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A new oofamily of dinosaur egg from the Upper Cretaceous of Tiantai Basin, Zhejiang Province, and its mechanism of eggshell formation

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Here we describe new types of dinosaur eggs found from the Late Cretaceous Chichengshan Formation in the Tiantai Basin, Zhejiang Province. On the basis of such characters as small spheroid or near-spheroid, columnar layer composed of three zones, the outer zone consisted of stalagmite-like or coralliform secondary shell units, we established two new oogenera, one new and one combination oospecies: *Stalicoolithus shifengensis* oogen. et oosp. nov. and *Coralloidoolithus shizuiwanensis* oogen. et comb. nov. In addition, re-examination of the holotype of *Shixingoolithus erbeni* from the Upper Cretaceous Pingling Formation, Guangdong Province reveals that it was erroneously attributed to Spheroolithidae, and should be transferred to stalicoolithid. Consequently, we established a new oofamily: Stalicoolithidae oofam. nov. Stalicoolthids represents a new model of dinosaur eggshell and thus sheds new light on the formation and evolution of amniotic eggshells.

dinosaur egg, stalicoolthids, Upper Cretaceous, Chichengshan Formation, Tiantai Basin

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The Tiantai Basin in Zhejiang Province is a very important locality for dinosaur eggs research. Since the dinosaur eggs were first found in 1958, a large number and verity of dinosaur eggs [1–9], turtle eggs [10], and dinosaur bones [11] have been found. The Upper Cretaceous strata of the Tiantai Basin consist of the Laijia Formation and the overlying Chichengshan Formation. The Laijia Formation is composed of lacustrine sediments such as red silty mudstones and granule conglomerates, with many layers of interbedded laminated tuffs. The Chichengshan Formation can be subdivided into two members. The lower member, which has yielded a large number of dinosaur eggs and bones, is composed of red conglomerates, sandstones, and silty mudstones with interbedded tuffs; whereas the upper member is composed of red conglomerates and sandstones interbedded with muddy siltstones. SIMS U-Pb zircon dating of the Laijia and Chichengshan formations indicated an age of 98–91 Ma (to be published elsewhere), corresponding to the early Late Cretaceous (Cenomanian-Turonian).

Since 2008, we have reported a large number of new types of dinosaur egg from the Tiantai Basin [6–9], and have undertaken some taxonomic revisions of dinosaur eggs described by other researchers [2–4]. Recently, we found more than a dozen eggs from the lower member of the Chichengshan Formation in Shuangtang, Qiaoxia and Brewery in the Tiantai Basin (Figure 1). These eggs have a distinctive eggshell microstructure not seen in other types of dinosaur egg. Based on both egg macrostructure and eggshell microstructure characteristics, we established in this paper one new oofamily, two new oogenera, one new oospecies, and one new binomial combination oospecies. The newly discovered dinosaur eggs are very important for understand the composition of the Tiantai dinosaur eggs oofauna and providing new materials to study the eggshell

