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DESCRIPTION AND REVIEW OF NON-AVIAN DINOSAUR EGGS FROM CRETACEOUS DEPOSITS OF THE MONGOLIAN GOBI DESERT

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ABSTRACT Mongolia has a long history of discoveries and research related to dinosaur eggs. Since the first scientific discoveries in the early 1920s, numerous eggs, eggshells, and nests have been collected by various international expeditions and have contributed significantly to our understanding of reproductive traits in dinosaurs. In this study, we report on non-avian dinosaur egg remains that were collected as part of the Korean-Mongolia International Dinosaur Expeditions and the joint expeditions between Japan and Mongolia. This research includes the first detailed descriptions of six ootaxa (*Collacoidoolithus* oosp., *Dendroolithus* oosp., *Macroelongatoolithus* oosp., *Paraspheroolithus irenensis*, cf. *Protoceratopsidovum minimum,* and cf. *Spheroolithus maiasauroides*) from Upper Cretaceous localities (Altan Uul I, Altan Uul IV, Bayanshiree, Shine Us Khudag and Shiluut Uul) in order to provide a current summary of dinosaur ootaxa and egg-producing localities from the Gobi Desert of Mongolia. A compilation of locality and formation data for these and other ootaxa from Mongolia reveals the egg-bearing Upper Cretaceous formations, except the Javkhlant Formation, have each yielded ten or more non-avian dinosaur ootaxa (Baruungoyot, Bayanshiree, Djadokhta, and Nemegt formations). Mongolia is thus among the richest countries with respect to abundance and diversity of dinosaur eggs.

KEYWORDS Upper Cretaceous, Gobi Desert, Mongolia, Dinosaur, Egg, Eggshell

INTRODUCTION

The first scientific discoveries of dinosaur eggs from Mongolia occurred nearly a century ago in Cretaceous strata of the Gobi Desert. During the Central Asiatic Expeditions, dinosaur egg remains were uncovered in the early 1920s by the American Museum of Natural History, which led to the sudden realization that dinosaurs had laid eggs (Andrews, 1932). Subsequent significant collections of dinosaur eggs, eggshells and nests were made during the Mongolian Paleontological Expeditions of the USSR Academy of Science (1946-1949), the Polish-Mongolian Paleontological Expeditions (1963-1971), and the Joint Soviet (Russian)-Mongolian Palaeontological and Geological Expeditions (since 1969) (see Mikhailov, 2000 for the summary). Importantly, these expeditions found additional egg-producing localities and increased the known diversity of dinosaur eggs in Cretaceous rocks of the southern Gobi Desert. From the 1990s onwards, Mongolian-international joint expeditions with the United States (American Museum of Natural History), South Korea (Korea-Mongolia International Dinosaur Expedition), and Japan (Hayashibara Museum of Natural Sciences expeditions, Hokkaido University Museum expeditions, etc.) continued to collect dinosaur eggs/nests from the Gobi Desert, yielding some remarkable discoveries. Such specimens include embryos in ovo, egg clutch-adult skeleton associations, and fossilized soft-shelled eggs, which have contributed significantly to our understanding of various nesting and reproductive traits (e.g.,

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eggshell types, nest types, egg pigmentation, brood-like behavior) within the dinosaur-bird lineage (e.g., Norell et al., 1995, 2001, 2018, 2020; Clarke et al., 1999; Weishampel et al., 2008; Fanti et al., 2012; Tanaka et al., 2015; Erickson et al., 2017; Wiemann et al., 2018).

This study focuses on the description of non-avian dinosaur egg remains that were collected as part of the Korean-Mongolia International Dinosaur Expeditions (KID) and the joint expeditions between Japan (Hokkaido University Museum) and Mongolia (Institute of Paleontology, Mongolian Academy of Sciences, MPC). The first detailed descriptions of all egg taxa (i.e., ootaxa) found at various localities are conducted in order to provide a summary of dinosaur ootaxa and egg-producing localities from the Gobi Desert of Mongolia, thus updating prior reviews (e.g., Sochava, 1969; Mikhailov, 1991, 2000; Sabath, 1991; Mikhailov et al., 1994).

REVIEW OF NON-AVIAN DINOSAUR EGGS FROM MONGOLIA

Some of the earliest discovered dinosaur eggs from Mongolia were studied by van Straelen (1925) and Brown and Schlaikjer (1940), the former of whom adopted light microscopy to describe the eggshell microstructures. After decades of collecting by various expeditions, dinosaur egg remains from Mongolia were described and classified, contributing to the development of a parataxonomy based on macro-features and microstructures of the eggs (e.g., Sochava, 1969; Mikhailov, 1991, 1994a, 1994b).

To date, more than twenty ootaxa are known from 46 localities in the Gobi Desert of southern Mongolia (Fig. 1 and see Appendix Table 1 for the list of egg-producing localities in Mongolia). Eight formations have produced these localities, most of which are Late Cretaceous in age with few (<10%) dating to the Early Cretaceous. To our knowledge, dinosaur egg sites have not been discovered in either Triassic or Jurassic deposits of Mongolia.

Eight egg families (i.e., oofamilies) have been recognized from Mongolia (Fig. 2 and see Appendix Table 2 for the measurements and outer surface morphology of non-avian dinosaur eggs in Mongolia). Eggs assignable to Dendroolithidae, Ovaloolithidae, Spheroolithidae, Elongatoolithidae, and Prismatoolithidae are common, whereas those attributable to Dictyoolithidae, Faveoloolithidae, and Stalicoolithidae are relatively rare (Mikhailov, 2000).

Dictyoolithidae eggs are relatively well documented from sites in China but are rarely reported from Mongolian sites. Eggs assigned to *Dictyoolithus* oosp. were identified from two localities, Nogoon Tsav and Algui Ulan Tsav (Ariunchimeg, 2000), although these specimens have not been described in detail.

Dendroolithidae eggs are commonly found in Upper Cretaceous formations of southern Mongolia, where two egg species, *Dendroolithus microporosus* and *D. verrucarius*, are currently recognized. Both of these oospecies are only known from Mongolia, and they can be differentiated from one another based on egg size and eggshell thickness (Appendix Table 2; Mikhailov, 1994b). Several egg clutches assignable to Dendroolithidae were reported at a single site in the Javkhlant Formation, from which colonial nesting and nest attendance behaviors in a possible therizinosaurian theropod have been inferred (Tanaka et al., 2019).

Faveoloolithidae eggs are found at several Upper Cretaceous localities in the Gobi Desert, notable for their large size and spherical shape. Although only a single oospecies, *Faveoloolithus ningxiaensis*, was recognized from Mongolia initially (Mikhailov, 1994b), it has been suggested that some of these eggs from the Algui Ulan Tsav locality are attributable to *Parafaveoloolithus* oosp., an oogenus known from Zhejiang and Henan provinces, China (Zhang, 2010).

Ovaloolithidae eggs are represented by two oospecies, *Ovaloolithus chinkangkouensis* and *O. dinornithoides*, from Upper Cretaceous deposits of Mongolia, the latter of which occurs only in Mongolia. These two oospecies differ with respect to eggshell thickness (primary range) and outer surface morphology (Appendix Table 2; Mikhailov, 1994b). An eggshell fragment assigned to *O. chinkangkouensis* along with embryonic remains (only possible metatarsals identified) adhered to the inner surface were described by Sochava (1972). The author suggested these few bones were similar to those of ceratopsian dinosaurs such as *Leptoceratops* and *Protoceratops*, but a recent study revealed that *Protoceratops* laid soft-shelled eggs (Norell et al., 2020) and not hard-shelled eggs like *Ovaloolithus*.

Spheroolithidae eggs are known from most Upper Cretaceous formations in Mongolia (Bayanshiree, Djadokhta, Baruungoyot, and Nemegt formations). Three oospecies, *Paraspheroolithus irenensis*, *Spheroolithus tenuicorticus* and *Sp. maiasauroides* have been recognized in Mongolia, but our analysis finds that *Sp. tenuicorticus* is a junior synonym of *Pa. irenensis* (see

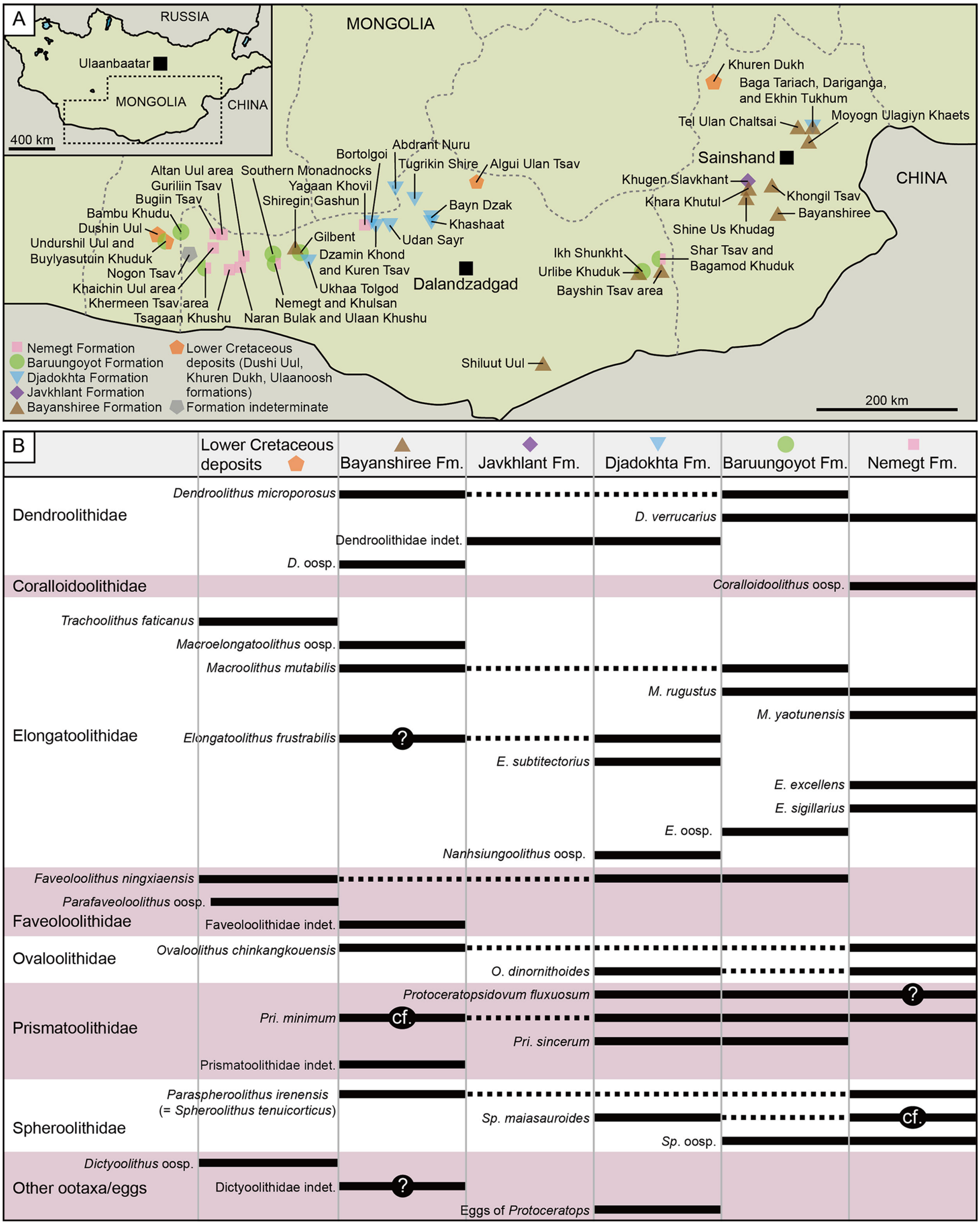

FIGURE 1. Summary of non-avian dinosaur egg localities and formations from Mongolia. **A**, approximate locations of fossil egg, eggshell and nest sites in Mongolia, based on Carpenter and Alf (1994), Mikhailov (2000), Watabe and Suzuki (2000a), Suzuki and Narmandakh (2004), Watabe and Tsogtbaatar (2004), Watabe et al. (2010a), Ishigaki et al. (2016), Saneyoshi et al. (2010); **B**, stratigraphic distribution of ootaxa (solid bars, ootaxon present; dashed bars, ootaxon currently absent). See Appendix Table 1 for the dataset of this figure.

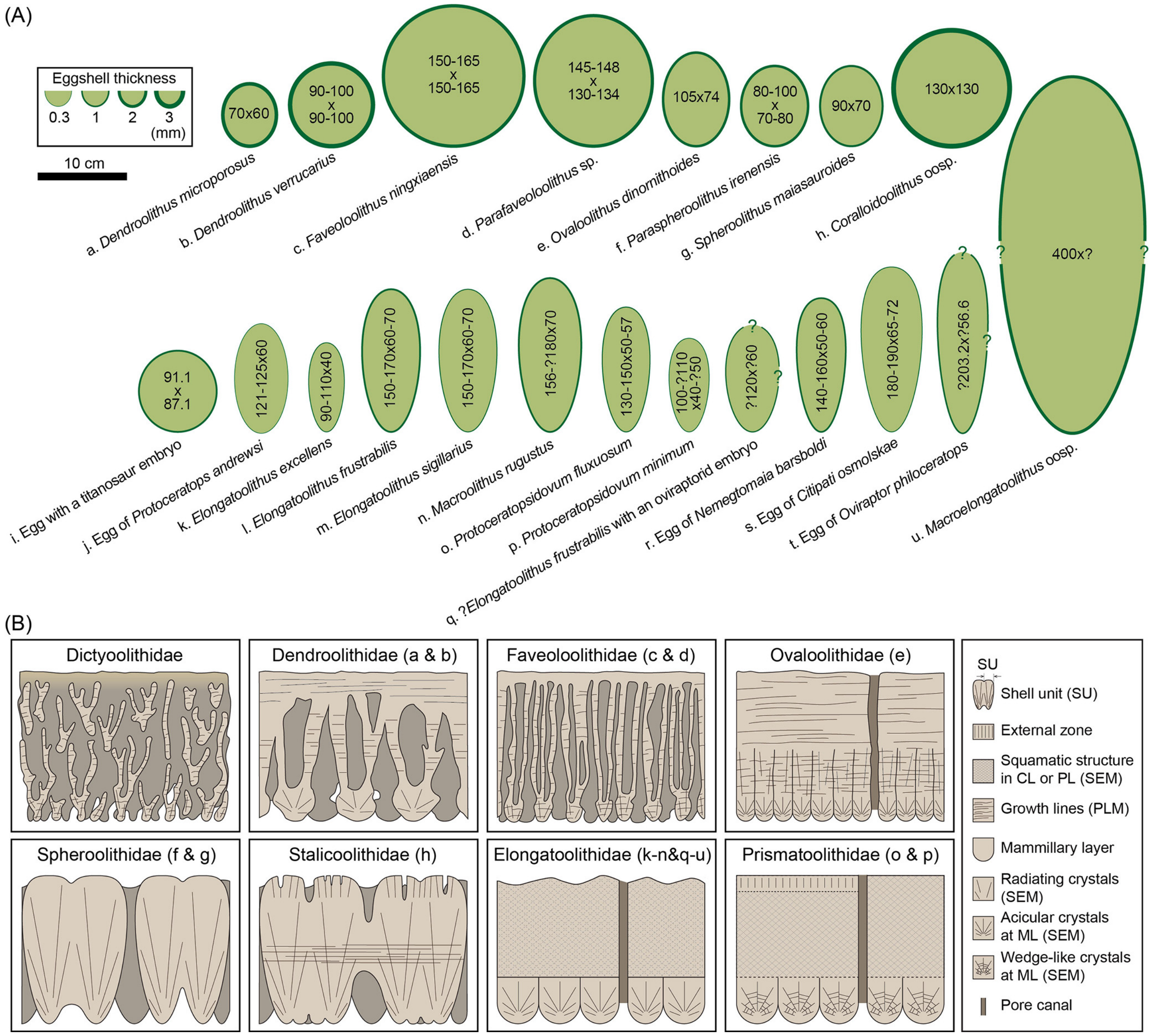

FIGURE 2. Comparisons of non-avian dinosaur eggs from Mongolia. **A**, comparison of egg size, shape, and eggshell thickness among ootaxa (size-known ootaxa only); **B**, schematic illustrations of eggshell microstructure (radial view) among oofamilies. Letters in parentheses for each oofamily correspond to letters (for ootaxa) in A. Note that *Protoceratopsidovum fluxuosum* and *Pro. sincerum* may be assignable to Elongatoolithidae and Montanoolithidae, respectively, rather than to Prismatoolithidae (Choi et al., 2022). See Appendix Table 2 for the dataset of this figure.

