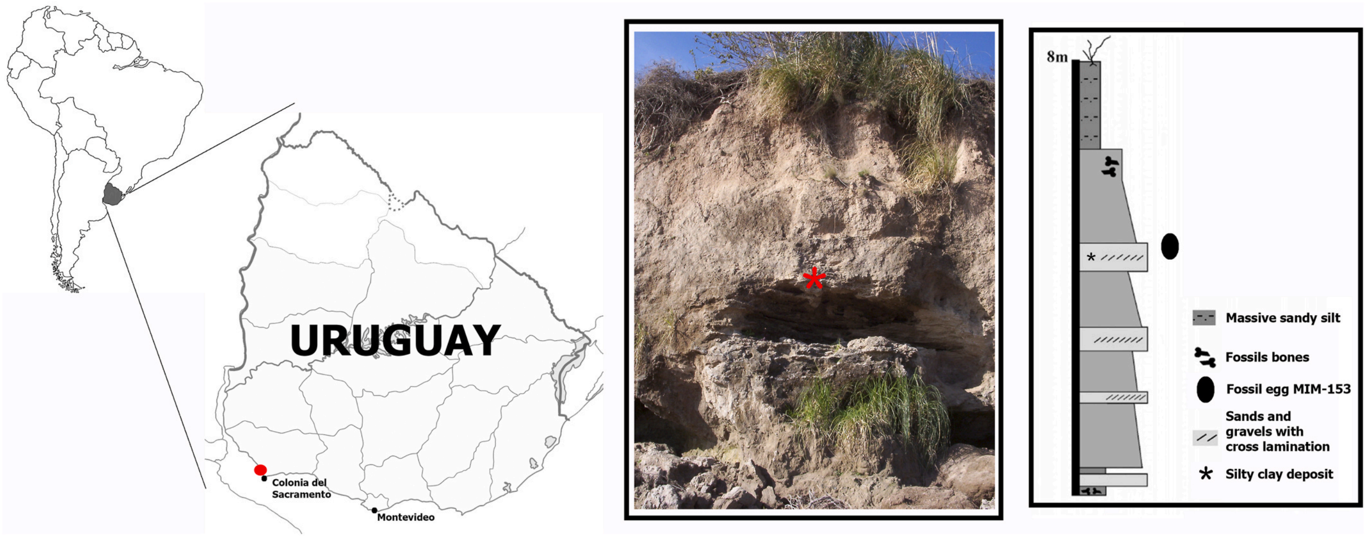

Fig. 1. Fossil locality (left) and, view of the coastal canyons and stratigraphic profile (right) where found the specimen studied. Red circle: El Caño locality; red star: place of the find, just above the silty clay deposit. Stratigraphic profile taken and modified from Corona et al. (2013).

ortodonta, *Microcavia* sp., *Glyptodon clavipes*, *Panochthus tuberculatus*, *Lestodon armatus*, *Toxodon platensis*, *Macrauchenia patachonica*, *Lagostomus* sp, *Catonyx cuvieri*, *Hemiauchenia* sp., *Vicugna* sp., *Catagonus* sp., *Hippidion principale*, *Equus neogaeus*, *Cerdocyon thous* and *Panthera onca* (Teisseire, 1928; Rinderknecht, 1999; Corona et al., 2013; Ubilla and Rinderknecht, 2014; Ubilla and Martínez, 2016; Manzuetti et al., 2018). This mammal association corresponds to the Lujanian regional stage/-age or SALMA (Cione and Tonni, 2005), which can be correlated with the Upper Pleistocene and Groenlandian formal stage/ages (Cohen et al., 2020). There have also been recorded fossil remains of land turtles like *Geochelone* sp. (Ubilla and Perea, 1999), freshwater mollusks (Martínez and Ubilla, 2004) and pollen, that reveal a dominance of herbs, since trees and shrubs are scarce (De Oliveira et al., 2011; Ubilla and Martínez, 2016).

Corona et al. (2013) obtained an optic ages of 16, 070 +- 930 kyr (UIC3039) from this locality based in a sediment sample taken 2–3 m below the stratigraphic level where the fossil eggs was collected.

3. Material and methods

3.1. Collection

The studied material consists of a complete fossil egg from “El Caño” locality (Colonia department; south-west of Uruguay), in ravines on the banks of the Río de la Plata, near the city of Colonia (Fig. 1). Its stratigraphic position probably corresponds to Upper Pleistocene (16.070 ± 930 years; UIC3039, Corona et al., 2013). This specimen is deposited in the Museo del Indio y la Megafauna (MIM), Cerros Azules (Maldonado, Uruguay), under the catalogue number of MIM 153.

3.2. Analysis

The fossil egg MIM 153 was scanned using the Somaton Sensation CT scanner at the Hospital de Clínicas "Dr. Manuel Quintela", Montevideo in order to verify the integrity of the material and corroborate the absence of embryonic or juvenile remains.

