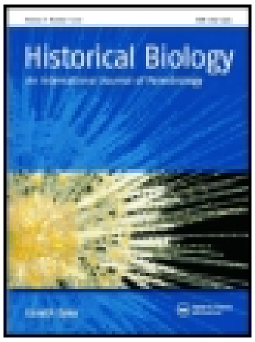

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ARTICLE

The first Similifaveoloolithidae (*Wormoolithus luxiensis* oogen. et oosp. nov.) from the Upper Cretaceous of Jiangxi Province, China

Xufeng Zhu[a,b,c], Kaiyong Fang[a,c,d], Qiang Wang[a,c], Li Deng[e], Yuchun Liu[e], Jun Wen[e], Xiaolin Wang[a,b,c] and Xuri Wang[f]

[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]University of Chinese Academy of Sciences, Beijing, China; [c]CAS Center for Excellence in Life and Paleoenvironment, Beijing, China; [d]School of Earth Sciences and Resources, China University of Geosciences, Beijing, China; [e]Pingxiang Museum, Pingxiang, China; [f]Key Laboratory of Paleontology and Stratigraphy of the Ministry of Natural Resources, Institute of Geology, Chinese Academy of Geological Sciences, Beijing, China

ABSTRACT

This study describes a new member of Similifaveoloolithidae from the Upper Cretaceous Zhoutian Formation of Jiangxi, China. The new ootaxon, *Wormoolithus luxiensis* oogen. et oosp. nov., is erected based on eggs collected from a partial clutch and represents the second oogenera of Similifaveoloolithidae. *Wormoolithus* shares some unique features with *Similifaveoloolithus* such as irregularly branched eggshell units, irregular cavities in the inner part of eggshell that are worm-like in tangential view and oblique pore canals in the outer part of the eggshell that show honeycomb-like structure in tangential view. And it is distinguished from the latter by longer polar axis and equatorial diameter and absence of compact layer. Although the clutch is not complete, the preserved parts show that the eggs are closely stacked in the nest. In addition, clay minerals that occur in pores and a high estimated water vapour conductance indicate a humid burial nest microenvironment.

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KEYWORDS
Similifaveoloolithidae; *Wormoolithus*; Jiangxi Province; Upper Cretaceous; Zhoutian Formation

Introduction

Similifaveoloolithidae is a rarely known oofamily whose representatives are reported only from several locations in China which consists of only one oogenera and three oospecies (Fang et al. 2003; Wang et al. 2006, 2011, 2013b; He et al. 2019). The first two ootaxa of this oofamily, *Similifaveoloolithus shuangtangensis* from Upper Cretaceous of Zhejiang and *S. gongzhulingensis* from Upper Cretaceous of Jilin were originally assigned to Dendroolithidae and Dictyoolithidae, respectively (Fang 2003; Wang et al. 2006) and were later reassigned to *Similifaveoloolithus* (Wang et al. 2011; Wang et al. 2013b), and the third ootaxon of this oofamily was excavated from Upper Cretaceous of Anhui. This study reports new materials of dinosaur egg recovered from Zhoutian Formation (K_2z) in Luxi county, Pingxiang, Jiangxi Province, China (Figure 1). Since the first discovery of dinosaur egg in 2002, over a hundred dinosaur eggs have been collected from this area, and two oospecies have been described, *Parafaveoloolithus pingxiangensis* (Zou et al. 2013) and *Undulatoolithus pengi* (Wang et al. 2013a). The new ootaxon represents the fourth member of Similifaveoloolithidae and the third erected oospecies from this area.

Geology

Pingxiang is located in the western part of Jiangxi province, and also in the west end of Ping-Le Depression, which is at the junction of Yangtze Plate and Southern Plate (Xu et al. 2011). The stratum bearing dinosaur egg is composed of red sandstone and silty mudstone, with gypsum layers in some place, which resembles Zhoutian Formation (K_2z). Zhoutian Formation is a set of inland lacustrine clastic rocks of the upper part of Ganzhou Group in Jiangxi Province, and it is sequenced above Maodian Formation (K_2m) and beneath Hekou Formation (K_2h) (Liu et al. 2003). It belongs to the early stage of Late Cretaceous.

Material and method

Material

At least eight pieces were recovered (Figure 2(a–g)) from a partial clutch which was found in a construction site (Figure 2(h)) and were separated before excavation. Among them, only one egg on PXMV-0021-1 is slightly deformed and has reliable data of equatorial diameter, and the others were deformed or broken by varies degrees, although the lengths of the polar axis of some specimens are still available (Table S1).

Eggshell characterisation

Histological section

Two eggshells from PXMV-0021-5 and one from PXMV-0021-7 were sampled for thin section preparation (Table S2). Each

