Eggs and clutches of the Spheroolithidae from the Cretaceous Tiantai basin, Zhejiang Province, China

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Numerous discoveries in the Tiantai basin of Zhejiang Province, China, enrich our understanding of the parataxonomy, paleobiology and taphonomic histories of fossil eggs from a diverse array of Cretaceous oofamilies. We describe the most abundant of these egg types catalogued in the Zhejiang Museum of Natural History, Spheroolithus cf. zhangtoucaoensis (oofamily Spheroolithidae). Scanning electron microscopy, here utilised for the first time on Spheroolithus eggs from Tiantai, and petrographic microscopy reveal 0.81–1.37-mm thick eggshell composed of a single structural layer of calcite with slightly flaring shell units, irregular pores, horizontal accretion lines and a sweeping extinction pattern under crossed polars. This contradicts previous reports of the presence of two structural layers in Tiantai Spheroolithus. Clutches consist of 2–13 eggs arranged in an irregular, single-layered pattern. As these eggs are among the oldest Asian examples of Spheroolithus currently known, they may shed light on the early evolution of this oogenus. This study establishes the definitive presence of the Spheroolithidae in the Tiantai basin, contra recent reports, and provides the framework for ongoing examination of egg diversity and taphonomy in the Tiantai basin.

**Keywords:** dinosaur; eggs; Spheroolithus; Cretaceous; Zhejiang Province; China

1. Introduction

Fossil eggs were first discovered in Cretaceous strata of Zhejiang Province in 1958 (Wang et al. 2000), and Mateer (1989) described the first eggs from the Tiantai basin (Figures 1 and 2). In 1990, highway construction, particularly that of the G15w (Shangsan) expressway north of Tiantai City, exposed additional Cretaceous bedrock in the 230 km² Tiantai basin (Jin et al. 2007), resulting in significant new discoveries. These and other previous studies reveal a diverse array of egg types including specimens referable to the Spheroolithidae, Dendroolithidae, Faveoololithidae, Ovaloololithidae, Prismatooololithidae, Elongatooololithidae and Testudooololithidae (Fang et al. 2000, 2003; Jin et al. 2007; Jackson et al. 2008; Wang et al. 2010).

The Zhejiang Museum of Natural History (ZMNH) in Hangzhou, China, houses hundreds, if not thousands, of fossil eggs from the Tiantai basin, providing an unprecedented sample. The majority of these eggs are spherical in shape and likely belong to the oogenus Spheroolithus Zhao, 1979 within the oofamily Spheroolithidae. Most of these eggs, however, come from construction sites and lack taphonomic data; furthermore, the vast majority of eggs in the museum collections remained unstudied until 2010. Beginning in that year, a grant from the National Science Foundation’s International Research Experience for Students (IRES) allowed nine students per year from Montana universities and colleges to conduct research on fossil eggs in the collections of the ZMNH. This ongoing research focuses on three primary aspects: (1) identification and description of the eggs and their microstructural characteristics, (2) assessment of the variation of eggs within different size categories and (3) understanding their diagenetic history.

The research presented here represents the first and essential step in accomplishing the goals of the IRES project, namely the identification and description of the fossil eggs comprising the first of the three size categories identified in the ZMNH collections. The IRES project research is important for several reasons. First, reports of new oospecies from China are often only brief descriptions that lack differential diagnoses and scanning electron imaging of the eggshell structure. Inadequate descriptions often lead to difficulty in comparing the eggs to existing oospecies from other localities, both within China and worldwide, and in assessing the validity of new ootaxa. Here, we examine Spheroolithus eggs from the Tiantai basin with scanning electron microscopy (SEM) for the first time. Second, future work by the IRES study will provide an assessment of the diversity of ootaxa within the Tiantai basin. Comparisons of egg diversity between Tiantai and other Chinese basins will help to examine previous assertions about the ‘primitive’ nature of the Tiantai egg...
fauna (Wang, Wang, Jiang, et al. 2012; He et al. 2013), based on Zhao’s (1993) hypotheses of evolutionary trends in eggshell structure. Finally, because many fossil eggs in China come from construction sites and lack precise geographic coordinates, knowledge of the diagenetic history of the eggs in the ZMNH collections may provide a better understanding of these and other specimens that lack sedimentologic and taphonomic context.

