New dinosaur egg material from Yunxian, Hubei Province, China resolves the classification of dendroolithid eggs

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The oofamily Dendroolithidae is a distinct group of dinosaur eggs reported from China and Mongolia, which is characterized by branched eggshell units and irregular pore canals. The ootaxonomic inferences, however, were rarely discussed until now. A colonial nesting site was recently uncovered from the Qinglongshan region, Yunxian, Hubei Province, China. More than 30 dendroolithid egg clutches outcrop on the Tumiaoling Hill, including an extremely gigantic clutch containing 77 eggs. All clutches were exposed in the Upper Cretaceous fluvial-deposited Gaogou Formation. In this study, we emend the diagnosis of the oogenus *Placoolithus* and assign all dendroolithid eggs from the Tumiaoling Hill to a newly emended oospecies *Placoolithus tumiaolingensis* that shows greatly variable eggshell microstructure. Moreover, our study also disentangles the previous vexing classification of dendroolithid eggs. We conclude that *Dendroolithus tumiaolingensis*, *D. hongzhaiziensis*, and *Paradendroolithus qinglongshanensis*, all of which were previously reported from Yunxian, should be assigned to the newly emended oospecies *Placoolithus tumiaolingensis*.

Key words: Dendroolithidae, *Placoolithus*, colonial nesting, Cretaceous, China, Yunxian, Tumiaoling Hill.

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Introduction

Dinosaur eggs are roughly categorized into two groups based on their eggshell microstructure: avian-like vs. reticulated-like (Zhao 1994). Represented by loosely arranged branched eggshell units and large cavities between eggshell units, dendroolithid eggs were assigned to the latter (Zhao 1994). The oofamily Dendroolithidae and its subsidiary oogenus *Dendroolithus* were erected based on six slightly oval *Dendroolithus wangdianensis* eggs (Zhao and Li 1988). The clutch of six *D. wangdianensis* eggs was discovered in the Upper Cretaceous Gonganzhai Formation of Wangdian, Anlu, Hubei Province, China (Zhao and Li 1988). Six years later, two new oospecies, *D. verrucarius* and *D. microporosus* were reported from the Upper Cretaceous Baruungoyot Formation of Mongolia (Mikhailov 1994). These spherical to slightly ellipsoid eggs were considered to be produced by ornithopods or sauropod dinosaurs, yet pending for more evidence such as embryo-containing eggs (Mikhailov 1991, 1994, 1997; Mikhailov et al. 1994).

Zhao and Zhao (1998) described a clutch of oblate eggs from the Xichuan Basin, Henan Province, China, and attributed the oblate eggs to a new oogenus, *Placoolithus*, mainly based on the oblate shape and presence of asymmetrically branched eggshell units. Some eggshell fragments from the same locality, however, were assigned to a new oospecies *Dendroolithus xichuanensis* (Zhao and Zhao 1998). In the same year, a huge number of dinosaur eggs were discovered in the Xixia Basin of Henan Province, and Yunxian, Hubei Province, in China. The eggs from the Xixia Basin of Henan Province were assigned to *D. furcatus*, *D. dendriticus*, *D. sanlimiaoensis*, and *D. zhaoyingensis* (Fang et al. 1998), while the eggs from Yunxian, Hubei Province represented three new oospecies, *D. hongzhaiziensis*, *D. tumiaolingensis*, and *Paradendroolithus qinglongshanensis* (Zhou et al. 1998).

These previous studies thus indicated a great variety of eggshell microstructure in dendroolithid eggs. Yet, a new

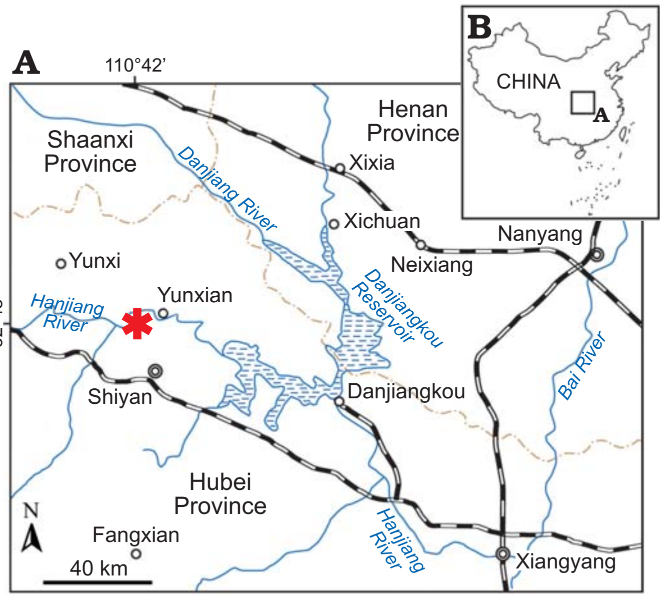

Fig. 1. **A**, **B**. Map of the location of dendroolithid eggs (asterisk) in Yunxian, Hubei Province, China.

study suggested that, except *D. wangdianensis*, *D. xichuanensis*, *D. tumiaolingensis*, and *Placoolithus taohensis*, the ootaxonomy of all dendroolithid eggs was controversial due to their poor preservation and a limited amount of thin sections of eggshells (Zhao et al. 2015). For instance, *D. verrucarius* and *D. microporosus*, which were previously reported from the Baruungoyot Formation of Mongolia, were re-assigned to stalicoolithid eggs in recent studies (Wang et al. 2012; Zhao et al. 2015). Although eggshell units have several branches near outer surface of eggshell, the parataxonomic position of Phaceloolithidae from Hunan Province, China is still doubtful (Zeng and Zhang 1979; Zhao et al. 2015). Despite large pore canals and branched eggshell units, the eggs with *Torvosaurus* embryo from the Lourinha Formation of Portugal reported by Araujo et al. (2013) should be assigned to faveoloolithid eggs based on the honeycomb-like eggshell microstructure. The acicular, elongated blade-shaped calcite crystals and large pore openings are not seen in dendroolithid eggs.