Systematic Paleontology). Although the egg sizes and eggshell thicknesses are similar, *Pa. irenensis* and *Sp. maiasauroides* can be differentiated based on the outer surface morphology (i.e., generally no ornamentation for *Pa. irenensis,* whereas prominent sagenotuberculate ornamentation for *Sp. maiasauroides*: Appendix Table 2). In the Altan Uul area, a perinatal *Saurolophus angustirostris* was found in association with *Spheroolithus* eggshells (Dewaele et al., 2015).

Stalicoolithidae eggs were not recognized in Mongolia until recently. Wang et al. (2012a) pointed out that some dendroolithid eggshells previously reported in Mongolia belong to Stalicoolithidae. Our study confirms the occurrence of Stalicoolithidae (*Coralloidoolithus*) in the Nemegt Formation of Mongolia (see Systematic Paleontology).

Elongatoolithidae is the most diverse oofamily known from strata of the Gobi Desert, and account for about half of the ootaxa known from Mongolia. Whereas *Trachoolithus faticanus* is restricted to Lower Cretaceous deposits, *Elongatoolithus*, *Macroolithus*, *Macroelongatoolithus*, and *Nanhsiungoolithus* are all known from Upper Cretaceous formations. These ootaxa have been differentiated from one another based on egg size, eggshell thickness, spacing of ridges on the outer surface, and/or relative thickness of the mammillary layer to the continuous layer (Mikhailov, 1994a). Specimens of eggs associated with skeletal remains from Mongolia were the first to provide conclusive evidence that elongatoolithid eggs were laid by oviraptorosaur theropods (Norell et al., 1994, 1995).

Prismatoolithidae eggs are documented from many Upper Cretaceous localities of the Gobi Desert. *Protoceratopsidovum* and *Prismatoolithus* are currently recognized from Mongolia; three oospecies have been identified within *Protoceratopsidovum* (Mikhailov, 1994a), including: *Pro*. *fluxuosum* that has linearituberculate ornamentation, and *Pro*. *minimum* and *Pro*. *sincerum* that both have a smooth eggshell surface. Choi et al. (2022) argue that *Pro*. *minimum* and *Pro*. *sincerum* can be distinguished from one another based on the ultrastructure of the mammillary layer (i.e., wedge-like crystals in *Pro*. *minimum*, but acicular crystals in *Pro*. *sincerum*). They also argue that *Pro*. *fluxuosum* could be reassigned to the Elongatoolithidae and *Pro. sincerum* to Montanoolithidae based on microstructure and crystallography. Prismatoolithid eggs/eggshells from Mongolia are reported to have been found associated with troodontid skeletons (Grellet-Tinner, 2005; Pei et al., 2017).

In addition to the wide diversity of ootaxa listed above, in-ovo dinosaur embryos are known for fossilized soft-shelled eggs from Mongolia which have not been classified using the parataxonomy. A clutch of eggs and embryos of *Protoceratops andrewsi* was reported from Ukhaa Tolgod (Erickson et al., 2017; Norell et al., 2020) for which geochemical analyses revealed that these eggs were soft-shelled.

MATERIALS AND METHODS

Over 300 eggshell fragments and partial eggs recovered from the areas of Altan Uul (Altan Uul I and IV), Bayanshiree, Shine Us Khudag, and Shiluut Uul were examined. The original egg diameter of *Coralloidoolithus* oosp. was estimated from the curvature of the partially-preserved egg, following Ribeiro et al. (2014). Eggshell thickness was measured with either a digital caliper (Mitutoyo CD-15CPX, precision of ±0.02 mm) or a digital micrometer (Mitutoyo CPM30-25 MJ, precision of ±2 μm). Macro- and microscopic structures of eggshell fragments were examined via scanning electron microscopy (SEM: Hitachi TM1000 and TM3000) and polarized light microscopy (PLM: Nikon Eclipse 50iPOL) instruments housed at the Royal Tyrrell Museum of Palaeontology, Drumheller, Canada, the Nagoya University Museum, Nagoya, Japan, and Sapporo Medical University, Sapporo, Japan. Descriptive terminology for eggshell generally follows Mikhailov (1991). Although Mikhailov (1997) considered *Paraspheroolithus* synonymous with *Spheroolithus*, we use the term '*Paraspheroolithus*' following the argument of Shen et al. (2023) (see discussions therein).

Institutional Abbreviations — **DNHM**, Dalian Natural History Museum, Dalian, China; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; **KID**, Korean-Mongolia International Dinosaur Expeditions; **MPC**, Institute of Paleontology, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia; **PIN**, Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; **PMRE**, Beijing Museum of Natural History, Beijing, China; **TMNH**, Tianjin Museum of Natural History, Tianjin, China.

SYSTEMATIC PALEONTOLOGY

Oofamily SPHEROOLITHIDAE Zhao, 1979

Oogenus *PARASPHEROOLITHUS* Zhao, 1979 emend. Zhao et al., 2015

PARASPHEROOLITHUS IRENENSIS (Young, 1954, 1965; Zhao and Jiang, 1974) Zhao, 1979 emend. Zhao et al., 2015

(Figs. 3A-C and 4A-E)

Holotype — The holotype specimen was not originally designated but selected as TMNH No. 40.095 by Zhao et al. (2015), which included four complete eggs and two egg impressions from a partial clutch collected from Shandong Province, China (Upper Cretaceous Jiangjunding Formation).

Referred Specimens — Partially preserved eggs from two clutches (eight and three eggs, respectively: MPC-D uncatalogued) and isolated eggshell fragments [MPC-D 100/1065 (n = 11) and MPC-D 100/1066 (n = 42)]. *Spheroolithus tenuicorticus* from Shiluut Uul (PIN 4476-4: Mikhailov, 1994b) is herein

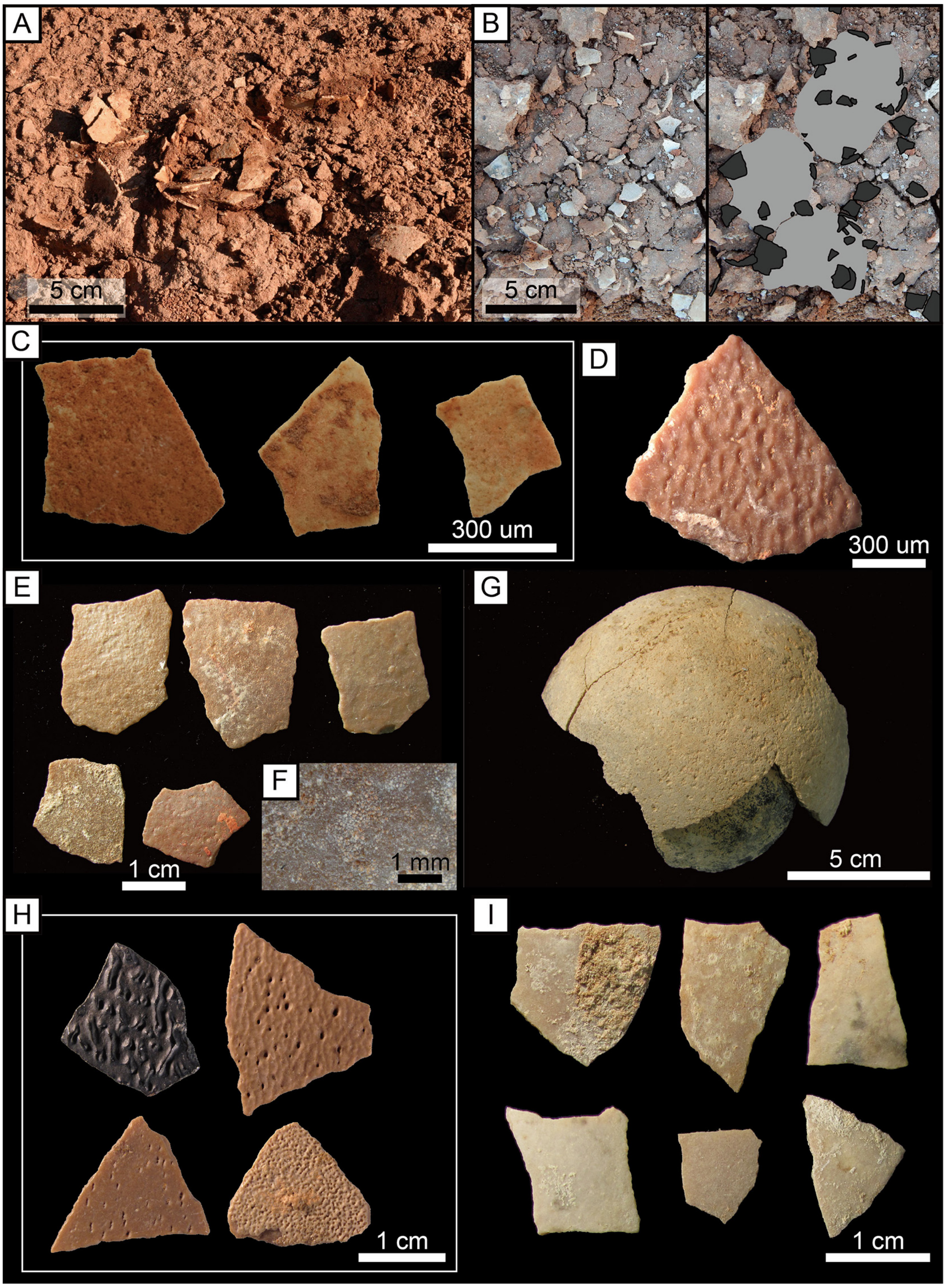

FIGURE 3. Selection of fossil eggs and eggshells examined in this study. **A**, partial clutch of *Paraspheroolithus irenensis* from Shiluut Uul, containing eight eggs and embryonic bones (only three eggs are visible in photograph whereas embryos are not visible); **B**, scattered eggshell fragments on a partial clutch of three *Pa. irenensis* eggs (left: original photograph, right: original photograph with light gray shadows of three eggs and darker shadows of eggshell fragments) from Shiluut Uul; **C**, rough outer surface of *Pa. irenensis* (MPC-D 100/1065); **D**, reticulated outer surface of cf. *S. maiasauroides* from Altan Uul IV (MPC-D 100/1060); **E**, rough outer surface of *Dendroolithus* oosp. from Bayanshiree (MPC-D 100/1063); **F**, magnification of outer surface of E; **G**, partial egg of *Coralloidoolithus* oosp. from Altan Uul I (MPC-D 100/1045); **H**, linearituberculate to smooth outer surface of *Macroelongatoolithus* oosp. from Bayanshiree (MPC-D 100/1064); **I**, smooth outer surface of cf. *Protoceratopsidovum minimum* from Bayanshiree (MPC-D 100/1062).

considered a junior synonym of *Pa. irenensis*.

Locality, Horizon, and Age — Egg and eggshell specimens examined in this study were recovered from a red-brown mudstone layer at the Shiluut Uul locality (N42.17.160; E105.44.604), a site located approximately 80 km southeast of Nomgon in Ömnögovi Aimag, Mongolia. The mudstone layer is part of the red beds of the Upper Cretaceous (Cenomanian to early Santonian?) Bayanshiree Formation.

Description — At least two clutches of *Paraspheroolithus irenensis* have been recovered from Shiluut Uul, containing at least eight and three eggs each (Fig. 3A, B); the larger clutch contains some embryonic remains (which will be described in a future study). The eggs are spherical to subspherical (diameter ~70-80 mm) in shape. All eggs were missing their upper halves due to erosion, whereas the lower halves were still imbedded in the mudstone layer. Abundant scattered eggshell fragments were found in the same horizon as the eggs, and were usually small in size (<20 mm in length).

Eggshell thickness ranges from 0.94 to 1.56 mm with a mean value of 1.25 mm (n = 52). The outer surface of the eggshell is smooth to rough and lacks a conspicuous ornamentation pattern (Fig. 3C). Round to oval pore openings are present on the outer surface. The eggshell consists of a single layer of closely-spaced fan-shaped shell units each made up of densely-packed acicular crystals (prolatospherulitic shell units: Fig. 4A-C). In radial thin section, the shell unit margins are poorly defined in the upper three-quarters to one-half of the eggshell. A sweeping extinction pattern and subhorizontal growth lines are visible through the shell units under PLM (Fig. 4B). The shell unit bases, which are composed of acicular crystals radiating from the core, are finger-like in shape and densely packed with little to no space between them (Fig. 4A-C). Pore canals appear irregular in shape along their length and are unbranching (assigned to prolatocanaliculate) (Fig. 4D). They vary in diameter and cross-sectional shape, from round to oval or somewhat irregular, with relatively smooth pore walls (Fig. 4E).

Comparisons — The eggs and eggshells (MPC-D 100/1065 and 100/1066 and uncatalogued specimens) are assignable to the oofamily Spheroolithidae based on the presence of prolatospherulitic shell units, but lack sagenotuberculate ornamentation (Table 1). Of the two oogenera within the oofamily Spheroolithidae, *Paraspheroolithus* and *Spheroolithus*, the specimens examined are attributable to *Paraspheroolithus* because of a scarcity of interstices between the finger-shaped bases of the shell units. These specimens are assignable to *Pa. irenensis* because all attributes of eggshell morphology are shared with this ootaxon, and the egg width and eggshell thickness are within the ranges of *Pa. irenensis*. Currently, *Paraspheroolithus* has only one valid oospecies, *Pa. irenensis* (see the review of *Paraspheroolithus* in Shen et al., 2023).

Remarks — Only a single spheroolithid ootaxon, *Spheroolithus tenuicorticus* had been reported previously from the Shiluut Uul locality (Mikhailov, 1994b). Although described as oval in shape [elongation index (100 × egg width / egg length): 71.43 - 76.92?] with weak sagenotuberculate ornamentation or a smooth outer surface (Mikhailov, 1994b), the ootaxon presently lacks sufficient description or illustration of the eggshell microstructure. The microstructure of *Sp. tenuicorticus*, according to Mikhailov (1994b), is similar to that of *Pa. irenensis*; the only differences noted between the two oospecies are a more elongate egg and thinner eggshell in *Sp. tenuicorticus*. Because egg shape and eggshell thickness of *Sp. tenuicorticus* are shown to largely overlap with these ranges for *Pa. irenensis* (Fig. 5), we consider *Sp. tenuicorticus* to be a junior synonym of *Pa. irenensis*. Thus, a single spheroolithid ootaxon (*Pa. irenensis*) is currently known from the Shiluut Uul locality.

