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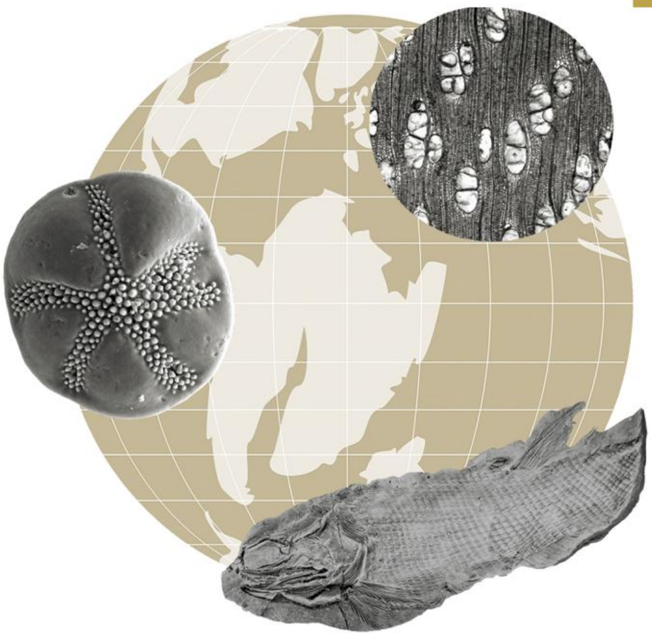

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FIRST RECORD OF FAVEOLOOLITHIDAE EGGSHELLS FROM THE LATE MAASTRICHTIAN OF THE LAGO COLHUÉ HUAPI FORMATION, GOLFO SAN JORGE BASIN, ARGENTINA

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Running Header: CARDOZO *ET AL*: FAVEOLOOLITHIDAE EGGSHELLS FROM CHUBUT GROUP

Short Description: First record of Faveoloolithidae eggshells in the late Maastrichtian of the Lago Colhué Huapi Formation, Golfo San Jorge Basin, Argentina

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Abstract. This study reports the first occurrence of Faveoloolithidae eggshells from "the upper section" (late Maastrichtian) of the Lago Colhué Huapi Formation, Chubut Group, in the Golfo San Jorge Basin, Argentina. A total of 161 eggshell fragments were examined using a binocular microscope, petrographic microscope, and scanning electron microscope. The specimens show morphological features consistent with the oofamily Faveoloolithidae, including a dinosauroid-spherulitic basic organization, a filispherulitic structural morphotype and a multicanaliculate pore system. However, as evidenced in others South American record, their well-developed external ornamentation and greater thickness distinguish them from other ootaxa within the oofamily; therefore, they are assigned to Faveoloolithidae indet. These eggshell fragments were recovered within deposits interpreted as low energy, shallow water bodies, developed in floodplain environments near the coastline. These levels are characterized by a remarkable abundance of hadrosaurid remains and, to date, the absence of sauropod fossils. Although an association with hadrosaurids might be suggested, a titanosaurian affinity cannot be excluded, as these sauropods are traditionally linked to Faveoloolithidae eggshells. This uncertainty reflects the complexity of taxonomic assignments in fragmentary oological records.

Keywords. Eggshells. Faveoloolithidae. Dinosauria. Chubut. Golfo San Jorge Basin.

Resumen. PRIMER REGISTRO DE CÁSCARAS DE HUEVO FAVEOLOOLITHIDAE EN EL MAASTRICHTIANO TARDÍO DE LA FORMACIÓN LAGO COLHUÉ HUAPI, CUENCA DEL GOLFO SAN JORGE, ARGENTINA. Este trabajo presenta el primer registro de cáscaras de huevo Faveoloolithidae en "la sección superior" (Maastrichtiano tardío) de la Formación Lago Colhué Huapi del Grupo Chubut, en la Cuenca del Golfo San Jorge, Argentina. Se analizaron 161 fragmentos de cáscaras de huevos bajo lupa binocular, microscopio petrográfico y microscopio electrónico de barrido. Los especímenes muestran características morfológicas consistentes con la oofamilia Faveoloolithidae, tales como tipo básico de organización dinosauroide-esferulítico, un morfotipo estructural filiesferulítico y sistema poral multicanaliculado. Sin embargo, como se evidencia en otros registros sudamericanos, la desarrollada ornamentación externa y el gran espesor, permiten diferenciarlos de los ootaxones formalmente establecidos para esta oofamilia, por lo que se asignan como Faveoloolithidae indet. Estos fragmentos de cáscaras fueron recuperados de depósitos interpretados como cuerpos de agua someros de baja energía, desarrollados en planicies de inundación y en entornos próximos a la costa. . Dichos niveles se caracterizan por una notable abundancia de restos de hadrosáuridos y hasta el momento la ausencia de restos de saurópodos. Aunque, podría sugerirse una asociación con hadrosáuridos, no puede excluirse una afinidad con saurópodos titanosaurios, tradicionalmente propuestos como los productores de cáscaras faveoloolítidas. Esta incertidumbre refleja la complejidad de las asignaciones taxonómicas en registros oológicos fragmentarios.

Palabras clave. Cáscaras de huevos. Faveoloolithidae. Dinosauria. Chubut. Cuenca del Golfo San Jorge.

FOSSIL OOLOGICAL REMAINS are exceptional sources of information about the reproductive strategies of extinct amniotes, including dinosaurs (Grellet-Tinner *et al*., 2006; Zelenitsky & Therrien, 2008; Salgado *et al*., 2009; Vila *et al*., 2010; Tanaka *et al*., 2015; Choi *et al*., 2020; Ezquerro *et al*., 2024). This type of fossil material provides insights into several aspects of their biology, such as incubation characteristics and modes (Seymour, 1979; Deeming, 2006; Grellet-Tinner *et al*., 2004, 2006; Varricchio *et al*., 2013; Tanaka *et al*., 2018; Dhiman *et al*., 2022). They also elucidate the paleoenvironmental conditions associated with nesting sites (Horner, 1984; Nadon, 1993; Cojan *et al*., 2003; Bojar *et al*., 2005; Liang *et al*., 2009; Fiorelli *et al*., 2012; Paik *et al*., 2012; Kim *et al*., 2022, 2025). Collectively, these studies contribute significantly to understanding archosaurian ecology. To date, the fossil record of dinosaur eggs and eggshells has been documented on all continents except Oceania and Antarctica (Paik *et al*., 2012).

Among the different types of dinosaur eggs described and classified (see Mikhailov 1991; references cited therein), the oofamily Faveoloolithidae Zhao and Ding 1976 is particularly noteworthy. It was first reported in Upper Cretaceous deposits in China and Mongolia (Sochava, 1969; Zhao & Ding, 1976). The occurrence of these eggshells has been documented primarily in Upper Cretaceous deposits from both the Northern and Southern Hemispheres, with particularly notable examples reported from Asia and South America (see Tab. 1).

The Lago Colhué Huapi Formation (Coniacian – Maastrichtian; Casal *et al*., 2015) crops out in the Golfo San Jorge Basin (Fig. 1), and it is notable for its extensive and diverse paleontological record (Casal *et al*., 2016, 2022; Ibiricu *et al*., 2021, and references therein). However, dinosaur eggshells are rare in this formation, and the first discoveries were reported by Casal *et al*. (2020), Ibiricu *et al*. (2021) and Cardozo *et al*. (2022a, b, 2023) from the uppermost levels of the unit. These levels are assigned to the late Maastrichtian based on the presence of palynomorphs that are biostratigraphically diagnostic of that time interval (Vallati *et al*., 2016, 2020). In this context, the present contribution primarily aims to broaden the existing fossil record of these eggshells by analyzing the macro and microstructures of the fragments recovered from the uppermost levels of the Lago Colhué Huapi Formation. Furthermore, the study also seeks to infer aspects of the paleoenvironment in which the dinosaurs that produced these eggs lived.