Despite a report of dendroolithid eggs from mid-west Korea (Kim et al. 2009), the absence of eggshell micrographs in the report led to an uncertainty of their assignement. The distribution of dendroolithid eggs is thus currently geographically constrained in three Chinese provinces, including Henan, Hubei and Zhejiang Provinces (Fang et al. 1998, 2000; Zhao and Zhao 1998; Zhou et al. 1998; Zhao et al. 2015). Cohen et al. (1995) and Mikhailov (1997) suggested that therizinosauroids laid dendroolithid eggs because of the evidence of a dendroolithid egg containing a therizinosauroid embryo. While Kundrát et al. (2008) examined several in ovo dinosaur embryos and concluded that they are closest to *Neimongosaurus yangi* and *Erliansaurus bellamanus*, the description of eggshell microstructure was absent and thus the linkage between therizinosauroids and dendroolithid eggs remained unclear.

Unlike the rarity of embryo-containing eggs, dendroolithid eggs are commonly discovered in China. For instance, more than 4000 dendroolithid eggs were discovered from Yunxian, Hubei Province, representing a dinosaur colony in the Late Cretaceous period. The most remarkable locality is the Tumiaoling Hill in Yunxian, Hubei Province (Fig. 1). More than 30 egg clutches, each of which contained 20 eggs in average, were exposed on an 80 m long section outcropped by running water. The largest clutch containing 77 eggs is the most incredible one on the Tumiaoling Hill. While some of these eggs had been preliminarily studied by Zhou et al. (1998), the parataxonomic assignment of these eggs requires further investigation. Therefore, this study aims to resolve the parataxonomy of the eggs from the Tumiaoling Hill and accordingly provide an ootaxonomical revision of dendroolithid eggs.

Institutional abbreviations.—HYH, Hejiagou, Yunxian, Hubei Province, China; HOZ, Hongzhaizi, Yunxian, Hubei Province, China; HYQB, north slope of Qinglongshan, Yunxian, Hubei Province, China; QDENG, Qinglongshan Dinosaur-Egg Fossil Cluster National Geopark, Shiyan, Hubei Province, China; TML, Tumiaoling exhibition hall (part of QDENG), Hubei Province, China.

Material and methods

Since 1995, an unprecedented number of dinosaur eggs were discovered from Yunxian, Hubei Province, China (Li 2001). These dinosaur eggs were later protected by the QDENG. A whole outcrop of Gaogou Formation with numerous dinosaur eggs in Tumiaoling was secured by a gigantic in-situ exhibition hall. Six clutches, TML4, TML7, TML8, TML9, TML10, and TML14, are exposed on an outcrop composed of tawny muddy sandstone (Fig. 2). Egg size was measured by using a caliper. We collected eggshell samples from most eggs, embedded them in EXAKT Technovit 7200 one-component resin and cut with an EXAKT 300CP automatic microtome. Both radial and tangential sections were prepared by ground and polished to a thickness about 40–80 μm by using an EXAKT 400CP variable speed grinder-polisher with P500 and P4000 abrasive paper. The thin sections were viewed under normal and polarized light by using a Leica DM-RX polarized light microscope. Eggshell thickness, diameters and density of eggshell units were calculated by using aforementioned instrument. The eggshell fragments of TML4 were observed under a Hitachi S-3700N scanning electron microscope.