The egg remains (MPC-D 100/1065 and 100/1066) were likely laid by hadrosaurs as embryonic and neonatal bones of these dinosaurs have been found in close association with spheroolithid eggs from sites in China, Mongolia, and the USA (Horner and Makela, 1979; Hirsch and Quinn, 1990; Horner, 1999; Dewaele et al., 2015; Xing et al., 2022). From the Bayanshiree Formation of Mongolia, the non-hadrosaurid hadrosauroid *Gobihadros mongoliensis* has been reported from skeletal remains (Tsogtbaatar et al., 2019) and is thus a potential candidate for the producer of these eggs.

Oogenus *SPHEROOLITHUS* Zhao, 1979 emend. Zhao et al., 2015

SPHEROOLITHUS cf. *S. MAIASAUROIDES* Mikhailov, 1994b

(Figs. 3D and 4F-H)

Holotype — PIN 4228-2, compressed egg from Baga Tariach, Mongolia (middle Campanian Djadokhta Formation).

Referred Specimens — An isolated eggshell fragment (MPC-D 100/1060).

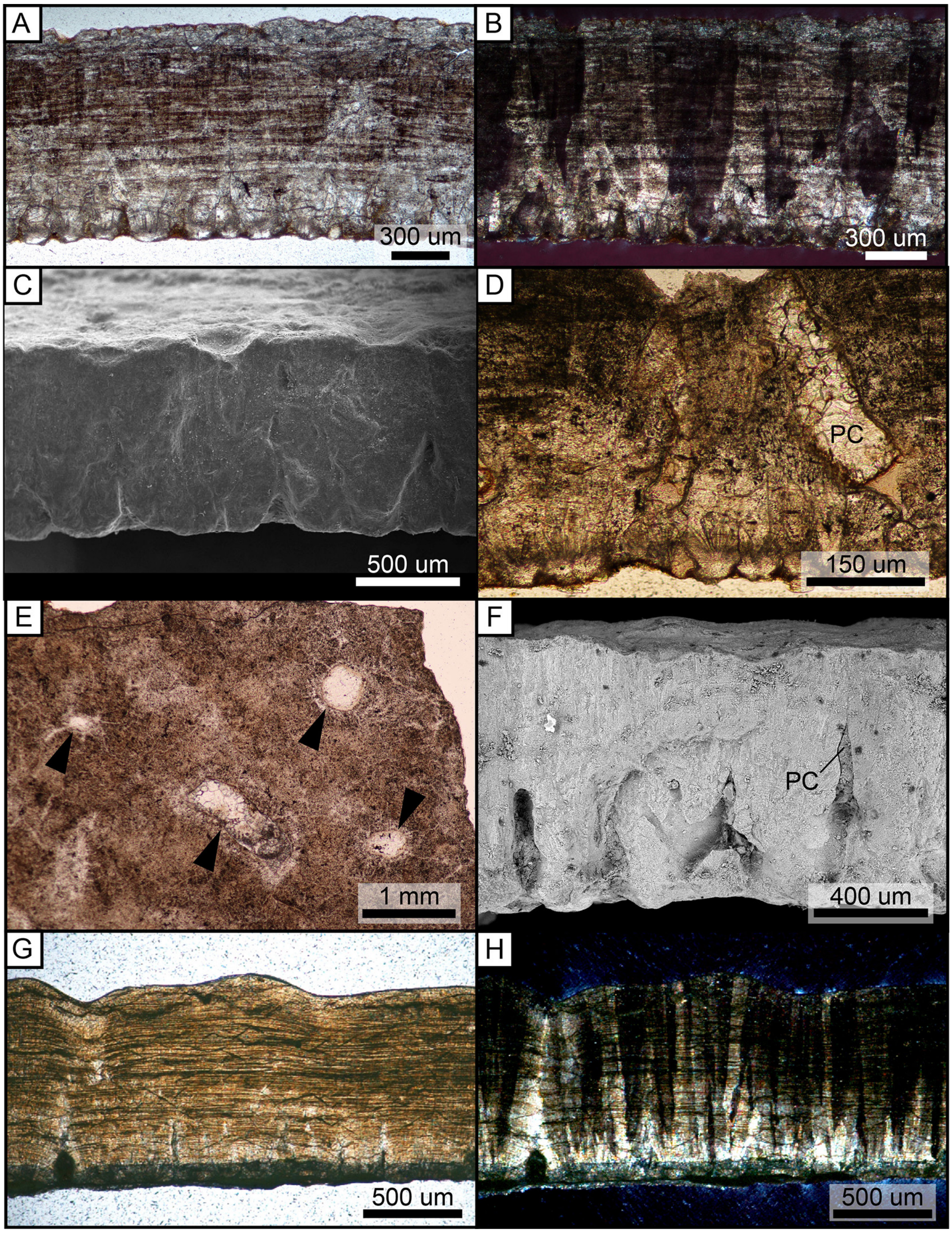

FIGURE 4. Photomicrographs of spheroolithid eggshells (A-E, *Paraspheroolithus irenensis*, MPC-D 100/1065; F-H, *Spheroolithus* cf. *S. maiasauroides*, MPC-D 100/1060). **A**, radial thin section of eggshell under polarized light, showing single layer of fan-shaped shell units with subhorizontal growth lines; **B**, radial thin section of A under cross-polarized light, showing sweeping extinction pattern; **C**, radial view of eggshell under SEM, showing fan-shaped shell units; **D**, radial thin section of eggshell under polarized light, showing oblique pore canal; **E**, tangential thin section of eggshell under polarized light, showing round to irregular pore canals with relatively smooth pore walls (black arrows); **F**, radial view of eggshell under SEM, showing single layer of fan-shaped shell units; **G**, radial thin section of eggshell under polarized light, showing fan-shaped shell units with subhorizontal growth lines; **H**, radial thin section of G under cross-polarized light, showing sweeping extinction pattern.

TABLE 1. Comparison of spheroolithid and related ootaxa. References: [1]this study; [2]Moreno-Azanza et al. (2014a); [3]Hirsch and Quinn (1990); [4]Zelenitsky and Hills (1997); [5]Sellés et al. (2014); [6]Xue et al. (1996); [7]Zhu et al. (2022); [8]Mikhailov (1994b); [9]Shen et al. (2023); [10]Young (1954); [11]Young (1965); [12]Zhao and Jiang (1974); [13]Zhao et al. (2015); [14]Bureau of Geology and Mineral Resources of Jilin Province (1992); [15]Jackson and Varricchio (2010); [16]Liu et al. (2013); [17]Chow (1951); [18]Mikhailov (2000); [19]Dawaele et al. (2015); [20]Xing et al. (2022). *Ootaxa that have been recently reassigned to *Stromatoolithus* by Zhao et al. (2015) and/or Zhu et al. (2022). **Incomplete egg. Parentheses include mean values or main ranges

Ootaxon	Egg length (mm)	Egg width (mm)	Mean EI	Eggshell thickness (mm)	Surface texture	Locality	Formation
Shiluut Uul *Paraspheroolithus irenensis*	?	70.00-80.00[1]	?	1.25[1]	Smooth[1]	Shiluut Uul, Mongolia[1]	Upper Cretaceous (Cenomanian to lower Santonian?) Bayanshiree Formation[1]
Altan Uul *Spheroolithus* cf. *S. maiasauroides*	?	?	?	0.97[1]	Prominent sagenotuberculate ornamentation[1]	Altan Uul IV, Mongolia[1]	Upper Cretaceous (upper Campanian to lower Maastrichtian) Nemegt Formation[1]
*Guegoolithus turolensis**	?	?	?	0.42-1.50 (0.815)[2]	Prominent sagenotuberculate ornamentation[2]	Teruel, Spain[2]	Lower Cretaceous (lower Barremian) Blesa, Camarillas, Upper El Castellar, and Mirambel formations[2]
Spheroolithus albertensis (egg of *Maiasaura peeblesorum*)*	100.00-120.00[3]	70.00-90.00[3]	72.73[3]	1.00-1.20[3]; 0.96-1.46 (0.98-1.22)[4]	Sagenotuberculate ornamentation[4]	Montana, USA[3] and Alberta, Canada[4]	Upper Cretaceous (Campanian) Two Medicine Formation (Montana)[3] and Upper Cretaceous (Campanian) Oldman and Dinosaur Park formations (Alberta)[4]
*Spheroolithus europaeus**	?	?	?	1.04-1.11 (1.07)[5]	Sagenotuberculate ornamentation[5]	Lleida, Spain[5]	Upper Cretaceous (upper Maastrichtian) Tremp Formation[5]
*Spheroolithus lamelliformae**	?	?	?	1.20-1.46 (1.33)[6]	'spots and curved strips' (prominent sagenotuberculate ornamentation)[6,7]	Shanyang, Shaanxi Province, China[6]	Upper Cretaceous Shanyang Formation[6]
*Spheroolithus maiasauroides**	90.00[8,**]	70.00[8,**]	77.78[8,**]	1.00-1.60 (1.20-1.50)[8]	Prominent sagenotuberculate ornamentation[8]	Baga Tariach and Bayn Dzak, Mongolia[8]	Upper Cretaceous (middle Campanian) Djadokhta Formation[8]
Paraspheroolithus irenensis, including *Paraspheroolithus jilinensis*	83.74[9]; 83.00-91.00 (87.00)[10]; 88.00-105.00 (93.73)[11]; 84.00-91.00 (86.75, 90.30)[12]; 83.00-99.00 (84.00)[13]; 87.00[14]	66.58[9]; 71.00-77.00 (73.75)[10]; 72.00-88.00 (78.91)[11]; 67.00-75.40 (68.25, 75.40)[12]; 67.00-88.00 (70.00)[13]; 81.50[14]	79.51[9]; 81.11, 86.10[10]; 84.19[11]; 83.50, 78.79[12]; 83.33[13]; 93.67[14]	1.05[9]; 1.10-2.60 (1.50-2.20), 1.10-3.00 (1.50-2.22)[10]; 1.50-2.20 (1.80)[12,13]; 2.00[14]	Smooth to rough and a very weak reticulate ornamentation (sagenotuberculate ornamentation)[9,10]	Gongzhuling of Jilin, Changtu of Liaoning, Erlian of Neimongolia, Laiyang of Shangdong, Xichuan and Xixia of Henan, Yunxian of Hubei, and Jinqu and Tiantai of Zhejiang, China[9]	Upper Cretaceous (Cenomanian) Quantou Formation (Jilin and Liaoning), Upper Cretaceous Earlian Formation (Neimongolia), Upper Cretaceous (Coniacian-Santonian) Jiangjunding Formation (Shangdong), Upper Cretaceous (Cenomanian-Turonian) Gaogou (or Zoumagang) Formation and (Coniacian-Santonian) Majiacun (or Zhaoying) Formation (Henan), Upper Cretaceous (Cenomanian-Turonian) Gaogou Formation (Hubei), and Upper Cretaceous Quixian and Chichengshan formations (Zhejiang)[9]

TABLE 1. Continued

Ootaxon	Egg length (mm)	Egg width (mm)	Mean EI	Eggshell thickness (mm)	Surface texture	Locality	Formation
Spheroolithus chiangchiungtingensis	81.00[12]	77.00[12]	95.06[12]	2.20[12]	Generally smooth but small nodes observed under microscopy[10,12]	Laiyang, Shangdong, China[12]	Upper Cretaceous (Coniacian-Santonian) Jiangjunding Formation[12]
Spheroolithus choteauensis	110.00[15,**]	95.00[15,**]	?	0.66-0.94[15]	Relatively smooth to ramotuberculate[15]	Montana, USA[15]	Upper Cretaceous (Campanian) Two Medicine Formation[15]
Spheroolithus quantouensis	90.00[16]	80.00[16]	88.90[16]	4.80-5.22[15]; 4.80-5.70[12]	Smooth[16]	Changtu, Liaoning, China[16]	Upper Cretaceous (Cenomanian) Quantou Formation[16]
Spheroolithus spheroides	68.00-81.00 (79.00)[10]; 81.00[12]; 74.00-90.00 (80.00)[13,16]	55.00-71.00 (64.67)[10]; 77.00[12]; 57.00-67.00 (62.33)[15]; 68.00[13]	81.94[10]; 95.06[12]; 78.51[15]; 85.00-90.50[13]	1.40-3.00[10]; 2.80-3.10[15]; 2.40-3.20[13]	Smooth[1,17]	Changtu, Liaoning and Laiyang, Shangdong, China[16]	Upper Cretaceous (Cenomanian) Quantou Formation (Liaoning) and Upper Cretaceous (Coniacian-Santonian) Jiangjunding Formation[16]
Spheroolithus tenuicorticus (= *Pa. irenensis*)	?	?	71.43-76.92?[8]	0.80-1.80 (1.00-1.30)[18]	No ornamentation or weak sagenotuberculate pattern[8]	Shiluut Uul, Mongolia[8]	Upper Cretaceous (Cenomanian to lower Santonian?) Bayanshiree Formation[1]
Spheroolithus eggshell of *Saurolophus angustirostris*	?	?	?	1.80[19]	Ramotuberculate or sagenotuberculate ornamentation[19]	Dragon's Tomb dinosaur locality, Mongolia[19]	Upper Cretaceous (upper Campanian to lower Maastrichtian) Nemegt Formation[19]
Spheroolithid egg of Lambeosaurinae	?	?	?	0.32-0.42[20]	?	Jiangxi, China[20]	Upper Cretaceous Hekou Formation[20]

TABLE 2. Comparison of egg size and eggshell thickness in Stalicoolithidae. Parentheses indicate mean values.

Ootaxon	Egg length (mm)	Egg width (mm)	Eggshell thickness (mm)	Reference
Coralloidoolithus oosp.	130.0	130.0	2.53-3.95 (3.24)	This study
Coralloidoolithus shizuiwanensis	93.6	81.9	1.80-2.60	Wang et al. (2012a)
Shixingoolithus erbeni	105.0-125.0	99.0-123.0	2.30-2.60	Zhao et al. (1991)
Stalicoolithus shifengensis	95.4	88.9	3.90-4.00	Wang et al. (2012a)

Locality, Horizon, and Age — The single eggshell fragment was recovered from the Altan Uul IV locality (N43.36.101; E100.27.102), which is located approximately 58 km northwest of Gurvantes in Ömnögovi Aimag, Mongolia. The exposures belong to the Upper Cretaceous (upper Campanian to lower Maastrichtian) Nemegt Formation.

Description — The outer eggshell surface exhibits a reticulated pattern of ridges (sagenotuberculate ornamentation), with an average width of 0.4 mm (Fig. 3D). The eggshell is 1.05 mm thick when the ornamentation height is included, and 0.97 mm with the ornamentation excluded. Oval pore openings are visible between the ridges on the outer surface. The eggshell consists of adjacent fan-shaped shell units (prolatospherulitic) that interlock at one-third to three-fifth of the eggshell thickness (Fig. 4F-H). Under SEM, acicular crystals are observed to radiate from the bases and occur throughout the shell units (Fig. 4F). In radial thin section, a sweeping extinction pattern is visible under PLM through the slender wedges that comprise the shell units (Fig. 4G, H). Multiple growth lines that roughly parallel the outer surface are also visible (Fig. 4G). Pore canals are non-branching, but their diameter varies throughout the length (prolatocanaliculate pore system) (Fig. 4F).

