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New forms of dictyoolithids from the Tiantai Basin, Zhejiang Province of China and a parataxonomic revision of the dictyoolithids

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Abstract Dinosaur eggs collected from the Upper Cretaceous Chichengshan Formation in the Tiantai Basin of Zhejiang Province are referable to the oofamily Dictyoolithidae. On the basis of general external shape, size, eggshell thickness, and eggshell composed of 3–4 superimposed slender shell units with a reticulate organization, a new oogenus and two oospecies, *Paradictyoolithus zhuangqianensis* oogen. et oosp. nov., and *P. xiaxisanensis* oogen. et oosp. nov., are erected. The Dictyoolithidae is previously represented by one oogenus and four oospecies, *Dictyoolithus hongpoensis*, *D. neixiangensis*, *D. jiangi*, and *D. gongzhulingensis*, all of which are known exclusively from the Cretaceous of China. We re-examined the holotypes of the four oospecies, established a new oogenus *Protodictyoolithus*, and propose only *D. hongpoensis* belong to the *Dictyoolithus*, the other that three species of *Dictyoolithus* should be reassigned to *Protodictyoolithus neixiangensis* comb. nov., *P. jiangi* comb. nov. and *Similifaveoolithus gongzhulingensis* comb. nov., respectively.

Key words Tiantai Basin, Zhejiang Province, China; Late Cretaceous; dinosaur eggs, dictyoolithids

Recently, we found some new forms of dinosaur eggs from the Tiantai Basin, Zhejiang Province, referable to the oofamily Dictyoolithidae. The Dictyoolithidae is previously represented by one oogenus, *Dictyoolithus* and four oospecies, *D. hongpoensis*, *D. neixiangensis*, *D. jiangi* and *D. gongzhulingensis*, all of which are known from the Cretaceous of China (Zhao, 1994; Liu and Zhao, 2004; Wang et al., 2006; Jin et al., 2010). Zhao (1993, 1994) described *Dictyoolithus* eggshells as comprised of three to five superimposed shell units and, on the basis of this interpretation, hypothesized an evolutionary trend in the calcification of dinosaur eggs. Previous descriptions of the dictyoolithid eggs are brief due to the scarcity of materials for comparison.

In this paper, detailed re-descriptions of holotypes of the aforementioned four oospecies

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and of some new materials from the Tiantai Basin, Zhejiang Province are presented along with comments on the parataxonomy of this group of eggs.

Dictyoolithidae Zhao, 1994

Revised diagnosis Eggs spherical or near-spherical. Outer surface smooth with grainy appearance or very low sculptured nodes. Radial view of eggshell with reticulate organization framed by irregular shell units. Shape of pore canals irregular. Pore walls separated into irregularly small blocks in tangential view.

***Dictyoolithus* Zhao, 1994**

Revised diagnosis Same as for the type oospecies *Dictyoolithus hongpoensis*.

***Dictyoolithus hongpoensis* Zhao, 1994**

Holotype Eggshell fragments from two broken eggs (IVPP RV 94001; Field No.79001).

Locality and horizon Hongpo, Chishuigou, Xixia County, Henan Province. Upper Cretaceous, Liuyemiao Formation.

Revised diagnosis Eggshell composed of more than five superimposed shell units with a reticulate organization in radial section.

Description The eggs are nearly spherical. The eggshells are 2.50–2.80 mm in thickness. Outer surface of the eggshell is smooth with grainy appearance or with very low sculptured nodes. Shell layer is composed of five or more superimposed shell units with a reticulate organization in radial section (Fig. 1A). Shell units vary in length and width, separated at their origin and forming interstices. In most cases, mammillary core (calcite nucleus) of the shell unit is poorly preserved by diagenetic changes, but some of them can be recognized under higher magnification (Fig. 1B). Tangential views show that all the pores connect to each other and the pore walls are separated into irregularly small blocks. Comparison of the shell units and pores in different levels of tangential sections reveals a considerable variation in shape (Fig. 1C-E).

Remarks Jin et al. (2010) reported *Dictyoolithus hongpoensis* from the Lishui Basin, Zhejiang Province. However, they observed microstructure of the eggshells in radial sections only. According to Zhang (2010), the faveoololithid eggshell structure in radial section resembles the reticular eggshell structure of dictyoolithid eggs, but the pores are numerous and closely spaced, forming a honeycomb in tangential section. It seems, therefore, an unresolved issue whether the Lishui eggs are referable to *Dictyoolithus hongpoensis*.

***Paradictyoolithus* oogen. nov.**

Etymology The prefix “para-”, Greek, is used to indicate the similarity in eggshell microstructure to the existing oogenus *Dictyoolithus*.

Type oospecies *Paradictyoolithus zhuangqianensis* oogen. et oosp. nov.