The dinosaur oogenus Spheroolithus, to which we assign the ZMNH sample, is known primarily from Upper Cretaceous rocks of North America, China, Mongolia and South Korea. It is the only oogenus with oospecies currently assigned to ornithischians (hadrosaurids) on the basis of associated embryonic remains (Horner and Makela 1979; Hirsch and Quinn 1990; Horner 1999). Thus, Spheroolithus eggs, clutches and nests form an important source of data on the reproductive strategies of a major dinosaur clade, Ornithischia, for which eggs otherwise likely remain unidentified. Possible exceptions include eggs assigned to neoceratopsians (Mikhailov 1994a; Balanoff et al. 2008). However, Protoceratopsidovum eggs (Mikhailov 1994a) have not yet been found with embryos in ovo, and Balanoff et al.’s (2008) identification of embryonic remains within a small, Late Cretaceous Mongolian egg as neoceratopian conflicts with the avian-like structure of the enclosing eggshell (Jackson and Varricchio 2010).

Macrostructural similarities between the Spheroolithidae and Chinese eggs referred to Dendroolithidae that contain therizinosaurid embryos (Manning et al. 1997; Kundrát et al. 2008) warrant caution in the assignment of Zhejiang Spheroolithus or any egg that lacks embryos in ovo to hadrosaurids. These similarities include slightly flaring shell units, dense horizontal accretion lines and irregular, unbranching pores (Zelenitsky 2004; Barta Personal observation 2012). In addition, the presence of Spheroolithus eggshell in the Upper Jurassic Morrison Formation of Utah (figure 5(C)–(E) in Zelenitsky et al. 2000), ‘prolatospherulitic’ eggshell in the Lower Cretaceous Cedar Mountain Formation of Utah (Zelenitsky et al. 2000) and cf. Spheroolithidae indet. eggshell in the Lower Cretaceous Blesa Formation of Spain (Canudo et al. 2010) all argue in favour of the existence of a broader phylogenetic distribution of spheroolithid eggshell structure outside Hadrosauridae, as definitive hadrosaurids are unknown from the Upper Jurassic and Lower Cretaceous (Prieto-Márquez 2010).

Previous research recognises two Spheroolithus oospecies, Spheroolithus zhangtoucaoensis Fang, Wang and Jiang, 2000 and S. jincunensis Fang, Lu, Jiang and Yang, 2003, from the Tiantai basin. These oospecies differ slightly in their macrostructural dimensions, eggshell thickness and in their stratigraphic position (see Section 6 for more details). Wang et al. (2011) recently synonymised these oospecies within the new oogenus and combination Mosaicoolithus zhangtoucaoensis, diagnosed primarily by the presence of secondary shell units (not previously documented in any Spheroolithus). Spheroolithus eggs and clutches from Tiantai basin are significant due to the temporal position of the Tiantai red beds as among the oldest egg-bearing Upper Cretaceous rocks in China (Wang, Wang, Jiang, et al. 2012; He et al. 2013). The only Chinese spheroolithid eggs as old as those of Tiantai basin are from the Gaogou Formation and its equivalents exposed in the numerous Cretaceous sedimentary basins of Henan Province (Liang et al. 2009). The Gaogou Formation and Tiantai basin occurrences of the Spheroolithidae additionally represent the oldest examples of this oofamily currently known from Asia. More detailed description and paratypical re-evaluation of previously described Tiantai Spheroolithus in this study may thus shed light on the early evolution of this oogenus, help to assess the validity of the reassignment of these eggs by Wang et al. (2011) and provide a basis for comparison with other members of the Spheroolithidae.