This will contribute to the reconstruction of the paleoecological conditions under which these organisms potentially nested or reproduced.

Institutional abbreviations. **UNPSJB** Universidad Nacional de la Patagonia San Juan Bosco, Comodoro Rivadavia, Chubut Province, Argentina.

Table 1

Figure 1.

GEOLOGICAL SETTING

The Golfo San Jorge basin is a predominantly extensional basin, located in central Patagonia, Argentina (Fig. 1.1–1.2). The genesis of the basin is linked to the fragmentation of the Gondwana supercontinent and the opening of the Atlantic Ocean in the Late Jurassic–Early Cretaceous interval (Fitzgerald, 1990; Figari *et al.*, 1999). Part of the Cretaceous sedimentary infill of the basin is represented by the Chubut Group (Lesta, 1968; Lesta & Ferello, 1972; among others), which comprises thick lacustrine and fluvial deposits with a significant volcaniclastic and pyroclastic component (Umazano *et al.*, 2008, 2012; Paredes *et al.*, 2007, 2021, among others). This continental sequence extends from the Barremian (Hechem & Strelkov 2002; Vallati, 2013) to the late Maastrichtian (Casal *et al.*, 2015; Vallati *et al.*, 2016, 2020). The Chubut Group includes the Pozo D-129, Matasiete, Castillo, Bajo Barreal, Laguna Palacios and Lago Colhué Huapi formations. Among these units, the Lago Colhué Huapi Formation (Coniacian–Maastrichtian; Casal *et al.*, 2015) comprises the most prolific in terms of paleontological content within the Chubut Group due to its exceptional record that reflects the rich biodiversity (Ibiricu *et al.*, 2021; Casal *et al.*, 2016, 2022; references cited therein). This unit comprises fluvial deposits developed in moderately to highly sinuous channelized systems and well-drained floodplains, under a context of high accommodation (Allard & Casal, 2013; Casal *et al*., 2015; Paredes *et al*., 2021). Depending on its to its position within the basin, the unit is overlain by the Salamanca Formation, Laguna Palacios Formation, or the ‘pre-Salamanca’ basalt (*sensu* Ferello, 1969), also called La Angostura Basalt by Clyde *et al*. (2014) (see Casal *et al*., 2015). The uppermost levels of the formation correspond to the informally defined ‘upper section’ of the unit (*sensu* Casal *et al*., 2016, 2020; Ibiricu *et al*., 2021, 2025), whose outcrops are well exposed at the headwaters of the Río Chico (Fig. 1.3–1.5). This section can be recognized by an increase in the sinuosity of fluvial channels (Casal *et al*., 2025). It, also differs from the middle and lower sections by reflecting warm, humid and no seasonal paleoclimatic conditions, and from a paleontological perspective, abundance of the hadrosaurids remains. (Casal *et al*., 2020; Ibiricu *et al*., 2021, 2025). Furthermore, a late Maastrichtian age has been proposed for this "upper section," based on its paleontological record and observed stratigraphic relationships (Vallati *et al*., 2016, 2017, 2020; Casal *et al*., 2020; Ibiricu *et al*., 2021).

MATERIALS AND METHODS

The fossil eggshells (n = 161) analyzed were recovered as rolled remains on the northern slope of the informally named 'Cerro del Hadro'. The specimens are housed in the vertebrate paleontology collection of the Universidad Nacional de la Patagonia San Juan Bosco (Repositorio Científico y Didáctico “Dr. Eduardo Musacchio”), and are catalogued as UNPSJB-PV 1082/205–/365. Eggshell thickness was measured using a Stainless Hardened Digital Calliper. Macrocharacter observations were conducted through both radial and tangential views using a Motic SMZ 168 binocular microscope at the Laboratorio de Bioestratigrafía “Dr Eduardo Musacchio” (UNPSJB). For microcharacter analysis thin sections were prepared and examined in radial and tangential orientations under a Zeiss Axioskop 40 petrographic microscope at the Laboratorio Patagónico de Petrotectónica (UNPSJB). These microscopic observations were performed using both crossed and parallel polarizers. The pore density was also measured using this same equipment, in tangential view, using a rectangular grid with 1 mm spacing. This methodology allowed for a systematic estimation of pore density, expressed as the number of pores per 100 mm² of surface area, following the criteria proposed by Mikhailov (1997). In addition, these characteristics were corroborated using a JEOL JSM-6510LV scanning electron microscope (SEM) at the UNPSJB.

A detailed description of the eggshells was made using the terminology established by Mikhailov (1991, 1997), which facilitated their taxonomic assignment to a specific oofamily.

RESULTS

SYSTEMATIC PALEONTOLOGY

Oofamily FAVEOLOOLITHIDAE Zhao and Ding, 1976

Oogenus indet.

A total of 161 fossil eggshells were recovered as rolled remains in “Cerro del Hadro” (Fig. 2) showing no evidence of transport and thickness values ranging between 3.71–5.82 mm (mean value= 4.44; SD= 0.53; n=161). The main micro and macrostructural features described below are summarized in Table 2. Radial sections reveal that the shell units develop through the branching of spherulites, growing in strong competition with each other (Fig. 3.1–3.3). This feature is consistent with the structural morphotype designated as filispherulitic by Mikhailov (1991). In addition, arched accretion lines are evident, extending transversely from the base throughout the thickness of the eggshell (Fig. 3.4). At the base of each shell unit, fused mammillae can also be seen (Figs. 3.3–

3.4), with an inter-mammillary spacing ranging from 0.62 mm to 1.50 mm (Mean=0.925 mm; Standard Deviation= 0.24; n=29). Irregularly shaped pore canals are positioned between these shell units (Fig. 3.3–3.4). In tangential views, these structures exhibit shapes ranging from circular to oval (Fig. 3.5), with diameters between 0.1–0.3 mm. Additionally, the external pore density is 655-671/100mm^2 (Mean= 663/100 mm^2= 6,63/mm^2; Standard Deviation=11, 3; n=2) . This arrangement and characteristic morphology correspond to a multicanaliculate pore system, as defined by Mikhailov (1991).

On outer surface of the eggshell fragments, nodular elevations can be clearly observed, forming the dome-shaped apex of each shell unit (Figs. 3.6). These nodes exhibit a subcircular to slightly elliptical morphology (Fig. 3.6–3.7), with diameters varying between 0.3 and 0.7 mm (mean value=0.42; Standard Deviation= 0.10; n=100). The external surface features are consistent with the compactituberculate ornamentation type defined in the classification of Mikhailov (1991). In thin section, under petrographic microscope observation in radial view, a distinctive fan-shaped extinction pattern becomes evident as the stage is rotated under crossed nicols. This optical property corresponds to the basic dinosauroid-spherulitic structural organization as outlined in the parataxonomic classification proposed by Hirsch and Quinn (1990) and Mikhailov (1991). Thus, these features collectively support the classification of the eggshells UNPSJB-PV 1082/205–/365 from the Lago Colhué Huapi Formation within the oofamily Faveoloolithidae (Zhao & Ding, 1976).

