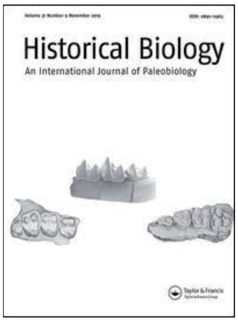

Historical Biology
An International Journal of Paleobiology

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/ghbi20

Restudy of the original and new materials of *Stromatoolithus pinglingensis* and discussion on some Spheroolithidae eggs

Xufeng Zhu, Qiang Wang & Xiaolin Wang

HISTORICAL BIOLOGY
https://doi.org/10.1080/08912963.2021.1910817

Taylor & Francis
Taylor & Francis Group

ARTICLE

Restudy of the original and new materials of *Stromatoolithus pinglingensis* and discussion on some Spheroolithidae eggs

Xufeng Zhu[a,b,c], Qiang Wang[a] and Xiaolin Wang[a,b,c]

[a]Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China); [b]CAS Center for Excellence in Life and Paleoenvironment, Beijing, China); [c]College of Earth & Planetary Sciences, University of Chinese Academy of Sciences, Beijing, China)

ABSTRACT
In this study, we restudied a rarely known oospecies from China, *Stromatoolithus pinglingensis*. Original materials from type locality Nanxiong, Guangdong Province as well as recently recovered materials from Shanyang, Shaanxi Province and Laiyang, Shandong Province are compared in this study. After detailed study about general and micro-structure of these eggshells, we are sure that this ootaxon cannot be placed within Spheroolithidae or any other oofamilies, though new oofamily cannot be erected due to lack of complete specimen. In the meantime, we reviewed some Spheroolithidae eggs from Asia, North America, and Europe. We propose that the Mongolia oospecies *Spheroolithus maiasauroides* is a synonym of *Stromatoolithus pinglingensis*. Eggs of *Maiasaura, Spheroolithus albertensis* from North America and *Spheroolithus europaeus* from Spain should be reassigned to *Stromatoolithus*. The Lower Cretaceous oospecies *Guegoolithus turolensis* from Spain should also be considered as ootaxon with close relationship to *Stromatoolithus* but not Spheroolithidae. The geographic distribution of Spheroolithidae may not be so wide as former researchers thought, and the producer of Spheroolithidae is back to unknown. The oogenus *Stromatoolithus* is associated with hadrosaurs, and may restrict to Hadrosauridae.

ARTICLE HISTORY
Received 20 February 2021
Accepted 27 March 2021

KEYWORDS
Stromatoolithus; Spheroolithidae; Late Cretaceous; China; dinosaur egg; parataxonomy

Introduction

Dinosaur eggs are of great significance for understanding the reproductive biology of dinosaurs. Direct evidence of correlation between eggs and their producers is rare. Some cases involve relationship of eggs to embryos or hatchlings (Horner and Weishampel 1988, 1996; Norell et al. 1994; Horner 1999; Cheng et al. 2008; Kundrát et al. 2008; Weishampel et al. 2008; Araújo et al. 2013; Shao et al. 2014; Pu et al. 2017), but there are often problems with the identity of the skeleton because even the most experienced taxonomists could sometimes be misled (Horner and Weishampel 1996). Some other cases reported related eggs with adult or nest (Hirsch and Quinn 1990; Norell et al. 1995; Dong and Currie 1996; Clark et al. 1999; Sato et al. 2005; Grellet-Tinner et al. 2006; Agnolin et al. 2012; Fanti et al. 2012; Jin et al. 2020). In all cases, the classification and identification of the eggs are more important since there are less experienced taxonomists working on dinosaur eggs than on bones.

Among all these egg–skeleton relations, the relation between *Maiasaura peeblesorum* (hadrosaurs) and its eggs is one of the rare cases that do not concern theropod. Hirsch and Quinn (1990) described eggs in clutches that associate with hadrosaur nesting areas in Upper Cretaceous Two Medicine Formation in Montana. Although this nesting area was reported with adults, hatchlings, and clutches (Horner and Makela 1979; Horner 1982; Hirsch and Quinn 1990; Mikhailov 1994), the eggs were not taxonomically assigned to any oofamily until Mikhailov assigned them to *Spheroolithus* sp. (Spheroolithidae) (Mikhailov 1997) for its similarity with the Mongolia oospecies *Spheroolithus maiasauroides* (Mikhailov 1994). Then, the eggs were assigned to *Spheroolithus maiasauroides* (Horner 1999, 2000), while Zelenitsky and Hills (1997) hold different view. However, the eggshell microstructure of both *Spheroolithus maiasauroides* and eggs of *Maiasaura* makes them questionable to be assigned to Spheroolithidae as this early established oofamily has been proved to be a hodgepodge of some later erected oofamilies like Ovaloolithidae (Mikhailov 1991) and Stalicoolithidae (Wang et al. 2012a). The type oospecies of Spheroolithidae, *Spheroolithus chiangchiungtingensis*, is so special that no similar ootaxon except *Spheroolithus megadermus* has come to our sight. We believe *Spheroolithus maiasauroides* and eggs of *Maiasaura* are more similar to *Stromatoolithus pinglingensis*, an oogenus and oospecies that was erected in Nanxiong Basin, Guangdong Province, China (Zhao et al. 1991). In this paper, both original and additional material of *Stromatoolithus pinglingensis* are described for comparison.

Stromatoolithus pinglingensis was erected based on 224 pieces of eggshells (IVPP RV 91,001) (Zhao et al. 1991). It was not assigned to an oofamily until Zhao placed it within Megaloolithidae as its first member in China (Zhao et al. 1999, 2015). Very little research has been carried out about it due to the incompleteness and scarcity of specimen (less than 300 eggshells in total, no complete eggs). In addition, the absence of detailed photograph and language (description in Chinese only) used in the original literature (Zhao et al. 1991) also adds to its obscurity. In recent years, new eggshell materials were collected from the Upper Cretaceous of two other localities, Shanyang of Shaanxi Province and Laiyang of Shandong Province, China, respectively, where Elongatoolithidae eggs are very common. Several eggshells with similar ornamentation were treated as Elongatoolithidae eggshells before they were

CONTACT Qiang Wang wangqiang@ivpp.ac.cn Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, 142 Xizhimenwai Street, Xicheng District, Beijing, China, 100044.

Published online 08 Apr 2021

thin sectioned in preliminary studies of diversity survey. However, after histological examination, we found that some of them can be attributed to *Stromatoolithus pinglingensis*. We carefully checked the rest specimens and found several more, and did a more detailed observation. Original materials of *Stromatoolithus pinglingensis* (IVPP V 18,542; IVPP V 18,543) from its type locality, Nanxiong, Guangdong Province were also restudied and described in detail for comparison. During the study, we compared *Stromatoolithus pinglingensis* with some North America and Mongolia materials that were placed within Spheroolithidae, and found them very similar in many aspects, therefore led to our doubt on the parataxonomic position of hadrosaur eggs and the distribution of Spheroolithidae.