2. Materials and methods

We systematically photographed and measured with calipers 370 eggs, including those both isolated and contained within clutches, from Tiantai basin in the ZMNH collection. The IRES group also collected taphonomic data on egg fracturing and sedimentologic data on the matrix inside and outside of eggs, including observations of reduction haloes commonly surrounding eggshell, to aid in future interpretation of taphonomic histories of eggs and clutches. The 116 eggs for which at least two macrostructural measurements (corresponding to the ‘A’- and ‘B’-axes in Figure 3) were obtained clustered into three size classes, the most abundant of which contains 94 eggs that measure 7–11 cm along the ‘A’-axis (Figure 4). This size class contains 15 clutches of between 2 and 13 eggs each. We sampled eggshell from representatives of this size class for microstructural examination. A detailed discussion of the other two size classes is beyond the scope of this paper; however, the largest diameter size class is probably assignable to Dendroolithidae and Faveoloolithidae (Jin
Figure 2. Geologic map of Tiantai basin, modified from Jin (2009), showing fossil egg localities (those with a white dot have produced eggs included in the current study). Q, Quaternary; N, Neogene Shengxian Formation; K₂C, Upper Cretaceous Chichengshan Formation; K₂L², upper member of Upper Cretaceous Liangtoutang Formation; K₂L¹, lower member of Upper Cretaceous Liangtoutang Formation; K₁T², upper member of Cretaceous Tangshan Formation; K₁T¹, lower member of Cretaceous Tangshan Formation; KV, Cretaceous subhyolite porphyry. Fossil localities 25 and 26, Tiantai Distillery; 27, ‘south of No. 2 mountain’, along Shangsan Expressway; 28–35, ‘profile of Nos 2–8 mountain’, along Shangsan Expressway; 38, south of Tiansi Village; 39 and 40, north of Tiansi Village; 43, Chengguan Paper Mill. See Jin (2009) for names of the other egg localities not included in the current study. Egg localities that are mapped as seemingly occurring in Quaternary rocks are interpreted as actually reflecting occurrences in Cretaceous outcrops that are too small in areal extent to be portrayed at the scale of mapping. Such an interpretation is consistent with the maps of Tiantai basin in Fang et al. (2003) and He et al. (2013), which both show a lesser mapped extent of Quaternary rocks and a greater extent of Cretaceous strata in the areas in question.
2009) and the smallest to Prismatoolithidae and as-yet-unidentified eggs (Barta, personal observation, 2012).

Eggshell samples ZMNH M8517 B and M8517 D1 C were mounted on aluminium stubs, coated with gold and imaged at 15 kV with a JEOL 6100 SEM. Samples M8517 F, M8535 D2 and M8572 D1 E were prepared as standard (30 µm) radial thin sections and examined with a Nikon Eclipse LV100POL petrographic microscope. Thin sections and SEM stubs for the above specimens are housed in the Department of Earth Sciences, Montana State University. ImageJ software allowed measurement of eggshell microstructural attributes from thin section images, which were then averaged. Measurements of shell thickness obtained from hand samples were considered inaccurate because of sediment or diagenetic deposits that covered the eggs.

3. Locality and geologic setting

Fossil eggs in the Tiantai basin occur in the Albian to Turonian Liangtoutang and Chichengshan formations of the Tiantai Group. The majority of the examined eggs come from the upper member of the Liangtoutang Formation, with a small subset (specimens M8545 A–J) from the Chichengshan Formation. Initial radiometric dates place the Liangtoutang Formation at 105.9–103.2 Ma (Albian) (Wang et al. 2000), whereas radiometric dates remain unreported for the Chichengshan Formation. Despite this, Wang et al. (2000) consider the formation to be Late Cretaceous in age. More recently, He et al. (2013) confirm a Cenomanian–Turonian age (98–91 Ma) for the Laijia and Chichengshan formations, based on SIMS U–Pb zircon dating of five stratigraphic sections in western, central and eastern Tiantai basin (Figures 1 and 2 in He et al. 2013). The Laijia Formation is equivalent to the lower Liangtoutang Formation, and the Chichengshan Formation as referenced by He et al. (2013) is equivalent to

Figure 3. Dimensions measured with calipers for 116 eggs in the ZMNH collections. A, longest ‘A-axis’; B, intermediate ‘B-axis’ (perpendicular to the A-axis); C, short ‘C-axis’ (perpendicular to the A- and B-axes).

Figure 4. Graph of A-axis versus B-axis length in centimetres (see Figure 3) measured for 116 eggs in the ZMNH collection. Diamonds represent the medium size class of 94 eggs assigned to S. cf. zhangtoucaoensis in this study. Xs represent the largest size class, probably referable to Dendroolithidae and Faveoloolithidae (Jin 2009). Plus signs represent the smallest size class, probably referable to partial eggs of Prismatoolithidae and other unidentified ootaxa. Triangles represent outliers. See online supplementary information for a full list of museum numbers, measurements and locality names for all specimens.
the upper Liangtoutang and Chichengshan formations of Wang et al. (2000) (Fang et al. 2003). The Liangtoutang Formation primarily consists of poorly sorted red siltstones and fine-grained sandstones and contains abundant root traces and burrows in the lower part of the formation. The Liangtoutang lithology may reflect shallow lacustrine (Wang et al. 2000) or lakeshore deposition with periods of subaerial exposure as evidenced by terrestrial arthropod traces (Martin and Varricchio 2011). The Chichengshan Formation consists of purple to red-grey mudflow conglomerates intercalated with argillaceous siltstone (Wang et al. 2000; Jackson et al. 2008). Mateer (1989) interprets the Chichengshan Formation (then called the Laijia B Formation) as alluvial fan deposits.