CONTACT Qiang Wang wangqiang@ivpp.ac.cn
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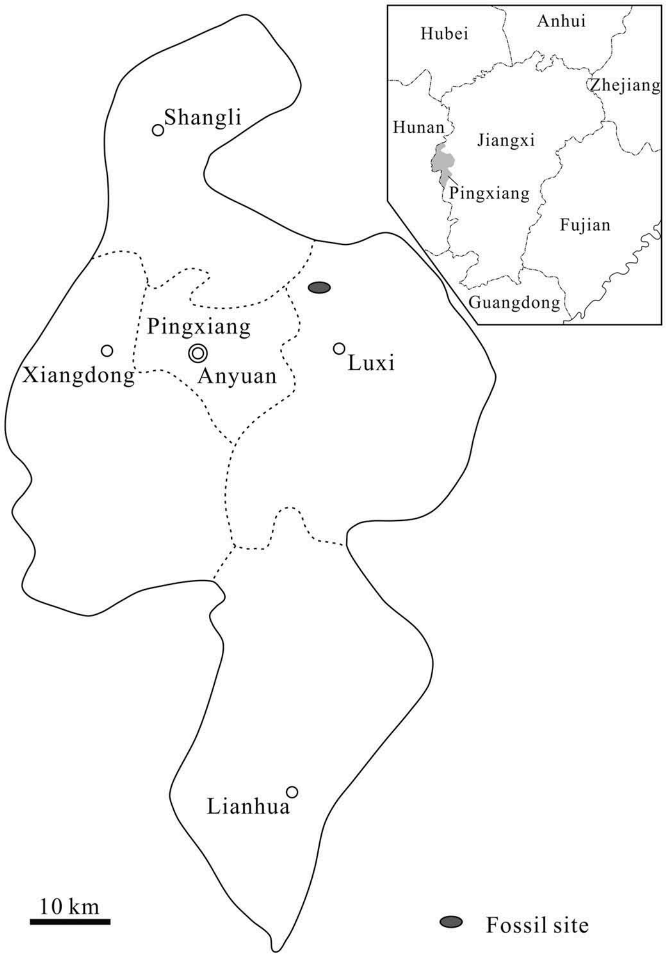

Figure 1. Location of the fossil site of PXMV-0021.

eggshell was separated into two parts and embedded in EXAKT Technovit 7200 resin for the preparation of both radial and tangential sections. Then, each block was cut with an EXAKT 300CP automatic microtome before being ground and polished to about 30 μm with an EXAKT 400CP variable speed grinder-polisher. These thin sections were examined and photographed under a ZEISS Axio imager A2m polarised light microscope.

Laser scanning confocal microscopy (LSCM)

Fluorescence microscopy has been used to detect organic structural remains in carbonate samples (Russo et al. 2006), but very few studies have used this method to check fossil eggshells (Jackson et al. 2010). Another method, cathodoluminescence microscopy, has been used to determine the extent of diagenetic modification in fossil eggshell (Grellet-Tinner et al. 2010). Fluorescence microscopy has the potential to partially replace it as different types of excitation will result in the emission of the same spectra (complete or incomplete) (Machel et al. 1991), and its relatively low energy makes it more suitable to detect organic structural remains.

LSCM is an optical imaging technique developed to overcome some limitations of traditional fluorescence microscopy. When using a traditional fluorescence microscope, the entire thin section is illuminated by the light source, and the resulting fluorescence is detected by a camera at the same time, which includes a high proportion of unfocused background signals. On the contrary, a confocal microscope uses a laser beam as point illumination and a pinhole in an optically conjugate plane in front of the detector to get rid of unfocused signals as only fluorescence signals that are very close to the focal plane can be detected, therefore producing a higher resolution of fluorescence images. Usually, in order to obtain an image with good quality under a regular fluorescence microscope, a thin section of a sample is needed, but a polished surface is sufficient for LSCM observation.

Stub of 111129-8 was polished for LSCM examination on the degree of diagenetic modification and possible organic remains. The scanning was performed with Olympus FV 3000 LSCM and FV 31S-SW software.

Scanning Electron Microscopy (SEM) and Back Scattered Electron-Energy Dispersive Spectrometer (BSE-EDS)

Three unlabelled eggshell from PXMV-0021–5 was sampled for SEM and BSE-EDS examination. The first one was broken radially and etched with 5% HAc for 3 min. The second one's fracture surface was polished before etched with 5% HAc for 3 min. After drying, they were coated with gold and observed under Zeiss EVO 25 SEM. The third eggshell was embedded in resin and cut radially. The exposed radial surface was polished and coated with carbon for BSE-EDS examination. BSE-EDS element mapping was obtained by Nova NanoSEM 450 field emission SEM with attached Oxford X-Max N80 EDS detector and Aztec software. Other BSE images were obtained with FEI Quanta FEG 650.

Water vapour conductance calculation

In this study, the method of estimating water vapour conductance mainly refers to Zhao et al. (2013), but some modifications have been made for the calculation of total pore area. The water vapour conductance ($G(H_2O)$) of the egg can be calculated with the following equation:

$$G(H_2O) = C \times D(H_2O) \times (R \times T)^{-1} \times A_p \times L_p^{-1}$$

where conversion constant (C) is 1.56 × 10^9(s mg)/(d mol) (Zhao et al. 2013), binary diffusivity between water vapour and air ($D(H_2O)$) is 0.292 cm^2/s at 303.15 K (Seymour 1979), gas constant (R) is 6.24 × 10^4(cm^3 mmHg)/(mol K), temperature (T) is 303.15 K. A_p is total pore area of an egg, and L_p is effective pore length. The pores of PXMV-0021 eggs are not of regular shape; therefore, in this study, A_p is calculated by the following formula:

$$A_p = A_s \times p,$$

where A_s is total surface area of an egg calculated following Hoyt's (1976, 1979) method and p (porosity) is a new parameter used here as the percentage of pore area under tangential view. Eggshell thickness is token for the value of L_p. In addition, egg mass (M) can be calculated with the regression equation given by Hoyt (1979), and the water vapour conductance of an avian