Diagnosis Eggs near-spherical. Eggshell thickness 1.8–2.2 mm. Three or four

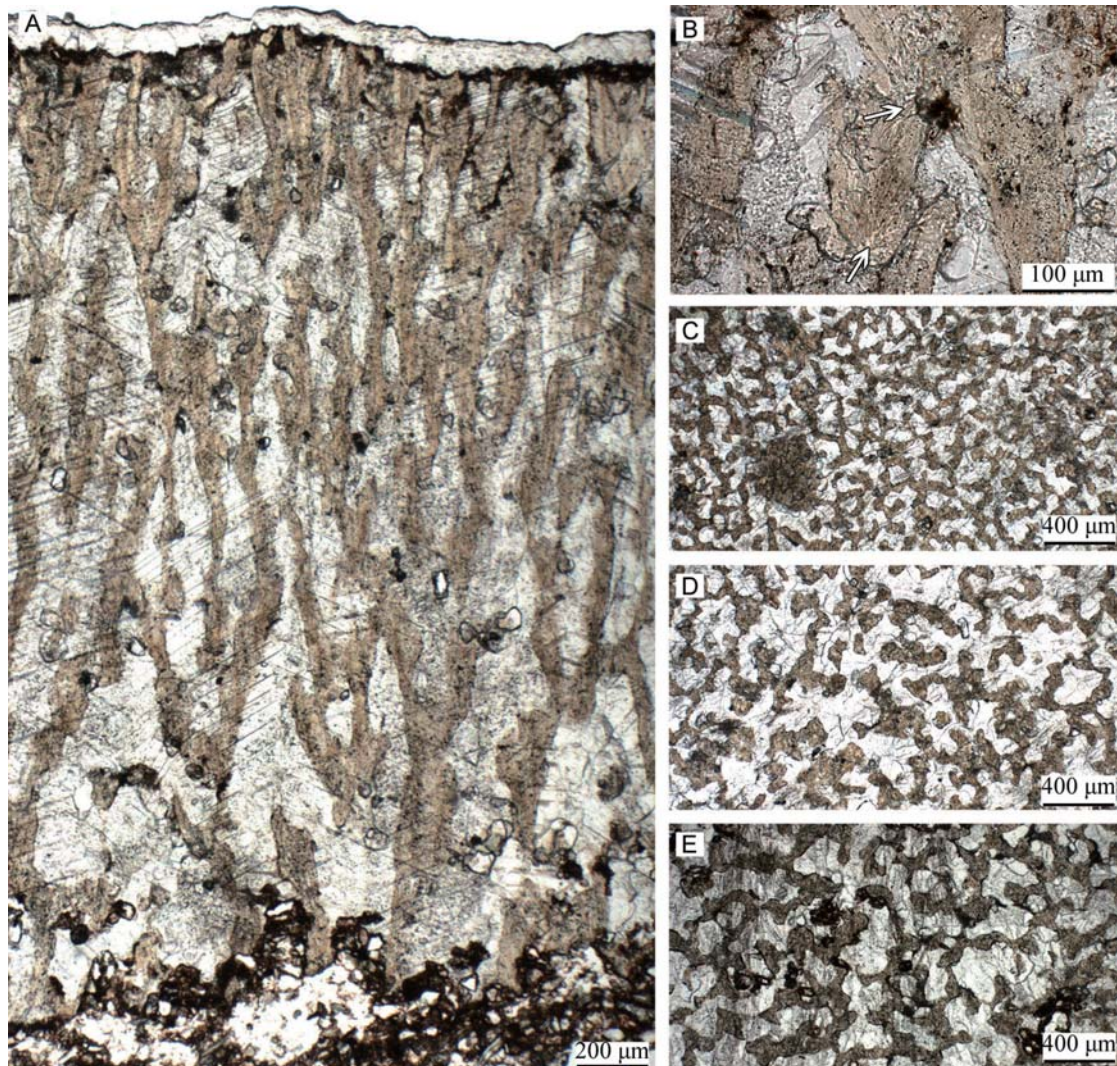


Fig. 1 Eggshell microstructure of *Dictyoolithus hongpoensis* Zhao, 1994

A. Radial section through the eggshell, showing five or more superimposed shell unit layers; B. Radial section through eggshell, arrows showing mammillary core (calcite nucleus) of the shell unit; C. Tangential section through near the outer surface of the eggshell, showing the more tightly interconnected shell units; D. Tangential section through the middle part of the eggshell, showing the random or interconnected shell units; E. Tangential section through near the inner surface of the eggshell, showing the interconnected eggshell units

superimposed shell units with a reticulate organization in radial section.

***Paradictyoolithus zhuangqianensis* oogen. et oosp. nov.**

Etymology From Zhuangqian, the name of the locality where the specimens were collected.

Holotype Three eggs represent a part of a nest (TTM18; Housed in Tiantai Museum, Zhejiang Province)(Fig. 2)

Locality and horizon Zhuangqian, Tiantai County, Zhejiang Province. Upper Cretaceous, Chichengshan Formation.



Fig. 2 Holotype of *Paradictyoolithus zhuangqianensis* oogen. et oosp. nov., TTM18

Diagnosis Eggshell composed of three or four superimposed shell units with a reticulate organization. Shell units connect to each other, forming a honeycomb-like structure in tangential section through the middle part of the eggshell.