4. Systematic paleontology

4.1 Family SPHEROOLITHIDAE Zhao, 1979

Included oogenera

Spheroolithus Zhao, 1979; Paraspheroolithus Zhao, 1979; Shixingoolithus Zhao, Ye, Li, Zhao and Yan, 1991 [see Wang, Wang, Zhao, et al. (2012) for referral of Shixingoolithus to Stalicoolithidae]

Type oospecies

Spheroolithus (= Oolithes) irenensis (Zhao and Jiang 1974) emend. Mikhailov 1994b

Included oospecies

Spheroolithus (= Oolithes) irenensis Zhao and Jiang, 1974 (originally Oolithes spheroides Young, 1954); S. (= Oolithes) megadermus Young, 1959; S. (= Oolithes) chiangchiungtingensis Zhao and Jiang, 1974; S. maiasaur-oides Mikhailov, 1994b; S. tenuicorticus Mikhailov, 1994b; S. albertensis Zelenitsky and Hills, 1997; S. zhangtoucaoensis Fang, Wang and Jiang, 2000; S. jincunensis Fang, Lu, Jiang and Yang, 2003 [see Wang et al. (2011) for reassignment of S. zhangtoucaoensis and S. jincunensis to Mosaicoolithus zhangtoucaoensis]; S. choteauensis Jackson and Varricchio, 2010

Oospecies Spheroolithus cf. zhangtoucaoensis Fang, Wang and Jiang, 2000

4.1 Diagnosis of Spheroolithidae

Prolatospherulitic shell units; 'prolatocanaliculate pore system; smooth, rough and sculptured surface (sagenotuberculate ornamentation); subspherical and ellipsoid eggs; “thick” (>2 mm) and medium thick (>1 mm) eggshells’ (Mikhailov 1991).
Table 1. List of occurrences of the Spheroolithidae.

| Formation(s) or Group                        | Age                        | Province or county | Country   | Reference                                      |
|---------------------------------------------|----------------------------|--------------------|-----------|------------------------------------------------|
| Kakauaut Formation                          | Maastrichtian              | Not stated         | Russia    | Godefroit et al. (2009)                        |
| Nemegt Formation                            | ?late Campanian or early Maastrichtian | N/A                | Mongolia  | Mikhailov (1994b)                             |
| Barun Goyot Formation                       | ?middle Campanian          | N/A                | Mongolia  | Sabath (1991) and Mikhailov (1994b)           |
| Djadokhta Formation                         | middle-late Campanian      | N/A                | Mongolia  | Mikhailov (1994b)                             |
| North Hom Formation                         | Maastrichtian              | Utah               | USA       | Bray (1999)                                    |
| Two Medicine Formation                      | late Campanian             | Montana            | USA       | Hirsch and Quinn (1990)                       |
| Oldman Formation                            | late Campanian             | Alberta            | Canada    | Zelenitsky and Hills (1997)                   |
| Lower and middle Wangshi Group              | Campanian-middle Maastrichtian | Shandong           | China     | Young (1954) and Zhao (1979)                  |
| Dongyuan Formation                          | Upper Cretaceous           | Guangdong          | China     | Fang et al. (2005)                            |
| Iren Dabasu Formation                       | Upper Cretaceous           | Inner Mongolia     | China     | Zhao and Jiang (1974)                         |
| Subashen Formation                          | Upper Cretaceous           | Xinjiang Autonomous Region | China | Zhao (1979)                                    |
| Gaogou, Majiacun, and Siguo formations and equivalents | Upper Cretaceous | Henan              | China     | Liang et al. (2009)                           |
| Liangtouyang and Chichengshan formations and equivalents | Upper Cretaceous | Zhejiang           | China     | Fang et al. (2000), Jin (2009), Yu et al. (2010) and Yu et al. (2012) |
| Seonso Conglomerate                         | Upper Cretaceous           | Chullanan-do       | South Korea | Huh and Zelenitsky (2002)                     |
| Goseong Formation                          | Campanian to Maastrichtian | Goseong County     | South Korea | Paik et al. (2012)                            |
| ?Lameta Formation                           | Upper Cretaceous           | Maharashtra        | India     | Mohabey (1996)                                |
| Not stated                                  | Upper Cretaceous           | Rio Negro          | Argentina | Maneta de Bianco and Köhler (2003)            |
| Cerro del Pueblo Formation                  | Upper Cretaceous           | Coahuila           | Mexico    | Aguillon-Martinez et al. (2004)               |
| ?Cedar Mountain Formation                   | Lower Cretaceous           | Utah               | USA       | Zelenitsky et al. (2000)                      |
| Blesa Formation                             | Lower Cretaceous           | Teruel             | Spain     | Canudo et al. (2010)                         |
| Morrison Formation                          | Upper Jurassic             | Utah               | USA       | Zelenitsky et al. (2000)                      |