Table 2

Figure 2

Figure 3

Figure 4

Figure 5

DISCUSSION

Taxonomic considerations and potential dinosaur affinities

The eggshell fragments UNPSJB-PV 1082/205–/365, recovered from the “upper section” (late Maastrichtian) of the Lago Colhué Huapi Formation, exhibit a series of diagnostic features. Among these are a filispherulitic structural morphotype (*sensu* Mikhailov, 1991), a multicanaliculate pore system (*sensu* Mikhailov, 1991), and external ornamentation consistent with the compactituberculata type (*sensu* Mikhailov, 1991). These characteristics support their assignment to the oofamily Faveoloolithidae, originally established by Zhao and Ding (1976) based on eggs and eggshells from the Upper Cretaceous of China and Mongolia exhibiting a filispherulitic morphotype and a multicanaliculate pore system. In contrast to the Lago Colhué Huapi Formation eggshells, the originally described specimens exhibit smooth to slightly rugose external surfaces lacking clear ornamentation (see Tab. 3). Additionally, Asian oogenera possess significantly thinner eggshells and narrower thickness ranges than the South America specimens (see Tab. 3). Consequently, the eggshells UNPSJB-PV 1082/205–/365 cannot be assigned to either *Faveoloolithus ningxiaensis* Zhao and Ding, 1976 or *Youngoolithus xiaguanensis* Zhao, 1979. Notably, the eggshells from the Lago Colhué Huapi Formation also differ from the oogenus *Hemifaveoloolithus* Wang *et al*. 2011 by exhibiting greater eggshell thickness and a well-developed outer surface ornamentation, features that are not observed in the Asian material (see Tab. 3). Furthermore, while the original description does not provide quantitative data on pore diameter or pore density per mm^2, subsequent studies (Zou *et al*., 2013; He *et al*., 2025) report values for these parameters. However, the methodology by which these measurements were obtained is not clear, making direct comparison with the materials studied here difficult. In any case, the pore diameters and pore densities reported for *Hemifaveoloolithus* are lower than those documented in the Lago Colhué Huapi specimens. On the other hand, as the original description of the oogenus *Hormoolithus* Wang *et al*. 2022 was not available for direct analysis, the present comparison relies on the data reported by He *et al*. 2025 (see Tab. 3). As with other Asian oogenera, the main differences are related to the eggshell thickness and external surface. Consequently, the assignment of the UNPSJB-PV 1082/205–/365 eggshells to this oogenus is not possible. Regarding the oogenus *Propagoolithus* Kim *et al*. 2019, the material from the Lago Colhué Huapi Formation exhibits significant variations in eggshell thickness and outer surface ornamentation, which are consistent with the patterns observed in comparison with other Asian oogenera discussed above. Patagonian specimens are characterized by thicker eggshells, a wider range of variation, as well as, a prominent external ornamentation, in contrast to *Propagoolithus*, in which ornamentation has been weakly reported. On the other hand, quantitative values for pore density were not provided in the original description of *Propagoolithus*. However, He *et al*. (2025) reassigned the oospecies *Parafaveoloolithus guoqingsiensis* to *Propagoolithus*, on the basis that it exhibits the diagnostic characteristics of *Propagoolithus* but lacks the defining features of *Parafaveoloolithus*. Based on this reassignment, those authors supplemented the missing pore density data for *Propagoolithus* using measurements from *P. guoqingsiensis* (see Tab. 3). In this context, these values are considerably lower than those reported in the Lago Colhué Huapi eggshells. Thus, these materials cannot be assigned to this specific oogenera. These differences also extend to the oogenus *Parafaveoloolithus* Zhang, 2010. Therefore, attributing the Lago Colhué Huapi Formation materials to this oogenus is also dismissed. It should be noted that *Duovallumoolithus* erected by Zheng *et al*.

(2018) is currently considered an invalid oogenus (He *et al*., 2025; Mao *et al*., in press) as its diagnostic features are well known within *Parafaveoloolithus*. For this reason, those authors reassigned *Duovallumoolithus shangdanensis* as *Parafaveoloolithus shangdanensis comb. nov*. In this context, its diagnostic characteristics are also incompatible with the materials studied here (see Tab. 3).

In this region, eggshells belonging to this oofamily have been found in Argentina and Uruguay (Fernández *et al*., 2022) and reported as Faveoloolithidae indet. or less frequently *Sphaerovum erbeni*. These eggshells show macro and microstructural characteristics that are comparable to those seen in the fragments UNPSJB-PV 1082/205–/365 from the Lago Colhué Huapi Formation. In particular, the material described herein shows broad similarities with other Argentinian records, in terms of eggshell thickness, pore diameter and external ornamentation (see Tab. 4). However, a certain degree of variability is evident when comparing quantitative parameters. For example, the thickness of the Chubut specimens (3.71–5.82 mm) falls within the range reported for Río Negro and partially overlaps with La Rioja and La Pampa. Also pore diameters (0.1–0.3 mm) are consistent with previously described values and the pore density per mm^2 recorded in this study is higher than in other Argentinian materials (see Tab. 4).

Furthermore, the macrostructural features which clearly separate South American record from Asian ootaxa, were also noticed in other materials documented from Cretaceous units across this region (Fernández, 2013; Fernández *et al*., 2022). Apart from differences in eggshell thickness and external ornamentation, South American eggs are strongly spherical, whereas Asian eggs are mostly sub-spherical or ellipsoidal (see Tab. 3).

Regarding *Sphaerovum erbeni* originally erected by Mones (1980) based on silicified eggs, Faccio (1994) later suggested its inclusion within the oofamily Faveoloolithidae, a proposal subsequently followed by Casadío *et al*. (2009). However, Grellet-Tinner *et al*. (2012) argued that *S. erbeni* should be regarded as *nomen dubium* because the characters observed in the holotype are strongly affected by diagenetic alteration. Although diagenetic processes can substantially modify its diagnostic features, the status *nomen dubium* should be regarded as provisional, pending the discovery of better-preserved material that may allow its taxonomic validity. On the other hand, it is important to mention that the oogenus *Paquiloolithus* established by Simon (2002) is unavailable at present, due to the original description and publication did not fulfil the criteria set out in the International Code of Zoological Nomenclature (Fernández *et al*., 2022). Thereby, and following these authors, this designation is not used in the present contribution, pending a formally valid erection in the future.

In summary, the eggshells from the Lago Colhué Huapi Formation differ from Asian faveoloolithid oogenera in several aspects. These include: (1) the presence of a well-developed external ornamentation; (2) a significantly greater eggshell thickness and a broader thickness range; (3) higher values of pore density per 100 mm^2. According to Fernández *et al*. (2022), the discrepancy between Asian and South American faveoloolithid might suggests the existence of an endemic group of sauropods that laid this type of eggs, restricted exclusively to the Upper Cretaceous of South America.

Although the identity of the producer of Faveoloolithidae eggs remains unknown, a possible affinity with titanosaurian sauropods has been proposed (Powell, 1985; Simón, 2006; Salgado *et al*., 2007; Grellet-Tinner & Fiorelli, 2010; Grellet-Tinner *et al*., 2012; Tanaka *et al*., 2018; Fernández *et al*., 2022, among others). This association is based on certain characteristics of the eggs, such as their large size, morphology, and spatial arrangement within the nest, which are comparable to those observed in megaloolithid egg clutches, also attributed to sauropods (Kim *et al*., 2009; Kundrát & Cruickshank, 2021; Fernández *et al*., 2022; references therein). It is important to highlight that the eggshells from the Lago Colhué Huapi Formation were recovered from the "upper section" of the unit. These levels are characterized by a high predominance of hadrosaurid remains and, to date, the absence of sauropod fossils (see Ibiricu *et al*., 2021; Casal *et al*., 2022; Caglianone *et al*., 2022). Among the materials identified at the same outcrop a small, amphicoelous vertebral centrum with an hourglass shape and 1.4 cm in length was found. This element, possibly belonging to a hatchling, shows clear affinities with the clade Ornithopoda (Cardozo *et al*., 2022b). Additionally, more recent discoveries include bone remains referred to Hadrosauridae, further expanding the fossil record of this dinosaur group in the youngest levels of the unit.