The techniques used on the preparation and analyses of eggshells are based on previous studies (Hirsch and Packard, 1987; Hirsch, 1979, 1989; Hirsch and Quinn, 1990). This work is framed within the concepts expressed by some authors (e.g. Grellet-Tinner and Norell, 2002; Grellet-Tinner et al., 2006, 2010) about the instability of the parataxonomy classification system. The description of the micromorphological characteristics of the eggshells is based on methodologies following by Grellet-Tinner and Norell (2002), Grellet-Tinner (2006) and Grellet-Tinner et al. (2006).

Micro-structural analysis of the eggshell was performed based on fragments extracted (approximately 1 cm^2) from the fossil egg specimen. Each eggshell fragment was cleaned and immersed into water in ultrasonic bath (Branson 1510 MT) to remove any trace of sediment. After the cleaning the removed eggshell fragments were broken into smaller fragments in order to be analyzed under TLM (Nikon SMZ800), PLM (Nikon Eclise 50i POL) and SEM (Jeol JSM-5900 LV). Under TLM, observations were made in radial view and external surface. Some eggshells were used to perform petrographic thin sections, which were made at the Laboratorio de Geología of the Facultad de Ciencias (Universidad de la República, Uruguay), using a PetroThin Buehler rock cutter. The resultant thin sections were observed under the PLM with transmitted light and polarized light and then were photographed. Eggshell preparation for the SEM analyses was made following Grellet-Tinner et al. (2006) methodology at the Laboratorio de Microscopía Electrónica of the Facultad de Ciencias (Universidad de la República, Montevideo-Uruguay). Macro-structural features were identified and photographed (Camera Nikon Digital Sight Fi1, Software NIS®F3.0). Measurements of the egg specimen (major axis and maximum diameter) and its eggshell samples (thickness) were taken using digital calipers (with 0.01 of measure error) and the IT program (UTHSCSA®Image tool), respectively. The resulting images were processed and edited with Adobe Photoshop® CS6.

4. Sistematic paleontology and description

Avialae Gauthier, 1986.
Neornithes Gadow, 1893.
Palaeognathae Pycraft, 1900.
Tinamiformes Huxley, 1872.
Tinamidae Gray, 1840.
Tinamidae *gen. et sp. indet.*

4.1. Specimen and locality

A complete egg (MIM-153) from the El Caño locality, near the city of Colonia del Sacramento (Department of Colonia. South-west of Uruguay) (Fig. 1).

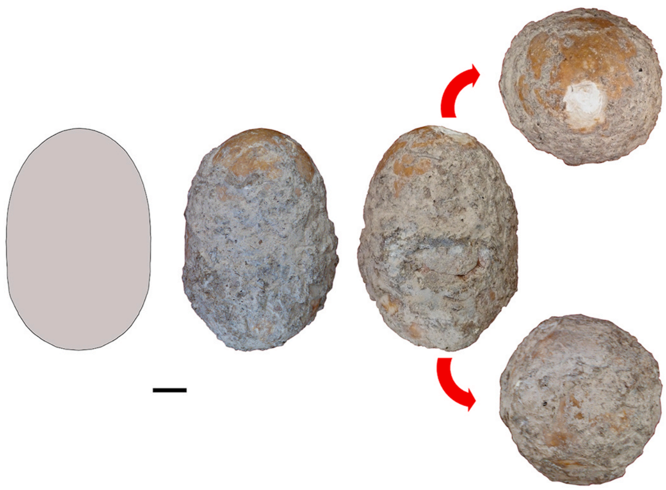

Fig. 2. Fossil egg MIM-153 in lateral and pole views. Scale 1 cm.

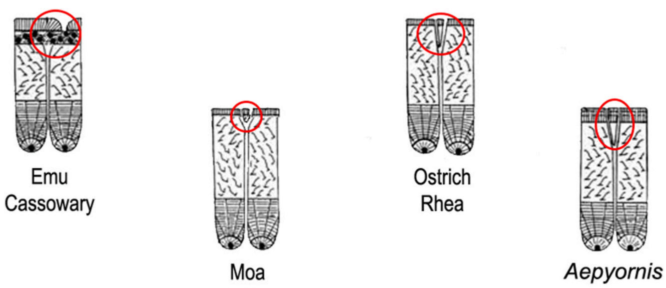

Fig. 3. Diagram of palaeognathae's eggshell units (Emu, Cassowary, Ostrich/Rhea and *Aepyornis* examples). Red circle: external apertures of the pores in a dichotomous way (Y type). Taken and modified from Mikhailov (1992) and Grellet-Tinner (2006).

4.2. *Age and horizon*

This specimen was found in layers of the Dolores Formation (Quaternary, Late Pleistocene-Early Holocene) (Fig. 1).