Note: Occurrences listed only as the 'prolatospherulitic morphotype' [Cedar Mountain Formation, Zelenitsky et al. (2000)] and where the spheroolithid identity of the eggshell is considered uncertain (Mohabey 1996) are marked with a '?' before the formation name.
with caution, as the incorporation of portions of staggered nucleation sites within the same plane of sectioning may lead to inaccurate measurements of the true spacing. Although measuring nucleation site spacing on the inner eggshell surface with SEM is ideal, we were unable to obtain such measurements, as diagenetic calcite overgrowth obscures all nucleation sites otherwise visible in radial view. The shell units display a radiating spherulite structure above the nucleation sites (Figure 6(B),(D),(E)). Pores are sparse and often difficult to identify in radial section; however, they appear irregular in shape and distribution and are more prevalent in the inner half of the eggshell (Figure 6(A),(B)). The inner portion of the eggshell displays extensive dissolution and the slightly undulating outer eggshell surface lacks ornamentation, possibly due to recent weathering. Extensive dissolution and possible recrystallisation of eggshell calcite characterise M8572 D1 E, likely contributing to its thinness. Eggshell thickness prior to alteration was probably closer to the values for M8517 F and M8535 D2, 1.37 and 1.16 mm, respectively.

### 6. Discussion

Microstructural features (Figure 6) including the presence of a single structural layer comprised of slightly flaring shell units, irregular pores and horizontal accretion lines, and a sweeping extinction pattern under crossed polars allows assignment of the eggshell to the oofamily Spheroolithidae. Shell thicknesses for all thin-sectioned specimens, including the extensively altered M8572 D1 E, fall within the observed shell thickness range for the Spheroolithidae (Mikhailov

| Specimen   | Eggshell thickness (mm) | Shell unit width (mm) | Distance between nucleation sites (mm) |
|------------|-------------------------|-----------------------|---------------------------------------|
| M8517 F    | Mean (of 40 measurements) = 1.37 | Mean (of 29 measurements) = 0.36 | Mean (of 3 measurements) = 0.24 |
|            | SD = 0.20               | SD = 0.08             | SD = 0.06                             |
| M8535 D2   | Mean (of 34 measurements) = 1.16 | Mean (of 19 measurements) = 0.31 | Not observed                          |
|            | SD = 0.24               | SD = 0.08             |                                       |
| M8572 D1 E | Mean (of 78 measurements) = 0.81 | Mean (of 13 measurements) = 0.26 | Not observed                          |
|            | SD = 0.19               | SD = 0.06             |                                       |
Differences in shell thickness among specimens may result from diagenetic alteration, intraspecific or interspecific variation, or differences in measurement techniques among investigators. The decrease, assuming an originally near spherical shape, in short axis dimensions of the eggs (~4.7 cm) likely results from lithostatic compaction. Partial clutches display an irregular, random or close-packed, single-layered arrangement of eggs similar to other clutches assigned to the Spheroolithidae; however, more complete clutches are necessary to assess this similarity.