This could suggest, in addition to the possible affinity with sauropods proposed by other authors, a potential association with hadrosaurids, given the abundance of this ornithopod clade in the levels where the eggshells UNPSJB-PV 1082/205–/365 were discovered. On the other hand, Kundrát and Cruickshank (2021) proposed an interesting hypothesis about convergent evolution based on the features observed in Faveoloolithidae eggshells. According to these authors, different groups of dinosaurs may have independently developed eggs with similar shell structures as an adaptive response to similar environmental conditions. The complex geometry and high pore density in these eggshells are interpreted as indicative of high conductance values (Deeming, 2006; Grellet-Tinner *et al*., 2012). These aspects would have made them particularly suitable for incubation in moist substrates (Grellet-Tinner *et al*., 2012).

However, based on the study of Early Cretaceous Spheroolithidae eggs from the Iberian Peninsula, Moreno-Azanza *et al*. (2014, 2017) indicated that the key structural features of ornithopod eggshells were already established by the Lower Cretaceous. These authors suggested that these characteristics persisted through time and could have extended into derived ornithopods. Although this pattern appears to be well supported for Laurasian records, the Gondwanan evidence points to regional pattern in eggshell morphological traits. Moreover, despite the relatively good representation of ornithopod dinosaurs in Gondwanan landmasses, Spheroolithidae eggs have not yet been documented. This makes Gondwanan record especially noteworthy as intriguing, suggesting that paleogeographical factors may have played a significant role.

Ootaxonomy and Biological Affinity: Implications from Faveoloolithidae Distribution

The apparent absence of Faveoloolithidae in North America, despite its occurrence in South America and Asia, raises important questions about the relationship between ootaxonomy and biological affinity. One potential scenario is that similar dinosaur clades inhabited these regions, but were either absent or less successful in North America. The other tentative scenario is that South American and Asian eggshells, despite their microstructural similarities and current classification within the same parataxonomic group (Faveoloolithidae), could have been produced by different dinosaur clades. Analysis on the microstructure and crystallography of extant and fossil eggshells have shown that similar microstructural patterns can evolve convergently in unrelated lineages, resulting in homoplastic features that may not necessarily reflect close phylogenetic relationships (Choi *et al*., 2023). In this context, the assignment of South American and Asian Faveoloolithidae eggs to a single ootaxon may not necessarily imply a monophyletic origin of their producers. Instead, these similarities could potentially reflect convergent evolution in eggshell structure among distinct and possibly unrelated lineages. Another case of uncertainty in the relationship between ootaxonomy and biological affinity was documented in Rumania (see Grigorescu *et al*., 2010 y Grigorescu, 2016), where a specific ootaxa (Megaloolithidae) usually linked to titanosaurian sauropods, have been reported in association with a different taxonomic group (Hadrosaurid).

Therefore, the distribution of Faveoloolithidae could not directly reflect the paleobiogeographic distribution of a single dinosaur clade, but rather the occurrence of similar eggshell morphologies in different contexts. In this sense, parataxonomy provides a useful tool for describing and comparing fossil eggs; however, it may also have certain limitations, as it could potentially mask biological diversity and evolutionary relationships.

Sedimentary paleoenvironment

The eggshell bearing levels of the Lago Colhué Huapi Formation are interpreted as part of a fining-upward succession attributed to a clean, low-energy, shallow, temperate water body (Vallati *et al*., 2016; Casal *et al*., 2020), possibly related to an abandoned meander.

Additionally, in stratigraphic levels interpreted as equivalent to these deposits, De Sosa Tomas *et al*. (2017) documented fossil plant remains with affinities to the family Arecaceae, comparable to the extant genus *Nypa*. At present, this genus is confined to coastal mangrove environments (De Sosa Tomas *et al*., 2017). This botanical affinity is further supported by the presence of *Spinizonocolpites*, a pollen genus unequivocally associated with Arecaceae, as reported by Vallati *et al*. (2016, 2020). This set of evidence would suggest a marine coastal proximity for these deposits.

This context allows for comparisons with other sedimentary paleoenvironments in South America and Asia where oological remains assigned to the oofamily Faveoloolithidae have also been recovered. For example, in Uruguay, eggshell fragments belonging to this oofamily have been reported in the Mercedes Formation (Campanian–Maastrichtian; Goso & Perea, 2004; Daners & Guerstein, 2004). Although this unit is predominantly of fluvial origin, the oological remains are found in thin lacustrine deposits with well-developed palustrine zones that laterally grade into fluvial facies. A similar paleoenvironment has been inferred for the Queguay limestones (Upper Cretaceous *sensu* Cabrera *et al*., 2018), with palustrine deposits also bearing oological remains. In both cases, no signs of marine influence have been recognized, leading to their interpretation as entirely continental environments.

In Argentina, the egg and eggshell bearing levels of the Allen Formation (Campanian–Maastrichtian; Ballent, 1980; Salgado *et al*. 2007) have been interpreted as brackish lagoon deposits developed in supratidal settings and associated with ephemeral fluvial channels (Simón 2006; Salgado *et al*. 2007). The paleoenvironmental setting of these levels shows clear similarities to those of the "upper section" of the Lago Colhué Huapi Formation (Vallati *et al*., 2016; De Sosa Tomas *et al*., 2017; Casal *et al*., 2020; Ibiricu *et al* 2021). In Asia, faveoloolithid eggs and eggshells have been preserved in facies representative of crevasse splay deposits in a proximal floodplain context (Kim *et al*., 2009; Kim *et al*., 2022), and more recently also in conglomeratic mid-channel bar deposits (Kim *et al*., 2025). Paleosol development occasionally occurs in the proximal floodplain facies, which would suggest a certain degree of temporal stability and interruptions in sedimentation with subaerial exposure. This type of deposit has been documented in the Sihwa Formation (Lower Cretaceous, Kim *et al*., 2025) and in sedimentary layers intercalated within the Daeri andesites, part of the Wido Volcanic

Complex (Coniacian–Santonian, *sensu* Paik *et al*., 2012; Kim *et al*., 2022). Oological remains have also been identified in deposits interpreted as unconfined flows associated with proximal floodplains in the Haman Formation (Albian, *sensu* Yoon *et al*., 2021), as well as in facies corresponding to a distal alluvial fan in the Gaogou Formation (Liang *et al*., 2009; Turonian–Campanian, *sensu* Xu *et al*., 2022). It has been proposed that eggs with a multicanaliculate pore system, like those attributed to Faveoloolithidae, would require some degree of moisture availability even under arid or semi-arid climatic conditions (Kim *et al*., 2009). In this sense, these authors suggest that the preferential nesting environments for these taxa would be located in fluvial environments, in areas near the main channel or in abandoned channels. The combination of stability, low-energy conditions, and moisture availability would make these sites suitable for incubation and embryonic development.

According to Paik *et al*. (2012), the diversity of sedimentary paleoenvironments associated with Cretaceous dinosaur nesting sites may reflect ecological variability in nesting site selection among dinosaurs. This relationship appears to be particularly evident in Asia, where the range of depositional environments is broader than in South America. As suggested by these authors, the presence of multiple dinosaur clades would have favored the utilization of a wide variety of available environments, thereby minimizing competition for nesting sites.