Figure 2. (Color online) Materials of PXMV-0021. (a1), (a2) PXMV-0021-1, two eggs (one nearly complete and was not deformed, the other broken) and four egg prints (indicated by black arrows, with remains of eggshells) preserved in rock; (a3) PXMV-0021-7, a broken piece of an egg from PXMV-0021-1, broken surfaces are marked as red dash lines; (b) PXMV-0021-2, a near-complete egg preserved in rock; (c) PXMV-0021-3, an egg preserving all eggshell but flattened; (d) PXMV-0021-4, a broken egg; (e) PXMV-0021-5, an broken egg; (f) PXMV-0021-6, an half complete and flattened egg, showing the complete side; (g) unlabelled specimen of rock preserving three egg prints, each attached to eggshells. Scale bar equals 10 cm. (h) PXMV-0021 in the field, eggs were stacked in partial clutch, and the egg marked with star refers to PXMV-0021-4.

egg ($G_b(H_2O)$) with equal mass can be estimated with the regression equation given by Ar and Rahn (1985).

State of preservation

The elemental mapping (Figure S1) shows that calcite cements do not only fill most space of the pores, but also cover the eggshell. However, the calcite cement does not contact with the eggshell unit directly, because original sediments, mainly clay minerals, invaded the pores in the first place, and act as barriers between the cements and the eggshell units.

Excited with 488-nm laser, an emission peak appears around 517 nm, and the detection wavelength was set between 500 and 600 nm. Boundary between the eggshell unit and pore is clear. Most position of eggshell units fluoresces dimly (Figure 3(a)) due to lattice defects, and bright fluorescence can only be seen along the edge of eggshell unit (Figure 3(c)). Surrounding the organic core (located at the inner most part of eggshell unit), there is a dark region (Figure 3(d)). Calcite cement in the pore or attached to the inner and outer surface of the eggshell does not fluoresce (Figure 3(b,d)). The calcite cement also occurs at the fracture (Figure 3(e)), which means the eggshell has already been fractured before the cementation of secondary calcite. Besides calcite, there are bright fluorescent mineral particles mixed with dim fluorescent clay minerals in the matrix.

Two causes are most likely to be responsible for the bright fluorescence along the edge of eggshell units, diagenetic alteration or enrichment of residual organic group. Diagenetic altered area tends to have a similar degree of fluorescence with calcite cement, as was observed by Grellet-Tinner and Makovicky (2006). Since calcite cement in the eggshell does not fluoresce, diagenetic alteration seems to be less possible.

Overall, the specimen did not undergo severe alteration, and calcite cements on outer surface protect the eggshell from severe mechanical and chemical erosions, making the microstructure observed reliable.

Systematic palaeontology

Oofamily **Similifaveoloolithidae** Wang et al. 2011

Emend diagnosis

Egg is spherical to ellipsoidal. Eggshell is composed of irregularly branched spherulitic eggshell units that are arranged in one layer. Pores originate from the inner surface as irregular cavities and is worm-like in tangential view; towards outer surface, the cavities gradually change into independent oblique pore canals, some of which often penetrates into the body of a single eggshell unit and shows honeycomb-like structure in tangential view. Adjacent eggshell units show the trend of fusion, which sometimes form a compact layer near the outer surface.

Oogenus ***Wormoolithus*** oogen. nov.

Etymology

The oogenus name refers to its worm-like structure in tangential view through the inner part of the eggshell, '*oolithus*', meaning 'stone egg' (Buckman 1859), ending for fossil oogenus.

Type oospecies

Wormoolithus luxiensis oogen. et oosp. nov.

Locality and horizon

As for the type oospecies.