Of the two oogenera (Spheroolithus, Paraspherooolithus) currently included within Spheroolithidae, some authors (Mikhailov 1997; Carpenter 1999) consider the holotype species of Paraspherooolithus (P. irenensis) synonymous with Spheroolithus [for a contrasting view see Zhao and Zhao (1998)]. The differences between the oogenera noted by Zhao and Zhao (1998) are attributable to variation in the width of pores separating the spherulites at the base of the shell units; however, similar ranges of variation in pore width are also present within individual eggs of each oogenus (Zhao and Jiang 1974, Plates I and II). Hence, we concur with the reasoning of Mikhailov (1997) and consider Paraspherooolithus a junior synonym of Spheroolithus. As our description of the ZMNH sample agrees with the emended diagnoses of Spheroolithus provided by Mikhailov (1994b, 1997), we assign the microstructurally examined specimens in this study to Spheroolithus. We tentatively extend this assignment to the additional eggs for which we made macrostructural measurements; however, confirmation requires further microstructural analysis.

Table 3 compares the holotypes of previously named Spheroolithus oospecies with the ZMNH sample and forms the basis for the following discussion. The Tiantai basin eggs reported here exhibit thinner eggshell than those of S. irenensis, S. megadermus and S. chiangchiungtingensis. If their lack of ornamentation represents a biological feature (an interpretation supported by the consistent lack of any obvious ornamentation among examined eggs from all localities and formations), then the ZMNH specimens differ from S. albertensis, S. choteauensis and S. maiasauroides, which all possess ornamentation. The ZMNH specimens further exhibit smaller dimensions and generally greater eggshell thickness than those of S. choteauensis. The Tiantai eggs and S. tenuicorticus differ mainly in their ratios of egg length to width (1.2 for the average dimensions of the Tiantai eggs versus ?1.3–1.4 for S. tenuicorticus). However, Mikhailov (1994b) noted that observations of the shape of S. tenuicorticus eggs were ‘made in the field and may not be confirmed’. Despite sharing an unornamented to weakly ornamented surface and similar ranges of eggshell thickness, we feel that given the possible macrostructural difference outlined above, as well as the great temporal and geographic separation of the ZMNH sample and S. tenuicorticus, assignment of the Zhejiang eggs to S. tenuicorticus is not parsimonious.

Previously identified spheroolithid oospecies from Tiantai basin include ‘Paraspherooolithus’ cf. shizuiwaensis (Fang et al. 2000), ‘P.’ irenensis (Jin 2009), ‘P.’
Table 3. Comparison of holotypes of previously named *Spheroolithus* oospecies with the ZMNH sample (this study).

| Ootaxon                                      | Reference                  | Holotype     | Province, country | Group or Formation(s) | Age                        | Egg size (cm) | Eggshell thickness (mm) | Surface ornamentation |
|----------------------------------------------|----------------------------|--------------|-------------------|------------------------|----------------------------|---------------|------------------------|----------------------|
| *S. (‘Paraspheroolithus’) irenensis*         | Zhao and Jiang (1974)      | IVPP V733?   | Shandong, China   | Wangshi Group          | Campanian to middle Maastrichtian | 9.0 × 7.5     | 1.5–2.2                | None                 |
| *S. megadermus*                              | Young (1959)               | IVPP V2337   | Shandong, China   | Wangshi Group          | Campanian to middle Maastrichtian | Not reported   | 5.5–5.8               | Not reported          |
| *S. chiangchiungtingensis*                   | Zhao and Jiang (1974)      | IVPP V730, V731 | Shandong, China | Wangshi Group          | Campanian to middle Maastrichtian | 8.1 × 7.7     | 2.2–2.85               | None?                |
| *S. maiasauroides*                           | Mikhailov (1994b)          | PIN 4228-2   | Mongolia          | Djadokhta Formation   | Middle to late Campanian     | 9.0 × 7.0     | 1.0–1.6                | Fine sagenotuberculate |
| *S. tenuicorticus*                           | Mikhailov (1994b)          | PIN 4476-4   | Mongolia          | Barun Goyot Formation  | Middle to late Campanian    | Not reported   | 0.8–1.8                | Weak impression of sagenotuberculate ornamentation |
| *S. albertensis*                             | Zelenitsky and Hills (1997)| RTMP 94.157.63 | Alberta, Canada  | Oldman Formation      | Late Campanian              | Not reported   | 0.98–1.22              | Sagenotuberculate     |
| *S. zhangtoucaoensis*                        | Fang et al. (2000)         | Slice No. Zhe-6-1 | Zhejiang, China | Chichengshan Formation | Turonian?                   | 9.0 × 4.0     | 1.0                    | Rough with indistinct tubercular ornament |
| *S. jincunensis*                             | Fang et al. (2003)         | Thin slice No. T-8? | Zhejiang, China | Laijia Formation      | Cenomanian?                 | 9.7 (length), 8.5 (width) | 1.3–1.5?              | Not reported          |
| *S. choteauensis*                            | Jackson and Varricchio (2010)| ES 113 and others | Zhejiang, China | Two Medicine Formation | Campanian                   | 11.0 × 9.5    | 0.66–0.94              | Ramotuberculate       |
| *S. cf. zhangtoucaoensis*                    | This study                 | N/A          | Zhejiang, China   | Liangtoutang and Chichengshan formations | Albion to Turonian | 9.0 × 7.8 × 4.7 | 0.8–1.4               | None?                |