Comparisons — The eggshell microstructure of MPC-D 100/1060 is comparable to that of *Stromatoolithus* as well as to those of other spheroolithid ootaxa with a prominent sagenotuberculate ornamentation (e.g., *Guegoolithus turolensis*, *Spheroolithus lamelliformae*, *Sp. albertensis*, *Sp. europaeus*, and *Sp. maiasauroides*: Table 1). These ornamented spheroolithid ootaxa were recently transferred to the oogenus *Stromatoolithus* because of morphological similarities (Zhu et al., 2022). According to Zhu et al. (2022), the (remaining) spheroolithids, which lack prominent ornamentation, differ from ornamented spheroolithids (i.e., *Stromatoolithus*) in that they have irregular pores in cross-section (i.e., unevenly pinched by surrounding shell units) and less conspicuous growth lines. However, Shen et al. (2023) more recently found that non-ornamented spheroolithid eggs could also possess features characteristic of ornamented spheroolithids (e.g., some pores are circular to sub-circular in cross section, subhorizontal to undulating growth lines continue through adjacent spherulitic shell units), suggesting that such features are transitional or shared between ornamented and non-ornamented spheroolithid ootaxa. Because of this, we presently consider *G. turolensis*, *Sp. lamelliformae*, *Sp. albertensis*, *Sp. europaeus*, and *Sp. maiasauroides* as distinct ootaxa, rather than synonyms of *Stromatoolithus*, until further investigations are conducted.

Compared to ornamented spheroolithid ootaxa, MPC-D 100/1060 has the most apparent differences with the ootaxon *G. turolensis* (ornamentation is significantly higher at one-fifth to one-third of the eggshell thickness: Moreno-Azanza et al., 2014a), whereas more subtle differences occur with *Sp. albertensis* (Zelenitsky and Hills, 1997), *Sp. europaeus* (Sellés et al., 2014), *Sp. maiasauroides* (Mikhailov, 1994b), and *Sp. lamelliformae* (Xue et al., 1996). These *Spheroolithus* oospecies are difficult to differentiate from one another as they are all characterized by sagenotuberculate ornamentation (which is extremely variable) and have similar eggshell thicknesses. The ornamentation ridges in MPC-D 100/1060 are wider than those of *Sp. europaeus* (180 µm in width), but similar measurement data are not provided for other oospecies. According to Mikhailov (1994b), *Sp. maiasauroides* eggshell from Mongolia has finer ornamentation than eggshells of the hadrosaur *Maiasaura peeblesorum* from North America (eggshells of *Maiasaura* were assigned to the oospecies *Sp. albertensis*: Zelenitsky, 2000), which also appears to be the case for MPC-D 100/1060. Although *Sp. maiasauroides* and *Sp. lamelliformae* (from Shaanxi Province of China: Xue et al., 1996) appear very similar, we tentatively assign MPC-D 100/1060 to *Sp. maiasauroides* due to geographic and stratigraphic considerations, as well as the fact that *Sp. maiasauroides* would be the senior synonym if these two oospecies cannot be differentiated.

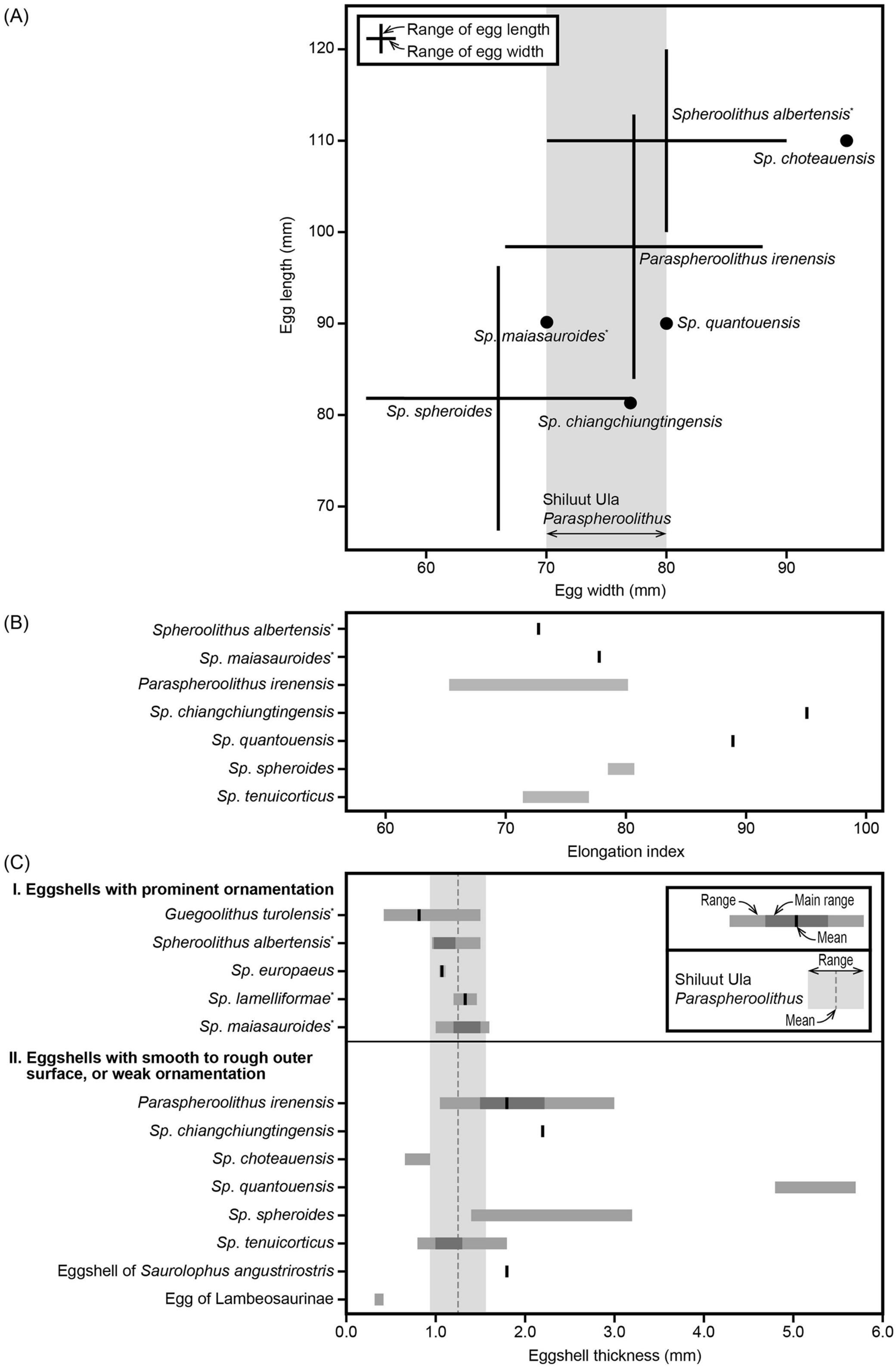

FIGURE 5. Comparisons of spheroolithid eggs. **A**, bivariate plot of egg length vs. egg width. Grey shaded area shows egg width of Shiluut Uul *Paraspheroolithus irenensis*; **B**, comparison of egg elongation index [100 × egg width (mm)/egg length (mm)] among ootaxa; **C**, comparison of eggshell thickness among ootaxa. Grey shaded area shows eggshell thickness of Shiluut Uul *Pa. irenensis* (MPC-D 100/1065 and MPC-D 100/1066).

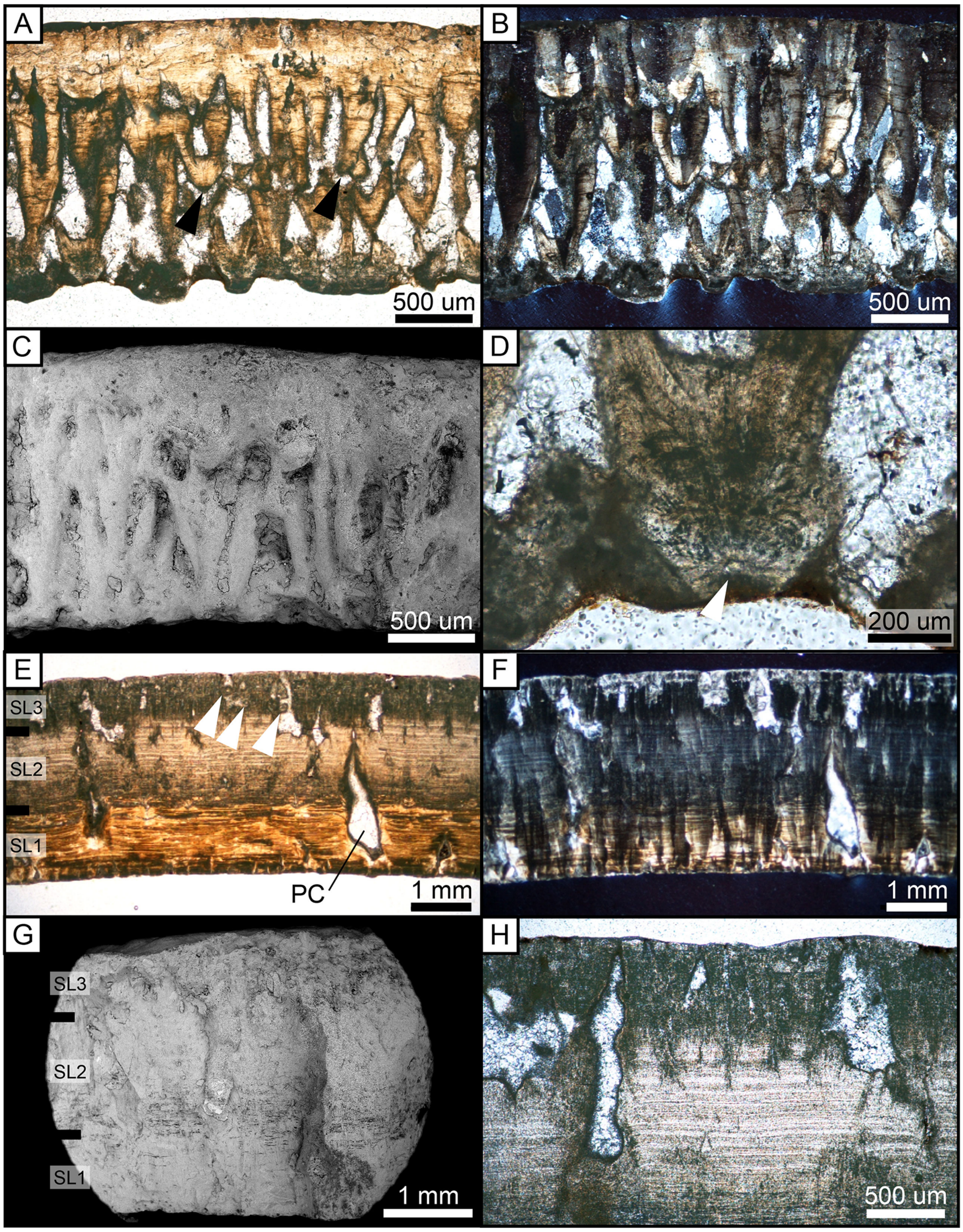

FIGURE 6. Photomicrographs of *Dendroolithus* oosp., MPC-D 100/1063 (A-D) and *Coralloidoolithus* oosp., MPC-D 100/1045 (E-H). **A**, radial thin section of eggshell under polarized light, showing shell units branching at mid-thickness of eggshell (black arrows); **B**, radial thin section of A under cross-polarized light, showing sweeping extinction pattern; **C**, radial view of eggshell under SEM, showing branched shell units; **D**, radial thin section of base of shell unit under polarized light, showing organic core (white arrow); **E**, radial thin section of eggshell under polarized light, showing three sublayers (SL1-3); **F**, radial thin section of E under cross-polarized light, showing narrow, columnar extinction pattern; **G**, radial view of eggshell under SEM, showing very porous layer in lower part of sublayer 2; **H**, radial thin section of upper part of eggshell under polarized light, showing narrow wedge-like structure with irregular aerial spaces.

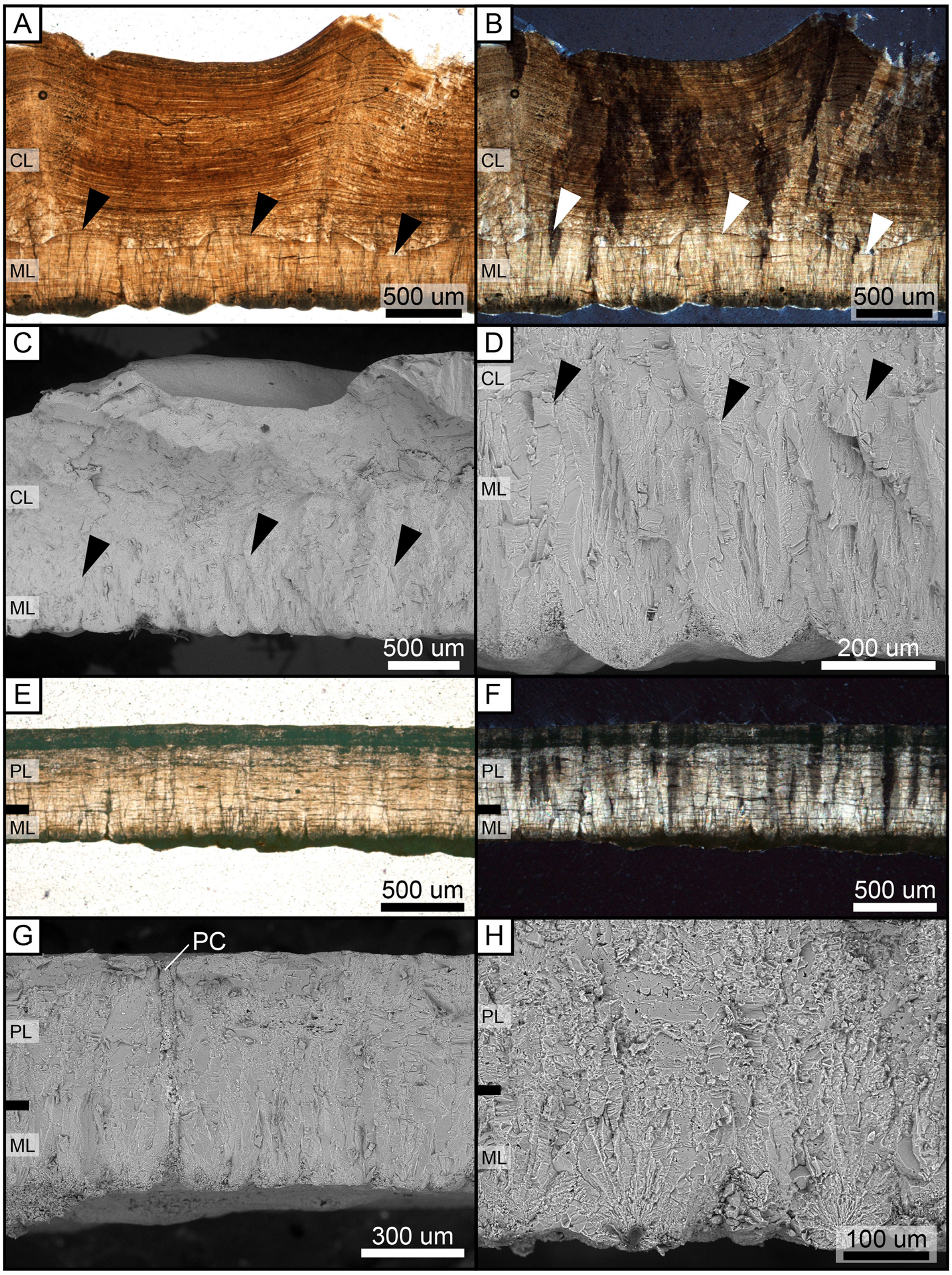

FIGURE 7. Photomicrographs of *Macroelongatoolithus* oosp., MPC-D 100/1064 (A-D) and *Protoceratopsidovum* cf. *Pro. minimum*, MPC-D 100/1062 (E-G) and MPC-D 100/1061 (H). **A**, radial thin section of eggshell under polarized light, showing two layers (ML and CL) delimited by undulating boundary (black arrows); **B**, radial thin section of A under cross-polarized light, showing undulating boundary between ML and CL (white arrows) and irregular extinction pattern; **C**, radial view of eggshell under SEM, showing two layers (ML and CL) delimited by undulating boundary (black arrows); **D**, radial view of ML under SEM, showing tall mammillae with overlying CL and CL boundary (black arrows); **E**, radial thin section of eggshell under polarized light, showing two layers (ML and PL) delimited by gradual boundary; **F**, radial thin section of E under cross-polarized light, showing prismatic extinction pattern; **G**, radial view of eggshell under SEM, showing straight, tubular pore canal (PC); **H**, radial view of ML, showing wedge-like crystals, and lower PL, showing squamatic structure, under SEM.