4.3. *Description*

This specimen corresponds to a slightly asymmetric ellipsoidal egg having major axis is of 71.6 mm and a maximum diameter of 46.5 mm in length (Fig. 2). The specimen has high diagenetic alterations (carbonate substitution) filled by consolidated carbonate matrix; however the 3D egg shape is well preserved and shows only a slight lateral compression. The poles of the egg are very similar, where the smaller pole is more flattened and less pointed compared with most other birds; indeed, in some species it is very difficult to determine which end is which (Cabot, 1992) (Fig. 2). The superficial ornamentation is smooth and avian type. The external apertures of the pores are in a dichotomous way (Y type – Fig. 3) (visible on the surface of the eggshell because the apertures of the pores are grouped in pairs – see Fig. 4), and have variable diameters (average of 100 μm), conforming a straight pore system. The eggshell thickness average is approximately 0.91 mm (see Fig. 4). The eggshell surface has carbonate minerals, which are common on levels of the Quaternary sedimentary unit. In radial view, the eggshell display three aprismatic layers (Fig. 4). Layer 1 -mammillary layer-has an average of 209.5 μm, showing an outward growth and a radial fibrous ultrastructure; however, growth core, spherulites or acicular crystals are difficult to observe due to the complete obliteration of the structures, and it is not possible to determine the limits of the shell units (Fig. 4). Layer 2 is larger (average of 704 μm), and has a prismatic arrangement of its crystals, which are more chaotic and posses vesicles (Fig. 4). Layer 3 is thinner than the previous layers (average of 176.6 μm), and has a vertical and compact arrangement of its crystals. This last layer corresponds to the "outer zone" of the shell of the parataxonomy nomenclature (Mikhailov, 1997). In the microstructures of the sub-horizontal layers, carbonate crystal growths are visualized, product of their recrystallization during the diagenesis.

5. Discussion

5.1. *Systematic and morphological comparisons*

The fossil egg here studied is assigned to class Aves due the presence of three layers on its microstructural eggshell with different thicknesses, slight asymmetry and the lack of superficial ornamentation. The assignation to order Palaeognathae is based on: 1) aprismatic condition of ultrastructural layers (a condition known to occur only in extinct and extant palaeognaths – Grellet-Tinner, 2000; Grellet-Tinner and Dyke, 2005); 2) apertures of the pores are in a dichotomous way (Y type); and 3) a larger layer 2 –prismatic layer-respect to the others (Grellet-Tinner, 2006). The relative thickness of layers (layer 2 thicker than layers 1 and 3) are mentioned by Grellet-Tinner (2006, Fig. 21A–D) and Grellet--Tinner and Dyke (2005, Fig. 1B) in reference to *Eudromia elegans* and *Rynchotus rufescens* eggshells, respectively. Layer thickness ratios are comparable to the layers observed in MIM 153 (see Figs. 4 and 6 of this work).

The Palaeognathae in comparison to Neognathae, is a clade limited to a few big flightless species (African and American ostriches, emus,

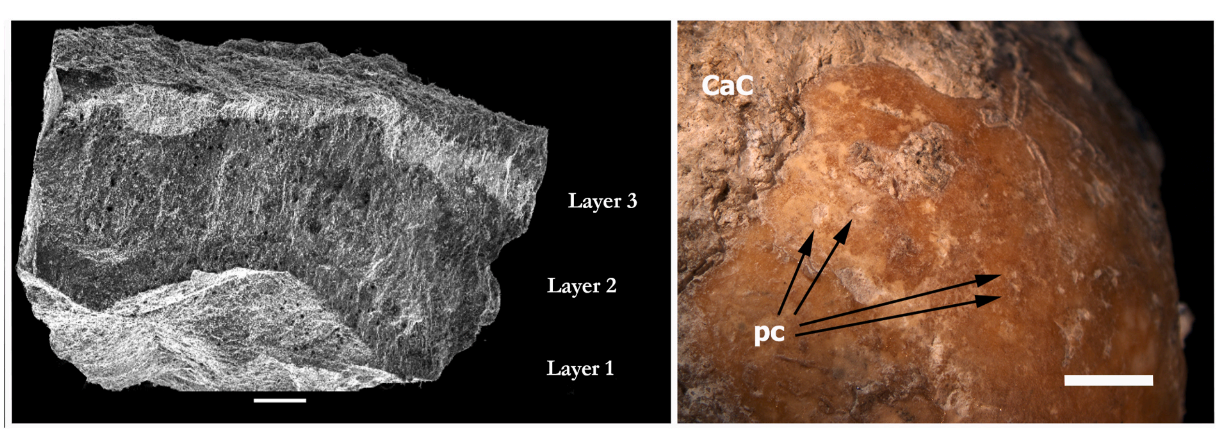

Fig. 4. Comparative SEM images showing eggshell thin sections. Scale 200 μm (left). Detail of the outer surface of the eggshell (pc: pore canal; CaC: carbonate of calcium – Scale: 0.5 cm) (right).