Systematic palaeontology

Oofamily Dendroolithidae Zhao and Li, 1988

Oogenus *Placoolithus* Zhao and Zhao, 1998

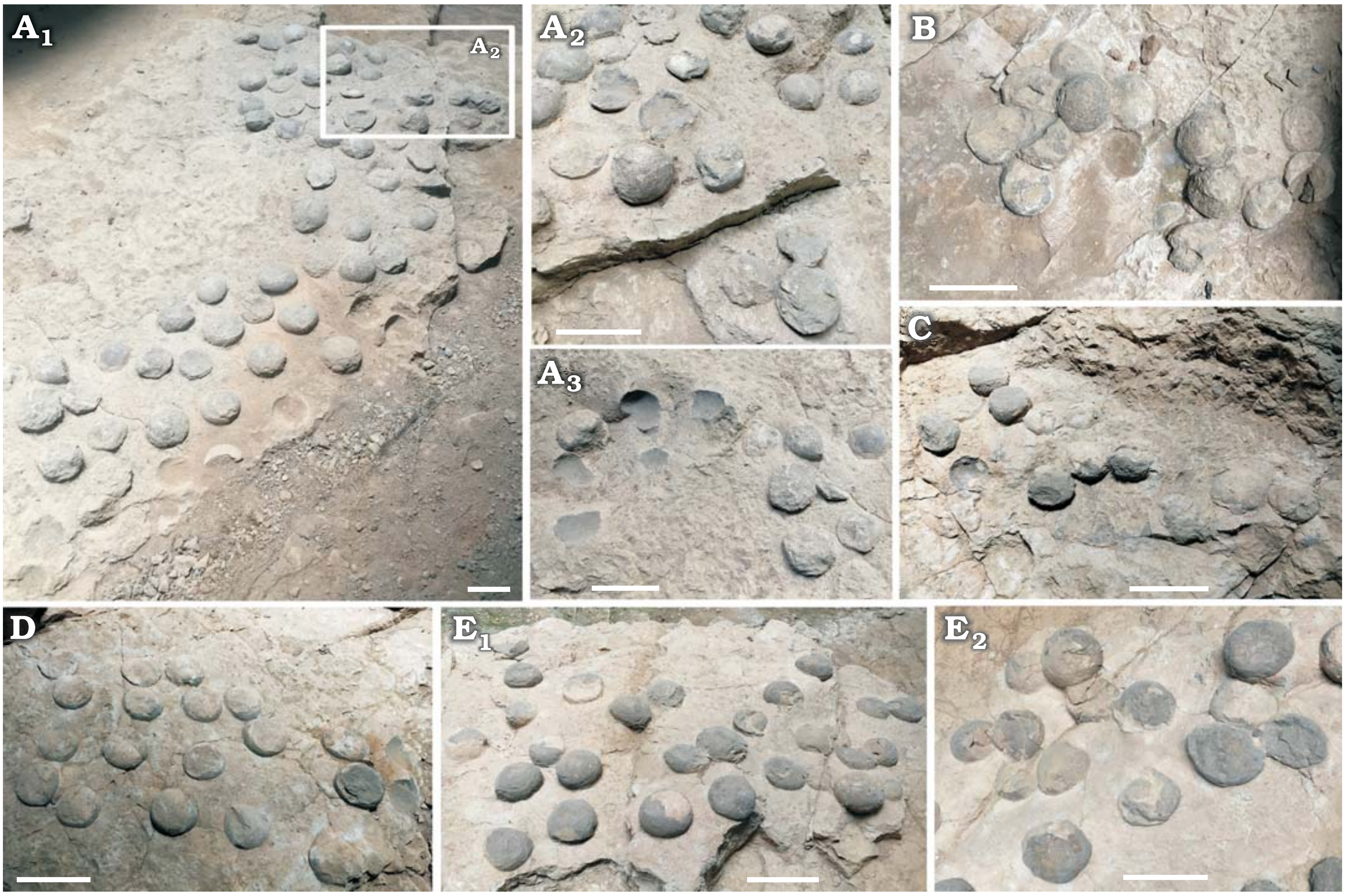

Fig. 2. Clutches of dendroolithid eggs of *Placoolithus tumiaolingensis* (Zhou, Ren, Xu, and Guan, 1998) comb. nov. from the Upper Cretaceous of the Tumiaoling outcrop, Yunxian, Hubei Province, China. **A**. TML 4; A_1, general view; A_2, the lower eggs; A_3, higher egg and egg impressions. **B**. TML 7. **C**. TML 9. **D**. TML 10. **E**. TML 14; E_1, general view; E_2, egg groups. Scale bars 20 cm.

Type oospecies: *Placoolithus taohensis* Zhao and Zhao, 1998; Majiacun Formation, Upper Cretaceous, Taohe, Xichuan, Henan Province, China.

Emended diagnosis (modified from Zhao and Zhao 1998).—The emended oogenus *Placoolithus* is characterized by the following unique combination of characters: oblate egg shape; an equatorial plane circular or sub-circular with long axis of 120–170 mm and short axis of 117–159 mm; eggshell thickness of 1.31–2.40 mm. Moreover, symmetric or asymmetric branches of eggshell unit usually appear in the middle part of the eggshell, and occasionally near the outer surface of the eggshell (Figs. 3A, 4).

Placoolithus tumiaolingensis (Zhou, Ren, Xu, and Guan, 1998) comb. nov.

Figs. 2–4, Table 1.

1998 *Dendroolithus tumiaolingensis* sp. nov.; Zhou et al. 1998: 3, pl. 1: 10–11.

1998 *Dendroolithus hongzhaiziensis* sp. nov.; Zhou et al. 1998: 4, pl. 1: 1–9.

1998 *Paradendroolithus qinglongshanensis* sp. nov.; Zhou et al. 1998: 4, pl. 2: 3–6.

Type material: Holotype: HYH 111, a complete egg (Zhou et al. 1998: pl. 1: 10–11). Paratype: HYH 1331–1337, a complete egg and a clutch with six eggs (Zhou et al. 1998).

Type locality: Tumiaoling Hill, Hejiagou Village, Yunxian, Hubei Province, China.

Type horizon: Gaogou Formation, Upper Cretaceous.

Material.—HOZ 11, a nearly complete egg (previously assigned to *Dendroolithus hongzhaiziensis*; Zhou et al. 1998: pl. 1: 1–9) from Hongzhaizi Hill, Hubei Province, China, Upper Cretaceous; HYQB 811–813, three incomplete eggs in a clutch (previously assigned to *Paradendroolithus qinglongshanensis*; Zhou et al. 1998: pl. 2: 3–6) from Qinglongshan Hill, Hubei Province, China, Upper Cretaceous; TML 4, TML 7–10, and TML 14, six egg clutches from the type locality.