Note: *Institutional abbreviations* – ES, Department of Earth Sciences, Montana State University, Bozeman, Montana; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; PIN, Paleontological Institute, Moscow, Russia; RTMP, Royal Tyrrell Museum of Paleontology, Drumheller, Alberta.
yangchengensis (Jin 2009), S. zhangtoucaoensis (Fang et al. 2000) and S. jincunensis (Fang et al. 2003). Eggs from Tiantai basin referred to ‘P’ cf. shizuiwanensis by Fang et al. (2000) were recently reassigned to the new oofamily Stalicoolithidae by Wang, Wang, Zhao, et al. (2012). Eggs of ‘P’ irensensis described by Jin (2009) from the Tiantai basin possess thicker eggshell than those of S. zhangtoucaoensis, S. jincunensis and the eggs in this study. The eggs referred by Jin (2009) to ‘P’ yangchengensis share similar macrostructural dimensions, shell thickness and microstructural attributes with S. zhangtoucaoensis, S. jincunensis and the eggs in this study, suggesting possible synonymy of the three oospecies and the ZMNH sample. However, due to the lack of detailed descriptions by previous authors and our lack of personal observations of the holotypes of ‘Paraspheroolithus’ oospecies, we consider a full review of the status of all oospecies previously assigned to ‘Paraspheroolithus’ as beyond the scope of this study.

Recently, Wang et al. (2011) synonymise the two Tiantai basin Spheroolithus oospecies, S. zhangtoucaoensis and S. jincunensis, and reassign them to the new oogenus and combination M. zhangtoucaoensis. However, they fail to utilise SEM to provide detailed microstructural comparisons to the holotype or other specimens of Spheroolithus. Thus, the validity of this claim remains difficult to evaluate. Furthermore, the features used by Wang et al. (2011) to unite these two Spheroolithus oospecies within Mosaicoolithus are either common to all Spheroolithus (spherical eggs, pore canals irregular in shape) or occur only near the margins of pore spaces and thus are potentially artefacts of dissolution [‘inlaid’ and secondary shell units that fill pore canals, and that based on Wang et al. (2011) appear to be shell units arising from nucleation sites located partway through the thickness of the eggshell]. The ZMNH specimens described in this study lack ‘inlaid’ and secondary shell units and thus are definitely not assignable to Mosaicoolithus. Previous investigation with both light microscopy and SEM of purported secondary shell units in Dictyoolithus hongpoensis reveals that such features are not present in that oospecies and are poorly documented in other Dictyoolithus (Jin et al. 2010). In light of these findings, SEM and cathodoluminescence should be utilised to determine whether the purported diagnostic secondary shell units of Mosaicoolithus are a biologic or diagenetic feature. In addition, in the originally published photomicrographs of radial sections of S. zhangtoucaoensis (Fang et al. 2000, Plate I, Figures 16 and 17) and S. jincunensis (Fang et al. 2003, Plate II, Figure 1), the eggshell does not clearly exhibit ‘inlaid’ or secondary shell units, though this may be due to the low resolution of the images. Furthermore, the eggshell thickness range (1.50–1.55 mm) given as diagnostic of M. zhangtoucaoensis by Wang et al. (2011) does not agree with the eggshell thickness of 1 mm stated in the diagnosis of S. zhangtoucaoensis by Fang et al. (2000). Due to the plesiomorphic or questionable nature of the diagnostic features attributed to Mosaicoolithus and their questionable presence in the holotype specimen of this ootaxon, we feel that the names S. zhangtoucaoensis and S. jincunensis should remain in use until a more detailed study of specimens referred to Mosaicoolithus can be made.