Description The eggs are near-spherical (Fig. 2), the average polar axis and equatorial diameter are 13.2 and 10.8 cm, respectively. The arrangement of the eggs in the nest is not clear. Eggshell thickness is 2.13–2.20 mm.

Radial view reveals the eggshell composed of three or four superimposed eggshell units with a reticulate organization (Fig. 3A). Shell units are slender (Fig. 3A), and the cone with mammillary core can be identified under higher magnification (Fig. 3B). In tangential sections, through nearly the outer and inner surface of the eggshell, all the pores connect to each other, and the pore walls become separated into irregularly small blocks (Fig. 3C, E), but in tangential section through the middle part of the eggshell, the shell units fuse together, forming a honeycomb-like structure (Fig. 3D).

Comparison and discussion Characteristics of the specimens described above are similar to those of *Dictyoolithus*, with a reticulate organization, and they should belong to the Dictyoolithidae. But the eggshell is composed of three or four of superimposed shell units, the shell units fuse together, forming a honeycomb-like structure in tangential section through the middle part of the eggshell. Therefore, these eggs are referred to a new dictyoolithid oogenus and oospecies, *Paradictyoolithus zhuangqianensis*.

***Paradictyoolithus xiaxisanensis* oogen. et oosp. nov.**

Etymology From “Xiaxisan”, the name of the locality where the specimens were collected.

Holotype TTM16, a clutch containing six eggs and an egg impression (Fig. 4A).

Referred specimen TTM17, a clutch containing four eggs and two impressions of eggs (Fig. 4B).

Locality and horizon Xiaxisan, Tiantai County, Zhejiang Province. Upper Cretaceous, Chichengshan Formation.

Diagnosis Eggs near-spherical. Eggshell composed of three or four superimposed shell units. Shell units are not fused near the outer surface.

Description Eggs near-spherical, the average polar axis and equatorial diameter are 13.9 and 11.7 cm, respectively (Table 1). Eggs irregularly arranges in the nest (Fig. 4A, B). Eggshell thickness is 1.80–2.00 mm.

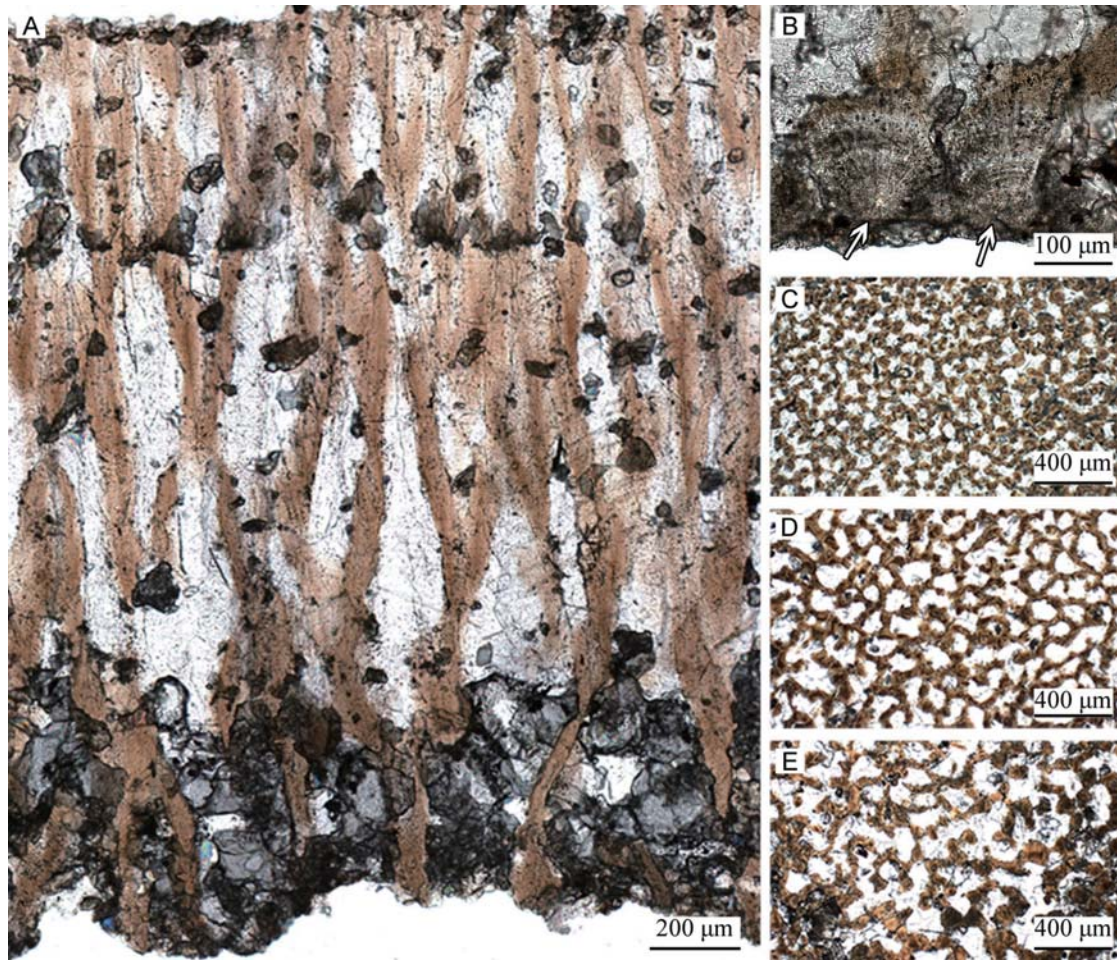


Fig. 3 Eggshell microstructure of *Paradictyoolithus zhuangqianensis* oogen. et oosp. nov.