This study provides a detailed description of *Stromatoolithus pinglingensis* and aims in the revision of this oospecies and some '*Spheroolithus*' eggs. These new specimens provide us with more information on the geological distribution and variation of *Stromatoolithus*, and help with the possible separation of similar ootaxa from the oofamily Spheroolithidae. The taxonomic affinity of *Stromatoolithus* is also discussed.

Geology

Three localities are involved in this study (Figure 1).

Nanxiong Basin is a NE-SW extending basin located in the north of Guangdong Province. The fossil-bearing Cretaceous stratum in the middle region of Nanxiong Basin, Nanxiong Group, is divided into Yuanpu Formation and Pingling Formation from bottom to top (Zhao et al. 1991). Materials involved in this study is collected from the Pingling Formation of Pingling-Datang section (CGY-CGD section), which is about 29 km northeast of Nanxiong. Pingling Formation is a set of fluvial deposition, which is mainly composed of interbedding purplish-grey conglomerate, pebbly sandstone, and purplish-red siltstone (Zhao et al. 2017). The age of Yuanpu Formation is Maastrichtian according to ^{40}K-^{40}Ar data (67.04 ± 2.31 Ma and 67.37 ± 1.49 Ma, Zhao et al. 1991), which also limits the earliest age of the overlying Pingling Formation (Zhao et al. 2017).

Shanyang Basin is one of the intermountain basins in the eastern part of the Qinling Mountains. It is about 22 km long in east-west direction and 5 km long in the north-south direction. The Cretaceous stratum in Shanyang Basin is named Shanyang

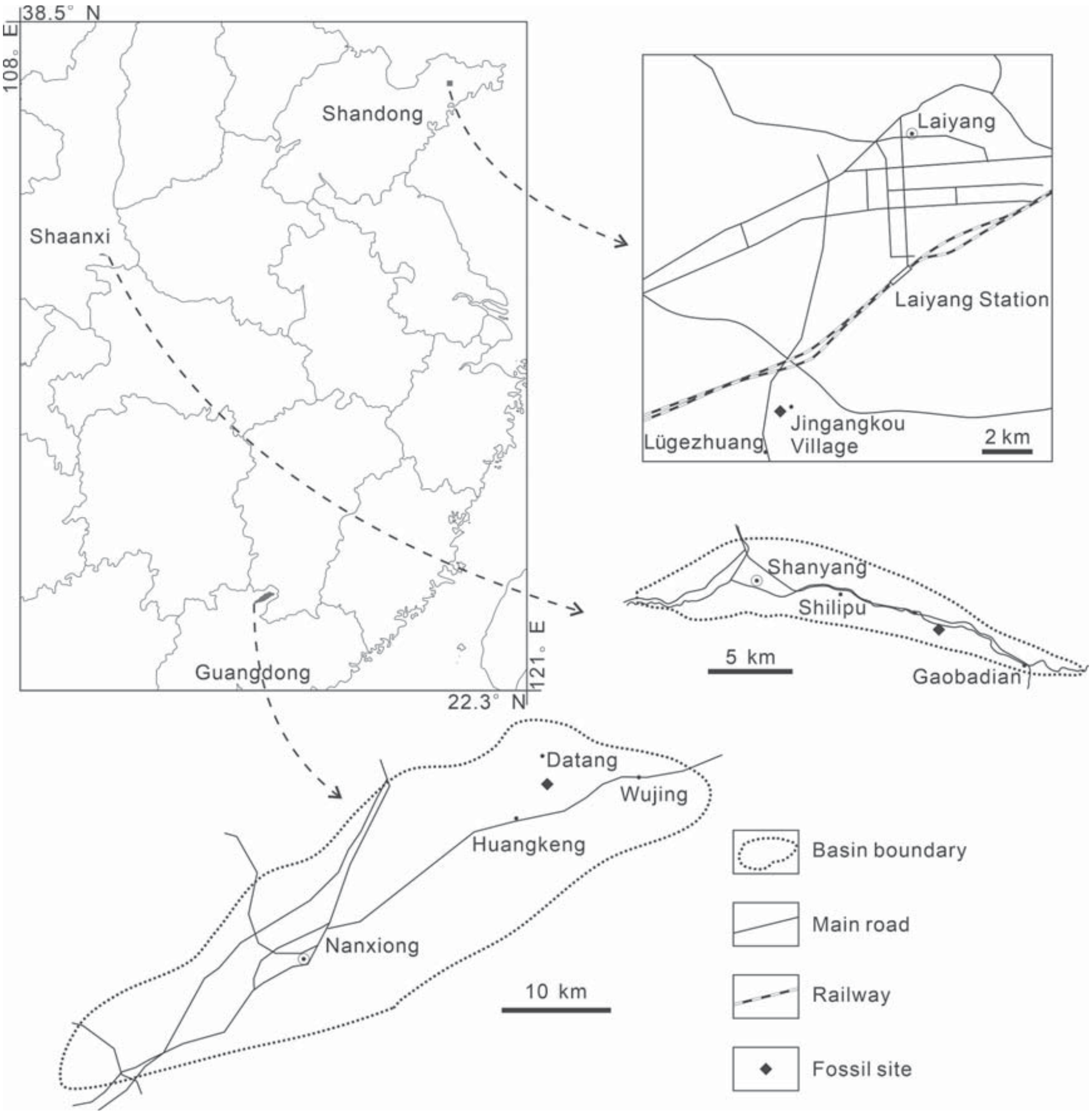

Figure 1. Map showing the localities of the specimens involved in this study.

Formation and it is subdivided into lower and upper members in Tangjiagou-Niupanggou section by Xue et al. (1987). The age of Shanyang Formation is Maastrichtian according to magnetostratigraphic data (70–65 Ma, Xue et al. 1994). The relationship of the lower member of Shanyang Formation and the Upper Devonian Liucen Formation is angular unconformity in this section. The lower member of Shanyang Formation starts with about 380 m of thick-bedded brownish red argillaceous conglomerate interbedded with mudstone or gravelly mudstone. The upper member of Shanyang Formation is composed of interbedding conglomerate, gravel-bearing sandstone, and brick red argillaceous siltstone. Calcareous concretions are very developed in the thick argillaceous siltstone beds. Beside eggshell fragments, Xue et al. (1996) also reported some bones of dinosaurs from Shanyang Formation in this area, including hadrosaurid, *Shantungosaurus* cf. *giganteus*.

Laiyang is in the east of Shandong Province and the northeast corner of Jiaolai Basin. The Upper Cretaceous in Laiyang is named Wangshi Group, which consists of Xingezhuang, Jiangjunding, and Jingangkou Formations in ascending order according to Hu et al. (2001). The latter two formations are known for a large number of excavated dinosaur bones and eggs. The age of Jingangkou Formation is estimated to be late Campanian according to an ^{40}Ar-^{39}Ar age (73 Ma) of a basalt sample obtained by Yan et al. (2003).