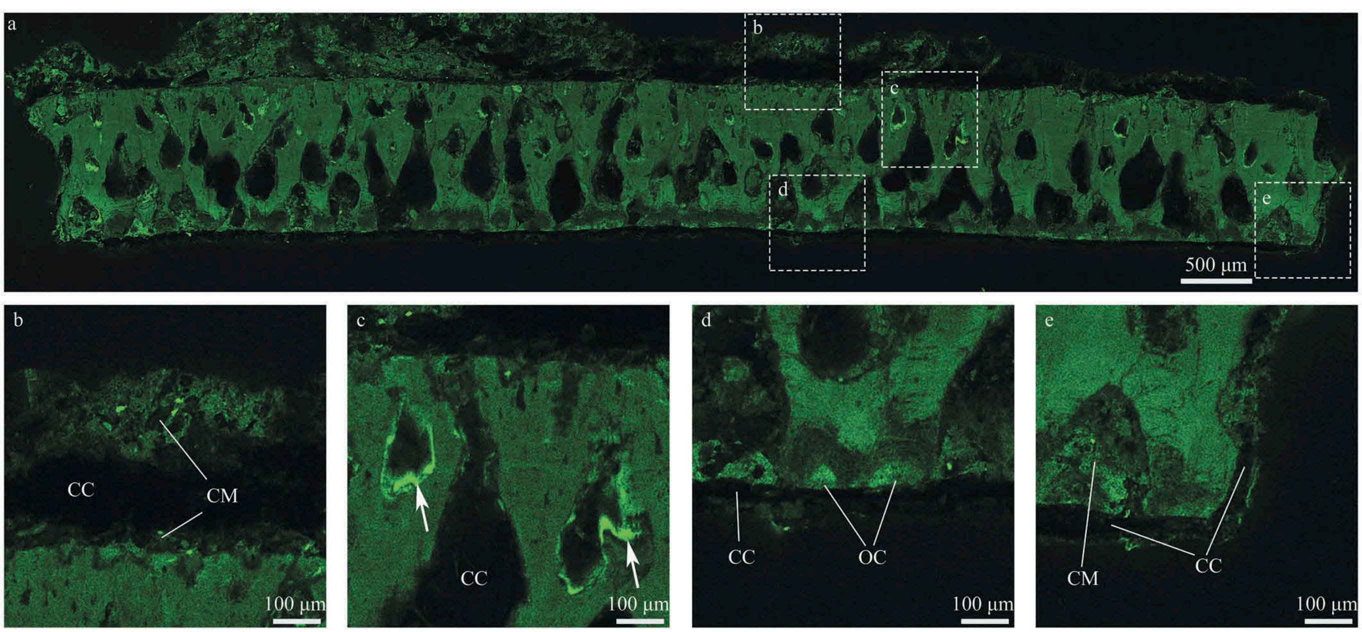

Figure 3. LSCM image of PXMV-0021-5. (a) In overall view, eggshell displays dim fluorescence; (b) calcite cement on outer surface does not fluorescence, while clay minerals fluorescence at different degrees; (c) pore filled with calcite cement does not fluorescence, and bright fluorescence along edges of the eggshell unit are marked with white arrows; (d) calcite cement on inner surface does not fluorescence, and the area around the organic core is darker; (e) some parts of the pore are filled with clay before calcite is cemented, and calcite cements also cover the fracture surface. CC, calcite cement; CM, clay minerals.

Diagnosis

As for the type oospecies.

Etymology

The oospecies name refers to the name of the county 'Luxi'.

Holotype

PXMV-0021, broken parts and single eggs from one partial clutch (Figure 2), housed in Pingxiang Museum.

Locality and horizon

About 1 km north from Xinxia Village, Luxi County, Pingxiang, Jiangxi Province, China; Zhoutian Formation (K_{2Z}), Upper Cretaceous.

Diagnosis

Similifaveoloolithidae eggs that can be distinguished from other known ootaxa of this oofamily by the following characteristics: eggs are closely stacked in clutch; egg is near spherical in shape (shape index is about 84); eggshell units do not form a well-developed compact layer, but with a trend of fusion.

Description

The eggs are probably unhatched as four better preserved eggs with relatively complete eggshell have no hatch window (Figure 2(a1,a2,a3,b,c)), and the other three eggs are broken irregularly with no signs of hatchling. Absence of absorption crater in radial sections also supports the judgement.

Clutch

Eggs are closely stacked in mudstone rather than distributed in a single layer (Figure 2(h)). Since the materials are not complete, it could only be representing a small part of a clutch.

Macro characteristics

Length of polar axis ranges 14.6–15.2 cm (14.9 cm in average), equatorial diameter is about 12.7 cm (Table S1), shape index (equatorial diameter/length of polar axis × 100) is about 84 (based on the egg on PXMV-0021-1 with reliable measurement). No ornamentation on outer surface.

General microstructure

Eggshell thickness ranges 0.95–1.15 mm (1.05 mm in average) and is composed of only one layer of eggshell units (Figure 4(a), Figure 5(a,b)), no secondary eggshell unit. Boundary between eggshell units is clear under polarised light (Figure 4(c)). Eggshell units are distributed unevenly.

Under SEM, the eggshell displays radial-tabular structure (Figure 5(c)). The radial pattern resembles the extinction pattern of radial sections under polarised light. And the tabular pattern is weak compared with the radial pattern and resembles the accretion lines under polarised light.

Eggshell unit

Spherulitic eggshell unit composed of crystals of calcite radiates from the organic core throughout the eggshell (Figure 4(c)), which shows cross extinction (Figure 4 (d2)). Under SEM, the space left by organic core can be seen at the bottom of eggshell units (Figure 5(d)). The organic core is surrounded by hollows left by membrane fibres that penetrate into the bottom of eggshell units (Figure S2). These diameters of these hollows range from one to several microns and are spatially distributed in a semi-spherical to spherical region that is about 180–200 μm in diameter. The hollow-rich area displays dark in LSCM (Figure 3(d)).

In radial view, eggshell unit usually branches irregularly and asymmetrically at the middle and outer parts of eggshell and often reunites soon after branching.

Pore system

Pores originate from the inner surface of the eggshell in the form of irregular cavities, which are worm-like in tangential view through the inner part of the eggshell (Figure 4(e)). Then, the cavities gradually change to more regular and isolated pore canals towards the outer surface. These pore canals do not grow sub-vertically towards outer surface; instead, they are slightly oblique. In the radial view, these pore canals are either tube-like when they are parallel to the radial section or oval if they crossed. Through the outer part of the eggshell, most pores show round or oval shape, and the proportion of worm-like shape pore decreases (Figure 4(f)); thus, the outer part of the eggshell shows honeycomb-like structure. The number of pore canals seen through the outer part of the eggshell are several times the number of the cavities below. In general, each cavity in the inner part of the eggshell seems to be linked to several (about two to four) pore canals above.