A. Radial section through the eggshell, showing three or four superimposed unit layers; B. Radial section through eggshell, arrows showing mammillary core (calcite nucleus) of the shell unit; C. Tangential section through near the outer surface of the eggshell, showing more closely arranged eggshell units with irregular pores; D. Tangential section through the middle part of the eggshell, showing the interconnected eggshell units forming honeycomb-like eggshell structure; E. Tangential section through near the inner surface of the eggshell, showing random eggshell units and irregular pores

Table 1 Egg measurements of *Paradictyoolithus xiaxishanensis* oogen. et oosp. nov. (mm)

Egg No.	Polar axis (a)	Equatorial (b)	Shape index (b/a×100%)	
TTM16	1	14.01	11.92	84.80
	2	13.31	10.72	80.56
	3	14.34	12.70	88.55
	4	14.97	11.95	79.79
	5	13.01	11.39	87.57
TTM17	1	13.04	12.23	93.80
	2	14.43	11.20	77.60
	3	14.40	11.98	83.20
	4	13.18	11.38	86.33

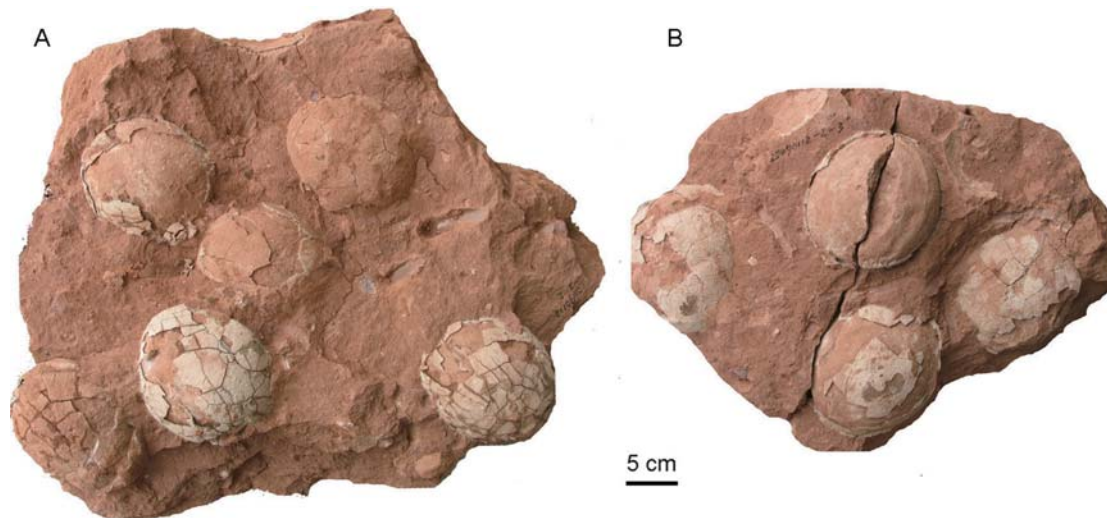


Fig. 4 *Paradictyoolithus xiashanensis* oogen. et oosp. nov.

A. TTM16 (holotype), a clutch containing six eggs and one egg impression; B. TTM17, a clutch containing four eggs and two egg impressions

Radial views show that the eggshell is usually composed of three or four superimposed shell units (Fig. 5A). Shell units are slender, and the cone with crescent-shaped layering is clearly defined under higher magnification (Fig. 5B). In tangential sections, all the pores connect to each other, and the pore walls become separated into irregularly small blocks (Fig. 5C–E).

Comparison and discussion These specimens should be assigned to *Paradictyoolithus* on the basis of general external shape and size, their slender shell units, and three or four superimposed shell units. However, the difference between these specimens and *Paradictyoolithus zhuangqianensis* is remarkable. The pores of the specimens described here connect to each other, and the pore walls become separated into small blocks, but the shell units of the *Paradictyoolithus zhuangqianensis* fuse together, forming a honeycomb-like structure in the middle part of the eggshell. Therefore, the specimens described here represent a new oospecies, *Paradictyoolithus xiashanensis*.

***Protodictyoolithus* oogen. nov.**

Etymology The prefix “proto-”, Greek, is used to indicate primitive characteristics of the eggshell in dictyoolithids.

Type oospecies *Protodictyoolithus neixiangensis*.