Materials and methods

Materials

All specimens were housed in IVPP.

Nanxiong materials came from the collection of Zhao Zikui, which were collected during field work (three times in 1983, 1984 and 1986, respectively, Zhao et al. 1991) of Sino-German joint group in Nanxiong Basin, Guangdong Province. The original materials contain eggshells from holotype IVPP RV 91,001 (field number CGD 063, CGD section, 60–63 m, 224 pieces), specimen IVPP V 18,542 (field number CGD 045, CGD section, 45 m, several eggshells mixed with elongatoolithid eggshell) and IVPP V 18,543 (field number CGD 101e, CGD section, 101 m, 53 pieces), all of which came from Pingling Formation, as documented by Zhao et al. (2015). Unfortunately, the holotype IVPP RV 91,001 is nowhere to be found. However, IVPP V 18,542 and IVPP V 18,543 contain enough eggshells that allow us to investigate the variation of ornamentation, and those with clean surface were selected for photography.

Seven fragments were collected from the upper member of Shanyang Formation during our field work in Shanyang Basin, Shaanxi Province in May 2014. Six of which were studied in diversity survey (IVPP V 26,961.1; IVPP V 26,962.1–2; IVPP V 26,963; IVPP V 26,964; IVPP V 26,965), and the remaining one (IVPP V 26,961.2) were later studied together with two additional fragments (IVPP V 26,966.1–2) collected in September 2019.

Four fragments (IVPP V 26,967.1–4) were collected from Jingangkou Formation in Laiyang, Shandong Province in May 2012, two of which were studied in diversity survey, the other two were studied in detail.

Methods

All sample preparation and observation were performed in the Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences. Ultrasonic cleaner was used to remove most of the matrix attached to the specimens, which were then observed under a Zeiss Stemi 2000 stereomicroscope. Eggshells without calcite cement were studied with a Zeiss EVO MA 25 SEM on both internal and external surface. The fresh fracture surface was also studied with SEM after etched with 5% acetic acid for one minute. Then, selected eggshells were mounted into resin for preparation of both radial and tangential sections (thickness is about 30 μm).

For Shanyang specimen, after examination under stereomicroscope, one of the corresponded resin blocks containing eggshell with complete microstructure was selected for SEM study on its radial surface. Most of the Nanxiong specimen IVPP V 18,543 do not have well-preserved mammillae according to examination under polarised light microscope (Zeiss Axio A2m), so one eggshell that is not thin sectioned was selected after checking under stereomicroscope. The observed surfaces of these two eggshells were first polished and then etched with 5% acetic acid for one minute.

Measurement of ornamentation was made on photographs of every eggshell with clean surface (27 samples in total). Eggshell thickness and pore diameter were measured on all micrographs of thin sections. All measurements were performed with ImageJ software. The specimens from Laiyang were too scarce to allow detailed study without over consumption, so the pore measurement of Laiyang specimens could not be done.

Institutional abbreviations

IVPP, Institute of Vertebrate Palaeontology and Palaeoanthropology (Beijing, China).

Systematic Palaeontology

Oofamily **Indet**

Oogenus ***Stromatoolithus*** (Zhao et al. 1991)

Included oospecies

Type oospecies, *Stromatoolithus pinglingensis*, (Zhao et al. 1991); *Stromatoolithus albertensis*, (= *Spheroolithus albertensis*, Zelenitsky and Hills 1997); *Stromatoolithus europaeus*, (= *Spheroolithus europaeus*, Sellés et al. 2014).

Original Diagnosis

As same as the original diagnosis of *Stromatoolithus pinglingensis*.

Amended Diagnosis

Surface strongly sculptured with sagenotuberculate ornamentation that is composed of scattered nodes to short or reticulated ridges. Eggshell is composed of one layer of spherulitic shell units that are highly fused. Evenly distributing parallel accretion lines that cross adjacent shell units are very developed, and are consistent with the undulation of the external surface. Pore systems are composed of tubular canals that are nearly perpendicular to the outer surface and may have slightly changing diameter. Pore openings can be circular, oval, or silt-like on the outer surface.

Known Distribution

Late Campanian to late Maastrichtian from China, Kazakhstan, Mongolia, Spain and North America.

Oospecies ***Stromatoolithus pinglingensis*** (Zhao et al. 1991)

Figure 2, 3, 4A–D, 5, 6A–F, 7A–C

1994 *Spheroolithus maiasauroides* Mikhailov, pl. 10, Figure 2.

1996 *Paraspheroolithus lamelliformae* Xue et al, pl. 9, Figure 2.