Relation between pore system and eggshell unit

With the description of eggshell unit and pore system, respectively, it can be revealed that the relation between them is very complicated, especially for the pore canals in the outer part of the eggshell. Since these pore canals are oblique, a pore canal can sometimes invade or even penetrate the body of a single eggshell unit, making it incomplete and branch in radial view. And it also explains the immediate reunion after branching. Pore canal can be seen within a single eggshell unit in tangential view of the outer part of the PXMV-0021-5 eggshell.

Accretion lines

Or growth lines. Near the organic core, the accretion lines grow in concentric arcs. As the eggshell unit grows, the accretion lines bend downwards where a pore canal penetrates the body of an eggshell unit (Figure 6(b)), which distinguishes it from false pore canal caused by a crack or

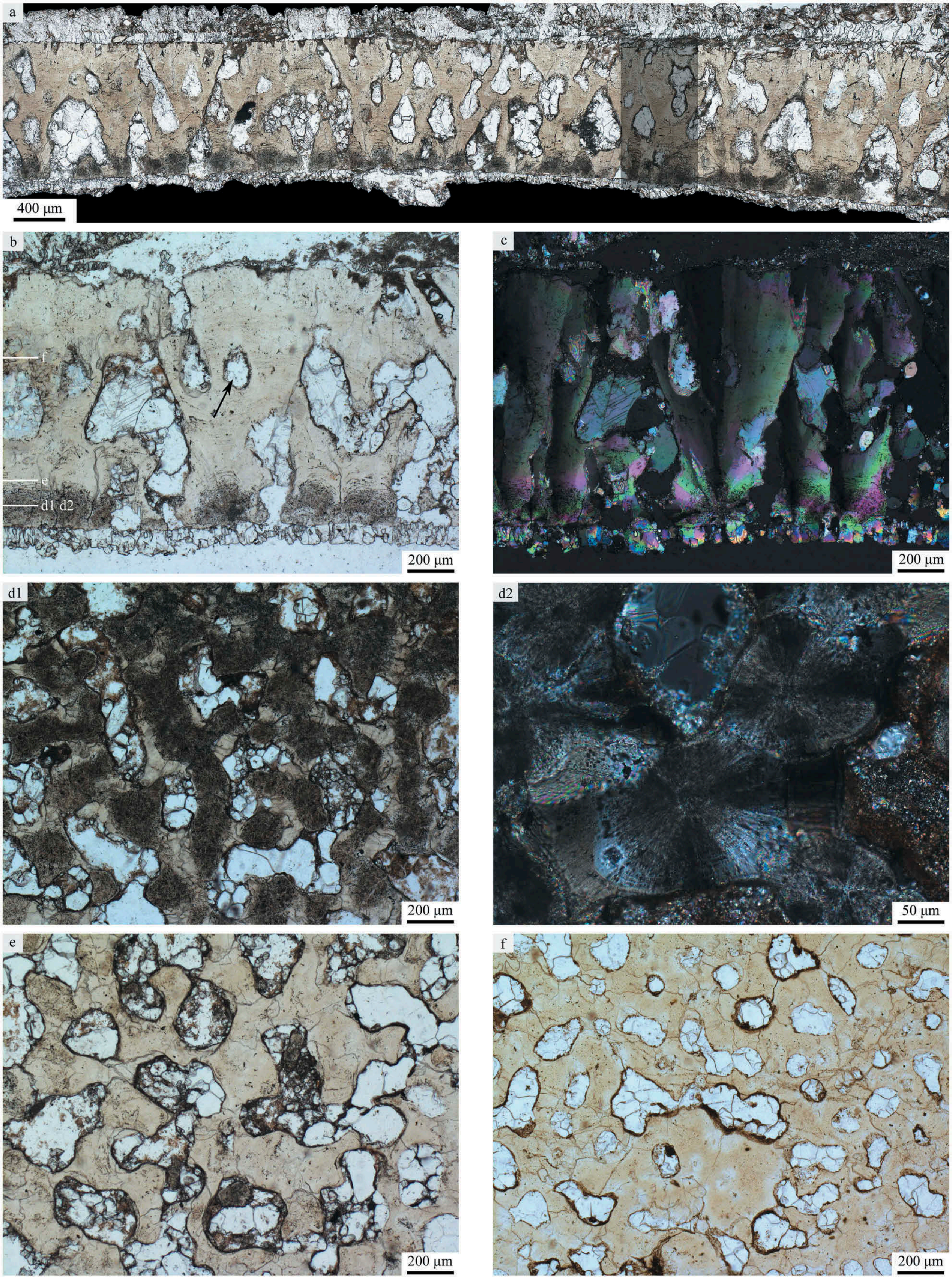

Figure 4. Microstructure of PXMV-0021-5. (a) Radial section under TL, shaded area refers to Figure 6(a); (b) radial section under TL, the black arrow in the middle marks a pore canal crossing the section; (c) radial section under PL; (d) tangential section near the inner surface, d1 under TL, d2 under PL; (e) tangential section through the inner part of the eggshell (46.73% porosity with more connected cavities) shows worm-like structure; (f) tangential section through the outer part of the eggshell (31.17% porosity with more independent pore canals) shows honeycomb-like structure. TL, transmitted light; PL, cross-polarised light.