The range of macrostructural dimensions of the ZMNH sample encompasses the dimensions previously described by Fang et al. (2003) for S. jincunensis. The shell thickness ranges for the ZMNH sample and S. jincunensis also partially overlap, though the upper limit to the range is higher for S. jincunensis. Only the stratigraphic position of the ZMNH eggs and S. jincunensis differs, as the ZMNH sample comes from the upper Liangtoutang and Chichengshan formations and S. jincunensis comes from the Laijia Formation, which is equivalent to the lower Liangtoutang (Fang et al. 2003).

The macrostructural dimensions, shell thickness and stratigraphic range of the ZMNH sample are all consistent with those of S. zhangtoucaoensis. The smooth surface of the eggshell in the ZMNH sample differs from the ‘rough’ eggshell surface with ‘indistinct tubercular ornament’ (Fang et al. 2000) previously described for S. zhangtoucaoensis, though this may be a taphonomic difference; furthermore, the surface texture of the eggs in the ZMNH sample appears similar to that of the S. zhangtoucaoensis egg described by Fang et al. (2003, Plate II, Figure 6). Fang et al. (2000, 2003) did not describe any clutches of S. zhangtoucaoensis or S. jincunensis; therefore, comparison with clutches in the ZMNH sample is not possible.

The overlap in macrostructural features among the ZMNH specimens, S. zhangtoucaoensis and S. jincunensis, argues in favour of the possible synonymy of the two oospecies, with S. zhangtoucaoensis retaining priority. However, brief microstructural descriptions, low-resolution photomicrographs and the lack of SEM images in the publications that diagnose these oospecies prohibit comparisons that could allow for a formal statement of synonymy. Until this issue and the validity of Mosaicoolithus are resolved, we choose to provisionally assign the ZMNH sample to S. cf. zhangtoucaoensis. Should the combination S. zhangtoucaoensis be upheld as valid upon further study, we recommend emendation of the original diagnosis of Fang et al. (2000) to remove references to the presence of mammillary and prismatic layers in eggshell of this oospecies. These layers are not present in the ZMNH sample or any other spheroolithid eggshell, which consists of a single structural layer of calcite (Mikhailov 1991). The above ootaxonomic issues emphasise that as the characters (shell thickness and surface ornamentation) most commonly used to diagnose Spheroolithus oospecies are susceptible to diagenetic and other taphonomic alteration, caution is warranted in utilising these characters as the sole diagnostic features for an oospecies.

The assignment of the eggs in this study to S. cf. zhangtoucaoensis establishes the definitive presence of the
Spheroolithidae in the Tiantai basin, as asserted by Fang et al. (2000, 2003), Jin (2009) and contra He et al. (2013). Thus, the purported absence of this oofamily (He et al. 2013) should not be used as evidence of the ‘primitive’ nature of the Tiantai egg fauna, if using Zhao’s (1993) hypothesised phylogeny of dinosaur eggs.

This study provides a detailed re-evaluation, utilising SEM for the first time, of Spheroolithus eggs from the Tiantai basin, Zhejiang Province, China. The eggs come from the Upper Cretaceous Liangtou tang and Chichengshan formations and are provisionally referable to S. cf. zhangtoucaoensis within the Spheroolithidae. This study clarifies previous descriptions of Spheroolithus from the Tiantai basin, specifically demonstrating that the eggshell consists of a single structural layer of calcite, as in other spheroolithids, contra previous diagnoses (Fang et al. 2000). It provides an initial attempt to test the potential synonymy of S. zhangtoucaoensis and S. jincunensis and the validity of Mosaicoolithus, though further work on these issues is needed. As these eggs represent some of the earliest known Spheroolithus in Asia, knowledge of their macrostructural and microstructural attributes may prove important to identifying any trends in the evolution of this oogenus.

In addition, this description forms the framework for future work on potential diagenetic alteration of eggs, including eggshell thinning and crushing that characterises many eggs in the ZMNH, and future paleoological studies of the diversity of fossil eggs in Zhejiang Province.

Supplementary information
A supplementary information file with a full list of museum numbers, measurements and locality names for all specimens can be accessed online.

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