Diagnosis.—The newly emended oospecies *Placoolithus tumiaolingensis* is featured by a shape index (egg width/length × 100%) of 80.03–99.28% (Table 1). The compact layer measures 1/10–1/4 of the eggshell. Moreover, the eggshell unit is slender and symmetrical, or rarely asymmetrical, divided into two branches in the middle part of the eggshell. The diameter of eggshell unit ranges from 0.05 to 0.25 mm and measures an average of 0.15 mm in tangential sections through the middle part of the eggshell. The density of eggshell units is 29–74 per mm^2 (Table 1).

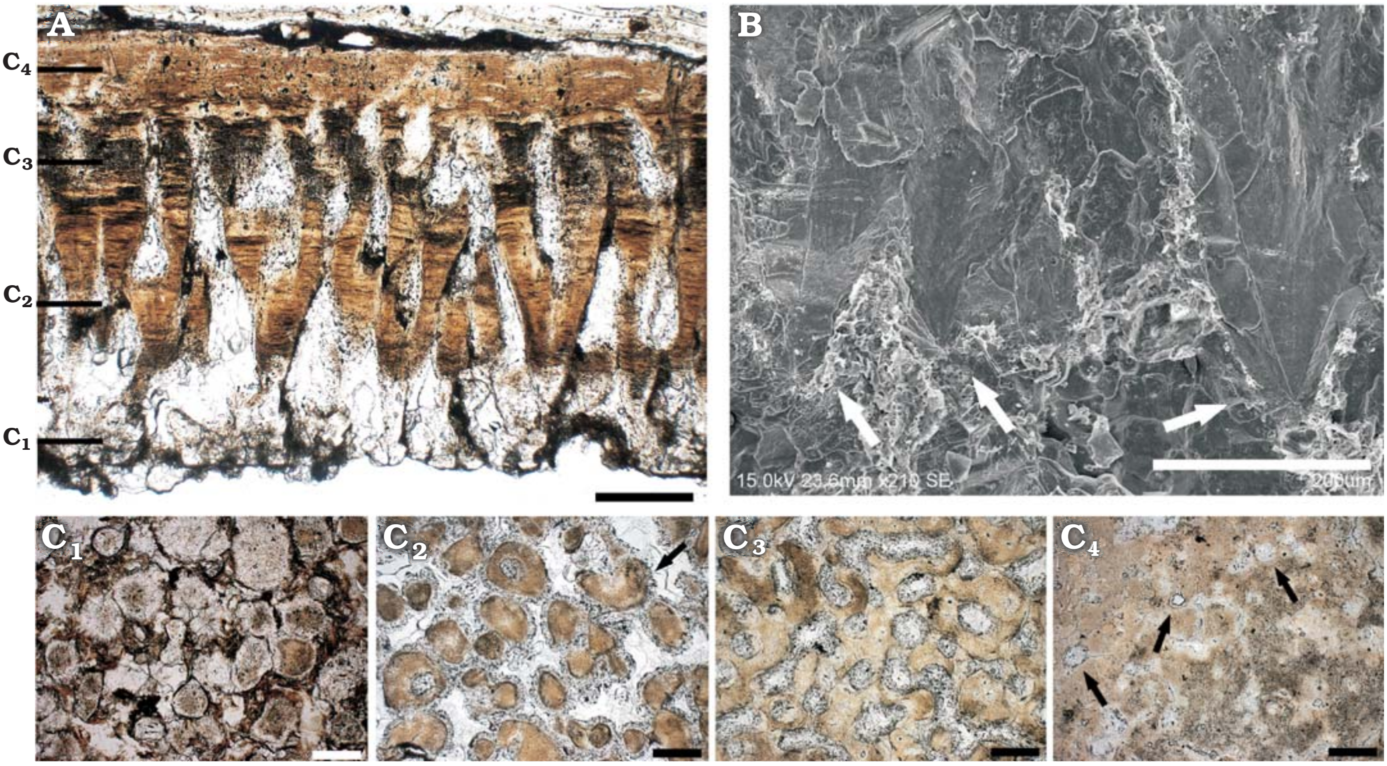

Fig. 3. Dendroolithid eggshell microstructure of *Placoolithus tumiaolingensis* (Zhou, Ren, Xu, and Guan, 1998) comb. nov. from the Upper Cretaceous of the Tumiaoling outcrop, Yunxian, Hubei Province, China. **A**. Radial thin section, lines at the left side indicate rough positions of C_1–C_4 in descending order. **B**. Secondary eggshell units (white arrows) in radial section (SEM). **C**. Tangential thin sections of eggshell, near the inner surface (C_1), in the middle part (C_2), near the outer surface (C_3), and through the compact layer (C_4); black arrows indicate a worm-like section formed by multiple eggshell units (C_2) and pore openings (C_4). Scale bars: A, 400 µm; B, C, 200 µm.