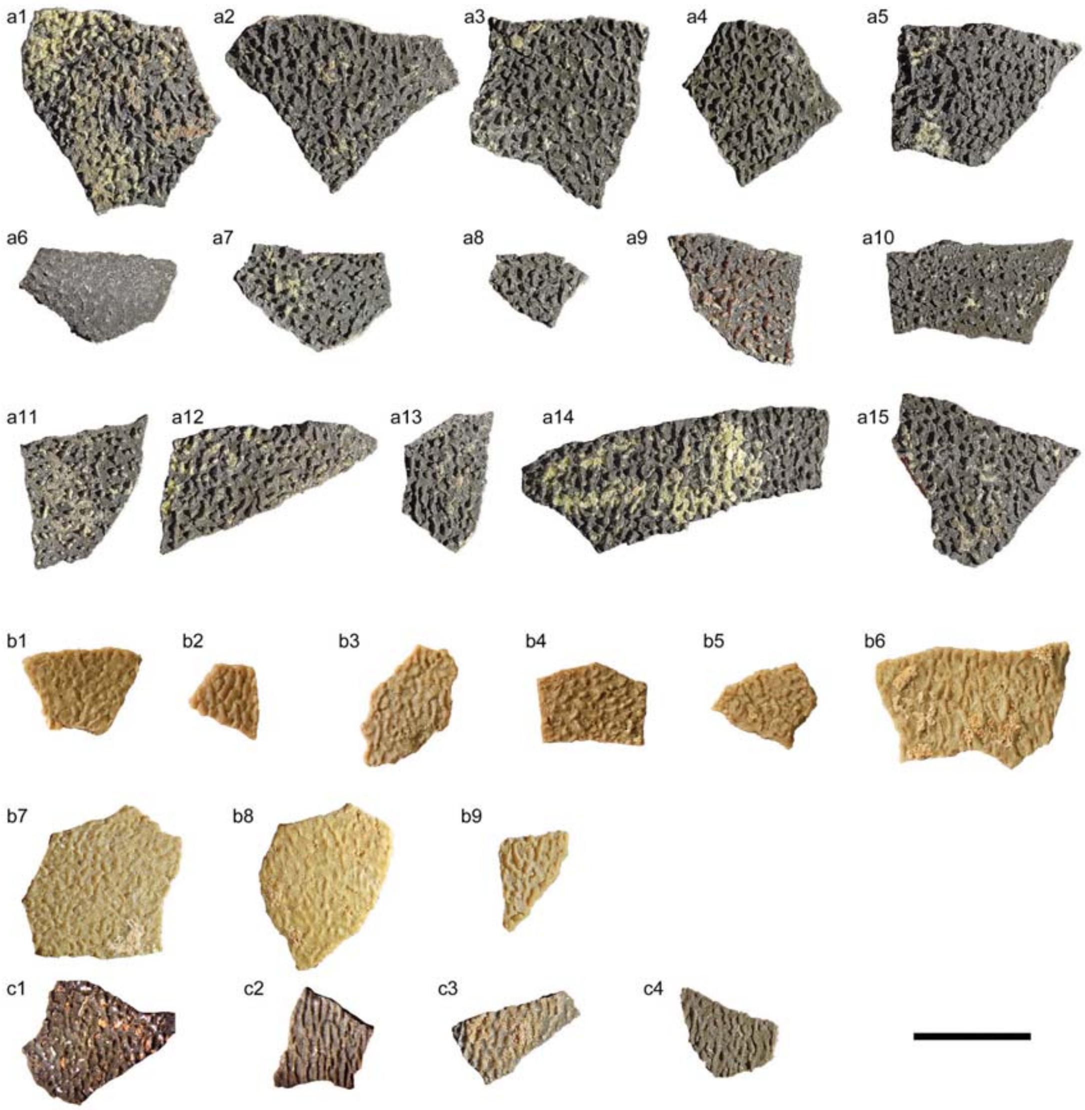

Figure 2. *Stromatoolithus pinglingensis* specimens involved in this study with clean surface. (a), 15 out of 53 eggshells of IVPP V 18,543 from Nanxiong, showing scattered nodes or slightly elongated nodes that are chained; (b), specimens from Shanyang, showing shallow nodes that are often elongated and connected into short ridges; (b1), IVPP V 26,961.1; (b2), IVPP V 26,962.1; (b3), IVPP V 26,962.1; (b4), IVPP V 26,963; (b5), IVPP V 26,964; (b6), IVPP V 26,965; (b7), IVPP V 26,961.2; (b8), IVPP V 26,966.1; (b9), IVPP V 26,966.1; (c), specimens from Laiyang, showing directionally arranged elongated nodes or short ridges that are connected reticulately; (c1), IVPP V 26,967.1; (c2), IVPP V 26,967.2; (c3), IVPP V 26,967.3; (c4), IVPP V 26,967.4. Scale bar equals 1 cm.

2012 'Spheroolithid eggshell' Lucas et al, Figure 6A–C, N, Figure 7A–C.

Neotype

IVPP V 18,543, 53 pieces of eggshell, plus 6 thin sections (110,-506–07, 110,506–08(1)–(2), 110,506–09, 110,506–10(1)–(2)).

Referred material

IVPP V 18,542, several eggshells mixed with elongatoolithid eggshells from 45 m of CGD section, Nanxiong, Guangdong Province; IVPP V 26,961.1–2, IVPP V 26,962.1–2, IVPP V 26,963–26,965, IVPP V 26,966.1–2, nine eggshells from Shanyang, Shaanxi Province; IVPP V 26,967.1–4, four eggshells from Laiyang, Shandong Province.

Known distribution

Late Campanian to late Maastrichtian from China, Kazakhstan, Mongolia and North America.

Type locality and horizon

Nanxiong, Guangdong Province. CGD section, 101 m, Pinging Formation, Nanxiong Group.

Original Diagnosis

Outer surface covered by unapparent worm-like ornamentation. Shell unit consists of cone and prisms are usually clustered in 2–3, wherein the organic fibres overlap. Pore canals are very developed. (Translated from Zhao et al. 1991).

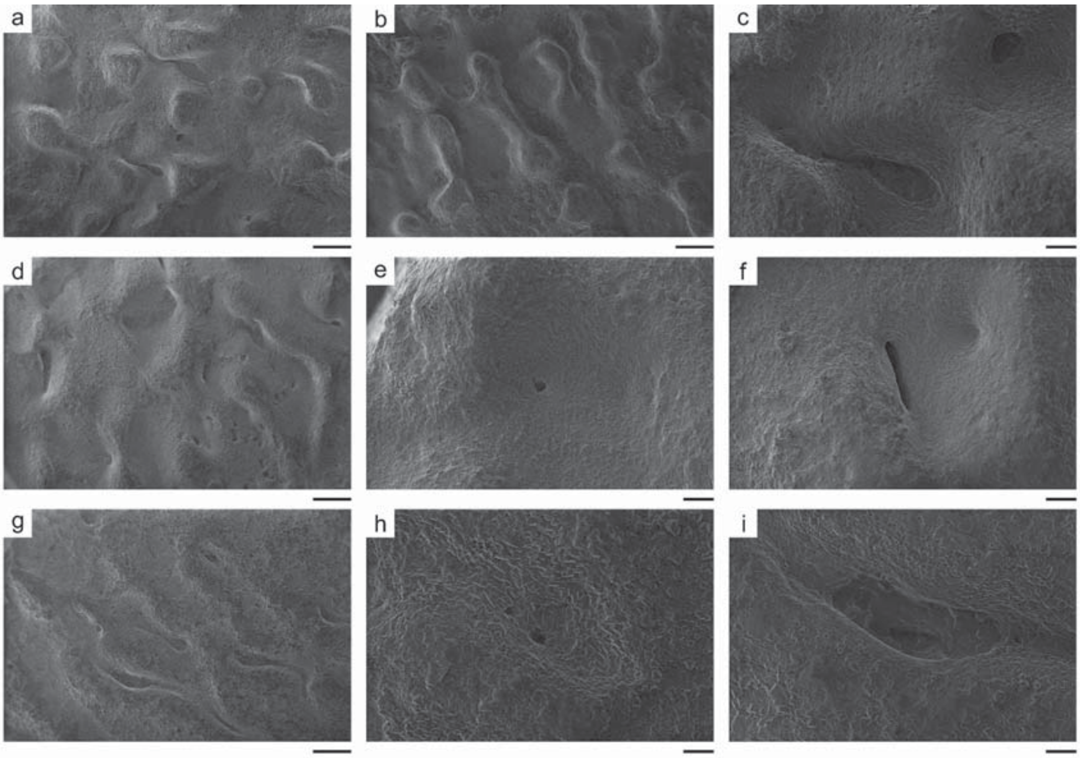

Figure 3. SEM image of the outer surface of *Stromatoolithus pinglingensis*. (a–c), Nanxiong specimen of IVPP V 18,543 (Figure 2a14); (a), scattered nodes; (b), elongated nodes that are connected in to chains and short ridges; (c), elongated and circular pore openings; (d–f), Shanyang specimen, IVPP V 26,966.1; (d), shallow nodes that are elongated into short ridges; (e), a small pore opening that is not aside the ridge; (f), a silt-like pore adjoining the ridge; (g–i), Laiyang specimen, IVPP V 26,967.4; (g), directionally arranged short ridges; (h), a small pore opening at the bottom of a pit; (i), an elongated pore opening between two ridges. Scale bar equals 500 μm for (a), (b), (d), (g) and 100 μm for (c), (e), (f), (h), (i).

