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SHORT COMMUNICATION

Dinosaur Eggs Associated with Crustacean Trace Fossils from the Upper Cretaceous of Jiangxi, China: Evidence for Foraging Behavior?

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ABSTRACT

We report the discovery of concentrated invertebrate inchnofossils in close association with a dinosaur nest from the Hekou Formation in Jiangxi Province, China. The seven dinosaurian eggs reported clearly belong to the Elongatoolithidae and burrow traces were most likely made by small crustaceans. This association prompts the question as to whether invertebrate activity had relations with the buried eggs. This may be just an occasional case or the eggs may have organically increased the content of organic matter in soil which attracted the crustaceans.

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Introduction

Dinosaur bones are frequently found with associated trace fossils, including those of invertebrates (Xing et al., 2013; Xing et al., 2016; Xing et al., 2017; Dal Sasso et al., 2018). These ichnofossil associations frequently offer novel paleoenvironmental clues (Xing et al., 2013; Xing et al., 2016). These associations also generally fall into two broad categories. One form is direct bone damage (Xing et al., 2013; Xing et al., 2016). Insects are one of the most reported invertebrate bone trace makers and may create grooves, striae, pits, bores, tubes, chambers, furrows or channels on dinosaur bones (Xing et al., 2013; Pirrone et al., 2014). Various marine invertebrates leave similar traces (Dal Sasso et al., 2018). In China, Xing et al. (2016) reported a Middle Jurassic bone boring ichnofossil case, among the oldest evidence of bone boring by terrestrial invertebrates.

The second form is the preservation of bones and traces in passive association without obvious erosion or damage to the former (Xing et al., 2013; Xing et al., 2017). Insect traces of *Taotieichnus* are associated with the skeleton of the prosauropod dinosaur *Yunnanosaurus* from the Lower Jurassic Lufeng Formation of China (Xing et al., 2013), for examples, while Middle Jurassic tetrapod burrows are preserved in association with the large sauropod *Omeisaurus* from the Sichuan Basin, China. These trace makers are probably involved in the decomposition of sauropod remains (Xing et al., 2016; Xing et al., 2017).

We report here on another ichnofossil association. In 2019, the Yingliang Stone Nature History Museum collected a nest dinosaur eggs with numerous associate invertebrate burrows from the Hekou Formation (Guifeng Group, Upper Cretaceous) of Shahe Town, Zhanggong District in Gan County, Ganzhou City, Jiangxi Province (Fig. 1).

Institutional abbreviations: YLSNHM = Yingliang Stone Nature History Museum

Geological setting

There is no current consensus on whether the Upper Cretaceous rocks of the Nanxiong Basin (Guangdong Province) and the Ganzhou Basin (Jiangxi Province) are part of a generalized Nanxiong Group/Nanxiong Formation, or should instead be divided into the Yuanfu, Zhutian, and Zhenshui formations (Fang et al., 2009). In Jiangxi Province, geologists divide the red sedimentary basins of the region into two groups: the Upper Cretaceous Ganzhou Group (Maodian and Zhoutian formations) as well as the Cretaceous-Paleogene Guifeng Group (Upper Cretaceous Hekou, Tangbian formations, and the Cretaceous-Paleogene Lianhe Formation) (Wen et al., 2016). Paleomagnetic studies have dated the Guifeng Group to 71.4 Ma – 65.0 Ma (Gu et al., 1991; Zuo et al., 1999).

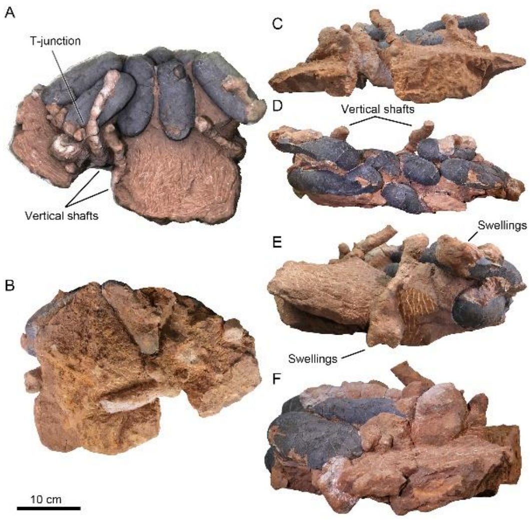

Fig. 1. Morphological features of *Thalassinoides* and dinosaur eggs in the Upper Cretaceous Hekou Formation, Ganzhou, Jiangxi, South China. The lines show the cross-cutting relationships between *Thalassinoides* and eggs.