Description.—*Size and structure of egg clutches* (Fig. 2, Table 1): TML 4 is the largest and best-preserved clutch at the Tumiaoling outcrop, containing 77 eggs in total. This clutch has an arc pattern, almost forming a half-ring, with an inner diameter of 3.06 m and an outer diameter up to 5 m (Fig. $2A_1$). Eggs are arranged randomly with intervals between each of them. Most eggs are at the same level, representing a single clutch. However, at one end of the nest, six eggs are slightly lower than the other eggs. The six eggs are separated from the other eggs by two fractures (Fig. $2A_2$). Moreover, at the other end of the nest, one egg and five egg impressions are slightly higher than the other eggs (Fig. $2A_3$). These 12 eggs at the two ends possibly represent other independent clutches.

TML 7 contains 15 eggs and one egg impression, almost forming a circle (Fig. 2B). All eggs contact adjacent ones directly, and some eggs superimpose others. No eggs are at the center of the nest except for an egg impression. The arc arrangement pattern of the TML 7 egg clutch may be due to the absence of some eggs.

The TML 8 egg clutch contains 20 eggs that are arranged randomly, all of which are separated from each other. TML 9 is composed of 13 eggs, with three or four eggs grouped together in a curved line (Fig. 2C).

TML 10 is similar to TML 9, 18 eggs and two egg impressions arranged in rows making six curved lines. Each line has three or four eggs except for the two egg impressions (Fig. 2D). The large gaps in the lines with three eggs may due to the absence of other eggs.

Table 1. Measurements of the dendroolithid eggs *Placoolithus tumiaolingensis*. *All eggs are partially exposed, only one parameter (diameter) can be measured. **The density of eggshell units is from a single tangential section.

Nest	Egg length (mm)	Egg width (mm)	Shape index (%)	Clutch size	Eggshell thickness (mm)	Diameter of eggshell units in the middle part of the eggshell (mm)	Density of eggshell units in the middle part of the eggshell (per mm^2)
TML 4	132.60–161.18	116.60–158.56	85.45–98.79	77	1.31–2.40	0.11–0.24	34–51
TML 7	130.42–148.04	125.96–137.54	85.71–97.68	16	1.52–1.68	0.08–0.16	47–53
TML 8	156.92–157.40	141.48–145.60	90.80–98.73	20	1.68–1.78	0.08–0.25	31–38
TML 9	135.12–145.40*	–	–	13	1.63–1.94	0.05–0.24	29–41
TML 10	131.68–148.90	128.50–139.28	91.54–99.28	20	1.50–1.78	0.08–0.20	63–74
TML 14	131.42–169.98	127.48–152.72	80.03–98.43	30	1.94–2.07	0.11–0.18	29**