Remarks — As for the spheroolithid *Pa. irenensis*, MPC-D 100/1060 was likely laid by a hadrosaurid. Perinatal remains of the hadrosaurids *Maiasaura peeblesorum* (from Montana) and *Saurolophus angustirostris* (from Mongolia) have been discovered in association with *Spheroolithus* eggshell (Horner and Makela, 1979; Dewaele et al., 2015).

Oofamily DENDROOLITHIDAE Zhao and Li, 1988, emend. Zhao et al., 2015
Oogenus DENDROOLITHUS Zhao and Li, 1988, emend. Zhao et al., 2015
DENDROOLITHUS oosp.
(Figs. 3E, F and 6A-D)

Referred Specimens — Isolated eggshell fragments (MPC-D 100/1063: n = 7).

Locality, Horizon, and Age — Eggshell specimens were recovered from the Bayanshiree type locality (N44.16.426; E109.54.373), which is located approximately 70 km south-southwest of Sainshand in Dornogovi Aimag, Mongolia. The exposures are part of the Upper Cretaceous (Cenomanian to lower Santonian?) Bayanshiree Formation.

Description — Eggshell thickness ranges from 1.55 to 2.04 mm with a mean value of 1.73 mm (n = 7). The outer surface of the eggshell is rough or shagreen. The eggshell is porous and abundant circular pore openings form honeycomb-like structures on the outer surface in places (Fig. 3E, F). Fan-shaped shell units that comprise the eggshell are sub-symmetrical and bifurcate at the base with further branching in the upper part of the shell units (dendrospherulitic shell units: Fig. 6A-D). It appears that shell units occasionally originated around mid-thickness of the eggshell and overlie the primary (lower) shell units (Fig. 6A), although these structures are likely just truncated branches of the primary shell units rather than additional shell units. The primary shell units have a core (which is integral to a shell unit) at the base near the inner shell surface (Fig. 6D), whereas the structures that appear to emanate near mid-thickness lack evidence of a core. This structure is similar to the secondary origin of extra-spherulites that lack organic cores (Moreno-Azanza et al., 2016). In the upper one-fifth of the shell thickness, the shell units are fused together forming a dense layer (Fig. 6A, B). Under PLM, a sweeping extinction pattern and subhorizontal growth lines were visible in radial view (Fig. 6B), and pore canals are irregular and branching (prolatocanaliculate pore system).

Comparisons — The eggshells MPC-D 100/1063 are comparable to those of other dendroolithid eggs, including *Dendroolithus* and *Placoolithus*. These specimens are assignable to *Dendroolithus* due to the presence of symmetrical shell units that bifurcate near the base (Zhao et al., 2015); *Placoolithus* has symmetrical or asymmetrical shell units that usually bifurcate around mid-thickness of the eggshell (Zhang et al., 2018). Most oospecies of *Dendroolithus* are between 1.5 and 2.5 mm in eggshell thickness (i.e., *D. dendriticus*, *D. microporosus*, *D. wangdianensis*, and *D. xichuanensis*), and few fall outside of this range (only *D. verrucarius* of 2.6-3.3 mm eggshell: Mikhailov, 1994b). Due to morphological similarities (including eggshell thickness) among oospecies, we assign MPC-D 100/1063 to *Dendroolithus* oosp.

Remarks — Embryonic remains discovered inside putative dendroolithid eggs from China and Portugal indicate that Dendroolithidae was likely laid by megalosauroids and therizinosaurs (Manning et al., 1997; Kundrát et al., 2008; Araujo et al., 2013; Ribeiro et al., 2014; Kundrát and Cruickshank, 2021). Attribution of MPC-D 100/1063 to therizinosaurs is more likely because megalosauroids are not found in Upper Cretaceous deposits of Mongolia.

Oofamily STALICOOLITHIDAE Wang et al., 2012a
Oogenus CORALLOIDOOLITHUS Wang et al., 2012a
CORALLOIDOOLITHUS oosp.
(Figs. 3G and 6E-H)

Referred Specimens — A partial egg and isolated eggshell fragments (MPC-D 100/1045: n = 694).

Locality, Horizon, and Age — Egg and eggshell specimens were recovered from the Altan Uul I locality (N43.34.881; E100.38.156), located approximately 52 km northwest of Gurvantes in Ömnögovi Aimag, Mongolia. The exposures belong to the Upper Cretaceous (upper Campanian to lower Maastrichtian) Nemegt Formation.

Description — Based on the curvature, the partially preserved egg was originally spherical with a diameter of approximately 13 cm (Fig. 3G). Eggshell thickness ranges from 2.53 to 3.95 mm with a mean value of 3.24 mm (n = 257). The outer surface of the eggshell is rough or shagreen and lacks conspicuous ornamentation. The eggshell consists of narrow, interlocking fan-shaped shell units (possibly prolatospherulitic) that often contain irregular fissures (Fig.

6E-G). At least three sublayers are recognizable within the eggshell, which are delimited by gradational boundaries. The inner sublayer is about 1.10 mm thick and includes the lower half of the shell units. The base of the shell units (0.20 mm thick) consists of an accumulation of cone-shaped spherites with radiating crystals. Overlying the shell unit bases, radiating crystals are visible under SEM and well-developed subhorizontal growth lines are visible under PLM. The middle sublayer has a lower (0.60 mm thick) very porous interval consisting of fine subhorizontal laminations (Fig. 6G) that gradually transitions into a denser, upper interval (0.85 mm thick). The upper sublayer (0.75 mm thick) consists of narrow, wedge-like structures with numerous irregular voids (Fig. 6H). Small globular structures (i.e., the 'secondary shell units' of Wang et al., 2012a) are occasionally visible within these voids (Fig. 6E). Regardless of structural differences between sublayers, a narrow columnar extinction pattern is observed throughout the eggshell under PLM (Fig. 6F). Pore canals are irregular in shape, and the diameter changes through the eggshell thickness (possibly prolatocanaliculate pore system) (Fig. 6E).

Comparisons — The spherical egg shape, thick eggshell (≥2.4 mm), and presence of at least three eggshell sublayers indicate that MPC-D 100/1045 belongs to Stalicoolithidae, an oofamily that contains three oogenera (i.e., *Coralloidoolithus*, *Shixingoolithus*, and *Stalicoolithus*). MPC-D 100/1045 differs from these oogenera with respect to egg size and eggshell thickness (Table 2). The microstructure, however, is comparable to that of *Coralloidoolithus* in that globular structures occur within the upper sublayer (Wang et al., 2012a), so we assign MPC-D 100/1045 to *Coralloidoolithus* oosp.

Remarks — Stalicoolithid eggs are mainly known from Lower and Upper Cretaceous deposits of China. As suggested by Wang et al. (2012a), some eggshells from Mongolia assigned to Dendroolithidae by Mihailov (1991, 1994b) may actually belong to Stalicoolithidae because they have the characteristic eggshell sub-layers (see Plate 24.7 of Mikhailov, 1991; Figure 7.6D of Mikhailov et al., 1994). The producer of stalicoolithid eggs has yet to be identified.

Oofamily ELONGATOOLITHIDAE Zhao, 1975
Oogenus MACROELONGATOOLITHUS Li et al., 1995
emend. Simon et al., 2019
MACROELONGATOOLITHUS oosp.
(Figs. 3H and 7A-D)

Referred Specimens — Isolated eggshell fragments (MPC-D 100/1064: n = 114).

Locality, Horizon, and Age — Bayanshiree type locality (N44.16.277; E109.54.530), which is located approximately 70 km south-southwest of Sainshand in Dornogovi Aimag, Mongolia. The exposures belong to the Upper Cretaceous (Cenomanian to lower Santonian?) Bayanshiree Formation.

Description — The outer surface texture of the eggshell is highly variable; eggshells exhibiting prominent short ridges and nodes (lineartuberculate, ramotuberculate and dispersituberculate ornamentation) are common (74% of 113 fragments), whereas those exhibiting coarse ridges (14%), fine reticulate ridges (0.9%) or a smooth surface (11%) are relatively uncommon (Fig. 3H). With the ornamentation height included, eggshell thickness ranges from 1.31 to 2.90 mm with a mean value of 1.90 mm (n = 112). Excluding the ornamentation height, eggshell thickness ranges from 1.22 to 2.39 mm with a mean value of 1.68 mm (n = 113). Two microstructural layers are visible in radial section, regardless of the outer surface texture: an inner mammillary layer (ML) and an outer continuous layer (CL), delimited by an abrupt undulatory boundary (Fig. 7A-C). The ML consists of cone-shaped mammillae and forms one-seventh to one-third of the eggshell thickness (Fig. 7D). Possible squamatic structures with small vesicles are present in the CL. Observations from PLM reveal a blocky to irregular extinction pattern and multiple fine growth lines that parallel the outer surface (Fig. 7B). Pore canals are straight and tubular (angusticanaliculate pore system).

Comparisons — Among elongatoolithids, both *Macroelongatoolithus* (1.11-3.23 mm) and *Macroolithus* (0.71-1.88 mm) have eggshells with a thickness of 1.6 mm (Tanaka et al., 2018). However, the relative thickness of the ML tends to be thinner in *Macroelongatoolithus* eggshell (ML : CL thickness ratio of 1 : 2-1 : 8: Simon et al., 2019) and thicker in *Macroolithus* eggshell (1 : 3: Zhao et al., 2015), indicating a *Macroelongatoolithus* affinity for MPC-D 100/1064.

Furthermore, *Macroelongatoolithus* eggs and eggshell fragments have been reported previously from the Bayanshiree locality (Iijima et al., 2011, 2012). The two eggs recovered are approximately 40 cm in length (Iijima et al., 2012), and significantly larger than other elongatoolithid ootaxa (Tanaka et al., 2018). MPC-D 100/1064 specimens are comparable to previously-described Bayanshiree *Macroelongatoolithus* eggshell, which has lineartuberculate, ramotuberculate, and dispersituberculate ornamentation and a mean eggshell thickness of

2.04 mm (Iijima et al., 2011, 2012).

Remarks — *Macroelongatoolithus* eggs are known to have been laid by large species of caenagnathid oviraptorosaur, based on the discovery of several eggs associated with a perinatal skeleton from Henan Province, China (Pu et al., 2017). Fused dentaries belonging to a large species of unnamed caenagnathid are also known from the Tsagaan Teg locality of the Bayanshiree Formation (Tsuihiji et al., 2015), and could be the producer of *Macroelongatoolithus* eggs from the formation.

Oofamily PRISMATOOLITHIDAE Hirsch, 1994 emend. Moreno-Azanza et al., 2014b
Oogenus PROTOCERATOPSIDOVUM Mikhailov, 1994b
PROTOCERATOPSIDOVUM cf. *Pro. MINIMUM* Mikhailov, 1994b
(Figs. 3I and 7E-H)

Holotype — PIN 4228-1, four incomplete eggs of a partial clutch from Baga Triach, Mongolia (middle Campanian Djadokhta Formation).

Referred Specimens — Isolated eggshell fragments from the localities of Shine Us Khudag (MPC-D 100/1061: n = 24) and Bayanshiree (MPC-D 100/1062: n = 22).

Locality, Horizon, and Age — Eggshell specimens were recovered from the Bayanshiree type locality (N44.16.426; E109.54.373) and the Shine Us Khudag locality (N44.22.857; E109.18.720), which are located approximately 70 km south-southwest and 87 km southwest, respectively, of Sainshand in Dornogovi Aimag, Mongolia. Outcrops at these localities belong to the Upper Cretaceous (Cenomanian to lower Santonian?) Bayanshiree Formation.

Description — The outer surface of the eggshell is smooth with scattered circular pore openings (Fig. 3I). Eggshell thickness ranges between 0.34 and 0.68 mm (mean value of 0.54 mm) for the Shine Us Khudag specimens (MPC-D 100/1061: n = 24) and between 0.34 to 0.80 mm (mean value of 0.61 mm) for the Bayanshiree specimens (MPC-D 100/1062: n = 22). The eggshell is composed of interlocking columnar shell units and consists of two structural layers, an inner ML and an outer prismatic layer (PL), delimited by a gradual boundary (Fig. 7E-G). The ML, representing one-quarter to one-third of the eggshell thickness, is composed of wedge-like crystals radiating from a core, whereas the PL is composed of well-developed squamatic structure with tiny vesicles (Fig. 7H). The uppermost part of the PL is dark in color under PLM, but no microstructural differences were identified under SEM, indicating a lack of an external zone or layer in these specimens, PLM also reveals a narrow columnar extinction pattern within the shell units (Fig. 7F). Pore canals are narrow, tubular and straight (angusticanaliculate pore system) (Fig. 7G).

Comparisons — MPC-D 100/1061 and MPC-D 100/1062 have a smooth outer surface and relatively thin eggshell (around 0.5-0.6 mm in thickness), features that are comparable to four prismatoolithid oospecies, including: *Prismatoolithus hirschi*, *Pri. tenuis*, *Protoceratopsidovum sincerum* and *Pro. minimum*. Particular characteristics of our specimens differ from those in the following oospecies: *Pri. tenuis* has a relatively thinner ML (ML : PL = 1 : 6: Vianey-Liaud and Crochet, 1993), *Pri. hirschi* has narrower and taller mammillae (ML : PL = 1 : 2-1 : 2.5: Jackson and Varricchio, 2010), and *Pro. sincerum* has acicular mammillae and an abrupt boundary between the ML and PL (Choi et al., 2022). With respect to *Pro. minimum*, although Choi et al. (2022) indicate the ML to PL boundary seems abrupt, other features (e.g., wedge-like crystals of the mammillae) are comparable to MPC-D 100/1061 and MPC-D 100/1062; we thus tentatively assign these specimens to *Pro. minimum*.

Remarks — Although a troodontid affinity is known for the oospecies *Prismatoolithus levis* (Varricchio et al., 2002), the taxonomic affinities of other ootaxa within the Prismatoolithidae are uncertain. Troodontid skeletons are apparently associated with prismatoolithid eggs/eggshells from Mongolia (Grellet-Tinner, 2005; Pei et al., 2017), although the oogenera and oospecies of these remains are unknown. The taxonomic affinity of *Protoceratopsidovum* eggs is also uncertain as no associated perinatal remains have been discovered with this ootaxon. The name *Protoceratopsidovum*, meaning eggs of *Protoceratops*, is clearly a misnomer as *Protoceratops* eggs are soft-shelled (Norell et al., 2020) and *Protoceratopsidovum* eggs share many characteristics (e.g., elongate eggs, asymmetrical egg shape, two microstructural layers) with known maniraptoran (e.g., oviraptorosaurs and deinonychosaurs) eggs (e.g., Zelenitsky and Therrien, 2008; Varricchio and Barta, 2014; Choi et al., 2022). Based on the variation in characteristics among *Protoceratopsidovum* oospecies (Varricchio and Barta, 2014; Choi et al., 2022), it is possible that the known *Protoceratopsidovum* oospecies are attributable to different maniraptoran clades (e.g., oviraptorosaur, dromaeosaurid, and troodontid).