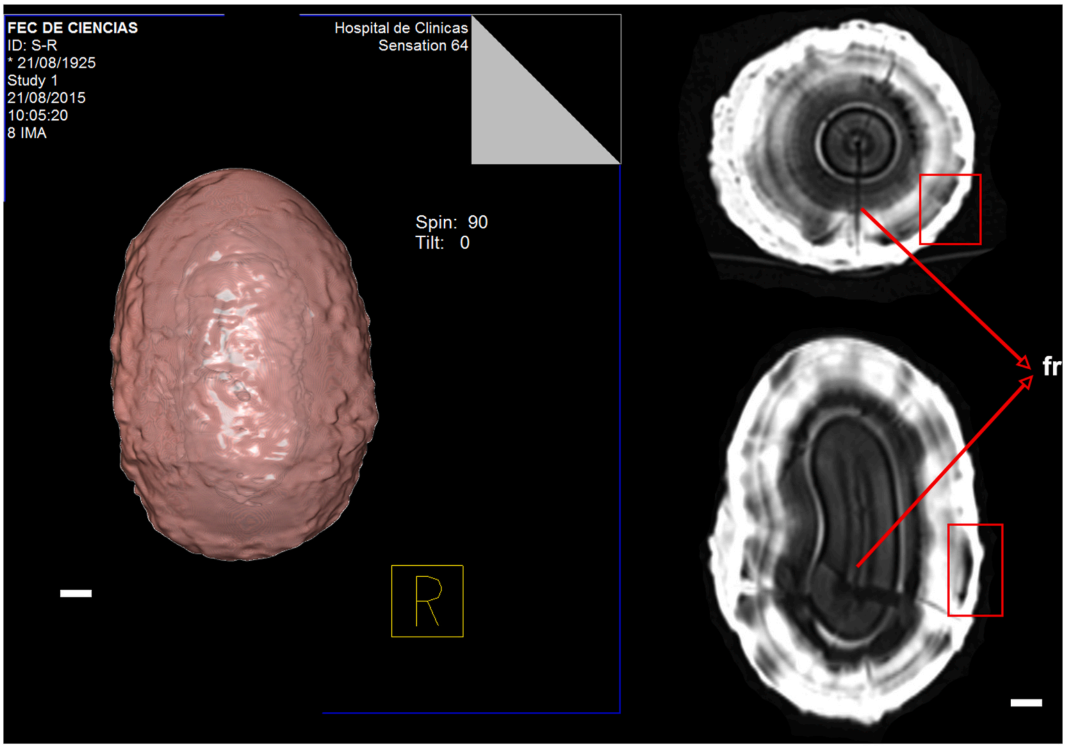

Fig. 5. 3D reconstruction on CT scanner. Scale 1 cm (left). Cross-sectional (up right) and longitudinal tomographic (down right) images of the fossil egg MIM-153 (red squares: details of the eggshell; fr: internal and external fractures – Scale: 1 cm).