In this context, the faveoloolithid eggshell bearing levels from the "upper section" of the Lago Colhué Huapi Formation share paleoenvironmental similarities with those of the Allen Formation, particularly with the development of shallow water bodies within floodplain settings and in areas proximal to the coastline. In contrast, in Asia, eggs assigned to Faveoloolithidae are preserved in a wide range of paleoenvironmental contexts. This difference would preliminarily suggest relatively homogeneous and restricted nesting environments in South America, in contrast to the broader diversity of habitats exploited by dinosaurs in Asia.

CONCLUSION

The macro and microstructural characteristics of the UNPSJB-PV 1082/205–/365 eggshells support their assignment to the oofamily Faveoloolithidae. However, given the significant differences in distinctive external ornamentation and eggshell thickness compared to formally established ootaxa, it is not possible to attribute them specifically to any of these. Therefore, the eggshells from the Lago Colhué Huapi Formation are classified as Faveoloolithidae indet. pending further evidence for a more precise classification.

Additionally, the paleoenvironmental context interpreted for the eggshell-bearing levels in the upper section of the Lago Colhué Huapi Formation exhibits significant similarities to the paleoenvironment proposed for the oological remains in the Allen Formation. In both cases, the deposits are associated with shallow water bodies developed within floodplain environments, in settings close to the sea.

Moreover, the eggshell fragments UNPSJB-PV 1082/205–/365 expand the known geographic distribution of Faveoloolithidae in South America, representing the southernmost record of this oofamily reported worldwide to date. These materials also exhibit similarities and are comparable to other previously documented specimens from Argentina and Uruguay. Furthermore, their discovery represents the first record of eggshells belonging to the Faveoloolithidae oofamily from the Chubut Group in the Golfo San Jorge Basin. The fragments were recovered from the "upper levels" of the Lago Colhué Huapi Formation, where hadrosaurid remains are predominant and, to date, no sauropod fossils have been found. This preliminarily suggests ornithopods as a possible producer of these reproductive structures. Nevertheless, as previously mentioned, this type of eggshell has traditionally been linked to sauropod dinosaurs. Therefore, obtaining new evidence and/or expanding the fossil record in the study area are crucial to clarifying the taxonomic identity of the producer of these reproductive structures more precisely.

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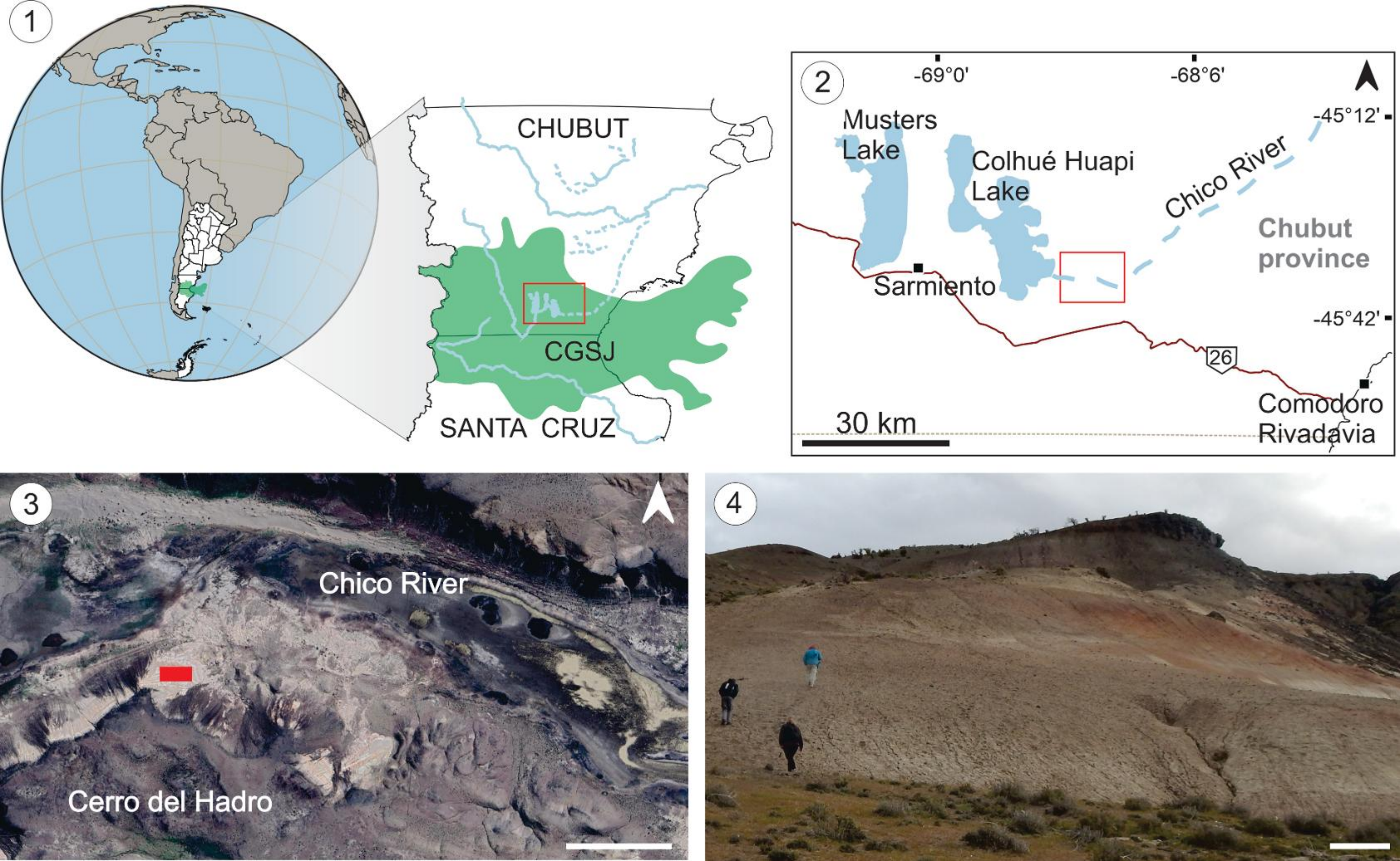
Figure captions

Figure 1. 1, Location map of the Argentinian Republic within the American continent and a closer view (green area) of the Golfo San Jorge basin (CGSJ) in central Patagonia. The red rectangle indicates the area of interest; **2,** Detailed view of the study site at the headwaters of the Chico River, Chubut Province, Argentina. The red rectangle indicates the provenance of the fossil eggshells analyzed in this study (modified from Ibiricu *et al*., 2025); **3,** Aereal view of the informally named "Cerro del Hadro" on the southern margin of the Chico River. Image from Landsat/Copernicus 2023; Google Earth, accessed December 2023. Scale bar equals 250 m. The red rectangle indicates the excavation site; **4,** Outcrop photograph of the Lago Colhué Huapi Formation at "Cerro del Hadro." Scale bar equals 2 m.

Figure 2. Stratigraphic section of the “Cerro del Hadro” where eggshells fragments were found (modified from Casal *et al*., 2020).