Diagnosis Eggshell composed of two to four superimposed shell units. Shell units near the outer surface of eggshell are laterally interlocking, with some tendency of fusion.

***Protodictyoolithus neixiangensis* (Zhao, 1994) comb. nov.**

Holotype Two eggs (IVPP RV 94002; Field No.79007)(Fig. 6).

Locality and horizon Shibangou, Chimei, Neixiang County, Henan Province. Upper Cretaceous, Zhaoying Formation.

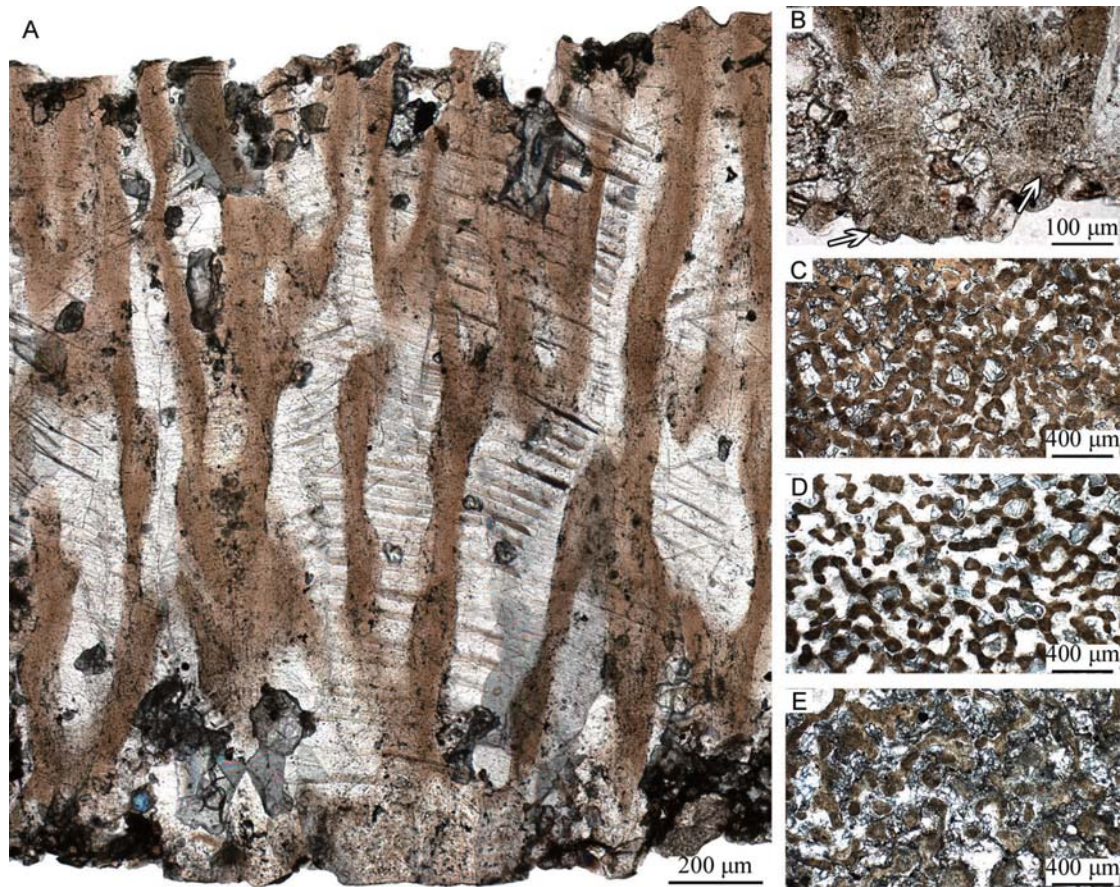


Fig. 5 Eggshell microstructure of *Paradictyoolithus xiaxishanensis* oogen. et oosp. nov.

A. Radial section through the eggshell, showing three or four superimposed eggshell unit layers; B. Radial section through the eggshell, arrows showing mammillary core (calcite nucleus) of the shell unit; C. Tangential section through near the outer surface of the eggshell, showing the interconnected eggshell units; D. Tangential section through the middle part of the eggshell, showing the random or interconnected eggshell units, some shell units interconnected with each other and forming a round pore canal; E. Tangential section through near the inner surface of the eggshell, showing the random or interconnected eggshell units



Fig. 6 Holotype of *Protodictyoolithus neixiangensis* (Zhao, 1994) comb. nov., IVPP RV 94002

Revised diagnosis Eggshell composed of two or three superimposed shell units. Shell units fused near the outer surface.

Description Eggs are spherical in shape, with polar axis about 12.0 μm (Fig. 6). Eggshell thickness is 1.50–1.70 mm. Eggshell is composed of two or three superimposed eggshell units with a reticulated organization in radial section (Fig. 7A). In some portion, very short shell units are arranged in a single layer beneath the outer surface of the eggshell (Fig. 7A). Mammillary core (calcite nucleus) of the shell unit can be recognized under higher magnification (Fig. 7E, F). Tangential views of the eggshells show that the shell units and pore canals display considerable variation in shape (Fig. 7B–D).