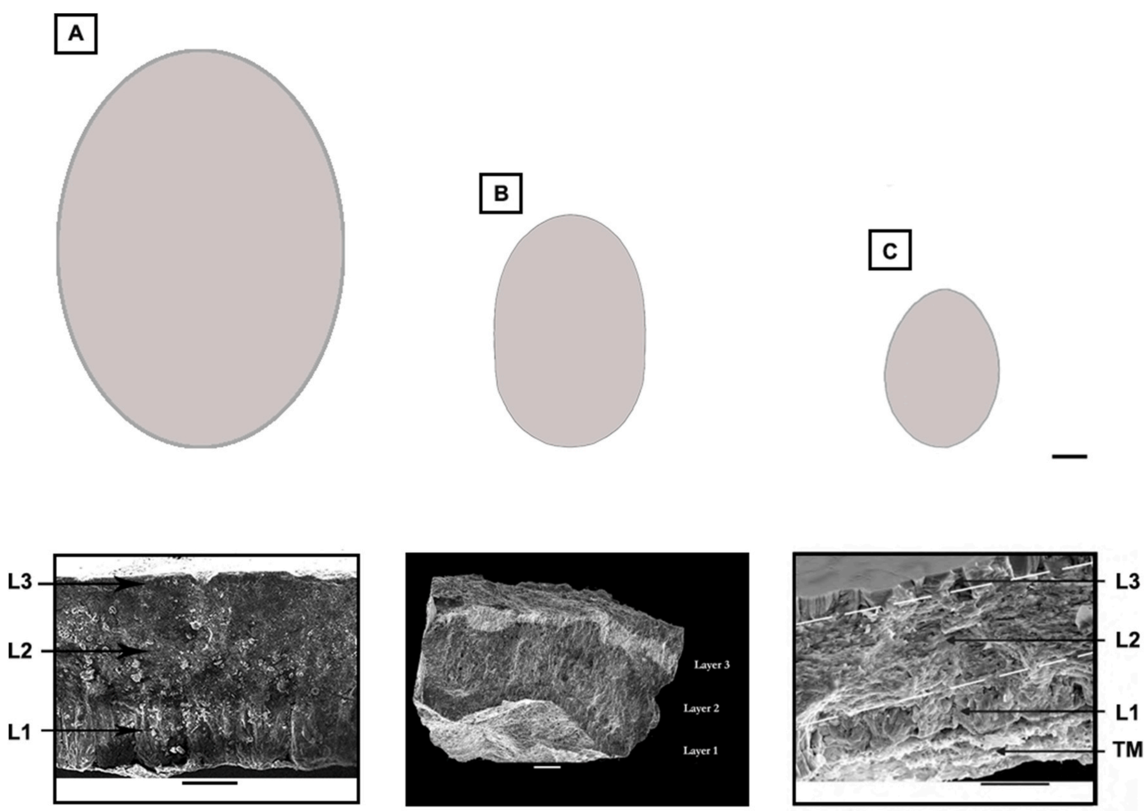

Fig. 6. Macro and micromorphology comparative scheme of the fossil egg, MIM-153, with other eggs of extant palaeognath birds. A: *Rhea americana*; B: MIM-153; C: *Eudromia elegans* (TM: testaceous membrane; L1: layer 1; L2: layer 2; L3: layer 3 – Scales: 1 cm (up), 200 μm (A and B down), 80 μm (C down). Images of *Eudromia elegans* taken and modified from Grellet-Tinner (2006).

cassowaries), the small nocturnal *Kiwi* from New Zealand, and the *Tinamou* family, which comprises over 40 small South American species that retained flight (Grellet-Tinner, 2006). Due to its oological and osteological features, the paleognath clade (ratites and tinamous) is assigned by several authors as a monophyletic group (e.g. Rich, 1980; Lee et al., 1997; Grellet-Tinner, 2006). Considering this, the tinamid eggs are larger in comparison with the size of these birds, but smaller than Rheidae eggs, in addition that all the fossil egg features showed in this work, suggest that MIM-153 is a tinamid specimen (Fig. 6).

5.2. Taphonomic implications

Throughout the taphonomic history of a fossil egg or eggshell, its original mineralogical composition is either replaced or recrystallized according to the physic-chemical conditions of the diagenetic environment. The fossil egg studied here display recrystallization by calcium carbonate. Also show an exaggerated increase in the diameter of the porous channels, as a result of the chemical dissolution (Grellet-Tinner et al., 2010) (Fig. 4). In addition, micromorphology is quite altered, in some cases making it difficult to observe structures of diagnostic importance. This process is also reflected in its macromorphology, which show aggregates of calcium carbonate matrix in the surface of the eggshell and inside of the material (Figs. 4 and 5).

CT analysis allows discarding the presence of embryonic or juvenile remains inside the fossil egg. Also, it is clearly shown in the images how the eggshell is distinguished from the sedimentary/crystalline fill (Fig. 5). These observations, plus the presence of typically oological macro and micromorphological features described above, allow us to reject the idea that the studied material corresponds to a calcareous concretion, and is indeed a fossil egg. In addition, internal fractures of this filling are observed in the images that are projected to the exterior of the eggshell. This is because the egg suffered post-fossilization fragmentation.

6. Concluding remarks

We describe a new fossil egg in an exceptional state of preservation. The microstructure, shape and size of the egg indicate affinities with fossil tinamid species. The bird that produced this egg belonged to an unknown fossil tinamid species from the Late Pleistocene of Uruguay. However, this material corresponds to the first record of a fossil avian egg from Uruguay and the first complete fossil avian egg from the Quaternary of South America.

Credit author statement

Andrés Batista: Conceptualization, Methodology, Validation, Investigation, Resources, Writing – original draft, Writing – review & editing, Visualization, Project administration. Washington Jones: Conceptualization, Investigation, Resources, Writing – original draft, Writing – review & editing, Project administration. Andrés Rinderknecht: Conceptualization, Writing – review & editing, Project administration.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

Angst, D., Buffetaut, E., Lécuyer, C., Amiot, R., Smektala, F., Giner, S., Méchin, A., Méchin, P., Amoros, A., Leroy, L., Guiomar, M., Tong, H., Martinez, A., 2015. Fossil avian eggs from the Palaeogene of southern France: new size estimates and a possible taxonomic identification of the egg layer. Geol. Mag. 152, 70–79.

Anderson, A., 1989. Prodigious Birds: Moas and Moas-Hunting in NewZealand. Cambridge University Press, Cambridge, ISBN 0-521-35209-6, pp. 17–238.

Apolinaire, E., Turnes, L., 2008. Diferenciación específica de rheidos a partir de fragmentos de cáscaras de huevo. Su aplicación en sitios arqueológicos del Holoceno Tardío. In: Berón, M., Luna, L., Bonomo, M., Montalvo, C., Aranda, C., Carrera Aizpitarte, M. (Eds.), Mamül Mapu: pasado y presente desde la arqueología pampeana. Editorial Libros del Espinillo (Ayacucho, Pcia. De Buenos Aires), pp. 253–260, 1666-2105.