Figure 3. 1, Radial view of eggshell fragment UNPSJB-PV 1082/205 showing the branching pattern of shell units. Scale bar equals 5mm; **2,** Radial view of fragment UNPSJB-PV 1082/206 obtained via SEM. Scale bar equals 500 µm; **3,** Thin section of eggshell UNPSJB-PV 1082/209 under parallel nicols, the area outlined in the black rectangle is shown in detail in 4. Scale bar equals 2 mm; **4,** Thin section of eggshell UNPSJB-PV 1082/209 under crossed nicols. Scale bar equals 2 mm; **5,** Tangential view showing pore canals, indicated by pink arrows. Scale bar equals 0.5 mm; **6,** External ornamentation of eggshell fragments /205/206/207/208 observed in hand sample. Scale bar equals 0.5 mm; **7,** Outer surface under scanning electron microscope (SEM) of eggshell UNPSJB-PV 1082/206. Scale bar equals 500 µm. Abbreviations: **PC**, pore canal; **N**, nodes; **MB**, mammillary base.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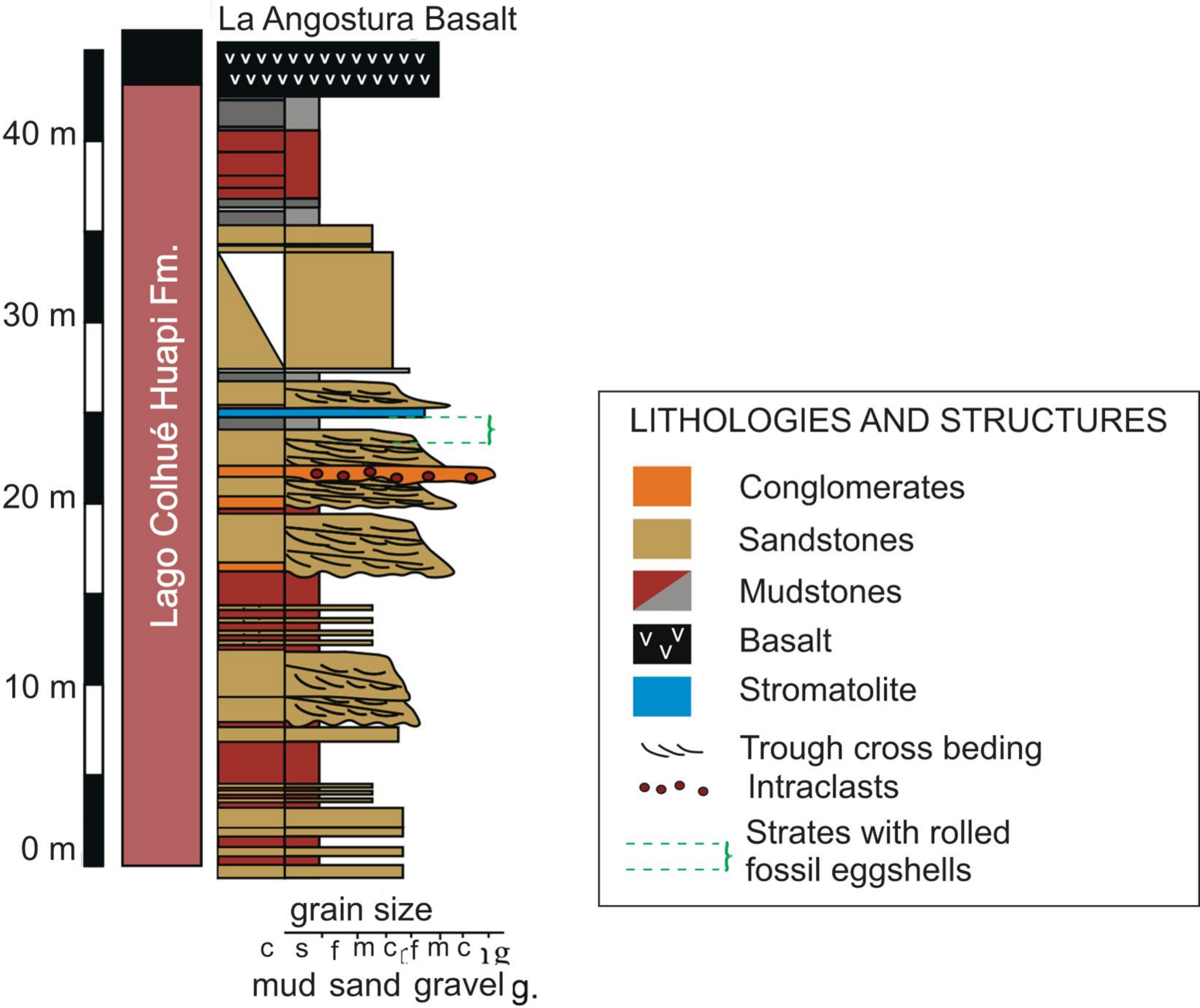
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LITHOLOGIES AND STRUCTURES
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Sandstones
Mudstones
Basalt
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Trough cross beding
Intraclasts
Strates with rolled fossil eggshells

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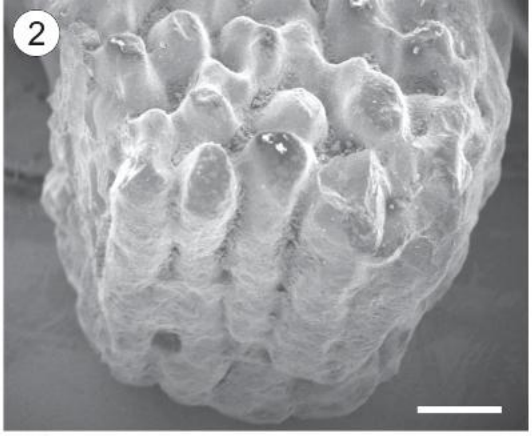

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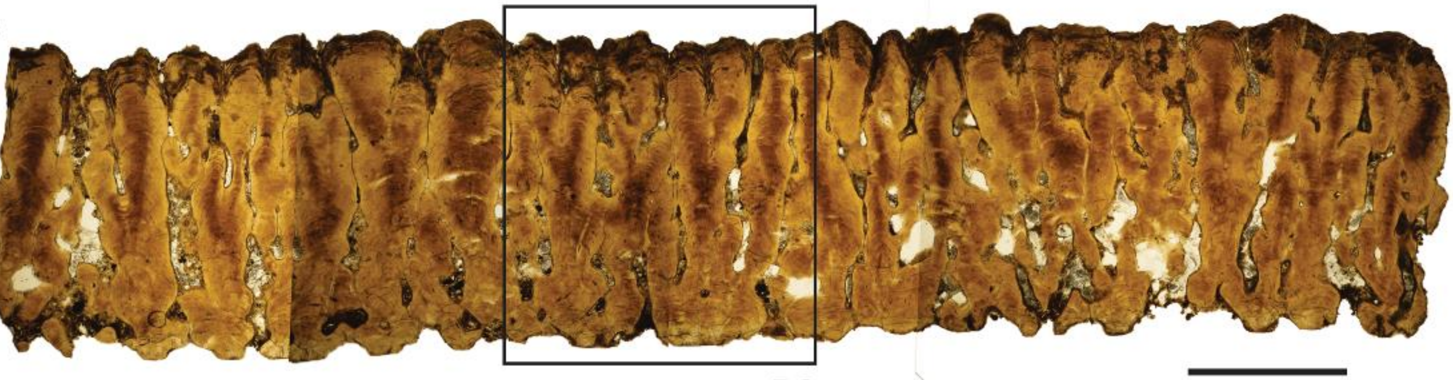