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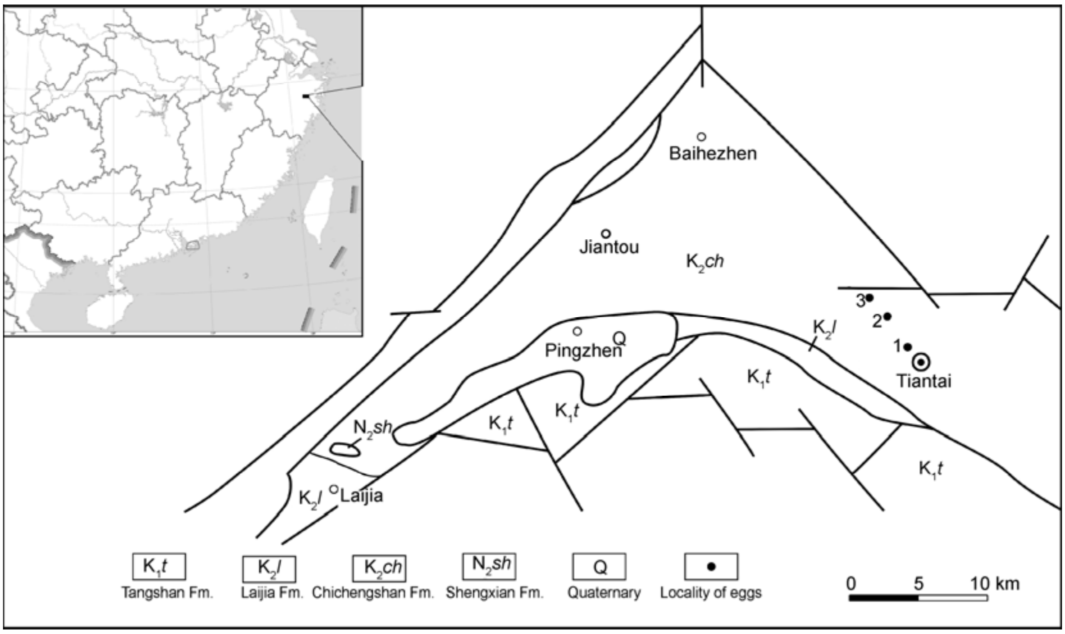

Figure 1 Dinosaur eggs localities and geological units of the Tiantai Basin, Zhejiang Province (modified from Wang et al. [1]). 1, Brewery; 2, Shuangtang; 3, Qiaoxia.

formation and evolution of the dinosaur eggs in the Cretaceous.

1 Systematic paleontology

Stalicoolithidae oofam. nov.

Etymology. From *Stalicoolithus*.

Known oogenera. *Stalicoolithus*, *Coralloidoolithus*, *Shixingoolithus*.

Diagnosis. Small spheroid or nearly spheroid eggs, irregularly arranged in the nest. Eggshell thickness, 2.4–4.0 mm. Outer surface of the eggshell is coarsely decorated. Cone layer is thin with 0.18–0.25 mm thick, about 1/20–1/4 of eggshell thickness. Three distinct zones of the columnar layer: (1) Horizontal growth lines develop in the inner zone. (2) Light and dark bands with varying thickness and lengths develop in the medial zone. (3) Secondary eggshell units are loosely arranged in the outer zone. The pore cannel is irregular.

***Stalicoolithus* oogen. nov.**

Etymology stalic-, Greek, "stalagmite-like", in reference to stalagmite-like arrangement of the second eggshell units in the outer layer of the eggshell columnar layer.

Diagnosis. Same as the type and only known oospecies.

***Stalicoolithus shifengensis* oogen. et oosp. nov.**

Etymology shifeng, from the ancient name of Tiantai County.

Holotype. A complete egg (TTM29) (Figure 2), housed in Tiantai Museum, Zhejiang Province.

Locality and horizon. Shuangtang, Tiantai County, Zhejiang Province; the first member of the Chichengshan Formation, Upper Cretaceous.

Diagnosis. Small spheroid egg with the polar axis about 9.54 cm and shape index 93.19. Eggshell thickness 3.90–4.00 mm. Cone layer is thin, about 1/20 of eggshell thickness. Columnar layer consists of the inner, medial, and outer zone. The medial zone is thick, with a thickness of 1.60–1.70 mm. There are some parallel light-colored streaks in the lower part of the medial zone. The outer zone is consisted of the loosely arranged stalagmite-like secondary eggshell units. There are 80–100 second eggshell units per square millimeter.

Description. A complete spheroid egg (Figure 2). The polar axis is 9.54 cm, and the equatorial diameter is 8.89 cm,

Figure 2 *Stalicoolithus shifengensis* oogen. et oosp. nov. holotype (TTM29).

with shape index 93.19. Outer surface of the eggshell is coarsely decorated. The eggshell thickness is 3.90–4.00 mm.

There is no obvious boundary between the cone layer and the columnar layer (Figure 3a). Cone layer is 0.18–0.20 mm in thickness, about 1/20 of the eggshell thickness. Cones are round, oval or irregular in shape, and tightly packed in the tangential section through the middle part of the cone layer (Figure 3b). There are 24–28 cones per square millimeter.