Balanoff, A.M., Rowe, T., 2007. Osteological description of an embryonic skeleton of the extinct elephant bird, Aepyornis (Palaeognathae: ratitae). J. Vertebr. Paleontol. 27 (Suppl. 4), 1–53.

Bertelli, S., Chiappe, L.M., 2005. Earliest tinamous (Aves: palaeognathae) from the Miocene of Argentina and their phylogenetic position. Contrib. Sci. (Los Angel.) 502, 1–20.

Brodkorb, P., 1963. Catalogue of fossil birds. Bulletin of Florida State Museum 7, 179–293.

Brum, L., 2009. Análisis arqueofaunístico de huevos de ñandú (*Rhea americana*) en un sitio prehistórico del litoral atlántico uruguayo. In: Bourlot, T., Bozzuto, D., Crespo, C., Hecht, A., Kuperszmit, N. (Eds.), Entre pasados y presentes II: estudios contemporáneos en Ciencias Antropológicas. Fundación de Historia Natural Féliz de Azara, Argentina, Buenos Aires, 978-987-23545-1-0. 323-339.

Cabot, J., 1992. Order tinamiformes. In: del Hoyo, J., Elliot, A., Sargatal, J. (Eds.), Handbook of the Birds of the World, vol. 1. Lynx Edicions, Barcelona, pp. 112–138.

Campbell, K.E., 1979. The non-passerine Pleistocene avifauna of the talara tarseeps, Northwestern Perú. Royal Ontario museum. Life Sci. Contrib. 118, 1–203.

Carpenter, K., Hirsch, K., Horner, J., 1994. Dinosaurs, Eggs and Babies. Cambridge University Press, New York, p. 392.

Cenizo, M.M., Tambussi, C.P., Montalvo, C.I., 2012. Late miocene continental birds from the cerro azul formation in the pampean region (central-southern Argentina). Alcheringa 36 (1), 47–68.

Chiappe, L.M., 1991. Fossil birds from the miocene pinturas formation of southern Argentina. J. Vertebr. Paleontol. 11, 21–22.

Cione, A., Tonni, E.P., 2005. Bioestratigrafía basada en mamíferos del Cenozoico superior de la provincia de Buenos Aires, Argentina. En. In: de Barrio, R.E., Etcheverry, R.O., Caballé, M.F., Llambías, E. (Eds.), Relatorio del XVI° Cong. Geol. Arg. La Plata, pp. 183–200.

Cohen, K.M., Finney, S.C., Gibbard, P.L., Fan, J.-X., 2020. The ICS International chronostratigraphic chart. Episodes 36, 199–204.

Corona, A., Perea, D., McDonald, H.G., 2013. *Catonyx cuvieri* (Xenarthra, Mylodontidae, Scelidotheriinae) from the late Pleistocene of Uruguay, with comments regarding the systematics of the subfamily. J. Vertebr. Paleontol. 33 (5), 1214–1225.

Deeming, D.C., Ruta, M., 2015. Egg shapes changes at theropod-bird transition, and a morphometric study of amniote eggs. R. Soc. open sci. 1, 140311. https://doi.org/10.1098/rsos.140311.

De Oliveira, K., García, J., Daners, G., Ubilla, M., Goso Aguilar, C., Bistrichi, C., 2011. Contribucao palinofloristica para o cenario do Pleistoceno superior-Holoceno inferior na bacia do Rio Santa Lucia, Sul de Uruguai. In: Souza Carvalho, I., Kumar, N., Strohschoen, O., Cunha, C. (Eds.), Paleontología: cenários de Vida, vol. 3. Interciencia, Rio de Janeiro.

Gadow, H., 1893. Vogel. II. Systematischer theil. Pp. 1–303. In: Klassen und Ordnungen des Their-Reichs (H. G. Bronn. C. F. Winter, Leipzig, Germany.

Gauthier, J., 1986. Saurischian monophyly and the origin of birds. In: The Origin of Birds and the Evolution of Flight (K. Padian. California Academy of Science, San Francisco, California.

Gill, B.J., 2006. A catalogue of moa eggs (Aves: Dinornithiformes). Rec. Auckl. Mus. 43, 55–80.

Goso, H., 1972. Cuaternario. Programa de Estudio y Levantamiento de Suelos. Ministerio de Ganadería Agricultura y Pesca, Informe interno, Montevideo, p. 12.

Gray, G.R., 1840. A List of the Genera of Birds, with Their Synonyma an Indication of the Typical Species of Each Genus. Compiled from Various Sources. - pp. i-viii [= 1-8], i-ii [= 1-2]. Richard & Taylor, London, England, pp. 1–80.