Amended Diagnosis

Stromatoolithus eggs with the following variations. Outer surface ornamentation resembles sagenotuberculate ornamentation, and are composed of nodes that can be slightly elongated to form chains or short ridges that sometimes connected into a network. Diameter of nodes ranges 0.42–0.60 mm. Eggshell thickness ranges 1.03–1.56 mm excluding ornamentation and 1.20–1.73 mm when including. Diameter of mammillae ranges 96–240.8 μm. Diameter of pores ranges 43.5–160.4 μm in the middle part of the eggshell.

Description

Surface ornamentation

The ornamentation type of *Stromatoolithus pinglingensis* can be classified as sagenotuberculate (Figure 2). No specimen with smooth outer surface was observed. For Nanxiong materials, the eggshell surface is scattered with small nodes (Figure S1). Most of the nodes are nearly round while some of them are slightly elongated (Figure 3(a)) or connected in chains of two to four occasionally, and sometimes they can even form short ridges (Figure 3(b), Figure S2). Eggshells from Shanyang have nodes that are often elongated, connected, or fused into reticulated ridges, while some specimens have scattered nodes that are regularly round (Figure 3(d)). Laiyang specimens show reticulated short ridges formed by elongated nodes that are sometimes hardly distinguishable from each other, and the short ridges are slightly directionally arranged (Figure 3(g)). The density and diameter (or width if nodes are oval or elongated) of the nodes range 103.1–140.1 per cm^2 and 0.42–0.60 mm, respectively (Table 1).

General microstructure

Ranges of eggshell thickness are as in Table 1. The eggshell is composed of one layer of shell units that are highly fused together, and the boundary between adjacent shell units are not clear unless there is a pore canal (Figure 4). The eggshell shows radial-tabular ultrastructure under SEM (Figure 5(b, e, h)).

Shell unit

The spherulitic shell unit is composed of calcite crystals that radiate in wedges from the organic core, and does not branch. These wedges show sweeping extinction beneath ornamentations, and are columnar at places where the shell units are more compact so that most of the wedges had no room to grow laterally (Figure S5, Figure S6, Figure S7). The mammillae are nearly round in tangential view (Figure 6(a, d)), the density is 348.7 per cm^2 for a Nanxiong specimen and 587.4 per cm^2 for a Shanyang specimen. The diameter of the mammilla ranges 99.8–227 μm for Nanxiong specimen and 96–240.8 μm for Shanyang specimen (Table 1). The top of shell unit that contributes to the ornamentation is usually more pointed rather than domed as in Megaloolithidae.

Pore system

Most pore systems are composed of tubular canals that have slightly changing diameter. Pore canals start at conjunctures of shell units and extend sub-vertically to the surface. In tangential view, the canals are usually circular or elliptical in shape (Figure 6(b–c, e, f)), and only a small number of them show

Figure 4. Radial sections of *Stromatoolithus pinglingensis* and *Spheroolithus chiangchiungtingensis* under light microscope (unpolarised). (a–d), *Stromatoolithus pinglingensis*; (a), Nanxiong specimen IVPP V 18,542; (b), Nanxiong specimen, IVPP V 18,543; (c), Shanyang specimen, IVPP V 26,961.1; (d), Laiyang specimen, IVPP V 26,967.2; (e), *Spheroolithus chiangchiungtingensis*, IVPP RV 74,002. Scale bar equals 1 cm.

irregular shape at the lower part of the eggshell (Figure 6(b, e)). The density of pores is 155.1–385.8 per cm^2 for Nanxiong and Shanyang specimens (Table 1), which are equal or lower than the values of a typical tubocanaliculate type ootype such as Megaloolithidae (0.05–0.2 mm, 400–500 per cm^2, Mikhailov 1997). There are two types of pore opening on the outer surface of the eggshell (Figure S3, Figure S4). One is simply circular or oval, which usually appears far away from the nodes (Figure 3(e, h)). The other is more commonly seen, which is usually slightly elongated and appears at the root of elongated nodes (Figure 3(c, i)). Sometimes the pore openings can be silt-like in shape (Figure 3(f)), indicating rimocanaliculate pores like in Ovaloolithidae.

Accretion lines

Accretion lines are very developed and almost evenly distributed throughout the eggshell (Figure 4(a–d), Figure 7(a–c)). They originate as concentric arcs centring organic cores, and horizontally connected as parallel growth lines when adjacent shell units come to fuse. In the meanwhile, at places beneath the ornamentation, the accretion lines arch up with the undulation. The accretion line bends downward at pore canals (Figure 5(e, j)) as it does in other ootaxa, which could help exclusive the possibility of diagenetic process such as cracking (Hirsch 1994; Choi et al. 2019). In tangential section, the accretion lines are concentric around pores (Figure 6(c, f), Figure S8, Figure S9).

Remarks

Materials from these three localities are comparable in thickness and general microstructure, and the major variation among them is the surface ornamentation. IVPP V 18,543 (Figure 2(a), Figure 3(a–b)) from Nanxiong shows ornamentation of nodes that are mostly scattered, with some linked in chains or fused into short ridges. Shanyang specimens (Figure 2(b), Figure 3(d)) exhibit comparable diameter and density of nodes with Nanxiong specimens, but the nodes and ridges are slightly lower. Laiyang specimens (Figure 2(c), Figure 3(g)) are more dominated by short ridges or chains that sometimes form a network and have a smaller node diameter (0.44 mm in average compared with 0.60 mm for Nanxiong specimens and 0.58 mm for Shanyang specimens). One can easily confuse specimen that has directionally arranged short ridges with some elongatoolithid eggshell that has reticulated ridges (*Paraelongatoolithus* for example, Wang et al. 2010a) solely by its ornamentation, just as we did in the first place. The pores of Nanxiong specimens and Shanyang specimens have equivalent diameter, but the latter are higher in density. These differences could be a coincidence due to the scarcity of materials from Shanyang and Shandong, and is also very possible to be caused by the variation of ornamentation within an egg or an oospecies, as the directionally arranged short ridges indicate a possible oval shape of the egg. Although we do not exclude the possibility that the specimen from Shanyang and Laiyang might be new oospecies of *Stromatoolithus*, but the lack of material makes it insufficient for us to draw such a conclusion. In this paper, we temporary treat the