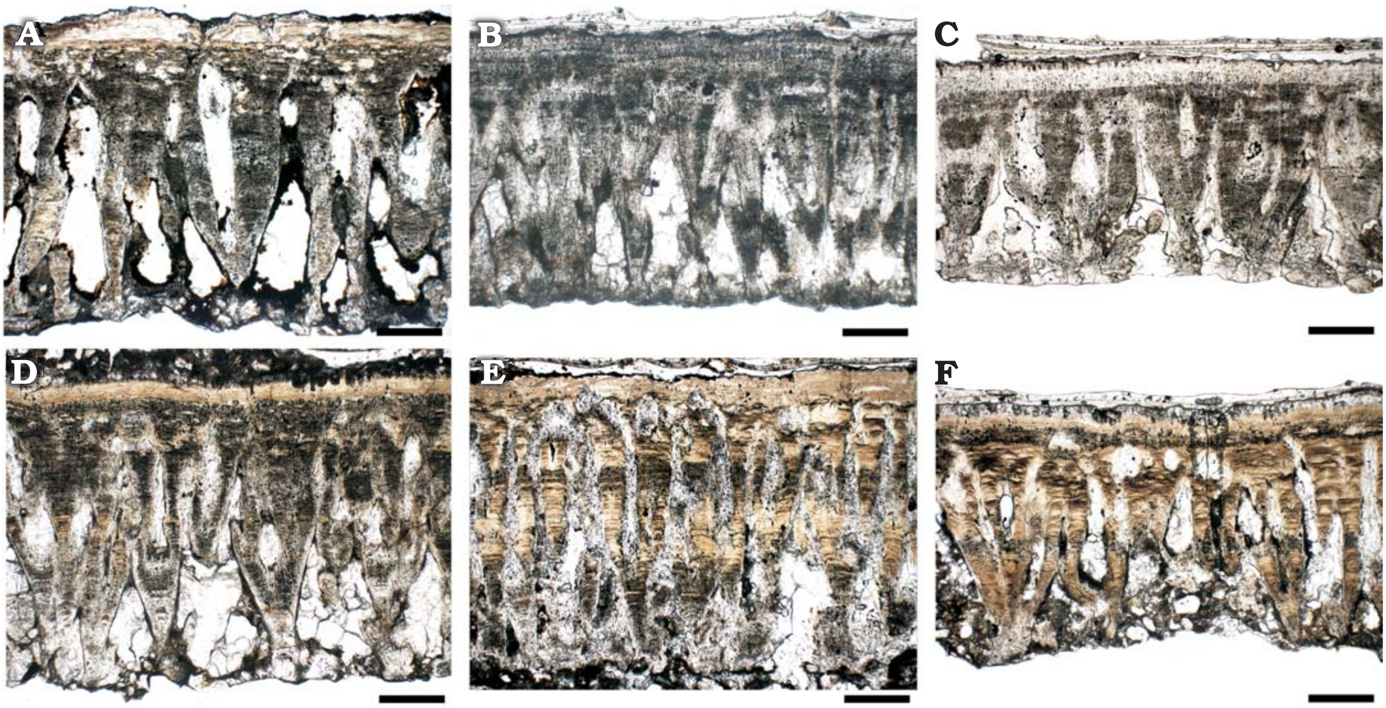

Fig. 4. Radial thin sections showing variety of dendroolithid eggshell microstructure of *Placoolithus tumiaolingensis* (Zhou, Ren, Xu, and Guan, 1998) comb. nov. from the Upper Cretaceous of the Tumiaoling outcrop, Yunxian, Hubei Province, China. **A**. TML 9, few branches. **B**. TML 10, fasciculate branches. **C**. TML 4, thinner eggshell. **D**. Eggshell from TML 4 with the *Dendroolithus tumiaolingensis* (Zhou, Ren, Xu, and Guan, 1998) microstructure from the Upper Cretaceous of the Tumiaoling outcrop, Yunxian, Hubei Province, China. **E**. Eggshell from TML 4 with *Dendroolithus hongzhaiziensis* (Zhou, Ren, Xu, and Guan, 1998) microstructure from the Upper Cretaceous of the Tumiaoling outcrop, Yunxian, Hubei Province, China. **F**. Eggshell from TML 8 with *Paradendroolithus qinglongshanensis* (Zhou, Ren, Xu, and Guan, 1998) microstructure from the Upper Cretaceous of the Tumiaoling outcrop, Yunxian, Hubei Province, China. Scale bars 400 μm.

The TML 14 clutch yields 30 eggs, representing a relatively large clutch at the Tumiaoling outcrop (Fig. $2E_1$). Like TML 4, it has a significant arc pattern, with a diameter of 1.82 m. The space between adjacent eggs is larger than the one in TML 4. There are no obvious patterns in the arrangement of the eggs, but in a part of the nest, every four eggs are grouped together and are in direct contact with each other (Fig. $2E_2$), possibly indicating that they were laid successively like sea turtles (Miller 2017).

Eggshell microstructure (Figs. 3, 4): The eggshell units of the eggs usually contain two symmetrical branches. Most of the eggshell units branch in the middle part of the eggshell, while the others divide near the inner surface of the eggshell. Sometimes, one of the two branches subdivides into two smaller branches near the outer surface of eggshell. There is little difference in diameter between the main stem and two branches of an eggshell unit. Near the outer part of eggshell, a branch becomes thicker and fuses with adjacent ones to form a distinct layer (referred to as compact layer in this study; Fig. 3A). The fused compact layer is usually absent or very thin in weathered eggshells (Fig. 4A, E). In the most complete eggshells, the compact layer occupies about 1/4 of the eggshell thickness (Fig. 4B). Horizontal dark lines are distributed evenly in the branched eggshell units, while horizontal accretion lines only appear in the compact layer (Figs. 3A, 4A, C–F). This observation probably indicates that the dark lines in the branched eggshell units are remains of organic fibers that are very rare in the compact layer (Zhao 1993). Several secondary eggshell units are observed under SEM, forming an extra layer inside of the calcitic eggshell (Fig. 3B). Secondary eggshell units have diagenetic or biological origins, which can be identified by cathodoluminescence or electron backscatter diffraction (Moreno-Azanza et al. 2016). Despite the absence of chemical evidence, the ultrastructural features, growth orientation and size of the secondary eggshell units that correspond to the eggshell units growing from the inner surface of eggshell indicate that they are indeed secondary eggshell units. They may result from the growth arrest of lower eggshell units, which have been reported in dictyoolithid and faveoloolithid eggs (Zhao 1993; Wang et al. 2013; Zou et al. 2013; Zhao et al. 2015); however, more evidence is required to test this hypothesis.

Tangential sections show that eggshell units are round with a distinct radial structure near the inner surface of eggshell (Fig. $3C_1$). In the middle and inner parts of the eggshell, round or worm-like sections through eggshell unit(s) are separated from each other. A worm-like section represents a merged chain of two to several round sections through multiple eggshell units (Fig. $3C_2$). Near the outer surface of the eggshell, the eggshell units fuse together, forming a honeycomb-like structure (Fig. $3C_3$). Pores are round or irregular in shape, but most of them terminate beneath the outer surface of the eggshell (Fig. 3C$_4$).

It should be noted that the eggs from the Tumiaoling Hill display various eggshell thicknesses, diameters and density of eggshell units. Moreover, the position of bifurcation in an eggshell unit also presents great intra- and inter-clutch variety in the same locality. The eggs of the TML 8 and TML 14 clutches have the most representative eggshell microstructure as described above. However, the other clutches have eggs with unusual eggshell microstructure. For instance, the eggshell unit of eggs in the TML 9 clutch are very thick with few branches (Fig. 4A), while the bunched eggshell units observed in TML 10 usually have more than three branches splitting near the inner surface of the eggshell (Fig. 4B). The space between two adjacent eggshell units is very large in the inner part of the eggshell but absent in the outer part (Fig. 4B). Thus, the density of eggshell unit in the middle part of eggshell is extremely high in the TML 10 clutch (Table 1). In the TML 4 clutch, the largest clutch from the Tumiaoling Hill, there seems to be "two types" of eggs. The eggs in one half of the TML 4 clutch yield thicker eggshells (1.78–2.40 mm) than those in the other half (1.31–1.58 mm). Our measurement of eggshell thickness shows that the thicker-shelled eggs and thinner-shelled eggs mixed randomly in the TML 4 clutch. The thicker-shelled eggs in TML 4 exhibit similar eggshell microstructure to those in TML 14. However, the thinner eggshells in radial section show highly weathered outer and inner surfaces, indicating that only the branches of eggshell units and the bottom of compact layer are preserved (Fig. 4C). We suggest that the thinner eggshells are a result of weathering instead of a distinct ootaxonomic feature. The eggs with thinner eggshell thus cannot be regarded as a different oospecies, indicating that all eggs in the TML4 clutch are assignable to a single oospecies.