Grellet-Tinner, G., 2000. Phylogenetic interpretations of eggs and eggshells. In: Bravo, A. M., Reyes, T. (Eds.), First International Symposium on Dinosaur Eggs and Babies, 61-75. Isona I Conca Dellà, Catalonia.

Grellet-Tinner, G., 2006. Phylogenetic interpretation of eggs and eggshells: implications for phylogeny of Palaeognathae. Alcheringa 30, 141–182.

Grellet-Tinner, G., Norell, M., 2002. An avian egg from the campanian of Bayn Dzak, Mongolia. Note, Journal of Vertebrate Paleontology 22 (3), 719–721.

Grellet-Tinner, G., Dyke, G., 2005. The eggshell of the Eocene bird *Lithornis*. Acta Paleontologica Polonica 50 (4), 831–835.

Grellet-Tinner, G., Chiappe, L.M., Norell, M., Bottjer, D., 2006. Dinosaur eggs and nesting behaviors: a paleobiological investigation. Palaeogeogr. Palaeoclimatol. Palaeoecol. 232, 294–321.

Grellet-Tinner, G., Corsetti, F., Buscalioni, A., 2010. The importance of microscopic examinations of eggshells: discrimination of bioalteration and diagenetic overprints from biological features. J. Iber. Geol. 36, 181–192.

Grellet-Tinner, G., Spooner, N., Worthy, T., 2016. Is the "Genyornis" egg of a mihirung or another extint bird from the Australian dreamtime? Quat. Sci. Rev. 133, 147–164. https://doi.org/10.1016/j.quascirev.2015.12.011.

Guthrie, D.A., Thomas, H.W., Kennedy, G.L., 2000. A new species of extinct late Pleistocene puffin (Aves: alcidae) from the southern California channel Islands. In: Proceedings of a Fifth California Islands Symposium. U.S. Dept. of the Interior Minerals Management Service. Pacific OCS Region (published as CD) MMS 99-0038, 525–30.

Hechenleitner, M., Grellet-Tinner, G., Fiorelli, L., 2015. What do giant titanosaur dinosaus and modern Australasian megapodes have in common? PeerJ 3, e1341. https://doi.org/10.7717/peerj.1341.

Hirsch, K.F., 1979. The oldest vertebrate egg? J. Paleontol. 53 (5), 1068–1084.

Hirsch, K.F., 1989. Upper Jurassic dinosaur eggs from Utah. Science 243, 1711–1713.

Hirsch, K.F., Packard, M.J., 1987. Review of fossil eggs and their shell structure. Scanning Microsc. 1 (1), 383–400.

Hirsch, K.F., Quinn, B., 1990. Eggs and eggshell fragments from the upper cretaceous two medicine formation of Montana. J. Vertebr. Paleontol. 10 (4), 491–511.

Huxley, T., 1872. A Manual of Anatomy of Vertebrated Animals. D. Appleton and Company, p. 234.

Huynen, L., Gill, B.J., Millar, C.D., Lambert, D.M., 2010. Ancient DNA reveals extreme egg morphology and nesting behavior in New Zealand's extinct moa. Proceedings of the National Academy of Sciences of the USA 107, 16201–16206.

Ksepka, D., 2011. March of the Fossil Penguins. https://fossilpenguins.wordpress.com/tag/eggs/.

Lee, K., Feinstein, J., Cracraft, J., 1997. The phylogeny of ratite birds: resolving conflicts between molecular and morphological data sets, 173-208. In: Mindell, D. (Ed.), Avian Molecular Evolution and Systematics. Yale University Press, New Haven.

Manzuetti, A., Perea, D., Rinderknecht, A., Ubilla, M., 2018. New canid remains from Dolores Formation, late pleistocene-early Holocene, Uruguay. J. Mamm. Evol. 25, 391–396.

Martínez, S., Ubilla, M., 2004. El cuaternario en Uruguay. In: Veroslavsky, G., Ubilla, M., Martínez, S. (Eds.), Cuencas Sedimentarias del Uruguay: Geología, Paleontología y Recursos Naturales-Cenozoico. DIRAC, Montevideo, pp. 195–227.

Medina, M.E., Hospitaleche, C.A., Turnes, L., Apolinaire, E., Pastor, S., 2011a. Huevos de Rhea pennata en el Holoceno Tardío de la provincia de Córdoba (Argentina): implicaciones ambientales, zoogeográficas y arqueológicas. ARCHAEOFAUNA (20), 157–169.

Medina, M., Pastor, S., Apolinaire, E., Turnes, L., 2011b. Late Holocene subsistence and social integration in Sierras of Córdoba (Argentina): the South-American ostrich eggshells evidence. J. Archaeol. Sci. 38 (9), 2071–2078.

Medina, M.E., Picasso, M.B., Campos, M.R., Avila, N.C., 2019. Tarsometatarsus, eggshells, and the species level identification of large-sized flightless birds from Boyo Paso 2 (Sierras of Córdoba, Argentina). Int. J. Osteoarchaeol. 29 (4), 584–594.