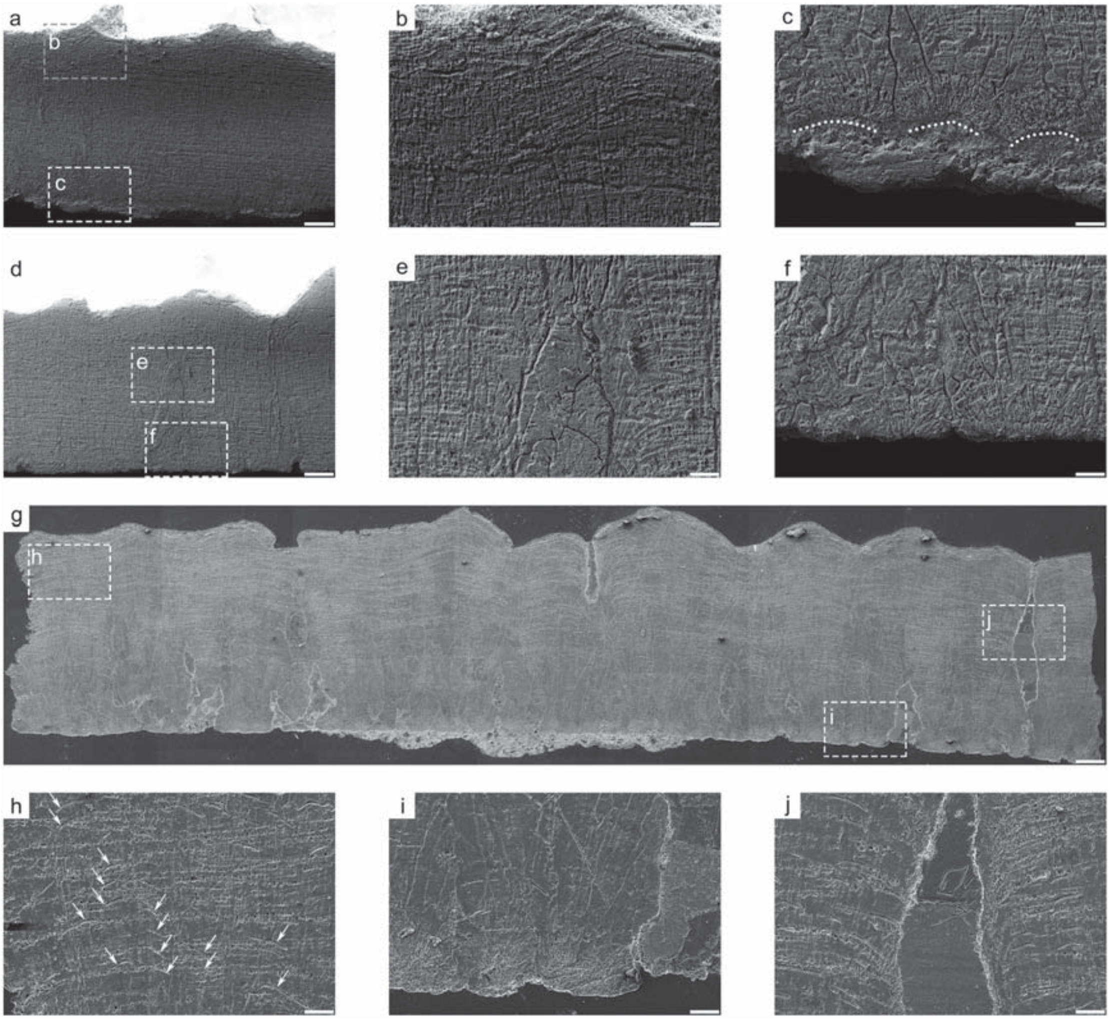

Figure 5. SEM microphotography of *Stromatoolithus pinglingensis*. (a–f), Radial view of an eggshell from Nanxiong specimen IVPP V 18,543; (b), enlargement showing radial-tabular ultrastructure, the transverse pattern is corresponded to accretion lines; (c), possible absorption craters protected by sediments (below) indicated by dotted lines suggesting incubated nature of the eggshell; (e), enlargement of the microstructure showing down-ward bending accretion lines approaching the pore canal; (f), enlargement of mammillae that are unprotected by sediments and eroded at their bottom; (g–j), Radial view of an eggshell from Shanyang specimen, IVPP V 26,961.1; (h), enlargement showing radial-tabular ultrastructure, arrows pointing out two sets of cleavage indicate possible recrystallisation; (i), enlargement of mammillae; (j), enlargement of a pore canal showing change of diameter of pore canal and down-ward bending of accretion lines approaching the pore canal. Scale bar equals 200 μm for (a), (d), (g) and 50 μm for (b), (c), (e), (f), (h), (i), (J).

specimens from three localities as one oospecies. Possible future erection of new oospecies will require statistically more eggshell materials from Shanyang and Laiyang or complete eggs.

For Nanxiong material, the mammilla structure of IVPP V 18,543 (Figure 5(c)) is not very complete compared with IVPP V 18,542 (Figure 5(i)). No mammillae can be identified from all IVPP V 18,543 eggshells with clean inner surface. SEM examination from one of the specimens shows structures that can be identified as absorption craters (Figure 5(c)) on mammillae that are covered with sediments. This structure is unseen on exposed mammillae of the same eggshell (Figure 5(f)), which could be possibly due to erosion during exposure. The craters at the centre of mammillae are usually interpreted as the result of calcium resorption by an embryo (Kurzanov and Mikhailov 1989; Hirsch and Quinn 1990; Karlsson and Lilja 2008; Tanaka et al. 2011). It indicates that IVPP V 18,543 eggshells could have been incubated, and to some extent explains why the inner surface was so incomplete while the ornamentations are well preserved. The combination of calcium absorption by an embryo and erosion might have caused the incompleteness of the inner surface of IVPP V 18,543.

The Shanyang specimens seem to have been more diagenetically altered than Nanxiong specimens. The Shanyang specimens show many small parallel cleavage surfaces within the eggshell under SEM (Figure 5(h)) that may be caused by partial recrystallisation, and its tangential section is not as clean as in Nanxiong specimen in equivalent position (Figure 6(b, c, e, f)).