The nest and associated traces reported here were preserved in the Hekou Formation, which has historically been placed in and considered equivalent to the Paleocene Guifeng Formation and the lower section of the Upper Cretaceous Nanxia Group (Department of Geology and Mineral Resources of Jiangxi Province, 1997). The Hekou Formation is now redefined as a red fluvial coarse-grained clastic deposit, overlying the Zhoutian Formation of the Ganzhou Group and underlying the Tangbian Formation of the Guifeng Group (He et al., 2017). The Hekou Formation is mainly composed of red conglomerates and glutenites, interbedded with a small amount of sandstone, siltstone, and locally interspersed tuff (Department of Geology and Mineral Resources of Jiangxi Province, 1997). Maastrichtian dinosaur fossils, including eggs assigned to *Oolithes spheroides* and *Oolithes* sp (Mikhailov et al., 1996), are known from the Hekou Formation (Chen et al., 2015; Liang et al., 2015; He et al., 2017). The Hekou Formation extends into Nanxiong, Guangdong, and is comparable with the Dafeng/Yuanpu Formation in the lower section of the Nanxiong Formation (Wu et al., 2002; Chen et al., 2015; Liang et al., 2015).

Methods and materials

One specimen, YLSNHM00998 consists of seven eggs and five invertebrate burrow traces. The *ex-situ* fossil was photographed using a Canon EOS (5D Mark III) digital camera from different viewpoints in a series of 30 overlapping images under artificial lighting conditions. A scale-corrected digital surface model (resolution = 0.217 mm/pix; point density > 20 points/mm2) was created from methods adapted from Falkingham et al. (2018) and using Agisoft Metashape Professional Edition (version 1.5). The digital model was then positioned at the center of a cartesian coordinate system using Meshlab (64bit_fp v2016.12; Cignoni et al., 2008), and visualized using the ambient occlusion filter in CloudCompare (v2.6.1 64 bit; www.cloudcompare.org).

The egg shell and five invertebrate burrow traces were sampled, cleaned, and coated with gold. Samples were analyzed both petrographically and chemically in a Quanta 250 field emission gun scanning electron microscope (FEI Quanta 250 FEG-SEM) equipped with a Bruker Nano with X-Max 30 mm^2 detector energy dispersive X-ray spectrometer (Bruker Quantax 200 XFlash 6|30 EDS) at the Key Laboratory of Biogenic Traces & Sedimentary Minerals of Henan Province in Jiaozuo, China. The scanning electron microscope provided elemental analyses and micro-scale morphological details of the egg shell and burrow.

Egg morphology and shell histology

The eggs measure 14.9-16.5 cm long and have equatorial widths of 6.2-7.2 cm. The equatorial surface ornamentation is linearituberculate (consisting of densely packed ridges). The blunt ends show dotted ornamentation, while the acute ends are smooth. These characters, along with the elongate shape and paired arrangement of the eggs, are indicative of the Elongatoolithidae (Young, 1954), an oofamily common throughout the Cretaceous of Asia. The eggs are thus assignable to *Elongatoolithus elongatus* based on the characteristics proposed by Young (1954). The previous discoveries of several embryo-containing eggs and adult-associated clutches have confirmed elongatoolithid eggs belong to oviraptorosaurs (Norell et al. 1994; Norell et al. 1995; Dong & Currie, 1996; Norell et al., 2018).

Two pieces of eggshell were removed from two of the eggs and prepared as petrographical thin sections for histological studies (Fig. 2). The shell thicknesses were 1.1 and 1.2 mm. Two calcite layers, a mammillary and a continuous layer, separated by a smooth boundary, were identified. The thickness ratio of the mamillary layer to calcite layer is roughly 1:4.

Fig. 2. Eggshell microstructures of Elongatoolithidae egg in the Shahe tracksite, Jiangxi Province, China.