Comparison and discussion Compared to other members of the Dictyoolithidae, the species *Dictyoolithus neixiangensis* described by Zhao (1994) on the basis of eggs (IVPP RV 94002; Field No.79007) from Neixiang County, Henan Province, differ remarkably from *D. hongpoensis*, *Paradictyoolithus zhuangqianensis*, *P. xiaxishanensis* in eggshell thickness, the numbers of superimposition among the shell units, and the fused eggshell unit layer near the outer surface of the eggshell. Consequently, the Neixiang eggs should be assigned to a new oogenus, *Protodictyoolithus*.

***Protodictyoolithus jiangi* (Liu & Zhao, 2004) comb. nov.**

Holotype 4 more or less completely preserved eggs (D737, D738, D739, and D740; Housed in Dalian Natural Museum)(Fig. 8)

Locality and horizon Jiangjunding, Laiyang City, Shandong Province. Upper Cretaceous, Jiangjunding Formation, Wangshi Group.

Revised diagnosis Eggshell composed of two to four superimposed shell units. Shell units near the outer surface of the eggshell are small and interlocking.

Description Eggs are near-spherical in shape (Fig. 8), the average polar axis and equatorial diameter are 13.4 and 11.8 μm , respectively (measurements of the eggs according to Liu and Zhao, 2004: table 1).

Eggshell thickness is 1.50–1.65 mm. Two or three superimposed shell units form a reticulate organization (Fig. 9A). Occasionally, there are three or four superimposed relatively shorter shell units in some portion of the eggshell. Shell units near the outer surface of the eggshell are very short, and arranged in a single layer (Fig. 9A). Therefore, some pore canals may end blindly before reaching the surface of the eggshell (Fig. 9A, B). Mammillary core (calcite nucleus) of the shell unit is very clear (Fig. 9A). Comparative examination of the shell units and pore canals in different level of tangential sections shows a considerable variation in shape (Fig. 9C, D).

Comparison and discussion The species *Dictyoolithus jiangi* erected by Liu and Zhao (2004) on the basis of eggs from the Upper Cretaceous Jiangjunding Formation of Laiyang, Shandong Province, is similar to *Protodictyoolithus neixiangensis* in eggshell thickness, and the rarity of superimposition among the shell units. However, there are 3 or 4 relatively shorter superimposed shell units in some portion of the eggshell. Accordingly, these eggs should be referred to the oogenus, *Protodictyoolithus*.