Comparison

Parataxonomic position of Stromatoolithus pinglingensis

Zhao et al. (1999) assigned *Stromatoolithus pinglingensis* to oofamily Megaloolithidae for its similarity with French Megaloolithidae oogenera *Cairanoolithus* and *Dughioolithus*. So far, two oofamilies have been derived from Megaloolithidae, including Fusioolithidae (Fernández and Khosla 2015) and Cairanoolithidae (Sellés and Galobart 2016). *Dughioolithus* was synonymised with *Cairanoolithus* by Garcia and Vianey-Liaud (2001), and both oogenera were synonymised with a new oogenus, *Fusioolithus*

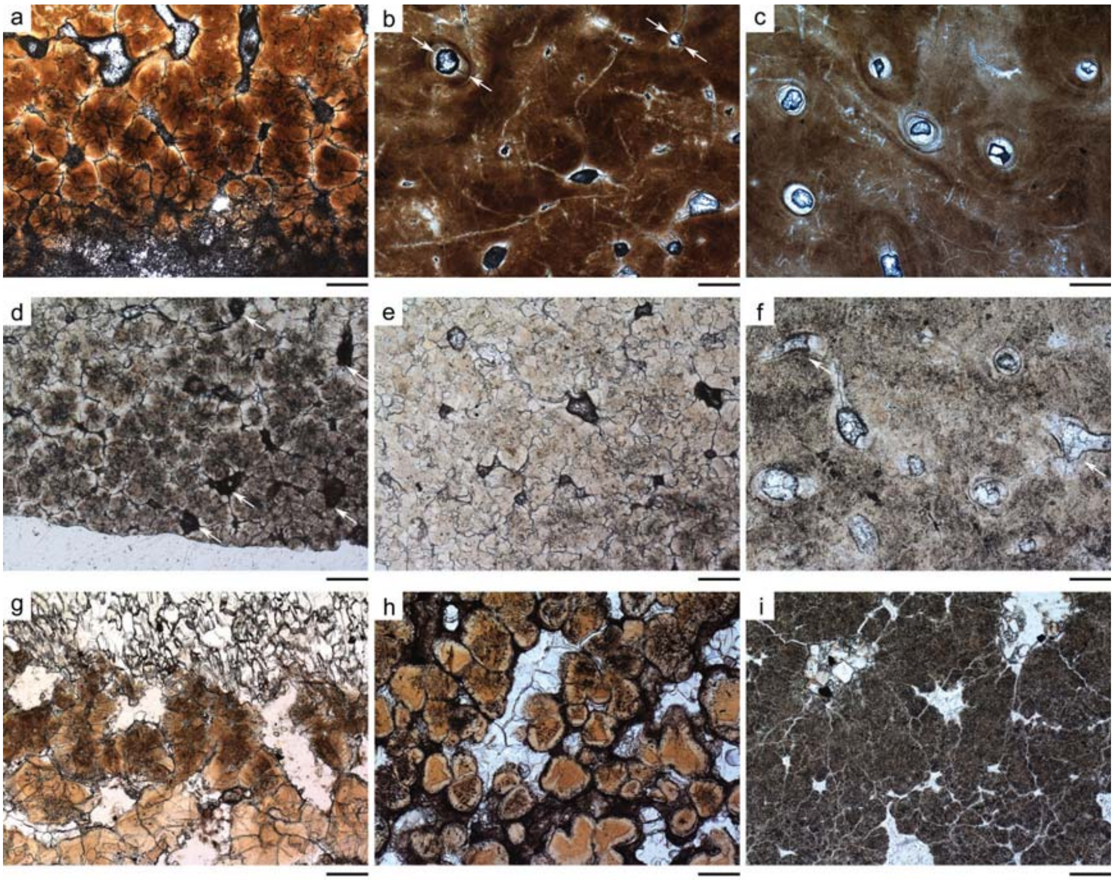

Figure 6. Tangential section of *Stromatoolithus pinglingensis* and *Spheroolithus chiangchiungtingensis* under light microscope (unpolarised). (a–c), *Stromatoolithus pinglingensis* from Nanxiong, IVPP V 18,542; (a), through mammillae; (b), through lower part of the eggshell, just above the mammillae, showing some pore canals circular to oval in tangential view and surrounded by concentrical accretion lines (pointed by white arrows) while others just start to form; (c), through middle part of the eggshell, showing nearly circular pore canals in tangential view, which were partially filled with syntaxial overgrew calcite, and were all surrounded by concentrical accretion lines; (d–f), *Stromatoolithus pinglingensis* from Shanyang, IVPP V 26,961.1; (d), through mammillae, showing compacted mammillae with some spaces filled with sediments among them that may related with pore opening on the inner surface (pointed by white arrows); (e), through lower part of the eggshell, just above the mammillae, showing pore canals that just start to form; (f), through middle part of the eggshell, showing nearly circular pore canals surrounded by concentrical accretion lines in tangential view, while a small number of them are not so regular in shape (pointed by white arrows); (g–i), *Spheroolithus chiangchiungtingensis* from Laiyang, IVPP RV 74,002; (g), through mammillae, showing loosely arranged mammillae compared to *Stromatoolithus pinglingensis*; (h), through middle part of the eggshell, showing loosely arranged wedges, and cavities among them; (i), through upper part of the eggshell, show cavities in irregular shape squeezed by shell units, and the structure of shell units are loose and mosaic in tangential view. Scale bars equal 200 μm.

under a new oofamily, Fusioolithidae, which was derived from several former members of Megaloolithidae that have partially fused shell units (Fernández and Khosla 2015). Soon after, a new oofamily, Cairanoolithidae was erected to contain *Cairanoolithus* (Sellés and Galobart 2016). All members of Megaloolithidae and Fusioolithidae have fan-shaped shell units that are either slender or short, and the border of adjacent units can be clearly observed or traced under polarised light, which makes the units easy to count. However, it is not the case for *Stromatoolithus pinglingensis*. Although the eggshell of *Stromatoolithus pinglingensis* shows sweeping distinction and occasionally reveals fan-shaped shell units, it is hard to determine the border of adjacent shell units. The fusion of shell units in *Stromatoolithus pinglingensis* is much greater than that in Fusioolithidae, and is to a similar degree with Cairanoolithidae. Besides, the surface of *Stromatoolithus pinglingensis* are usually covered with nodes, which can be scattered, linked in chains, or even merged into short ridges that is slightly directional arranged, and can be classified as sagenotuberculate type. It can be easily distinguished from the compactituberculate ornamentation of Megaloolithidae and Fusioolithidae, and from the nearly smooth surface of Cairanoolithidae. In addition, pore canals of *Stromatoolithus pinglingensis* are not so consistent in diameter compared to that of Megaloolithidae and Fusioolithidae. Therefore, *Stromatoolithus pinglingensis* should not be assigned to these oofamilies (Megaloolithidae, Fusioolithidae and Cairanoolithidae).

Stromatoolithus can be easily distinguished from all faveoloolithid eggs (oofamily Faveoloolithidae and Youngoolithidae, Zhang 2010) in sagenotuberculate ornamentation, fan-shaped shell units that are highly fused, and not of multicanaliculate type pore system.

Stromatoolithus differs from Similifaveoloolithidae (Zhu et al. 2019), Dendroolithidae (Zhang et al. 2018) and Dictyoolithidae (Wang et al. 2013b) in not having branched shell units and in the simpler structure of pore system. The pore systems of these oofamilies are usually described simply as prolatocanaliculate type, but is much more complex (with both canals and silt-like cavities) than in typical prolatocanaliculate ootaxa like Spheroolithidae. The branching of shell units on the radial section is related to the intrusion of oblique pore canals as in Similifaveoloolithidae or internal cavities as in Dendroolithidae (Zhu et al. 2019).