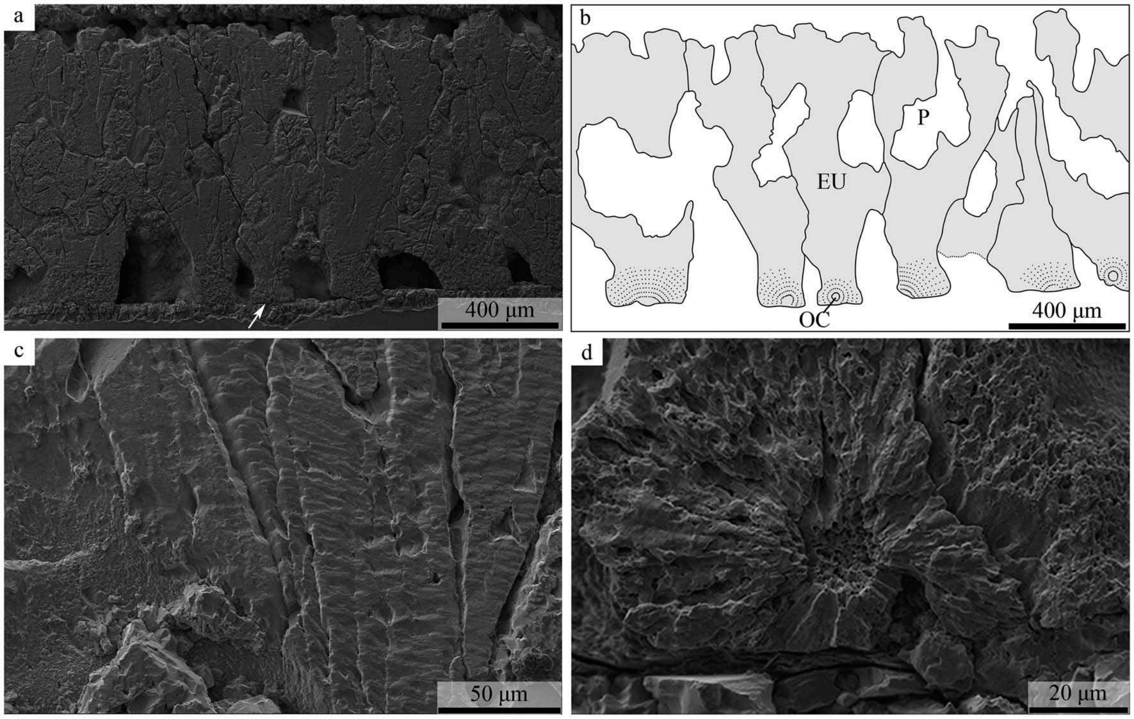

Figure 5. SEM images of PXMV-0021-5. (a) In radial view, boundaries are clear when etched with 5% HAC for 3 min, white arrow refers to (d); (b) line drawing of a, showing the arrangement of eggshell units (EU, as in grey) and the position of organic core (OC), pores (P); (c) middle part of the eggshell showing radial-tabular ultrastructure; (d) enlargement of the hollow left by organic core.

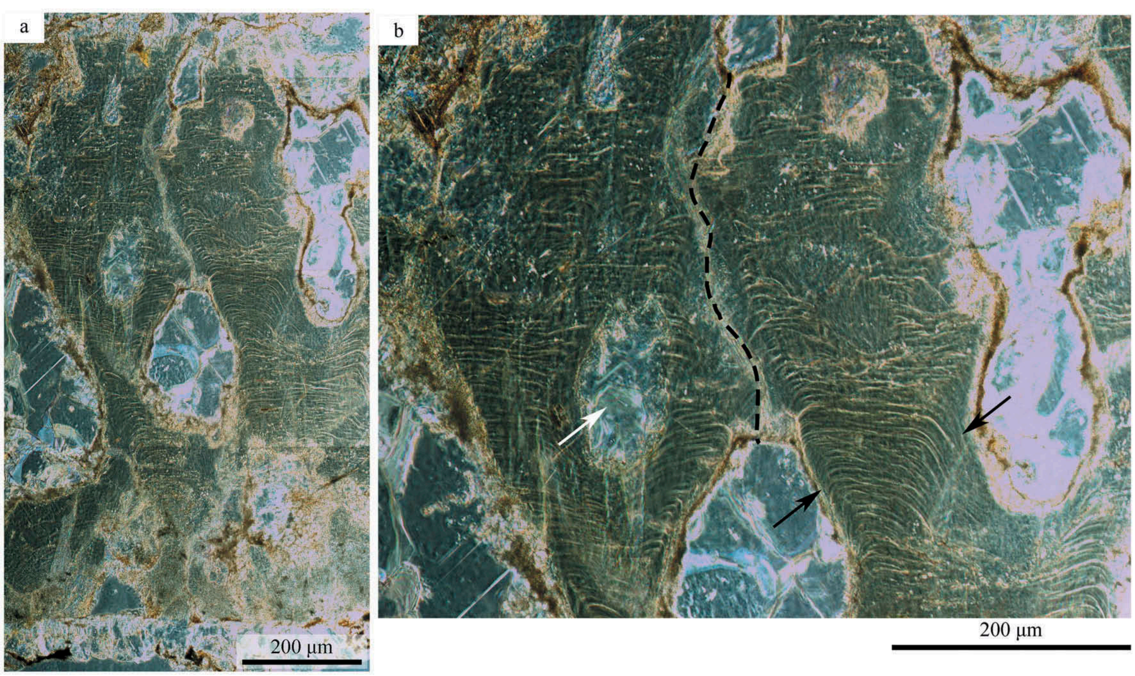

Figure 6. Accretion lines in radial section of PXMV-0021-5. (a) Differential interference contrast image of shaded area in Figure 4(a); (b) enlargement of the middle part of a, down turning curvature of accretion lines are indicated by black arrows, the dash line marks the boundary between two eggshell units, which is not crossed by accretion lines, the white arrow marks a pore canal crossing the section.

diagenetic process (Hirsch 1994; Choi et al. 2019). In addition, the accretion lines are usually restricted within each eggshell unit, and they also bend downwards and converge at its edge, where the calcite crystals of the eggshell unit only extend a little.