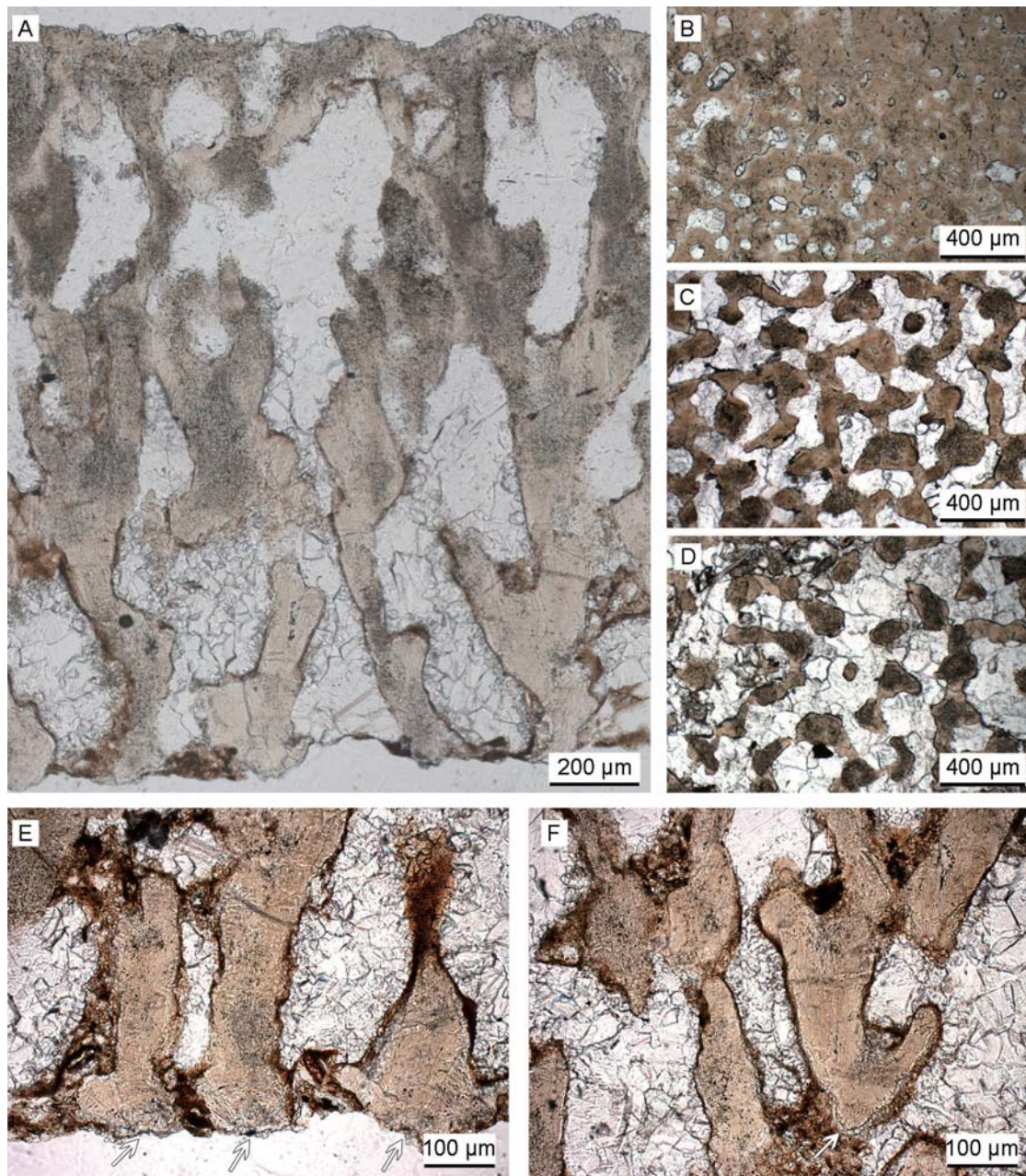


Fig. 7 Eggshell microstructure of *Protodictyoolithus neixiangensis* (Zhao, 1994) comb. nov.

A. Radial section through the eggshell, showing two or three superimposed unit layers; B. Tangential section through near the outer surface of the eggshell, showing the fused eggshell units and round or irregular pores; C. Tangential section through the middle part of the eggshell, showing interconnected eggshell units; D. Tangential section through near the inner surface of the eggshell, showing random or interconnected eggshell units; E–F, Radial section through the eggshell, showing mammillary core (arrows) of the shell unit

Similifaveoolithidae Wang et al., 2011

***Similifaveoolithus* Wang et al., 2011**

***Similifaveoolithus gongzhulingensis* (Wang et al., 2011) comb. nov.**



Fig. 8 Holotype of *Protodictyoolithus jiangi* (Liu & Zhao, 2004) comb. nov., D737–740

Holotype Two completely preserved eggs and two broken eggs (D09-1, D09-2, D09-3, and D09-4; Housed in Jilin University Museum of Geology)

Locality and horizon Liufangzi, Gongzhuling City, Jilin Province. Lower Cretaceous, Quantou Formation.

Revised diagnosis Eggshell composed of two or three superimposed shell units. Shell units of the third layer are small and fused near the outer surface of the eggshell.

Description Eggs are near-spherical in shape (see Wang et al., 2006: fig. 3), the average polar axis and equatorial diameter are 11.9 and 11.6 mm, respectively (measurements of the eggs according to Wang et al., 2006: table 1). Eggshell thickness is 1.40–1.70 mm. Radial views show that the eggshell is composed of two or three superimposed shell units. Shell units are very short and arranged in a single layer beneath the outer surface of the eggshell (see Wang et al., 2006: fig. 4C, D). Tangential views show shell units connect each other and that the pores are extremely numerous, and closely spaced, looking as a whole like a honeycomb organization (see Wang et al., 2006: fig. 4B).

Comparison and discussion Characteristics of the *Dictyoolithus gongzhulingensis*