Mercerat, A., 1897. Note sur les oisseaux fossiles de la République Argentine. An. Soc. Cient. Argent. 43, 222–240.

Mikhailov, K.E., 1992. The microstructure of avian and dinosaurian eggshell: phylogenetic implications. In: Campbell, K.E., red, J. (Eds.), Papers in Avian Paleontology Honoring Pierce Brodkorb, vol. 36. Natural History Museum of Los Angeles Conty. Science Series, pp. 361–373p.

Mikhailov, K.E., 1997. Fossil and recent eggshell in amniotic vertebrates: fine structure, comparative morphology and classification. Special Papers in Paleontology 56, 1–79p.

Miller, G.H., Magee, J.W., Johnson, B.J., Fogel, M.L., Spooner, N.A., McCulloch, M.T., Aycliffe, L.K., 1999. Pleistocene extinction of Genyornis newtoni: human impact on Australian megafauna. Science 283, 181–205.

Olson, S.L., Hearty, P.J., 2003. Probable extirpation of a breeding colony of Short-tailed Albatross (Phoebastria albatrus) on Bermuda by Pleistocene sea-level rise. Proceedings of the National Academy of Sciences of the USA 100, 12825–12829.

Olson, S.L., Hearty, P.J., 2013. Fossilized egg indicates probable breeding of Brown Pelican (Pelecanus occidentalis) on Bermuda in the Middle Pleistocene. Proc. Biol. Soc. Wash. 126, 169–177.

Panario, D., Gutierrez, O., 1999. The continental uruguayan Cenozoic: an overview. Quat. Int. 62, 75–84.

Picasso, M.B.J., Degrange, F.J., 2009. El género Nothura (Aves, Tinamidae) en el Pleistoceno (Formación Ensenada) de la provincia de Buenos Aires, Argentina. Rev. Mex. Ciencias Geol. 26, 428–432.

Pycraft, W.P., 1900. On the morphology and phylogeny of the palaeognathae (ratitae and crypturi) and Neognathae (carinatae). Trans. Zool. Soc. Lond. 15, 149–290.

Rich, P.V., 1980. The Australian Dromornithidae: a group of extinct large ratites. In: Campbell, K.E. (Ed.), Papers in Avian Paleontology Honoring Hildegarde Howard. Natural History Museum of Los Angeles County, Contributions of Science, vol. 330, pp. 93–103.

Rinderknecht, A., 1999. Estudios sobre la familia Glyptodontidae Gray, 1869. I. Nuevos registros para el Uruguay y consideraciones sistemáticas (Mammalia: cingulata). Comun Paleontol. Mus. Hist. Nat. Montev. 2 (31), 145–156 lám.1. Montevideo.

Tambussi, C., 1987. Catálogo crítico de los Tinamidae (Aves: tinamiformes) fósiles de la República Argentina. Ameghiniana 24, 241–244.

Tambussi, C., 1989. Las aves del Plioceno-tardío Pleistocenotemprano de la Provincia de Buenos Aires. Unpublished dissertation, Universidad Nacional de La Plata, Argentina.

Tambussi, C., Noriega, J., 1996. Summary of the avian fossil record from southern south américa. Münchner Geowissenschaftliche Abhandlungen 30, 245–264.

Tambussi, C., Tonni, E.P., 1985. Un Tinamidae (Aves: tinamiformes) del Mioceno tardío de La Pampa (República Argentina) y comentarios sobre los tinámidos fósiles argentinos. Revista de la Asociación Paleontológica Argentina 14, 4.

Tambussi, C., Noriega, J., Tonni, E.P., 1993. Late Cenozoic birds of Buenos Aires Province (Argentina): an attempt to document quantitative faunal changes. Paleoecology 101, 117–129.

Teisseire, A., 1928. Contribución al estudio de la geología y paleontología de la República Oriental del Uruguay. Región de Colonia. Anales de la Universidad 37 (122), 319–469 (Montevideo).

Tonni, E.P., 1977. Los tinámidos fósiles argentinos I. El género tinamisornis rovereto, 1914. Ameghiniana 14, 225–232.

Ubilla, M., Perea, D., 1999. Quaternary fossil vertebrates of Uruguay: a biostratigraphic, biogeographic and climate overview. Quat. S. Am. Antarct. Peninsula 12, 75–90.

Ubilla, M., Rinderknecht, A., 2014. Comparative analysis of Galea (rodentia, caviidae) and expanded diagnosis of *Galea ortodonta* Ubilla & Rinderknecht, 2001 (late Pleistocene, Uruguay). Geobios 47, 255–269.

Ubilla, M., Martínez, S., 2016. Geology and paleontology of the quaternary of Uruguay. In: Lohmann, G., Mysak, L.A., Notholt, J., Rabassa, J., Unnithan, V. (Eds.), Springer Briefs in Earth System Sciences. South America and the Southern Hemisphere. Springer Nature, Basel, p. 77.