Water vapour conductance

The length of polar axis (L) and equatorial diameter (D) are 15.2 cm and 12.7 cm, respectively, both were measured from the best-preserved egg on PXMV-0021-5. The effective length of pore (L_p) is 1.05 mm. Porosity (p) is 31.7%. After substituting these values in the equations, water vapour conductance ($G(H_2O)$) was 40,200.8 mg/(d mmHg). It should be noted that the value obtained here is only a rough estimation because the shape of the pore canals is not of regular shape like that of avian or maniraptoran eggs, and there is so far no suitable method for calculating the water vapour conductivity of such eggshells (Tanaka et al. 2015). Considering that the total pore area was obtained through the tangential section with smaller porosity, and the whole eggshell thickness is used as the effective pore length, the value of water vapour conductance is actually a small estimate.

The estimated egg mass is 1343.48 g, and an avian egg with equal mass has a water vapour conductance ($G_b(H_2O)$) of 140.2 mg/(d mmHg). The ratio of $G(H_2O)$ to $G_b(H_2O)$ is about 287.

Comparison and discussion

Wormoolithus can be assigned to the oofamily Similifaveoloolithidae based on the following combined features unique to the group: pores originate from inner surface as irregular cavities and are worm-like in tangential view; nearing outer surface, the cavities gradually change into independent oblique canals, some of which often penetrate into the body of a single eggshell unit, and show honeycomb-like structure in tangential view. These features are shared with the other oogenus of this group, *Similifaveoloolithus*.

Similifaveoloolithus is the type oogenus of Similifaveoloolithidae, all three oospecies of this group have a compact layer, which is absent in PXMV-0021 eggs. Since the radial section of PXMV-0021 shows little erosion and well-preserved microstructure, the absence of a compact layer is reliable. The hollows left by organic fibre were not observed in *Similifaveoloolithus*, which is probably caused by poor preservation of specimens, and so it is not used for the diagnosis. PXMV-0021 eggs are larger than all *Similifaveoloolithus* in polar length and equatorial diameter. The thickness of PXMV-0021 eggshell is thinner than *Similifaveoloolithus shuangtangensis* and *S. gongzhulingensis*, but is thicker than *S. qiyunshanensis*. *S. shuangtangensis* and *S. gongzhulingensis* have a spherical egg shape (shape index ranges 90–100), while *S. qiyunshanensis* is ellipsoidal in shape (shape index ranges 50–80), and PXMV-0021 eggs have an in-between near-spherical egg shape.

Spherulitic eggshell unit is a primitive form of eggshell unit shared by many oofamilies, and branched spherulitic eggshell unit is a common feature in Dendroolithidae, Dictyoolithidae and Similifaveoloolithidae (Zhao and Li 1988; Zhao 1994; Fang et al. 1998; Zhao and Zhao 1998; Zhou et al. 1998; Wang et al. 2013b), and some faveoloolithids also possess this character (Kim et al. 2019). The phrase 'branched eggshell unit' is usually used to describe the shape of the eggshell units in radial section, and it is a major diagnostic character in Dendroolithidae, the eggshell units of which usually branch more symmetrically and do not reunite until reaching the compact layer. In addition, eggshell units of Dendroolithidae rarely contact with each other beneath the compact layer. In tangential view, eggshell units of Dendroolithidae originate at the inner surface in round or oval shape and change into circular or semi-closed rings towards compact layer (Zhao and Li 1988). Dictyoolithidae also has branched eggshell units, and they also branch more regularly (usually with two branches), and several layers of such eggshell unit stack, forming a unique reticular structure in radial view (Zhao 1994; Wang et al. 2013b), and a single eggshell unit is often V-shaped three-dimensionally. Faveoloolithids can sometimes have branched eggshell unit which is tree-shaped (Kim et al. 2019), and if a faveoloolithid's inner surface is eroded, the slender branches can hardly be determined whether they belong to the same eggshell unit or not.

Pore systems of Similifaveoloolithidae are composed of cavities and slightly oblique pore canals, while irregular cavities are dominant at the inner part of the eggshell and transform into pore canals towards the outer surface. These features can sometimes be confused with Dendroolithidae and faveoloolithid eggs. In tangential section, the differences of pore systems between these groups are distinct. Eggs of Dendroolithidae display no honeycomb-like structure, as cavities appear at all layers other than the compact layer, and sub-vertically extending pore canal starts at the branching point of the eggshell and ends at the compact layer, which is not well connected with those cavities and probably makes little contribution to gas conductance. Zhang et al. (2018) used honeycomb-like structure to describe a layer located beneath the compact layer of a dendroolithid, but the tangential section shows that it actually consists of both silt-shaped or worm-shaped cavities and pore canals inside eggshell units. Furthermore, in the compact layer of the Dendroolithidae, pores are relatively far from each other and can be well distinguished from the typical honeycomb-like structure of a faveoloolithid. On the contrary, honeycomb-like structure appears at both the inner and outer parts of faveoloolithid eggs, and only at the innermost level of the eggshell can it be observed with worm-like structure, where eggshell units are still loose and pores are still transversely connected (Zhao 1979; Zhang 2010; Kim et al. 2019). In Similifaveoloolithidae, the honeycomb-like structure appears only at the upper half part of the eggshell. The distribution and morphology of the honeycomb-like structure may be the key to the relation of these groups.