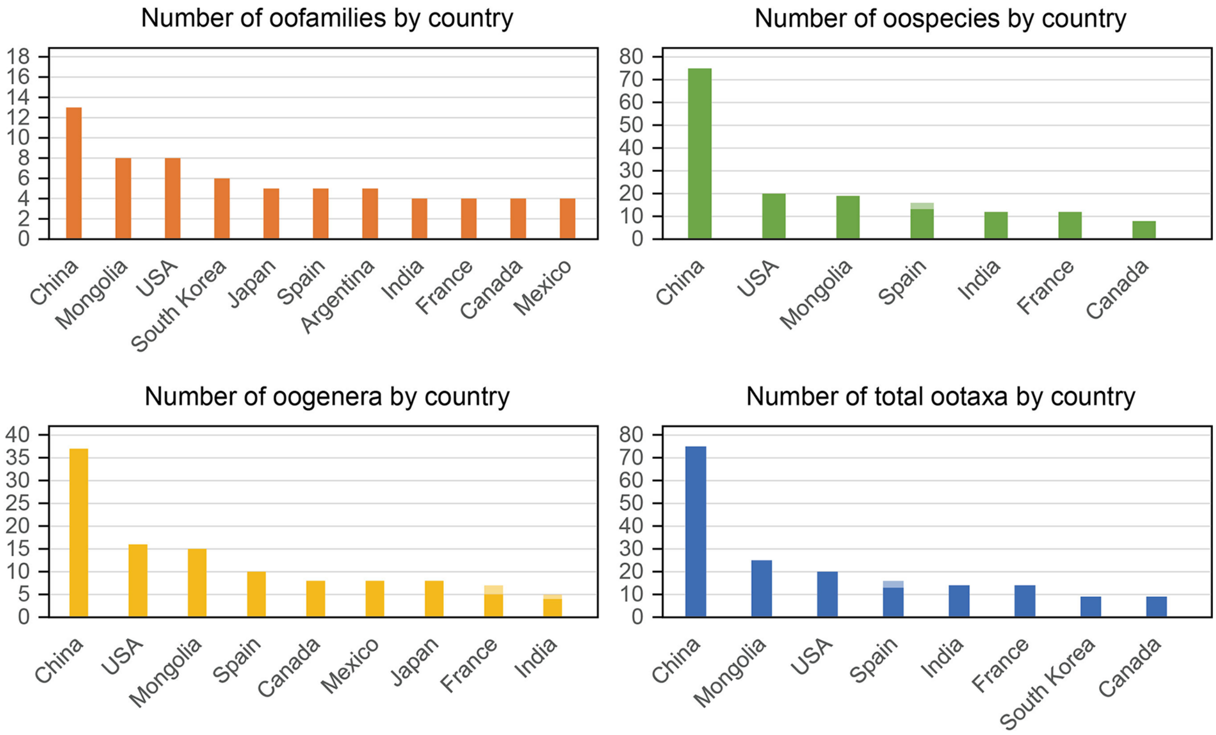

FIGURE 8. Numbers of non-avian dinosaur oofamilies, oogenera, and oospecies and the total numbers of non-avian dinosaur ootaxa recognized in various countries. Only egg specimens that were parataxonomically classified were included. See Appendix Table 3 for the dataset of this figure.

DISCUSSION

Fossil eggshells described in this study reveal new occurrences of ootaxa at several localities in the Gobi Desert, providing further insight into the diversity of non-avian dinosaur eggs from Mongolia. Six ootaxa, *Coralloidoolithus* oosp., *Dendroolithus* oosp., *Macroelongatoolithus* oosp., *Paraspheroolithus irenensis*, cf. *Protoceratopsidovum minimum,* and *Spheroolithus* cf. *S. maiasauroides*, were identified among eggshell specimens recovered at five localities, including Altan Uul I, Altan Uul IV, Bayanshiree, Shine Us Khudag and Shiluut Uul, during joint Mongolian expeditions with Korea (KID) and with Japan (Hokkaido University Museum expedition). Although eggs from these localities were described/reported previously (e.g., Mikhailov, 1994b; Mikhailov et al., 1994; Ariunchimeg, 2000; Iijima et al., 2011, 2012), the current study recognizes at least one new ootaxon from each locality, except at Bayanshiree. A compilation of locality and formation data for these and other ootaxa from Mongolia reveals the egg-bearing Upper Cretaceous formations, except for the Javkhlant Formation, have each yielded ten or more non-avian dinosaur ootaxa (Baruungoyot, Bayanshiree, Djadokhta, and Nemegt formations) (Fig. 1). Whereas each of these latter formations has produced several eggshell localities, only one eggshell locality is known from the Javkhlant Formation explaining the small number of ootaxa known from this formation. Lower Cretaceous deposits in Mongolia also have few localities and ootaxa compared to Upper Cretaceous deposits, a trend also found in strata of China (Wang et al., 2012b).

China and Mongolia are among the richest places with respect to abundance and diversity of dinosaur eggs (Fig. 8). Each country has produced more than twenty ootaxa attributable to non-avian dinosaurs. Abundant dinosaur eggs have been collected from individual basins in China (e.g., Laiyang or Jiaolai Basin of Shandong Province, Xixia Basin of Henan Province, Tiantai Basin of Zhejiang Province, and Heyuan and Nanxiong basins of Guangdong Province: Dong, 2005; Wang et al., 2012b), although skeletal remains of dinosaurs are usually uncommon in such egg-rich strata. Mongolia is unique in that it preserves both egg and skeletal remains in the same formations. The Upper Cretaceous Bayanshiree, Djadokhta, Baruungoyot, and Nemegt formations each have produced more than ten ootaxa (Fig. 1), as well as skeletons of more than ten species of dinosaurs (e.g., Weishampel et al., 2004; Tanaka et al., 2021). For each formation, the taxonomic affinities of the ootaxa present are generally consistent with the known dinosaur taxa. For example, sauropods, therizinosaurs, and deinonychosaurs are known from the Bayanshiree Formation as are ootaxa attributed to these clades, including faveoloolithids, dendroolithids, and prismatoolithids, respectively. Finally, many significant discoveries of dinosaur eggs (several with closely associated skeletal remains) in Mongolia have shed light on nesting behaviors and other reproductive traits of particular dinosaurs.

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AUTHOR CONTRIBUTIONS

KT, FT, DKZ, YNL, KK, YK, GFF, TK. KT and DKZ designed the project, YNL, YK, and TK organized the fieldworks, KT, FT, DKZ, YNL, KK, and GFF collected specimens, TK prepared specimens, KT, YNL, KK, YK, and GFF gathered the data, KT conducted the analyses, KT, FT, and DKZ drafted the manuscript. All authors edited the manuscript.

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APPENDIX TABLE 1. List of non-avian dinosaur egg localities in Mongolia. **Ovaloolithus chinkangkouensis* has been divided into three oospecies: *O. mixtistriatus*, *O. monostriatus*, and *O. tristriatus* by Zhao (1979a). †Choi et al. (2022) indicate that *Protoceratopsidovum fluxuosum* and *Pro. sincerum* are maniraptoran eggs and could belong to Elongatoolithidae and Montanoolithidae, respectively. ‡Zhang (2010) suggested that some eggs of *Faveoloolithus ningxiaensis* from Algui Ulan Tsav are actually *Parafaveoloolithus* oosp. Abbreviations of 'Fm.' column: BG, Baruungoyot Formation; BS, Bayanshiree Formation; Dj, Djadokhta Formation; Du, Dushi Uul (/Doshuul/ Dushihin/ Duhih Ula) Formation; J, Javkhlant Formation; KD, Khuren Dukh Formation; N, Nemegt Formation; UN, Ulaanoosh Formation (formerly known as Barunbayan Formation)

Locality	Fm.	Dendroolithidae	Elongatoolithidae	Ovaloolithidae	Prismatoolithidae	Spheroolithidae	Other ootaxa/eggs
Abdrant Nuru[1-4]	Dj	Dendroolithidae indet.	*Elongatoolithus* oosp.			Spheroolithidae indet.	
Altan Uul area[5-15]	N	Dendroolithidae indet.	Elongatoolithidae indet.	*Ovaloolithus dinornithoides*	*Protoceratopsidovum minimum*	*Spheroolithus* cf. *S. maiasauroides*; *Spheroolithus* oosp. with perinatal *Saurolophus angustirostris*	*Coralloidoolithus* oosp.
Baga Tariach[6-8,12,16]	Dj				*Protoceratopsidovum minimum*	*Spheroolithus maiasauroides*	
Bagamod Khuduk[6]	BG						Dinosaur egg indet. (?*Protoceratopsidovum minimum*)
Bambu Khudu[6]	BG						Dinosaur egg indet.
Bayan Dzak (Bayan Zag)[5-8,12,16-21]	Dj		*Elongatoolithus frustrabilis*; ootaxonomically unassigned clutch associated with a skeleton of *Oviraptor philoceratops*		*Protoceratopsidovum fluxuosum*†; *Protoceratopsidovum sincerum*†	*Spheroolithus maiasauroides*	*Faveoloolithus ningxiaensis*‡
Bayanshiree[2,6,9,12,15,22-25]	BS	*Dendroolithus* oosp. (and/or Dictyoolithidae indet.)	*Macroelongatoolithus* oosp.; *Macroolithus mutabilis*		cf. *Protoceratopsidovum minimum*		Faveoloolithidae indet.
Baynshin Tsav area[6,9,12,23]	BS	*Dendroolithus microporosus*	Elongatoolithidae indet.				
Bortolgoi[12,21]	Dj		Elongatoolithidae indet.			Spheroolithidae indet.	
Bugiin Tsav[1,9-12,20,26]	N	*Dendroolithus verrucarius*	*Elongatoolithus sigillarius*; ootaxonomically unassigned eggs with oviraptorid embryos		*Protoceratopsidovum* oosp.	Spheroolithidae indet.	
Buylyasutuin Khuduk[6,8,27]	Du		*Trachoolithus faticanus*				

APPENDIX TABLE 1. Continued

Locality	Fm.	Dendroolithidae	Elongatoolithidae	Ovaloolithidae	Prismatoolithidae	Spheroolithidae	Other ootaxa/eggs
Dariganga[7]	BS			*Ovaloolithus chinkangkouensis**			
Dushin Uul[6]	Du						Dinosaur egg indet.
Dzamin Khond[1,9,10,12,20,28]	Dj		Elongatoolithidae indet. (including ?*Elongatoolithus subtitectorius*)			Spheroolithidae indet.	
Ekhin Tukhum (Ikh Eren?)[6]	BS						Dinosaur egg indet.
Gilbent[6]	BG	*Dendroolithus microporosus*					*Faveoloolithus ningxiaensis*[‡]
Guriliin Tsav[6-9,11,20]	N	Dendroolithidae indet.	*Elongatoolithus sigillarius*; *Macroolithus rugustus*; *Macroolithus yaotunensis*			*Paraspheroolithus irenensis*	
Ikh Shunkht[6-8,12,16,30]	BG	*Dendroolithus verrucarius*	*Macroolithus mutabilis*		*Protoceratopsidovum minimum*; *Protoceratopsidovum sincerum*[†]	*Spheroolithus* oosp.	*Faveoloolithus ningxiaensis*[‡]
Khaichin Uul area[6,8,11,12,20,30]	N	*Dendroolithus* oosp.	*Elongatoolithus* oosp.; ?*Macroolithus rugustus*				
Khara Khutul[6]	BS						Dinosaur egg indet.
Khashaat[5,20]	Dj		Elongatoolithidae indet.		*Protoceratopsidovum fluxuosum*[†]		
Khermeen Tsav area[1,5-9,11,12,15,16]	BG/N	*Dendroolithus microporosus; Dendroolithus verrucarius*	*Macroolithus rugustus*		*Protoceratopsidovum minimum*; *Protoceratopsidovum fluxuosum*[†]; *Protoceratopsidovum sincerum*[†]	*Spheroolithus maiasauroides*	?*Coralloidoolithus*; *Faveoloolithus ningxiaensis*[‡]
Khongil Tsav[1,9,31]	BS		*Macroolithus mutabilis*		Prismatoolithidae indet.		Dinosaur egg indet.
Khugen Slavkhant[32]	J	Dendroolithidae indet.					
Khulsan[6-8,16]	BG	*Dendroolithus microporosus; Dendroolithus verrucarius*			*Protoceratopsidovum minimum*; *Protoceratopsidovum fluxuosum*[†]		*Faveoloolithus ningxiaensis*[‡]

APPENDIX TABLE 1. Continued

Locality	Fm.	Dendroolithidae	Elongatoolithidae	Ovaloolithidae	Prismatoolithidae	Spheroolithidae	Other ootaxa/eggs
Khuren Dukh[7]	KD						*Faveoloolithus ningxiaensis*‡
Kuren Tsav[6]	?						Dinosaur egg indet.
Moyogn Ulagiyn Khaets (Mogoin Ulaagiin Hets / Mogoin Bulak?)[6,7]	BS			*Ovaloolithus chinkangkouensis**			
Naran Bulak[6,12]	N						Dinosaur egg indet.
Nemegt[5,7,9,10,12,33,34]	BG/N	*Dendroolithus verrucarius*	*Elongatoolithus* oosp.; ootaxonomically unassigned clutch with a brooding *Nemegtomaia barsboldi*	*Ovaloolithus dinornithoides*	*Protoceratopsidovum fluxuosum*†		
Nogon Tsav[9,10,12]	?		?*Elongatoolithus* oosp.				*Dictyoolithus* oosp.; Faveoloolithidae indet.
Algui Ulan Tsav (= Ologoy Ulaan Tsav)[1,7,12,19,30,35,36]	UN						*Dictyoolithus* oosp.; *Parafaveoloolithus* oosp.‡; ootaxonomically unassigned egg with a possible titanosaur embryo
Shar Tsav[2,12,37]	N	Dendroolithidae indet.	Elongatoolithidae indet.			Spheroolithidae indet.	
Shiluut Uul (Shiljust Ula)[3,6,7,15]	BS	*Dendroolithus microporosus*				*Paraspheroolithus irenensis* (= *Spheroolithus tenuicorticus*)	
Shine Us Khudag[9,15]	BS			*Ovaloolithus chinkangkouensis**	*Protoceratopsidovum* cf. *Pro. minimum*		
Shiregin Gashun[6]	BS					*Spheroolithus* oosp.	
Southern Monadnocks[1]	BG						Dinosaur egg indet.
Tel Ulan Chaltsai (Tel Ulan Ula)[1,6,7,9,10,12,38]	BS		?*Elongatoolithus frustrabilis*	*Ovaloolithus chinkangkouensis** with a partial embryo			
Tsagaan Khushu[3,5-12,16]	N	Dendroolithidae indet.	*Elongatoolithus excellens*; *Macroolithus rugustus*	Ovaloolithus dinornithoides	?*Protoceratopsidovum fluxuosum*†	*Spheroolithus* oosp.	