Thickness of the columnar layer is 3.70–3.80 mm. The columnar layer can be divided into three zones: inner, medial, and outer zone (Figure 3a).

Thickness of the inner zone is 1.00–1.10 mm, with distinct horizontal growth lines (Figure 3a). Columns with wedge-like and boundaries between each other are visible under crossed nicols. Pore cannels are irregular; there is little second eggshell unit development in some pores (Figure 3c, d).

Thickness of the medial zone is 1.60–1.70 mm. Columns are tightly packed and interlocking, thus forming a continuous zone. The lower part of medial zone has some gray streaks of various widths, in which filled with secondary calcite particles (Figure 3e). This may be similar to those found in eggshell of extant birds, such as *Casuarius*. There are numerous irregular pore canals in the upper part of the medial zone (Figure 3a). In the tangential section through the lower part of the medial zone, pores are round or oval, about 0.10–0.41 mm wide (Figure 3f). In the tangential section through the upper part of the medial zone, the diameter of pores varies 0.06–0.30 mm, and the number of pores increases upward to the eggshell surface. Some secondary eggshell units within pore canals can be observed in radial section or the tangential section (Figure 3a, g, h).

Thickness of the outer zone is 1.00–1.10 mm. This zone is composed of stalagmite-like secondary eggshell units (Figure 3a, i, j). These second eggshell units are 0.06–0.20 mm in diameter. There are 80–100 secondary eggshell units per square millimeter.

Pore cannels are irregular (Figure 3a). These canals vary in diameter, and are, for the most part, thicker in the middle and upper of the eggshell. Many small secondary eggshell units are present in most of the canals (Figure 3a, h, i).

Comparison and discussion. *Stalicoolithus shifengensis* has spheroid morphotype, three distinct zones of the columnar layer, and occurrence of numerous, tiny secondary eggshell units within the pore canals, significantly different from other dinosaur egg types [2–5,12–14] found in the world. Thus, it is considered to be a new oofamily, oogenus and oospecies: Stalicoolithidae oofam. nov., and *Stalicoolithus shifengensis* oogen. et oosp. nov.

***Coralloidoolithus* oogen. nov.**

Etymology coralloid-, Latin word, “coral-like”, in reference to the coral-like arrangement of the second eggshell units in the outer layer of the eggshell columnar layer.

Diagnosis. Same as for type and only known oospecies.

***Coralloidoolithus** shizuiwanensis* **oogen. et comb. nov.**

Paraspheroolithus shizuiwanensis Fang et al., 1998

Paraspheroolithus cf. *shizuiwanensis* Fang et al., 2000

Referred specimens. An incomplete nest composed of six nearly complete and three broken dinosaur eggs (TTM2) (Figure 4a), an incomplete nest composed of five nearly complete and one broken dinosaur eggs (IVPP V16966.1) (Figure 4e), one nearly complete and two broken dinosaur eggs (IVPP V16966.2) (Figure 4c), one nearly complete dinosaur eggs (IVPP V16966.3) (Figure 4b), one nearly complete and two broken dinosaur eggs (IVPP V16966.4) (Figure 4d). these specimens save in the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences and Tiantai County Museum, respectively.

Locality and horizon. Qiaoxia (TTM2), (IVPP V16966.1–4), Tiantai County, Zhejiang Province; the first member of Chichengshan Formation, Upper Cretaceous.

Diagnosis. Eggs nearly spheroid. The average polar axis is 9.36 cm, average shape index is 87.50. Thickness of eggshell is 2.60 mm. Thickness of the cone layer is 0.20–0.25 mm, about 1/10 of the eggshell thickness. There are 20–24 cones per square millimeter. The columnar layer is divided into the inner, medial and outer zone. There are brown bands with varying thickness in the medial zone. The outer zone is composed of coralline-like secondary eggshell units.

Description. Eggs are nearly spheroid. The average polar axis is 9.54 cm, the average equatorial diameter is 8.89 cm, and average shape index is 87.5 (Table 1). Outer surface of the eggshell is coarsely decorated. Thickness of eggshell is 1.80–2.60 mm.