Remarks.—The distinct characters of the eggs from the Tumiaoling Hill, such as branched eggshell units (do not form several layers), a compact layer in the upper part of eggshell, and separated eggshell units on tangential sections, indicate that their eggshell microstructure are similar to those of the oofamily Dendroolithidae (Zhao and Li 1988; Zhao and Zhao 1998; Zhao et al. 2015). Incidentally, the features of Mongolian dendroolithid eggs summarized by Mikhailov (1997) actually refer to Stalicoolithidae (Wang et al. 2012). Thus, we only compare eggs from the Tumiaoling Hill to dendroolithid eggs from Hubei, Henan, and Zhejiang Provinces of China. The eggshell microstructure of *Dendroolithus wangdianensis* from Anlu, the type oospecies of *Dendroolithus*, is almost the same as that of our studied eggs. However, the eggs from Anlu are ellipsoid in shape (Zhao and Li 1988; Zhao et al. 2015), whereas our studied eggs are more spherical. Both of them are not influenced by lithographic compaction. According to a recent study on the shape of avian eggs (Stoddard et al. 2017), egg shape diversity is predominantly determined by geometric and material properties of the egg membrane, which are hereditary characteristics of parental animals. Hence, dendroolithid eggs from Yunxian and Anlu probably belong to different oospecies despite similar eggshell microstructural characters. Although no complete eggs were discovered, *D. xichuanensis* from the Xichuan Basin, Henan Province shows peculiar eggshell microstructure, such as very small branches near the cones. The slender stem of a *D. xichuanensis* eggshell unit bifurcates into two branches near the outer surface of eggshell (Zhao and Zhao 1998; Zhao et al. 2015). Such eggshell microstructure was not observed in the studied specimens. As mentioned above, these materials have extremely variable eggshell microstructure, the microstructure of some thick eggshells from the TML 4 clutch are consistent with those of *D. tumiaolingensis* (Fig. 4D) and *D. hongzhaiziensis* (Fig. 4E). The microstructure of an egg from the TML8 clutch is consistent with those of *Paradendroolithus qinglongshanensis* (Fig. 4F), indicating that these three oospecies are assignable to the same ootaxon. As the oospecies *D. tumiaolingensis* was named prior to *D. hongzhaiziensis* and *Paradendroolithus qinglongshanensis*, the latter two names should be discarded. Ultimately, all eggs reported in this study are assignable to the same oospecies *D. tumiaolingensis*. On the other hand, *Placoolithus taohensis* eggs from the Xichuan Basin have similar shapes, sizes and clutch patterns with those of the eggs from the Tumiaoling Hill (Table 2). However, the eggshell units of *Placoolithus taohensis* are mostly asymmetrically bifurcated (Zhao and Zhao 1998; Zhao et al. 2015), which is a unique feature to this oospecies. According to these comparisons, we move the oospecies *D. tumiaolingensis* to the oogenus *Placoolithus* and amend a new oospecies *Placoolithus tumiaolingensis*.

Table 2. Comparison of the eggs from the Tumiaoling Hill and other known dendroolithid eggs in China.

Ootaxon	Egg size (mm)	Shape index (%)	Eggshell thickness (mm)	Ratio of compact layer to eggshell thickness	References
Placoolithus tumiaolingensis	130–170×117–159	80.03–99.28	1.31–2.40	1/10–1/4	this paper
Placoolithus taohensis	120–134×118–130	95.2–100.0	1.70–1.90	1/5	Zhao and Zhao 1998
Dendroolithus wangdianensis	145–162×110–130	70.5–84.5	1.70–2.10	1/4	Zhao and Li 1988
Dendroolithus dendriticus?	140×133	95.0	1.5	1/6–1/5	Fang et al. 1998; Zhao et al. 2005
Dendroolithus sanlimiaoensis?	152×126	82.9	1	1/7	Fang et al. 1998; Zhao et al. 2005
Dendroolithus furcatus?	141×128	90.8	1	–	Fang et al. 1998; Zhao et al. 2005
Dendroolithus cf. *D. dendriticus*?	130–140×60	43–46	1	–	Fang et al. 2000; Zhao et al. 2005

A comprehensive comparative study between dendroolithid eggs from the Xixia Basin of Henan Province and the Tiantai Basin of Zhejiang Province and the eggs from the Tumiaoling Hill is likely unavailable since previous photographs of eggshell radial sections of the specimens from Henan and Zhejiang Provinces are undiagnostic (Fang et al. 1998: pl. 18: 3, 7–12; Fang et al. 2000: pl. 1: 18–20) and the amount of thin sections is rare. Although the loosely arranged eggshell units of *D. dendriticus*? contrast sharply with the tightly arranged eggshell units of *Placoolithus tumiaolingensis*, the eggshells of *D. sanlimiaoensis*? and *D. furcatus*? are much thinner than *Placoolithus tumiaolingensis* (Table 2). Therefore, more thin sections of the specimens from Henan and Zhejiang Provinces are needed for a defined conclusion.