APPENDIX TABLE 1. Continued

Locality	Fm.	Dendroolithidae	Elongatoolithidae	Ovaloolithidae	Prismatoolithidae	Spheroolithidae	Other ootaxa/eggs
Tugrikin Shire (Toogreek)[1,6,8,9,12,16,20,28]	Dj		*Elongatoolithus frustrabilis*; ?*Elongatoolithus subtitectorius*		*Protoceratopsidovum minimum*; *Protoceratopsidovum sincerum*†		
Udan Sayr[6-9,12,16,19-21,23,28]	Dj		*Elongatoolithus subtitectorius; Nanhsiungoolithus* oosp.	*Ovaloolithus dinornithoides*	*Protoceratopsidovum* oosp.		
Ukhaa Tolgod[39-47]	Dj		?*Elongatoolithus frustrabilis* (with a *Citipati osmolskae* embryo); clutch (?*Elongatoolithus frustrabilis*) with brooding *Citipati osmolskae*		*Prismatoolithus* oosp. (associated with a skeleton of *Almas ukhaa*); ootaxonomically unassigned eggs with a juvenile *Byronosaurus jaffei*		ootaxonomically unassigned clutch with embryos of *Protoceratops andrewsi*
Ulaan Khushu[9,10]	N	*Dendroolithus verrucarius*					
Undurshil Uul[6]	BG		*Elongatoolithus* oosp.				
Urlibe Khuduk[48,49]	BS	Dendroolithidae indet.	Elongatoolithidae indet.		Prismatoolithidae indet.		
Yagaan Khovil[12,20,21,28]	N?	Dendroolithidae indet.	Elongatoolithidae indet.			Spheroolithidae indet.	

References: 1, Watabe and Suzuki (2000b); 2, Watabe and Suzuki (2000c); 3, Watabe and Suzuki (2000d); 4, Watabe (2004); 5, Sabath (1991); 6, Carpenter and Alf (1994); 7, Mikhailov (1994b); 8, Mikhailov (1994a); 9, Ariunchimeg (2000); 10, Watabe and Suzuki (2000a); 11, Watabe et al. (2010b); 12, Watabe et al. (2010a); 13, Dewaele et al. (2015); 14, Graf et al. (2018); 15, this study; 16, Mikhailov et al. (1994); 17, van Straelen (1925); 18, Brown and Schlaikjer (1940); 19, Suzuki and Watabe (2000a); 20, Suzuki and Watabe (2000b); 21, Saneyoshi et al. (2010); 22, Watabe et al. (1998); 23, Suzuki and Watabe (2000c); 24, Iijima et al. (2012); 25, Iijima et al. (2012); 26, Weishampel et al. (2008); 27, Kurzanov and Mikhailov (1989); 28, Watabe and Tsogtbaatar (2004); 29, Suzuki et al. (2010); 30, Sochava (1969); 31, Lee et al. (2017); 32, Tanaka et al. (2019); 33, Fanti et al. (2012); 34, Funston et al. (2016); 35, Grellet-Tinner et al. (2011); 36, Kundrát and Cruickshank (2021); 37, Watabe et al. (2004); 38, Sochava (1972); 39, Clark et al. (1999); 40, Norell et al. (1994); 41, Norell et al. (2001); 42, Norell et al. (2018); 43, Norell et al. (2020); 44, Grellet-Tinner (2005); 45, Grellet-Tinner et al. (2006); 46, Erickson et al. (2017); 47, Pei et al. (2017); 48, Ishigaki et al. (2016); 49, Noda and Hayashi (2021)

APPENDIX TABLE 2. List of non-avian dinosaur eggs known from Mongolia. *Ootaxa known also from outside of Mongolia but data presented here are based on Mongolian specimens. [†]Eggshell thickness excluding the height of ornamentation. Parentheses indicate mean values or main ranges. Abbreviations: L, egg length; ST, eggshell thickness; W, egg width.

Oofamily	Ootaxon/ taxon	L (mm)	W (mm)	ST (mm)	Outer surface morphology	Reference of egg
Dendroolithidae	*Dendroolithus microporosus*	70.0	60.0	1.5-3.0 (2.0-2.7)	Primarily unsculptured	Mikhailov (1994b)
	Dendroolithus verrucarius	90.0-100.0	90.0-100.0	1.8-4.3 (2.6-3.3)	Rough and nodose, lacking any clear ornamentation (eroded by numerous ravines surrounding wartlike projections of repeated spherulites)	Mikhailov (1994b)
Dictyoolithidae	*Dictyoolithus* oosp.*	?	?	?	?	Ariunchimeg (2000)
Elongatoolithidae	*Elongatoolithus excellens*	90.0-110.0	40.0	0.3-0.9 (0.4-0.7)[†]	Linearituberculate ornamentation	Mikhailov (1994a)
	Elongatoolithus frustrabilis	150.0-170.0	60.0-70.0	0.8-1.5 (1.1-1.3)[†]	Linearituberculate ornamentation	Mikhailov (1994a)
	Elongatoolithus sigillarius	150.0-170.0	60.0-70.0	0.3-1.1 (0.4-0.8)[†]	Linearituberculate ornamentation	Mikhailov (1994a)
	Elongatoolithus subtitectorius	?	?	0.5-0.9 (0.7-0.8)[†]	Linearituberculate ornamentation	Mikhailov (1994a)
	Macroelongatoolithus oosp.*	400.0	?	~2.9 (2.0)	Linearituberculate ornamentation	Iijima (2012)
	Macroolithus mutabilis	>170.0?	?	1.3-2.0 (1.5-1.8)[†]	Linearituberculate ornamentation	Mikhailov (1994a)
	*Macroolithus rugustus**	165.0-?180.0	70.0	0.8-1.5 (1.1-1.3)[†]	Linearituberculate ornamentation	Sochava (1969); Mikhailov (1994a, 2000)
	Macroolithus yaotunensis	?	?	?	?	Ariunchimeg (2000)
	Nanhsiungoolithus oosp.*	?	?	?	?	Ariunchimeg (2000)
	Trachoolithus faticanus	?	?	0.3-0.5	Linearituberculate ornamentation	Mikhailov (1994a)
	Clutch with the holotype skeleton of *Oviraptor philoceratops*	203.2?	56.6?	1	Linearituberculate ornamentation	van Straelen (1925); Andrews (1932); Brown and Schlaikjer (1940); Norell et al. (2018)
	Clutches (?*Elongatoolithus frustrabilis*) with brooding *Citipati osmolskae*	180.0-190.0	65.0-72.0	0.5-0.6	Linearituberculate ornamentation	Clark et al. (1999); Grellet-Tinner et al. (2006); Norell et al. (2018)
	Clutch with a brooding *Nemegtomaia barsboldi*	140.0-160.0	50.0-60.0	1.0-1.2	Linearituberculate ornamentation	Fanti et al. (2012)

APPENDIX TABLE 2. Continued

Oofamily	Ootaxon/ taxon	L (mm)	W (mm)	ST (mm)	Outer surface morphology	Reference of egg
	Egg (?*Elongatoolithus frustrabilis*) with an oviraptorid embryo	120.0?	60.0?	0.5-1.0	Linearituberculate ornamentation	Norell et al. (1994, 2001); Mikhailov (2014)
	Eggs with oviraptorid embryos	?	?	0.7-1.0 (0.9)	Linearituberculate ornamentation	Weishampel et al. (2008)
Faveoloolithidae	*Faveoloolithus ningxiaensis*	150.0-165.0	150.0-165.0	1.8-2.6	Smooth or rough	Mikhailov (1994b)
	Parafaveoloolithus oosp.	145.0-148.0	130.0-134.0	1.8-2.5	Smooth	Sochava (1969); Mikhailov (1994b)
Ovaloolithidae	*Ovaloolithus chinkangkouensis**	?	70.0-80.0	1.4-3.0 (2.2-3.0)	Fine-corrugated ornament of sagenotuberculate ornamentation	Mikhailov (1994b)
	Ovaloolithus dinornithoides	105.0	74.0	1.3-1.6 (1.5-1.8)	No ornamentation or weak sagenotuberculate ornamentation at poles	Mikhailov (1994b)
	Eggshell (*Ovaloolithus chinkangkouensis*) with a partial indeterminate embryo	?	?	2.2-2.8	Small tubercles	Sochava (1972); Mikhailov (1994b)
Prismatoolithidae	*Protoceratopsidovum fluxuosum*	130.0-150.0	50.0-57.0	0.3-1.4 (0.6-0.7)	Lineartuberculate ornamentation	Mikhailov (1994a)
	Protoceratopsidovum minimum	100.0-?110.0	40.0-?50.0	0.3-0.7	Smooth	Mikhailov (1994a)
	Protoceratopsidovum sincerum	?	?	0.4-1.2 (0.6-0.7)	Smooth	Mikhailov (1994a)
	Clutch with juveniles of *Byronosaurus jaffei*	?	?	0.5	Smooth	Grellet-Tinner (2005)
	Prismatoolithus oosp. with the holotype skeleton of *Almas ukhaa*	?	?	0.4	Smooth	Pei et al. (2017)
Spheroolithidae	*Paraspheroolithus irenensis* (including *Spheroolithus tenuicorticus*)*	80.0-100.0	70.0-80.0	0.8-2.2 (1.0-2.0)	Smooth to rough, or weak sagenotuberculate ornamentation at poles	Mikhailov (1994b, 2000)
	Spheroolithus maiasauroides	90.0	70.0	1.0-1.6 (1.2-1.5)	Sagenotuberculate ornamentation	Mikhailov (1994b)
	Eggshells (*Spheroolithus* oosp.) with perinatal *Saurolophus angustirostris*	?	?	1.6-2.0 (1.8)	Between ramotuberculate and sagenotuberculate ornamentation	Dewaele et al. (2015)
Stalicoolithidae	*Coralloidoolithus* oosp.*	130.0	130.0	2.5-4.0 (3.2)	Rough or shagreen	This study
Other eggs	Clutch with *Protoceratops andrewsi* embryos	121.0-125.0	60.0	0.3	?	Erickson et al. (2017); Norell et al. (2020)
	Brooding troodontidae	?	?	?	?	Erickson et al. (2007)
	Egg with a titanosaur embryo	91.1	87.1	1.0-1.4	Eroded but occasionally nodes	Grellet-Tinner et al. (2011)

APPENDIX TABLE 3. List of non-avian dinosaur ootaxa in each country. Only egg specimens that were parataxonomically classified were included. **Subtiliolithus hyogoensis* is considered as a non-avian theropod eggshell (see Tanaka et al., 2020)

Region	Country	Oofamily	Oogenus	Oospecies
Africa	Morocco	Megaloolithidae	*Megaloolithus*	*Megaloolithus magharebiensis*
Africa	Morocco		*Pseudomegaloolithus*	*Pseudomegaloolithus atlasi*
Africa	Morocco	Prismatoolithidae	*Prismatoolithus*?	
Africa	Tanzania	Megaloolithidae		
Asia	China	Dendroolithidae	*Dendroolithus*	*Dendroolithus alimiaoensis*
Asia	China			*Dendroolithus dendriticus*
Asia	China			*Dendroolithus furcatus*
Asia	China			*Dendroolithus sanlimiaoensis*
Asia	China			*Dendroolithus wangdianensis*
Asia	China			*Dendroolithus xichuanensis*
Asia	China		*Phaceloolithus*	*Phaceloolithus hunanensis*
Asia	China		*Placoolithus*	*Placoolithus taohensis*
Asia	China			*Placoolithus tiantaiensis*
Asia	China			*Placoolithus tumiaolingensis*
Asia	China	Dictyoolithidae	*Dictyoolithus*	*Dictyoolithus hongpoensis*
Asia	China		*Paradictyoolithus*	*Paradictyoolithus xiaxishanensis*
Asia	China			*Paradictyoolithus zhuangqianensis*
Asia	China		*Protodictyoolithus*	*Protodictyoolithus jiangi*
Asia	China			*Protodictyoolithus neixiangensis*
Asia	China	Dongyangoolithidae	*Dongyangoolithus*	*Dongyangoolithus nanmaensis*
Asia	China		*Multifissoolithus*	*Multifissoolithus megadermus*
Asia	China			*Multifissoolithus chianensis*
Asia	China	Elongatoolithidae	*Elongatoolithus*	*Elongatoolithus andrewsi*
Asia	China			*Elongatoolithus elongatus*
Asia	China			*Elongatoolithus magnus*
Asia	China			*Elongatoolithus taipinghuensis*
Asia	China			*Elongatoolithus yuanshutensis*
Asia	China		*Heishanoolithus*	*Heishanoolithus changii*
Asia	China		*Lepidotoolithus*	*Lepidotoolithus guofenglouensis*
Asia	China		*Macroelongatolithus*	*Macroelongatolithus xixiaensis*
Asia	China		*Macroolithus*	*Macroolithus rugustus*
Asia	China			*Macroolithus yaotunensis*
Asia	China		*Nanhsiungoolithus*	*Nanhsiungoolithus chuetienensis*
Asia	China		*Paraelongatoolithus*	*Paraelongatoolithus reticulatus*
Asia	China		*Undulatoolithus*	*Undulatoolithus pengi*
Asia	China	Faveoloolithidae	*Duovallumoolithus*	*Duovallumoolithus shangdanensis*
Asia	China		*Faveoloolithus*	*Faveoloolithus ningxiaensis*
Asia	China			*Faveoloolithus zhangi*
Asia	China		*Hemifaveoloolithus*	*Hemifaveoloolithus muyushanensis*

APPENDIX TABLE 3. Continued

Region	Country	Oofamily	Oogenus	Oospecies
Africa	Morocco	Megaloolithidae	*Megaloolithus*	*Megaloolithus magharebiensis*
Africa	Morocco		*Pseudomegaloolithus*	*Pseudomegaloolithus atlasi*
Africa	Morocco	Prismatoolithidae	*Prismatoolithus*?	
Africa	Tanzania	Megaloolithidae		
Asia	China	Dendroolithidae	*Dendroolithus*	*Dendroolithus alimiaoensis*
Asia	China			*Dendroolithus dendriticus*
Asia	China			*Dendroolithus furcatus*
Asia	China			*Dendroolithus sanlimiaoensis*
Asia	China			*Dendroolithus wangdianensis*
Asia	China			*Dendroolithus xichuanensis*
Asia	China		*Phaceloolithus*	*Phaceloolithus hunanensis*
Asia	China		*Placoolithus*	*Placoolithus taohensis*
Asia	China			*Placoolithus tiantaiensis*
Asia	China			*Placoolithus tumiaolingensis*
Asia	China	Dictyoolithidae	*Dictyoolithus*	*Dictyoolithus hongpoensis*
Asia	China		*Paradictyoolithus*	*Paradictyoolithus xiaxishanensis*
Asia	China			*Paradictyoolithus zhuangqianensis*
Asia	China		*Protodictyoolithus*	*Protodictyoolithus jiangi*
Asia	China			*Protodictyoolithus neixiangensis*
Asia	China	Dongyangoolithidae	*Dongyangoolithus*	*Dongyangoolithus nanmaensis*
Asia	China		*Multifissoolithus*	*Multifissoolithus megadermus*
Asia	China			*Multifissoolithus chianensis*
Asia	China	Elongatoolithidae	*Elongatoolithus*	*Elongatoolithus andrewsi*
Asia	China			*Elongatoolithus elongatus*
Asia	China			*Elongatoolithus magnus*
Asia	China			*Elongatoolithus taipinghuensis*
Asia	China			*Elongatoolithus yuanshutensis*
Asia	China		*Heishanoolithus*	*Heishanoolithus changii*
Asia	China		*Lepidotoolithus*	*Lepidotoolithus guofenglouensis*
Asia	China		*Macroelongatolithus*	*Macroelongatolithus xixiaensis*
Asia	China		*Macroolithus*	*Macroolithus rugustus*
Asia	China			*Macroolithus yaotunensis*
Asia	China		*Nanhsiungoolithus*	*Nanhsiungoolithus chuetienensis*
Asia	China		*Paraelongatoolithus*	*Paraelongatoolithus reticulatus*
Asia	China		*Undulatoolithus*	*Undulatoolithus pengi*
Asia	China	Faveoloolithidae	*Duovallumoolithus*	*Duovallumoolithus shangdanensis*
Asia	China		*Faveoloolithus*	*Faveoloolithus ningxiaensis*
Asia	China			*Faveoloolithus zhangi*
Asia	China		*Hemifaveoloolithus*	*Hemifaveoloolithus muyushanensis*