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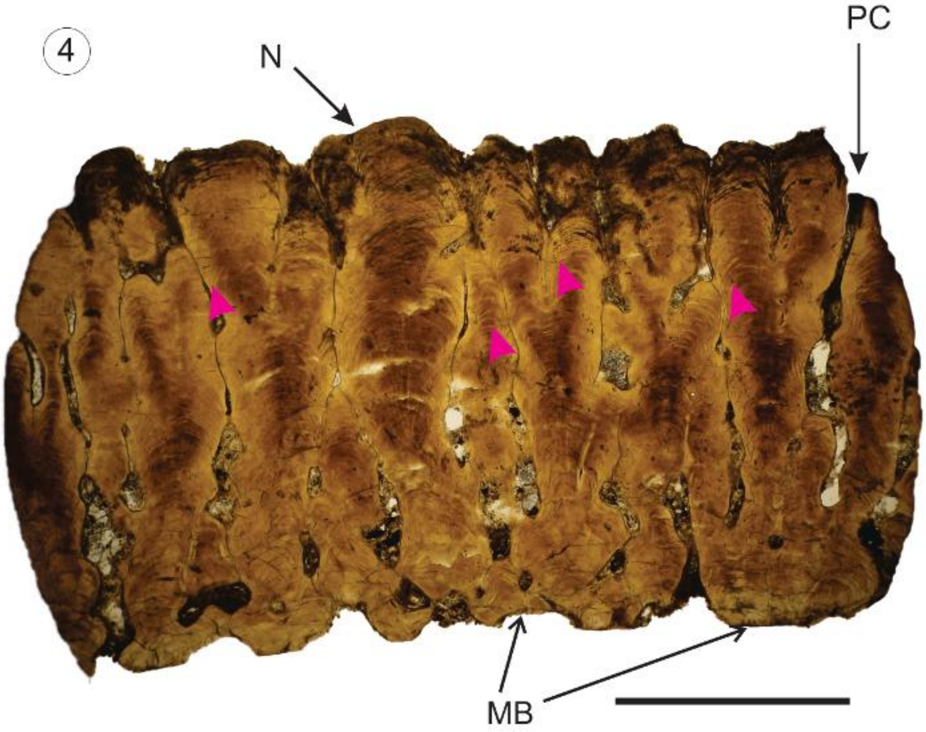

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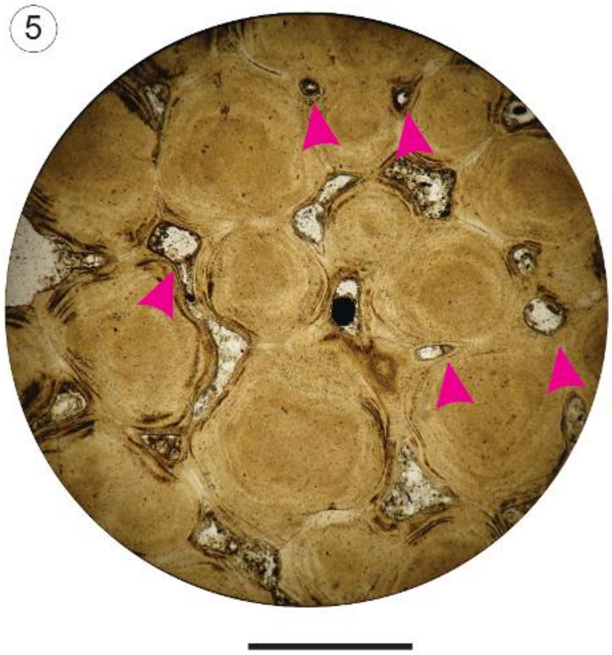

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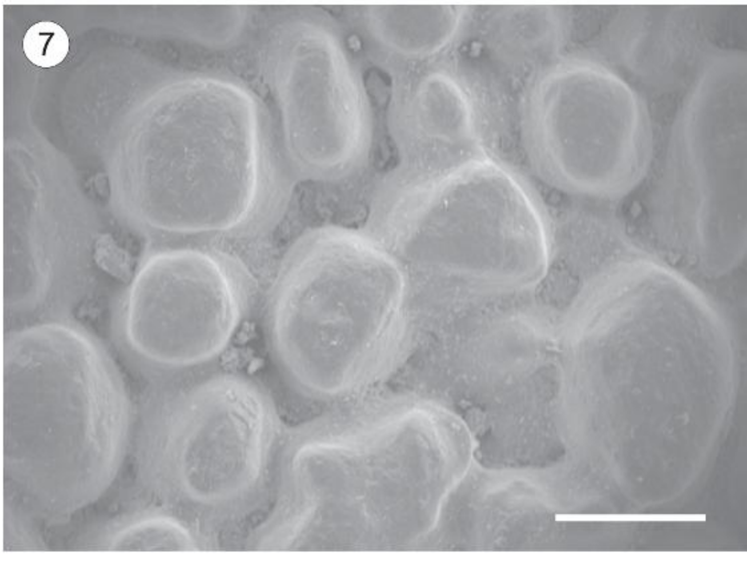

TABLE 1. Faveoloolithidae worldwide record (modified from Fernández *et al*., 2022 and He *et al*., 2025)

Region	Country	Oogenus	Locality and Province/Department	Formation and age	References
South America	Argentina	Faveoloolithidae indet	Salitral Moreno, Río Negro	Allen Fm (Campanian─Maastrichtian)	Powell (1985); Simón (2006)
		Faveoloolithidae indet	Salitral Ojo de Agua, Río Negro	Allen Fm (Campanian─Maastrichtian)	Salgado *et al*. (2007); Fernández (2013)
		Faveoloolithidae indet	Salinas de Trapalcó-Salitral de Santa Rosa, Río Negro	Allen Fm (Campanian─Maastrichtian)	Salgado *et al*. (2007); Fernández (2013)
		Faveoloolithidae indet	Yaminué, Río Negro	Allen Fm (Campanian─Maastrichtian)	Manera de Bianco (1996)
		Faveoloolithidae indet	Gonzalito I, Río Negro	Allen Fm (Campanian─Maastrichtian)	Fernández *et al*. (2017)
		Sphaerovum	La Pampa	Colorado Fm (Campanian─Maastrichtian)	Casadío *et al*. (2002)
		Sphaerovum	Sanagasta Valley, Sanagasta, La Rioja	Los Llanos Fm (Campanian─Maastrichtian)	Hünicken *et al*. (2001); Tauber (2007); Grellet-Tinner and Fiorelli (2010)
		Sphaerovum	Ita-i-cora, Entre Ríos	Puerto Yeruá Fm (Late Cretaceous)	De Valais *et al*. 2003
	Uruguay	*Sphaerovum*	Quebracho, Paysandú	Guichón Fm (Turonian─Santonian)	Goso and Perea (2004); Soto *et al*. (2012)
		Sphaerovum	Forestal Caja Bancaria Quarry, Paysandú	Mercedes Fm (Maastrichtian)	Alonso-Zarza *et al*. (2011); Cabrera *et al*. (2018); Veroslavsky *et al*. (2019)
		Sphaerovum	White Quarry, Paysandú	Queguay Fm (Maastrichtian)	Veroslavsky *et al*. (2019)
		Faveoloolithidae indet	Algorta, Río Negro	Mercedes Fm (Maastrichtian)	Mones (1997); Faccio (1994); Faccio and Montaña (1994)
		Sphaerovum	Palmitas, Soriano	Mercedes Fm (Maastrichtian)	Mones (1980); Faccio *et al*. (1990)
Asia	China	*Hemifaveoloolithus*	Muyushan Tunnel, Zhejiang	Chichengshan Fm (Upper Cretaceous)	Wang *et al*. (2011)
		Parafaveoloolithus	Xiuning County, Anhui Province	Xintan Fm (Lower Cretaceous)	Mao *et al*. (in press)
		Parafaveoloolithus	Xixia County, Henan Province	Zhaoying Fm (Upper Cretaceous)	He *et al*. (2025)