There is no visible boundary between the cone layer and the columnar layer (Figure 5a). The cone layer is thin, 0.20–0.25 mm in thickness, about 1/10 of the eggshell thickness. Cones tightly arrange. In tangential section through the cone layer, cones are round or oval in shape, there are 20–24 cones per square millimeter (Figure 5b).

The columnar layer is 2.25–2.40 mm thick and consists of the inner, medial and outer zone (Figure 5a). Thickness of the inner zone is 0.75–0.80 mm. Columns are tightly packed, with uniform brown streaks. In tangential section through the inner zone, pores are round, oval or irregular in shape, and their diameter varies between 0.08–0.30 mm. Most of them are filled with secondary eggshell units (Figure 5c).

Thickness of the medial zone is 1.05–1.10 mm. Columns are tightly packed, there are a number of brown streaks with varying width (Figure 5a). In tangential section through the inner layer, pores are round or oval in shape, diameter is 0.06–0.14 mm in lower part of the medial zone, number of the pores is reduced (Figure 5d); diameter is 0.10–0.34 mm in upper part of the medial zone, number of the pores increases, and some of them have secondary eggshell units (Figure 5e).

Thickness of the outer layer is 0.55–0.60 mm, and consists of coralline-like secondary eggshell units. In most cases,

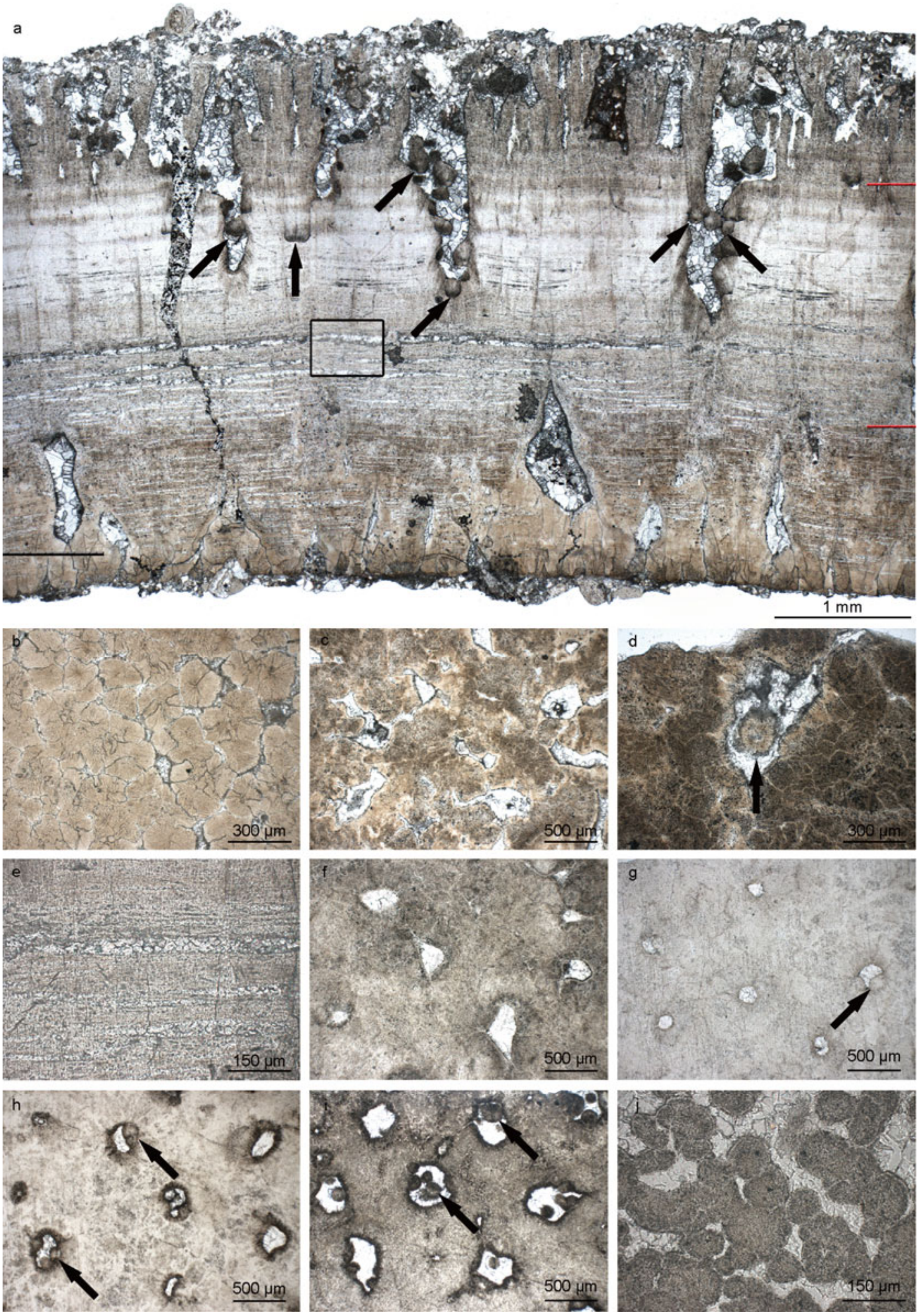

Figure 3 *Stalicoolithus shifengensis* oogen. et oosp. nov. eggshell microstructure. a. Radial section of eggshell, showing the unclear boundary of the cone layer and the columnar layer (black line), the cone layer thin, cones tightly packed; the lower part of the medial zone in the columnar layer has gray streaks of various widths; the outer zone composed of a number of stalagmite-like secondary eggshell units (red line showing the boundary between the inner and medial, and between medial and outer zone); pores irregular in shape, a number of secondary eggshell units (arrow) developed in pores; b. Tangential section through the cone layer, showing tightly arranged cones and little boundary in cones; c, d. Tangential section through the inner zone of the columnar layer, showing irregular pore canals in shape; d. showing the secondary eggshell units (arrow) in pores; e. Showing gray band in the lower part with irregular secondary calcite particles (magnified of a. box part); f–h. Tangential section through the medial zone of the columnar layer, showing the change of the round or oval shape pores in the different part of the eggshell; i, j. Tangential section through the outer zone of the columnar layer, i showing secondary eggshell units (arrow) in pores, j showing the round or oval secondary eggshell units in shape.