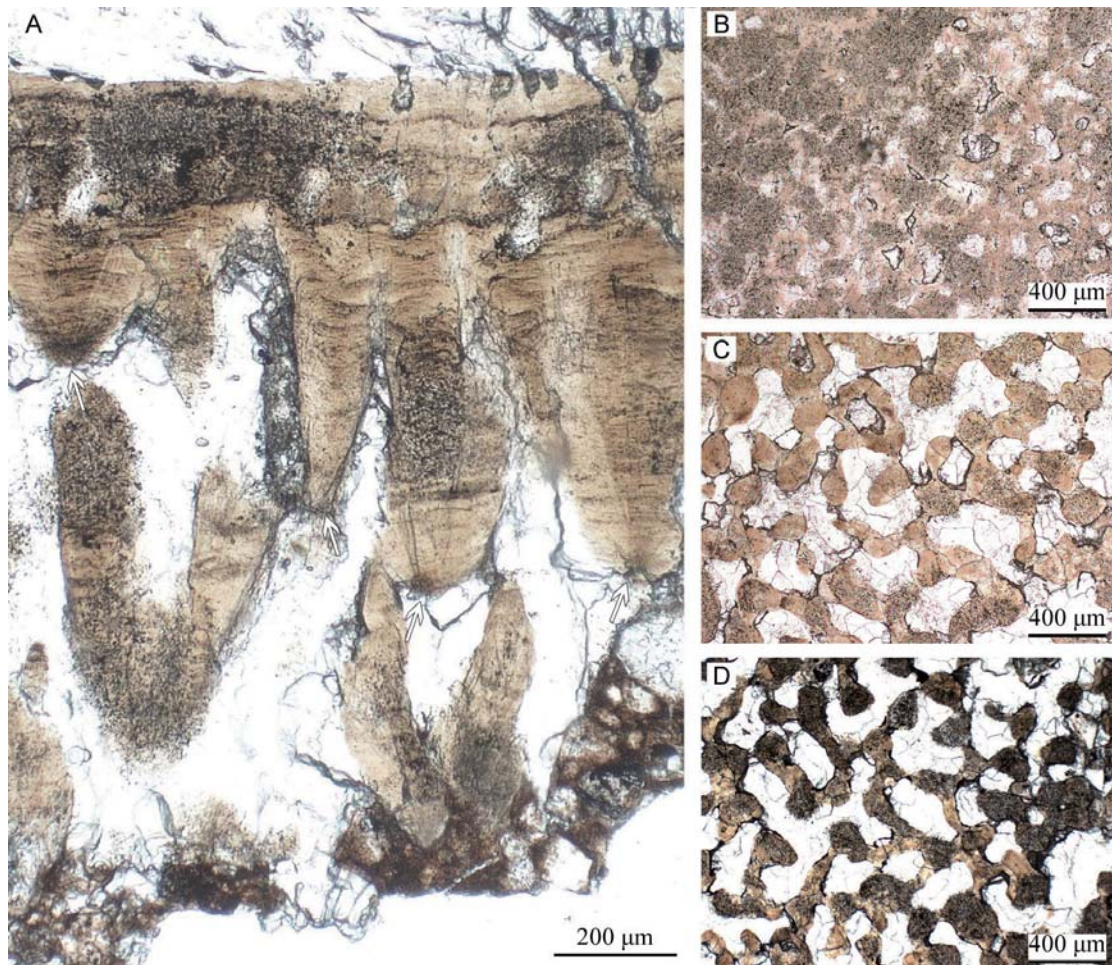


Fig. 9 Eggshell microstructure of *Protodictyooolithus jiangi* (Liu & Zhao, 2004) comb. nov.

A. Radial section through the eggshell, showing two or three superimposed unit layers, eggshell units are thicker and fused near the outer surface of the eggshell, arrows showing mammillary core (calcite nucleus) of the shell unit; B. Tangential section through near the outer surface of the eggshell, showing the fused eggshell units and the round or irregular pores; C. Tangential section through the middle part of the eggshell, showing interconnected eggshell units; D. Tangential section through near the inner surface of the eggshell, showing the random or interconnected eggshell units

eggshell described by Wang et al. (2006), are more similar to those of *Similifaveoolithus shuangtangensis* Wang et al., 2011 than to those of dictyooolithids. In tangential section through middle part of the eggshell, shell units connect each other in eggshells of *Similifaveoolithus*, but shell units are separated as irregularly small blocks in eggshells of dictyooolithid. The eggshell is thicker than that of *S. shuangtangensis* which is 1.05–1.20 mm, but the fused layer beneath the outer surface of the eggshell is thinner than the latter. Consequently, the specimens should be referred to the *Similifaveoolithus*.

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浙江天台盆地晚白垩世网形蛋类新类型 及网形蛋类的分类订正

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摘要: 记述了产自浙江省天台盆地的网形蛋类新材料, 建立一新蛋属——拟网形蛋属 (*Paradictyoolithus* oogen. nov.), 两个新蛋种: 庄前拟网形蛋 (*Paradictyoolithus zhuangqianensis* oogen. et oosp. nov.) 和下西山拟网形蛋 (*P. xiaxisanensis* oogen. et oosp. nov.)。在此基础上, 重新系统描述其他已知4种网形蛋属成员的结构特征, 并对网形蛋类的分类进行了订正: 网形蛋属 (*Dictyoolithus*) 仅保留红坡网形蛋 (*D. hongpoensis* Zhao, 1994) 一个蛋种; 建立一新蛋属: 原网形蛋属 (*Protodictyoolithus* oogen. nov.), 将发现于河南西峡盆地的内乡网形蛋 (*D. neixiangensis* Zhao, 1994) 和发现于山东莱阳盆地的蒋氏网形蛋 (*D. jiangi* Liu & Zhao, 2004) 分别修订为: 内乡原网形蛋 (修订种) (*Protodictyoolithus neixiangensis* (Zhao, 1994) comb. nov.) 和蒋氏原网形蛋 (修订种) (*P. jiangi* (Liu & Zhao, 2004) comb. nov.); 此外, 发现于吉林公主岭早白垩世的公主岭网形蛋 (*D. gongzhulingensis* Wang et al., 2006) 并不属于网形蛋类, 而应归入似蜂窝蛋类 (*Similifaveoolithus*), 将其修订为公主岭似蜂窝蛋 (修订种) (*Similifaveoolithus gongzhulingensis* (Wang et al. 2006) comb. nov.)。

关键词: 浙江天台盆地, 晚白垩世, 恐龙蛋, 网形蛋类

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