	Parafaveoloolithus	Pingxiang City, Jiangxi Province	Zhoutian Fm (Upper Cretaceous)	Zou *et al*. (2013)
	Parafaveoloolithus	Tiantai County, Zhejiang Province	Chichengshan Fm (Upper Cretaceous)	Zhang (2010)
	Parafaveoloolithus	Tiantai County, Zhejiang Province	Laijia Fm (Upper Cretaceous)	Zhang (2010)
	Parafaveoloolithus	Heyuan City, Guangdong Province	Dongyuan Fm (Upper Cretaceous)	Fang *et al*. (2005); Zhao *et al*. (2015)
	Parafaveoloolithus	Xixia County, Henan Province	Zoumagang Fm (Upper Cretaceous)	Fang *et al*. (1998); Zhao *et al*. (2015)
	Parafaveoloolithus	Shangluo City, Shaanxi Province	Lijiacun Fm (Upper Cretaceous)	Zheng *et al.* (2018) He *et al*. (2025)
	Hormoolithus	Heyuan City, Guangdong Province	Dongyuan Fm (Upper Cretaceous)	Wang *et al*. (2022)
	Youngoolithus	?	Neixiang County, Henan Province	Zhao (1979); Zhang (2010)
	Propagoolithus	Tiantai County, Zhejiang Province	Chichengshan Fm (Upper Cretaceous)	Fang *et al*. (2000); Wang *et al*. (2011); He *et al*. (2025)
	Faveoolithus	Xixia County, Henan Province	Gaogou Fm (Upper Creataceous)	Zhou and Han (1993); Zhang and Li (1998); Zhou and Feng (2002)
	Faveoolithus	Xichuan County, Henan Province	Gaogou Fm (Upper Creataceous)	Zhou and Han (1993); Zhang and Li (1998)
	Faveoolithus	Neixiang County, Henan Province	Gaogou Fm (Upper Creataceous)	Zhou and Han 1993
	Faveoolithus	Yun County, Hubei Province	Gaogou Fm (Upper Creataceous)	Zhou *et al*. (1998)
	Faveoolithus	Alxa, Inner Mongolia, China	?	Zhao and Ding (1976)
	Propagoolithus	Sinan (Shinan)-gun, Jeolla nam-do	?	Jo *et al*. (2023)
	Propagoolithus	Buan County, North Jeolla Province	The Daeri Andesite Wido Volcanics (Coniacian–Santonian)	Kim *et al*. (2019)
South Korea	*Faveoolithus*	Bosung County, Chullanam-do Province	Seonso Fm (Upper Cretaceous)	Huh and Zelenitsky (2002)
	Faveoloolithidae indet	Hwaseong City, Gyeonggi Province	Sihwa Fm (Lower Cretaceous)	Kim *et al*. (2025)
Mongolia	*Faveoolithus*	South and East Gobi provinces	Barun-Goyot Fm (Upper Cretaceous)	Mikhailov (1994)

TABLE 2. Morphological characteristics of the Lago Colhué Huapi Formation eggshells

Thick-ness (mm)	Average pore Density (per 100 mm^2)	Pore canals diameters (mm)	Pore system	Nodes diameters (mm)	Ornamenta-tion	Average inter-mammillary space (mm)	Structural morphotype	Structural organization
3.7—5.82	663	0.1—0.3	multicanali-culate	0.3—1	compacti-tuberculate	0.925	filispherulitic	dinosauroid–spherulitic

TABLE 3. Comparison between South American and Asian Faveoloolithidae oogenus (modified from He *et al.*, 2025)

Region	Oogenus	Egg morpho-logy	Size (mm)	Thick-ness (mm)	Pore Diameter (mm)	Pore Density (per 100 mm^2)	External surface	References
South America	Faveoolithidae indet	Spherical	180—220 (diame-ter)	3.50—7.5	0.06—0.9	663	Ornamen-ted with nodes	Simón (2006); Salgado *et al*. (2007); Casadío *et al*. (2002); Fernández (2013, 2017); this paper
	Sphaerovum	Spherical	150—170 (diame-ter)	4.20—5	?	?	Ornamen-ted with nodes	Mones (1980); Soto *et al*. (2012)
Asia	*Faveoolithus*	Subsphe-rical to Ellipsoidal	130.8—143.7 (lenght) 117.6—127.9 (width)	1.20—1.54	0.07—0.040	18	Smooth	Zhao and Ding (1976); Zhang (2010)
	Parafaveoloolithus	Subsphe-rical to Ellipsoidal	73.2—192 (lenght) 97.2—168 (width)	1.00—2.35	0.04—0.64	12 y 55	Smooth	Zhang (2010); Zou *et al*. (2013); Zheng *et al*. (2018); He *et al*. (2025); Mao *et al*. (in press)
	Hemifaveoloolithus	Spherical	130—137	1.60	0.03—0.12?	40—50?	Smooth	Wang *et al*. (2011); Zou *et al*. (2013); He *et al*. (2025)
	Propagoolithus	Subsphe-rical to Ellipsoidal	85—192 (lenght) 53—168 (width)	1.34—1.98	0.08—0.44	55—60	Smooth to Slightly nodulose	Zheng *et al*. (2018); Kim *et al* (2019); Jo *et al*.

							(2023); He *et al*. (2025)
Youngoolithus	Ellipsoidal	156.0—173.4 (lenght) 91.0—109.4 (width)	1.45—1.60	0.07—0.33	26	Smooth	Zhang (2010)
Hormoolithus	?	?	1.65—1.71?	0.10—0.35?	?	Smooth?	Wang *et al*. (2022); He *et al*. (2025)

TABLE 4. Macro and microstructural comparison between Argentinian Faveoloolithidae eggshells.

Province	Site	Formation and age	Egg morphology and diameter (cm)	Thickness (mm)	Pore Diameter (mm)	Pore Density (per mm2)	External surface	Nodes Diameter(mm)	References
Río Negro	Salitral Moreno, Río Negro	Allen Fm. (Campanian—Maastrichtian)	Spherical 20	3.85—6.70	0.06-1.5	1.64	Ornamented with nodes	0.22—1.27	Simón (2006)
	Salitral Ojo de Agua Salinas de Trapalcó Salitral de Santa Rosa	Allen Fm. (Campanian—Maastrichtian)	Spherical 18—21	3.5—7.5	0.16	?	Ornamented with nodes	0.32—0.8	Salgado *et al*. (2007); Fernández (2013)
La Pampa	Localities A and B, western edge of the Colorado basin	Colorado Fm. (Campanian—Maastrichtian)	Spherical 18	4.55—5.55	?	?	Ornamented with nodes	0.32—1.36	Casadío *et al*. (2002)
La Rioja	Sanagasta	Los Llanos Fm. (Campanian—Maastrichtian)	Spherical to subspherical	1.29/ 2.3 — 7.6/ 7.94	0.15—0.2	2.26	Ornamented with nodes	0.25—1.3	Hünicken *et al*. (2001); Tauber (2007); Grellet Tinner and Fiorelli (2010)
Chubut	Puesto El Colorado Ranch	Lago Colhué Huapi Fm. (Coniacian—Maastrichtian	?	3.71—5.82	0.1—0.3	6.63	Ornamented with nodes	0.3—0.7	This paper