Elongatoolithidae (Wang et al. 2013a), Macroelongatoolithidae (Wang et al. 2010b), Prismatoolithidae (Wang et al. 2018),

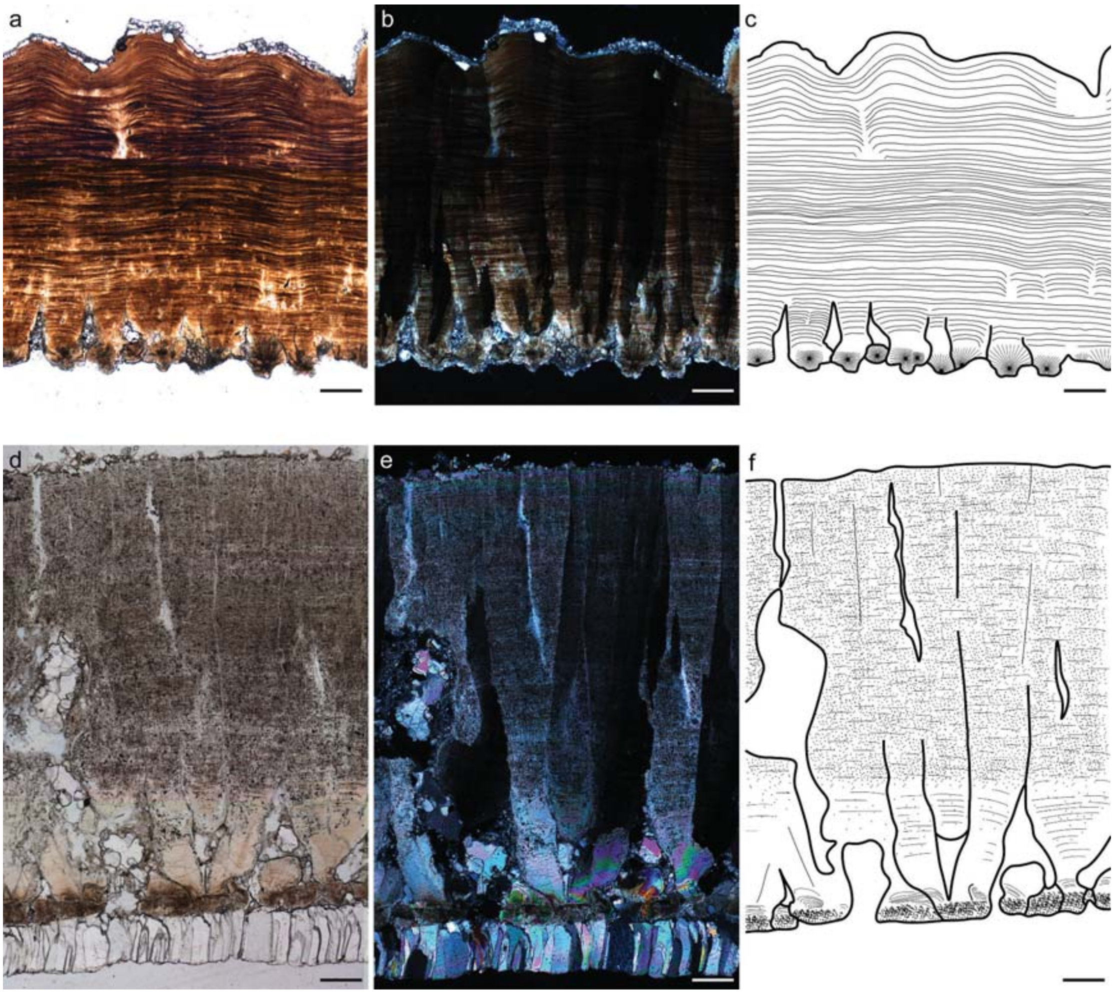

Figure 7. Comparison between radial view of *Stromatoolithus* and *Spheroolithus*. (a–c). *Stromatoolithus pinglingensis*, IVPP V 18,542, thin section No. 110,506–05-radial, showing evenly distributed accretion lines throughout the eggshell; (a), normal light; (b), cross polarised light; (c), line drawing of (a); (d–f), *Spheroolithus chiangchiungtingensis*, IVPP RV 74,002, showing relatively unapparent accretion lines; (d), normal light; (e), cross polarised light; (f), line drawing of (d). Scale bars equal 200 μm.

Table 1. Measurements of *Stromatoolithus pinglingensis* in this study.

Locality	Density (per cm^2)/ diameter (mm) of nodes	Density (per cm^2)/diameter (μm) of pore canal	Thickness without/ with ornamentation (mm)
Nanxiong	103.1–124.8*/ 0.59–0.60* (n = 14)	155.1–212.7/ 43.5–147.1 (n = 3)	1.16–1.56/1.29–1.73 (n = 2)
Shanyang	107.7–129.9*/ 0.57–0.59* (n = 9)	257.9–385.8/ 44.8–160.4 (n = 2)	1.11–1.49/1.22–1.63 (n = 5)
Laiyang	114.2–140.1*/ 0.42–0.45* (n = 4)	NA	1.03–1.15/1.20–1.31 (n = 1)

*, 95% confident interval.

Ovaloolithidae (Zhao 1979; Mikhailov 1991), and Stalicoolithidae (Wang et al. 2012a) eggs have clearly two structural layers at least, therefore cannot be compared with *Stromatoolithus* in microstructure.

It is easy to confuse *Stromatoolithus* with oofamily Spheroolithidae, especially for those who are more familiar with eggs of *Maiasaura* (Hirsch and Quinn 1990; Mikhailov 1994, 1997) but not *Spheroolithus chiangchiungtingensis* (Zhao and Jiang 1974; Zhao 1979). However, *Stromatoolithus pinglingensis* differs from Spheroolithidae in having more complex ornamentation and a regular pore system. The pore system of Spheroolithidae is typical of prolatocanaliculate, in which most pores on tangential sections are polygonal in the middle part of the eggshell (Figure 6(i)) as a result of space squeezed out by surrounding shell units. On the contrary, for *Stromatoolithus*, most tubular pores are regularly circular or oval with relatively smooth pore wall in tangential view and are concentrically surrounded by downward bending accretion lines (Figure 6(c, f)). Therefore, the pore system of *Stromatoolithus pinglingensis* should not be curtly assigned to prolatocanaliculate type, which is composed of irregular cavities with ‘large lacunae’ in the middle part of the eggshell, otherwise, the definition of prolatocanaliculate type pore system would be too vast to be used for parataxonomic purpose. The accretion lines of *Stromatoolithus* are distributed evenly throughout the eggshell, which is much more characteristic than that of Spheroolithidae eggs (Figure 7). In Spheroolithidae, the accretion lines are less apparent and can hardly be recognised in the upper part of the eggshell.

Here, although we would very much like to erect a new oofamily to contain *Stromatoolithus pinglingensis*, we decide not to do so for the moment because the materials described in this work contain no complete egg.