APPENDIX TABLE 3. Continued

Region	Country	Oofamily	Oogenus	Oospecies
Asia	China		*Parafaveoloolithus*	*Parafaveoloolithus guoqingsiensis*
Asia	China			*Parafaveoloolithus macroporus*
Asia	China			*Parafaveoloolithus microporus*
Asia	China			*Parafaveoloolithus pingxiangensis*
Asia	China			*Parafaveoloolithus tiansicunensis*
Asia	China			*Parafaveoloolithus xipingensis*
Asia	China			*Parafeveoloolithus fengguangcunensis*
Asia	China	Ovaloolithidae	*Ovaloolithus*	*Ovaloolithus huangtulingensis*
Asia	China			*Ovaloolithus laminadermus*
Asia	China			*Ovaloolithus mixtistriatus*
Asia	China			*Ovaloolithus monostriatus*
Asia	China			*Ovaloolithus nanxiongensis*
Asia	China			*Ovaloolithus sangequanensis*
Asia	China			*Ovaloolithus shitangensis*
Asia	China			*Ovaloolithus tristriatus*
Asia	China			*Ovaloolithus weiqiaoensis*
Asia	China	Polyclonoolithidae	*Polyclonoolithus*	*Polyclonoolithus yangjiagouensis*
Asia	China	Prismatoolithidae	*Laiyangoolithus*	*Laiyangoolithus lixiangensis*
Asia	China		*Prismatoolithus*	*Prismatoolithus tiantaiensis*
Asia	China			*Prismatoolithus gebiensis*
Asia	China			*Prismatoolithus heyuanensis*
Asia	China			*Prismatoolithus hukouensis*
Asia	China	Similifaveoolithidae	Similifaveoloolithus	*Similifaveoloolithus gongzhulingensis*
Asia	China			*Similifaveoloolithus shuangtangensis*
Asia	China		*Wormoolithus*	*Wormoolithus luxiensis*
Asia	China	Spheroolithidae	*Paraspheroolithus*	*Paraspheroolithus irenensis*
Asia	China		*Spheroolithus*	*Spheroolithus chiangchiungtingensis*
Asia	China			*Spheroolithus quantouensis*
Asia	China			*Spheroolithus spheroides*
Asia	China	Stalicoolithidae	*Coralloidoolithus*	*Coralloidoolithus chichengshanensis*
Asia	China			*Coralloidoolithus shizuiwanensis*
Asia	China		*Shixingoolithus*	*Shixingoolithus erbeni*
Asia	China		*Stalicoolithus*	*Stalicoolithus shifengensis*
Asia	China			*Stalicoolithus spheroides*
Asia	China	Umbellaoolithidae	*Umbellaoolithus*	*Umbellaoolithus xiuningensis*
Asia	China	Youngoolithidae	*Youngoolithus*	*Youngoolithus xipingensis*
Asia	China	(Oofamily incertae sedis)	*Mosaicoolithus*	*Mosaicoolithus zhangtoucaoensis*
Asia	China		*Parvoblongoolithus*	*Parvoblongoolithus jinguoensis*
Asia	China		*Stromatoolithus*	*Stromatoolithus pinglingensis*
Asia	China		*Taoyuanoolithus*	*Taoyuanoolithus dontingensis*

APPENDIX TABLE 3. Continued

Region	Country	Oofamily	Oogenus	Oospecies
Asia	India	Elongatoolithidae	*Ellipsoolithus*	*Ellipsoolithus khedaensis*
Asia	India		*Trachoolithus*	
Asia	India	Fusioolithidae	*Fusioolithus*	*Fusioolithus baghensis*
Asia	India	Megaloolithidae	*Megaloolithus*	*Megaloolithus cylindricus*
Asia	India			*Megaloolithus dholiyaensis*
Asia	India			*Megaloolithus dhoridungriensis*
Asia	India			*Megaloolithus jabalpurensis*
Asia	India			*Megaloolithus khempurensis*
Asia	India			*Megaloolithus matleyi*
Asia	India			*Megaloolithus megadermus*
Asia	India			*Megaloolithus mohabeyi*
Asia	India			*Megaloolithus padiyalensis*
Asia	India			*Megaloolithus walpurensis*
Asia	India	Spheroolithidae	*Spheroolithus?*	
Asia	Japan	Dongyangoolithidae	*Multifissoolithus*	*Multifissoolithus shimonosekiensis*
Asia	Japan	Elongatoolithidae	*Elongatoolithus*	
Asia	Japan	Prismatoolithidae	*Prismatoolithus*	
Asia	Japan		*Ramoprismatoolithus*	*Ramoprismatoolithus okurai*
Asia	Japan	Spheroolithidae	*Spheroolithus*	
Asia	Japan	Laevisoolithidae	*Subtiliolithus*	*Subtiliolithus hyogoensis**
Asia	Japan	(Oofamily incertae sedis)	*Himeoolithus*	*Himeoolithus murakamii*
Asia	Japan		*Nipponoolithus*	*Nipponoolithus ramosus*
Asia	Kazakhstan	Elongatoolithidae		
Asia	Kazakhstan	Spheroolithidae		
Asia	Mongolia	Dendroolithidae	*Dendroolithus*	*Dendroolithus microporosus*
Asia	Mongolia			*Dendroolithus verrucarius*
Asia	Mongolia	Dictyoolithidae	*Dictyoolithus*	
Asia	Mongolia	Elongatoolithidae	*Elongatoolithus*	*Elongatoolithus excellens*
Asia	Mongolia			*Elongatoolithus frustrabilis*
Asia	Mongolia			*Elongatoolithus sigillarius*
Asia	Mongolia			*Elongatoolithus subtitectorius*
Asia	Mongolia		*Macroelongatoolithus*	
Asia	Mongolia		*Macroolithus*	*Macroolithus mutabilis*
Asia	Mongolia			*Macroolithus rugustus*
Asia	Mongolia			*Macroolithus yaotunensis*
Asia	Mongolia		*Nansiungoolithus*	
Asia	Mongolia		*Trachoolithus*	*Trachoolithus faticanus*
Asia	Mongolia	Faveoloolithidae	*Faveoloolithus*	*Faveoloolithus ningxiaensis*
Asia	Mongolia		*Parafaveoloolithus*	
Asia	Mongolia	Ovaloolithidae	*Ovaloolithus*	*Ovaloolithus chinkangkouensis*

APPENDIX TABLE 3. Continued

Region	Country	Oofamily	Oogenus	Oospecies
Asia	Mongolia			*Ovaloolithus dinornithoides*
Asia	Mongolia			*Ovaloolithus turpanensis*
Asia	Mongolia	Prismatoolithidae	*Prismatoolithus*	
Asia	Mongolia		*Protoceratopsidovum*	*Protoceratopsidovum fluxuosum*
Asia	Mongolia			*Protoceratopsidovum minimum*
Asia	Mongolia			*Protoceratopsidovum sincerum*
Asia	Mongolia	Spheroolithidae	*Paraspheroolithus*	*Paraspheroolithus irenensis*
Asia	Mongolia		*Spheroolithus*	*Spheroolithus maiasauroides*
Asia	Mongolia	Stalicoolithidae	*Coralloidoolithus*	
Asia	Russia	Prismatoolithidae	*Prismatoolithus*	*Prismatoolithus ilekensis*
Asia	Russia	Spheroolithidae		
Asia	South Korea	Dendroolithidae		
Asia	South Korea	Dictyoolithidae	*Protodictyoolithus*	*Protodictyoolithus neixiangensis*
Asia	South Korea	Elongatoolithidae		
Asia	South Korea			*Macroelongatoolithus goseongensis*
Asia	South Korea	Faveoloolithidae	*Faveoloolithus*	
Asia	South Korea		*Propagoolithus*	*Propagoolithus widoensis*
Asia	South Korea	Ovaloolithidae		
Asia	South Korea	Spheroolithidae	*Spheroolithus*	
Asia	South Korea	(Oofamily incertae sedis)		*Reticuloolithus acicularis*
Europe	UK	Faveoloolithidae (or Dictyoolithidae)		
Europe	UK	Ovaloolithidae		
Europe	UK	Megaloolithidae		
Europe	France	Cairanoolithidae	*Cairanoolithus*	*Cairanoolithus dughii*
Europe	France		*Dughioolithus*	*Dughioolithus roussentensis*
Europe	France	Megaloolithidae	*Megaloolithus*	*Megaloolithus aureliensis*
Europe	France			*Megaloolithus mammillare*
Europe	France			*Megaloolithus microtuberculata*
Europe	France			*Megaloolithus petralta*
Europe	France			*Megaloolithus pseudomamillare*
Europe	France			*Megaloolithus siruguei*
Europe	France	Montanoolithidae	*Montanoolithus*	*Montanoolithus labadousensis*
Europe	France	Prismatoolithidae	*?Pseudogeckoolithus*	
Europe	France		*Prismatoolithus*	*Prismatoolithus carboti*
Europe	France			*Prismatoolithus matellensis*
Europe	France			*Prismatoolithus tenuis*
Europe	France	(Oofamily incertae sedis)	cf. *Ageroolithus*	
Europe	Portugal	Phaceloolithidae		
Europe	Portugal	Prismatoolithidae	*Preprismatoolithus*	

APPENDIX TABLE 3. Continued

Region	Country	Oofamily	Oogenus	Oospecies
Europe	Romania	Megaloolithidae	*Megaloolithus*	*Megaloolithus siruguei*
Europe	Spain	Cairanoolithidae	*Dughioolithus*	*Dughioolithus* cf. *roussetensis*
Europe	Spain	Fusioolithidae	*Fusioolithus*	*Fusioolithus baghensis*
Europe	Spain	Megaloolithidae	*Megaloolithus*	?*Megaloolithus pseudomamillare* (or *M. petralta*)
Europe	Spain			Maybe *Megaloolithus mammillare*
Europe	Spain			*Megaloolithus aureliensis*
Europe	Spain			*Megaloolithus petralta*
Europe	Spain			*Megaloolithus siruguei*
Europe	Spain	Prismatoolithidae	*Prismatoolithus*	aff. *Prismatoolithus matellensis*
Europe	Spain			*Prismatoolithus tenuis*
Europe	Spain			*Prismatoolithus trempii*
Europe	Spain		*Pseudogeckoolithus*	*Pseudogeckoolithus nodosus*
Europe	Spain		*Sankofa*	*Sankofa pyrenaica*
Europe	Spain		*Trigonoolithus*	*Trigonoolithus amoae*
Europe	Spain	Spheroolithidae	*Guegoolithus*	*Guegoolithus turolensis*
Europe	Spain		*Spheroolithus*	*Spheroolithus europaeus*
Europe	Spain	(Oofamily incertae sedis)	*Ageroolithus*	*Ageroolithus fontllongensis*
North America	Canada	Arriagadoolithidae	*Triprismatoolithus*	
North America	Canada	Montanoolithidae	*Montanoolithus*	*Montanoolithus strongorum*
North America	Canada	Prismatoolithidae	*Prismatoolithus*	*Prismatoolithus levis*
North America	Canada	Spheroolithidae	*Spheroolithus*	*Spheroolithus albertensis*
North America	Canada			*Spheroolithus* cf. *S. choteauensis*
North America	Canada	(Oofamily incertae sedis)	*Continuoolithus*	*Continuoolithus canadensis*
North America	Canada		*Porituberoolithus*	*Porituberoolithus warnerensis*
North America	Canada		*Reticuloolithus*	*Reticuloolithus hirschi*
North America	Canada		*Tristraguloolithus*	*Tristraguloolithus cracioides*
North America	Mexico	Prismatoolithidae	*Pseudogeckoolithus*	
North America	Mexico	Prismatoolithidae	*Prismatoolithus*	
North America	Mexico	Spheroolithidae	*Spheroolithus*	
North America	Mexico	Tubercuoolithidae	*Tubercuoolithus*	
North America	Mexico	(Oofamily incertae sedis)	*Disperituberoolithus*	
North America	Mexico		*Continuoolithus*	
North America	Mexico		*Porituberoolithus*	
North America	Mexico		*Tristraguloolithus*	
North America	USA	Arriagadoolithidae	*Triprismatoolithus*	*Triprismatoolithus stephensi*
North America	USA	Belonoolithidae	*Belonoolithus*	*Belonoolithus garbani*
North America	USA	Elongatoolithidae	*Macroelongatoolithus*	*Macroelongatoolithus carlylei*
North America	USA		*Spongioolithus*	*Spongioolithus hirschi*
North America	USA	Montanoolithidae	*Montanoolithus*	*Montanoolithus strongorum*

APPENDIX TABLE 3. Continued

Region	Country	Oofamily	Oogenus	Oospecies
North America	USA	Ovaloolithidae	*Ovaloolithus*	*Ovaloolithus tenuisus*
North America	USA			*Ovaloolithus utahensis*
North America	USA	Prismatoolithidae	*Preprismatoolithus*	*Preprismatoolithus coloradensis*
North America	USA		*Prismatoolithus*	*Prismatoolithus hirschi*
North America	USA			*Prismatoolithus jenseni*
North America	USA			*Prismatoolithus levis*
North America	USA		*Spheruprismatoolithus*	*Spheruprismatoolithus condensus*
North America	USA		*Tetonoolithus*	*Tetonoolithus nelsoni*
North America	USA	Spheroolithidae	*Spheroolithus*	*Spheroolithus albertensis*
North America	USA			*Spheroolithus choteauensis*
North America	USA	Tubercuoolithidae	*Dimorphoolithus*	*Dimorphoolithus bennetti*
North America	USA		*Tubercuoolithus*	*Tubercuoolithus tentonensis*
North America	USA	(Oofamily incertae sedis)	*Continuoolithus*	*Continuoolithus canadensis*
North America	USA		*Porituberoolithus*	*Porituberoolithus warnerensis*
North America	USA		*Stillatuberoolithus*	*Stillatuberoolithus storrsi*
South America	Argentina	Arriagadoolithidae	*Arriagadoolithus*	*Arriagadoolithus patagoniensis*
South America	Argentina	Faveoloolithidae		
South America	Argentina	Fusioolithidae	*Fusioolithus*	*Fusioolithus berthei*
South America	Argentina			*Fusioolithus baghensis*
South America	Argentina	Megaloolithidae		
South America	Argentina	Prismatoolithidae		
South America	Brazil	Elongatoolithidae?		
South America	Brazil	Megaloolithidae	*Megaloolithus*	*Megaloolithus pseudomamillare*
South America	Peru	Megaloolithidae	*Megaloolithus*	*Megaloolithus pseudomamillare*
South America	Uruguay	Faveoloolithidae	*Sphaerovum*	*Sphaerovum erbei*
South America	Uruguay	(Oofamily incertae sedis)	*Tacuarembovum*	*Tacuarembovum oblongum*