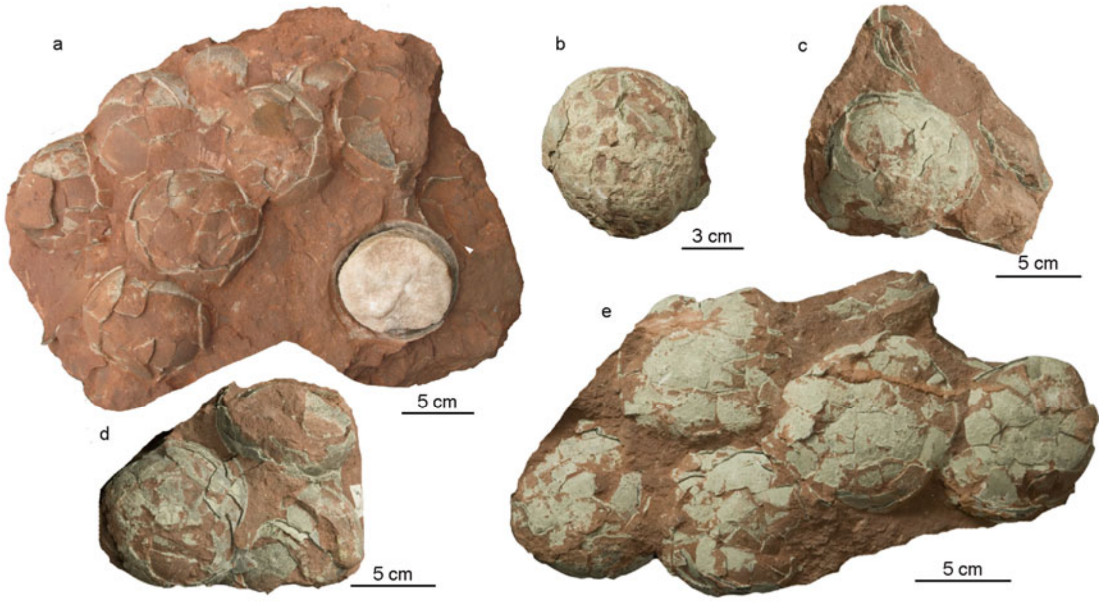

Figure 4 *Coralloidoolithus shizuiwanensis* oogen. et comb. nov. referred specimens. a. TTM2, an incomplete nest consists of nine dinosaur eggs; b–e. IVPP V16966, b. V16966.3 one nearly complete dinosaur egg; c. V16966.2 one nearly complete and two broken dinosaur eggs; d. V16966.4 one nearly complete and two broken; e. V16966.1 an incomplete nest consists of five complete and one fragmentary dinosaur eggs.

Table 1 Measurement of *Coralloidoolithus shizuiwanensis* (cm)

Specimens No.	Egg No.	Polar axis	Equatorial diameter	Shape index
TTM2	1	9.57	8.76	91.60
	4	8.84	7.26	82.13
	5	9.63	7.56	78.44
	6	9.19	6.85	74.52
V16966.1	1	10.01	8.25	82.42
	2	9.98	9.24	92.59
	3	8.72	8.20	94.04
	5	10.38	8.84	85.16
V16966.2	–	8.92	8.56	95.96
V16966.3	–	8.74	7.75	88.67
V16966.4	–	9.00	8.79	97.77

these secondary eggshell units can be recognized (Figure 5a). In tangential section through the outer zone, the secondary eggshell unit is round or oval in shape, and is 0.06–0.20 mm in diameter. There are 35–45 second eggshell units per square millimeter (Figure 5g). Pore cannels of the eggshell are irregular, often changing their course.

Comparison and discussion. Compared with *Stalicoolithus shifengensis*, eggs (TTM2 and V 16966.1–4) are similar to *Stalicoolithus shifengensis* in shape, and size of eggs, and eggshell microstructure. However, the eggshell thickness is 1.80–2.60 mm, thinner than that of the *Stalicoolithus shifengensis*, but, and there are a small amount of secondary eggshell units in the medial and outer zone of the columnar layer (Table 2). Thus, it is considered to be a new oogenus, *Coralloidoolithus*.

Paraspheroolithus shizuiwanensisi found in the Xixia Basin, Henan Province [21] (see Fang et al. [21] plate XVII, Figure 5) and *Paraspheroolithus* cf. *shizuiwanensis* from the Tiantai Basin, Zhejiang Province [6,7] (see Fang et al. [7] plate II, Figure 3) resemble *Coralloidoolithus*, especially with coralline-like arranged secondary eggshell units of the outer zone of the columnar layer, and this is never observed in paraspheroolithids. For this reason, we establish a new oogenus *Coralloidoolithus*, and *P*. *shizuiwanensisi* assembles *Coralloidoolithus shizuiwanensis*.

In addition, spherical eggs of prolatocanalicular structure [26] in *Dendroolithus microporosus* [27,28] found in Gobi, Mongolia, and *Spheroolithus* oosp. [29] found in the Bosung County, South Korea, are similar to *Coralloidoolithus shizuiwanensis* in eggshell microstructure characteristics,