Stratigraphic and geographic range.—Upper Cretaceous, Hubei Province, China.

Discussion

Previous studies (Mikhailov 1991, 1997; Mikhailov et al. 1994) used the terms "dendrospherulithic morphotype" and "prolatocanaliculate" to describe the calcareous eggshell structure and pore canals of the "dendroolithid eggs" recovered from Mongolia. According to his description, these eggs have a rough outer surface with irregular hillocks, nodes, and visible pore openings. The eggshell is composed of tightly arranged eggshell units that branch in the upper part of the eggshell. Pore canals are relatively irregular and isolated, swelling in the middle part or near the outer surface of the eggshell. The diameter of pore canal varies throughout the eggshell.

However, the description suggested by Mikhailov (1991, 1997) is contradictory to the characters of dendroolithid eggs (Zhao and Li 1988; Zhao and Zhao 1998; Zhao et al. 2015). Instead, Mikhailov's (1991, 1997) descriptions correspond with the newly erected oofamily Stalicoolithidae (Wang et al. 2012). Thus, the oospecies *D. verrucarius* and *D. microposus* are referable to the oofamily Stalicoolithidae, and probably the oogenus *Coralloidoolithus* (Wang et al. 2012). To avoid confusion, we posited that the misleading term "dendrospherulithic morphotype (Mikhailov 1991, 1997; Mikhailov et al. 1994)" should not be used to describe the eggs from Mongolia or other stalicoolithid eggs. It also cannot be used to describe dendroolithid eggs in terms of its original definition (Mikhailov 1991). The basic characters of dendroolithid eggs are branched eggshell units, large cavities in the inner part of eggshell, and a compact layer near the outer surface of eggshell. However, the eggshell microstructure in all oospecies of Dendroolithidae is so various that microstructural features fail to be a distinct character. Hence, egg shape is the only distinguishable character between *Dendroolithus* and *Placoolithus*. It is also crucial for the identification of dendroolithid eggs. Unfortunately, the clutch pattern of *D. wangdianensis* is unknown because the eggs were not excavated all together.

It is clear that *Placoolithus tumiaolingensis* shares the same macro-features with *Placoolithus taohensis*. Although the asymmetrical branches of eggshell units in *Placoolithus taohensis* have not been seen in *Placoolithus tumiaolingensis* so far, it is possible to observe such a character in *Placoolithus tumiaolingensis* eggs in the future because of the extremely variable eggshell microstructure of *Placoolithus tumiaolingensis*. If the hypothesis is true, *Placoolithus tumiaolingensis* would become a junior synonym of *Placoolithus taohensis*.

Another problem of the identification for dendroolithid eggs is the similarity between the oofamily Dendroolithidae and the oogenus *Protodictyoolithus* in Dictyoolithidae. *Protodictyoolithus* eggs that also have isolated branched eggshell units and the compact layer near the outer surface of eggshell seem to combine features of Dendroolithidae and Dictyoolithidae but share more features with dendroolithid eggs. Although some portions of the *Protodictyoolithus* eggshell (e.g., *Protodictyoolithus jiangi*) are composed of 2–3 layers of short eggshell units (Liu and Zhao 2004; Wang et al. 2013; Zhao et al. 2015), the same feature also occasionally appears in dendroolithid eggs, such as *Placoolithus tumiaolingensis*. Furthermore, the eggshell microstructures on tangential sections of *Protodictyoolithus* are almost the same as those of dendroolithid eggs, making the parataxonomic position of *Protodictyoolithus* doubtful. However, detailed comparisons between the eggs in *Protodictyoolithus* and Dendroolithidae are needed for a confirmed conclusion.

Dendroolithid eggs are remarkable among dinosaur eggs for their complicated eggshell microstructure. For this reason, the two-dimensional eggshell microstructures on different radial sections are greatly variable, making the identification of oospecies based on limited thin sections inaccurate. According to the observation of numerous eggs from Yunxian and the comparison between known oospecies of dendroolithid eggs, our results show that all dendroolithid eggs share very similar eggshell microstructure; hence, it is problematic to classify the dendroolithid eggs merely based on eggshell thin sections. If egg shape and nest structure of some kinds of dendroolithid egg are unknown, assigning them to any existing ootaxa of Dendroolithidae or establishing a new ootaxon hastily may lead to confusion.

Conclusions

A new oospecies *Placoolithus tumiaolingensis* from the Tumiaoling Hill, Yunxian, Hubei Province, China sheds light on the classification of dendroolithid eggs. According to the comparisons between egg clutches on the Tumiaoling Hill and other known dendroolithid eggs in China, *Dendroolithus tumiaolingensis*, *D. hongzhaiziensis*, and *Paradendroolithus qinglongshanensis*, all of which were previously reported from Yunxian, should be assigned to the newly emended oospecies *Placoolithus tumiaolingensis*, and we found that all dendroolithid eggs share very similar eggshell microstructure, egg shape and nest structure are crucial for the identification of dendroolithid eggs.

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