More importantly, pore systems of Similifaveoloolithidae differ from the other groups in how they interact with eggshell units. In faveoloolithid eggs, each pore canal is usually surrounded by several eggshell units (Zheng et al. 2018), and in some faveoloolithid like *Propagoolithus*, the eggshell units branch in a three-dimensional way like a tree (Kim et al. 2019), and the pore canals are actually walled up by multiple branches of these eggshell units, and it is also the case with other faveoloolithids (Zhang 2010; Zheng et al. 2018), except for that they are usually described as walled up with eggshell units. But as eggshell units of Similifaveoloolithidae can be penetrated by oblique pore canals, a pore canal can often be semi-encircled or sometimes totally encircled by a single eggshell unit in tangential view (Figure 4(f)), and causes its fast reunion in radial view. In Dendroolithidae, the pore canal within the body of a single eggshell unit extends sub-vertically, and the branches of an eggshell unit do not reunion until reaching compact layer. These findings make the understanding of the relationship between eggshell units and pore system crucial for the identification of these oofamilies and highlight the importance of the examination of tangential sections.

The compact layer is a structure found in all known members of Dendroolithidae, *Similifaveoloolithus* (Similifaveoloolithidae) and *Protodictyoolithus jiangi* (Dictyoolithidae). Among these groups, Dendroolithidae eggs have the most developed version of this structure which is significantly thick (up to 1/4 of the eggshell thickness) and distinct from the lower part of their eggshells as most eggshell units do not touch each other until this layer. *Protodictyoolithus jiangi* also has a distinct but relatively thinner compact layer, but the other oospecies of this oogenus, *Protodictyoolithus neixiangensis,* has only trends of fusion. *Similifaveoloolithus shuangtangensis* and *Similifaveoloolithus qiyunshanensis* both have a compact layer with similar relative thickness compared with Dendroolithidae eggs, and *Similifaveoloolithus gongzhulingensis* has a thinner one, but they all seem to be the simple results of consistent widening of the eggshell units, in which way the eggshell units began to touch each other before they reach compact layer. The function of the compact layer, however, is seldom discussed. Within these groups, only Dendroolithidae eggs have been reported to have a well-preserved clutch, and others have only single eggs or partially preserved clutch. Dendroolithidae eggs are usually arranged in the nest within a roughly horizontal level (Zhang et al. 2018). It seems eggs of Dendroolithidae were laid on flat ground and not buried by sands, and the compact layer prevents water loss as an adaption to a relative open, arid environment.

In extant birds, an egg laid by a non-burrowing bird could have a water vapour conductance twice as much as one laid by a burrowing bird (Birchard and Kilgore 1980). Water vapour conductance has been widely used by palaeontologists as an important index to study the microenvironment of the dinosaur nest (Seymour 1979; Mou 1992; Deeming 2006; Zhao et al. 2013). High ratio of $G(H_2O)$ to $G_b(H_2O)$ indicates that the nest microenvironment of *Wormoolithus luxiensis* should be very damp, as an arid environment would cause these eggs to dehydrate rapidly and fail to hatch. Considering that the eggs are closely stacked in the clutch, it is very likely that they were laid in a depression in the ground and were most likely buried by sand or soil just like the eggs of an extant sea turtle. Presence of clay mineral between eggshell unit and capping calcite cement also supports a burial incubation condition. Absence of a compact layer simply matches such condition since there is no need to prevent water loss. *Similifaveoloolithus qiyunshanensis* eggs were reported to have a clutch containing 10 eggs, which allows us to study its nest structure, and it was interpreted as laid in a buried nest because of their irregular arrangement and the highly porous nature of eggs (He et al. 2019). According to the photograph of the tangential section near the outer surface of *S. qiyunshanensis*, there are still numerous pores opening on its outer surface, which support the judgement of the nesting habit of its layer. Though possible, the nest structure of *Wormoolithus luxiensis* and *S. qiyunshanensis* cannot be simply extended to other Similifaveoloolithidae eggs, for the compact layers of *S. shuangtangensis* and *S. gongzhulingensis* are less porous and might significantly block the transportation of water vapour, which provides higher resistance to the arid environment.

Conclusions

The PXMV-0021 eggs are assigned to the new oogenus and oospecies, *Wormoolithus luxiensis*, and it is the fourth ootaxon of Similifaveoloolithidae. It expands the diversity and geographical distribution of this oofamily and represents its second oogenera.

The major diagnostic character of Similifaveoloolithidae against Dendroolithidae and Faveoloolithidae is discussed in this study. The way the eggshell units interact with its pore system is the major difference between these groups, which is important for identification.

Based on the arrangement of eggs in the partial clutch and the high estimated value of water vapour conductance, eggs of *Wormoolithus luxiensis* are stacked and buried in moist soil for incubation.

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Disclosure statement

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ORCID

Xufeng Zhu http://orcid.org/0000-0001-9731-6615

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