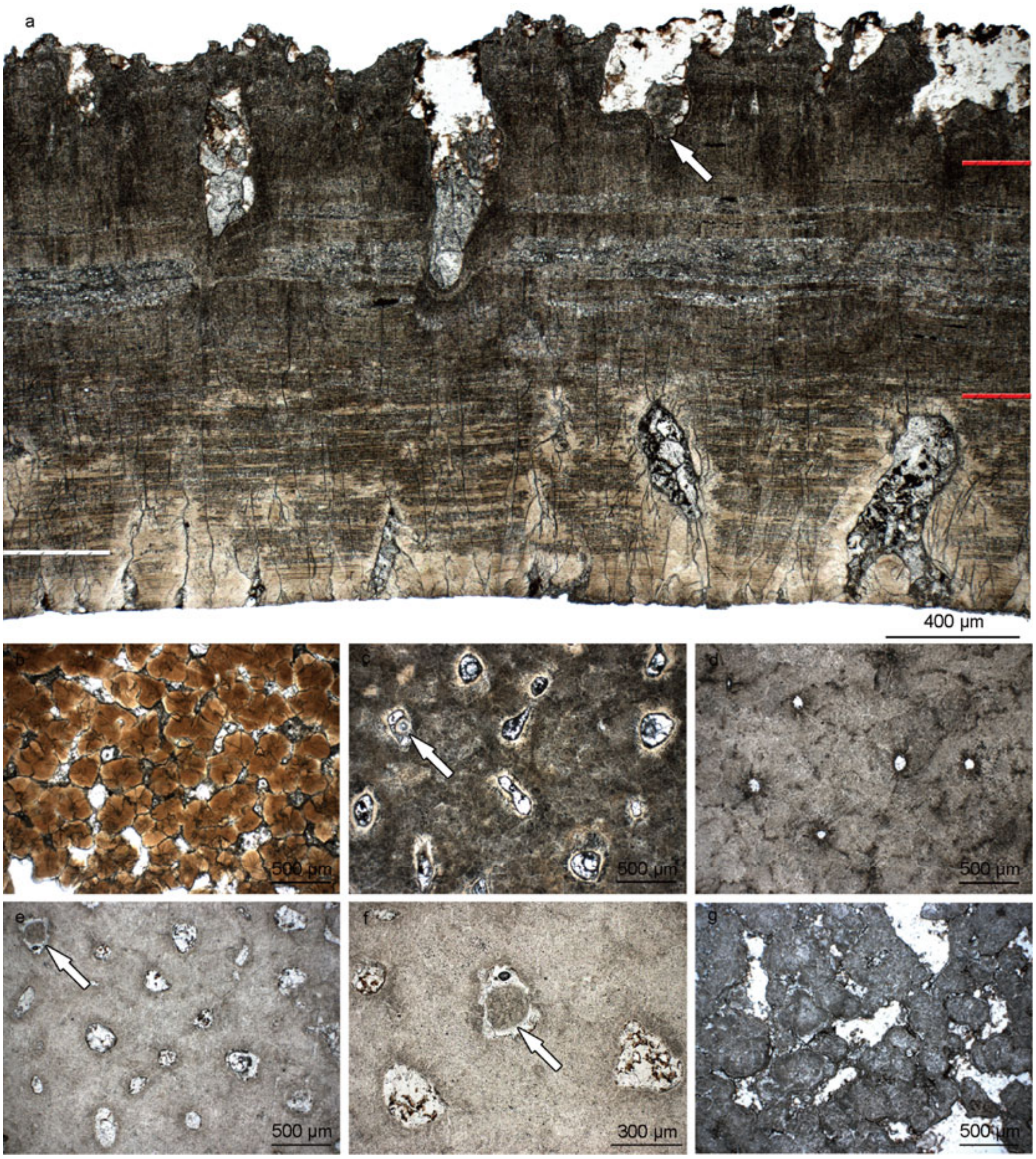

Figure 5 *Coralloidoolithus shizuiwanensis* oogen. et comb. nov. eggshell microstructure. a. Radial section of eggshell, showing an unclear boundary between the cone layer and the columnar layer (white line), the columnar layer consists of three zones: the inner, medial and outer zone (red line showing the boundary between the inner and medial, medial and outer zone), coralline-like secondary eggshell units (arrow) in the outer zone of the columnar layer; b. Tangential section through the cone layer, showing round or oval cones in shape; c. Tangential section through the inner zone, showing round, oval or irregular pores in shape, and secondary eggshell units within the pores (arrow); d. Tangential section through the medial zone, showing narrow diameter and reduce number of pores; e, f. Tangential section through the outer zone, showing enlarged diameter and increased number of pores, and secondary eggshell units (arrow) in some pores; g. Tangential section through the eggshell near the surface, showing irregular pores in shape, and secondary eggshell units.

Table 2 Characteristics comparison of *C. shizuiwanensis* and *S. shifengensis*

Characteristics		*C. shizuiwanensis*	*S. shifengensis*
Shape index		81.74	93.19
Thickness of the eggshell (mm)		1.80–2.60	3.90–4.00
Thickness of the cone layer (mm)		0.18–0.20	0.20–0.25
Thickness of the columnar layer	Inner zone (mm)	0.75–0.80	1.00–1.10
	Medial zone (mm)	1.05–1.10	1.60–1.70
	Outer zone (mm)	0.55–0.60	1.00–1.10
Cone number per mm^2		20–24	24–26
Second eggshell units number per mm^2		35–45	80–100

so they should belong to *Coralloidoolithus*, not *Spheroolithus* nor *dendroolithus*.

The eggshell microstructure of *Shixingoolithus erbeni* (oofamily Spheroolithidae) found in the Nanxiong Basin, Guangdong Province [30] is similar to that of *Stalicoolithus shifengensis* and *Coralloidoolithus shizuiwanensis*. But, some characteristics are different from them, such as the average polar axis is 12.5 cm, the cone layer thickness being 1/4 of the whole eggshell thickness. Re-make eggshell thin section of *S. erbeni* found secondary eggshell units in pore canals, so *Shixingoolithus erbeni* should belong to the member of Stalicoolithidae.

2 Eggshell formation mechanisms of stalicoolithids

Eggshell is formed in oviduct. The structure and physiological function of the oviduct of living birds and reptiles are significantly different [31–34]. This can also be reflected from the different eggshell microstructure of birds and reptiles [35,36]. On the basis of eggshell microstructure, Zhao [14,37] believed that different groups of dinosaur eggs are divided into two types of eggshell microstructure models. Members of elongatoolithids, prismatoolithids, and ovaloolithids have an avian-like eggshell structure, showing that the formation process of these types of dinosaur eggshells in oviduct is similar to that in living birds: firstly forming eggshell membrane, then the cone layer and the columnar layer. As a result, there is a clear demarcation between the eggshell membrane and the crystalline layer of the eggshell.

The other eggshell structure model represented by dictyoolithids, faveoloolithids, and dendroolithids differs from those birds, elongatoolithids, prismatoolithids, and ovaloolithids. The eggshell of these groups is composed of superimposed eggshell units which separated at their origin, thus showing a reticular or honeycomb-like organization. The mechanism and process of their eggshell formation have been different from those observed in extant birds. The fibers of eggshell membrane and eggshell units in these groups form more or less simultaneously, and then new components are formed over the first one. Additional eggshell units and fibers of eggshell membrane are repeatedly formed unitl growth of the crystalline eggshell units outstrips that of the eggshell membrane. In the end, the eggshell units are formed into reticulated or honeycomb-like organization.

Eggshell microstructure of stalicoolithids is peculiar, different from other groups of dinosaur eggs. By the large number of secondary eggshell units developed in the eggshell of stalicoolithids, it is showing that fibers of eggshell membrane and eggshell units may be formed more or less simultaneously, rather than sequentially. This is somewhat similar to that of dictyoolithids and fevoloolithids. But, the characteristics of tightly arranged eggshell units are clearly different from these dinosaur egg types and similar to those of elongatoolithids, prismatoolithids, and ovaloolithids. This is may be the convergence of eggshell formation mechanism between stalicoolithids and elongatoolithids etc.

Accordingly, it can be considered that the eggshell formation process of stalicoolithids consists of three phases: beginning of the eggshell formation, a large number of eggshell membrane fibers are secreted in oviduct, thereby providing nuclei centers for forming eggshell units. Then, the growth of both components is closely matched. Because of the tight arrangement of the eggshell units, only the fibers within pore canals formed nuclei center, and developed the second eggshell units. At the last of the eggshell formation, more fibers of eggshell membrane with nuclei center are secreted, and then a large number of second eggshell units are formed.

This shows that the characteristics of eggshell microstructure in stalicoolithids provide fresh evidence for studying eggshell formation mechanism and evolution of amniotic eggshell.

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