Ichnology

Thalassinoides suevicus

Three-dimensional burrow fills with the invertebrate ichnogenus *Thalassinoides* occur throughout the dinosaur eggs-bearing calcareous siltstone of the Upper Cretaceous Hekou Formation. Locally, long, vertical shafts are seen on bedding surfaces. Those closely associated with the eggs consist of 3.1–3.4 cm wide, smooth, unlined, branched channels, oriented roughly perpendicular to bedding. The burrows from both Y- and T-junctions. Some irregular swellings occur in the middle of the burrow segments, but not at the junctions. No scratches are present. The burrow fill is passive.

SEM-EDS features

SEM-EDS analysis indicates that the egg shell consists of a calcareous component, rich in calcium and oxygen (Fig. 3A-D). Sediments within the *Thalassinoides* burrow traces and the surrounding rock matrix contain clay minerals around siliceous minerals and are overall coarse and porous (Fig. 3E). The SEM mapping, reveals the egg shells to be dominated by Ca, O, and Si (Fig. 3C).

Discussion and Conclusion

The dinosaur egg fossils associate with the invertebrate ichnofossils which discovered in Jiangxi enrich our knowledge of the diversity of dinosaur egg fossils and ichnofossils of Cretaceous. This sample also prompts some information. *Thalassinoides* is usually interpreted as a feeding burrow (Fodinichnion), typically produced by infaunal deposit feeders, such as decapod crustaceans (Myrow, 1995; Nickell & Atkinson, 1995). The channel diameters fall within the range of crustacean burrowing channels, and the traces are consistent with the morphology of known crustacean channels (Nickell & Atkinson, 1995; Stieglitz et al., 2000; Monaco & Garassino, 2001; Carmona et al.,2004) for example: burrowing shrimps (Hasiotis & Mitchell, 1993; Nickell & Atkinson, 1995; Carvalho et al., 2007). The size of the burrow-makers can be estimated from the width of the channels (Xing et al., 2013; Xing et al., 2017). The trace makers were most likely small crustaceans, a little more than 3 cm in width.

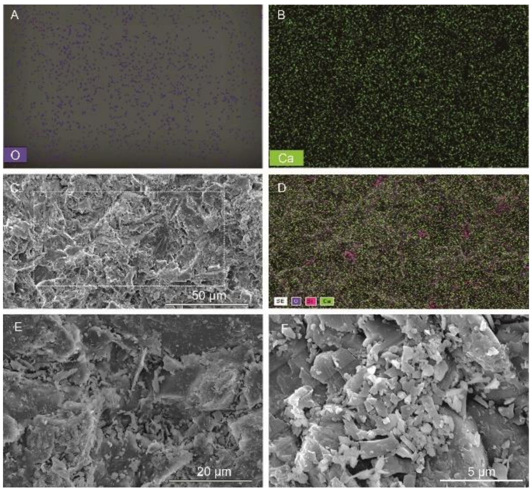

Fig. 3. Scanning electron microscope (SEM) images of the dinosaur egg shell and the symbiotic burrow. A, B, D. Elemental maps showing the component differences in the dinosaur egg shell. B. The mapping areas selected by the white dotted line box. E. Clay minerals and siliceous in the burrow. F. The carbonate minerals in the egg shell.

Although some of the channels abut and run in the tight association alongside the outer surfaces of the eggs, there is no clear record of the channels entering any of the eggs. Similarly, while the eggs are broken and fragmented in many spots, there is no clear indicator that this fragmentation is associated with the activities of the burrow makers, and such shell fragments are common in similarly preserved elongatoolithid nests, which lack any associated burrow traces (Codrea et al., 2002; Wang et al., 2018; He et al., 2019; Skutschas et al., 2019). Moreover, since the *Thalassinoides* burrows have only a few short branches, they cannot be confirmed as foraging traces (Nickell & Atkinson, 1995; Xing et al., 2013; Koy & Plotnick, 2010). A similarly small number of bifurcations are typical in the living nests of some marine crustaceans, which can be used for changing the direction of the creature or renewal of the water from different nest entrances (Nickell & Atkinson, 1995; Ziebis et al., 1996; Xing et al., 2013). As a small crustacean, it is even doubtful whether the trace-makers had the ability to pierce the more than 1 mm thick egg shells (Wang et al., 2018; Skutschas et al., 2019). Therefore, the *Thalassinoides* traces do not appear to document direct foraging. Or even more, the association between the two is just an accidental situation.

On the other hand, the dinosaur eggs had clearly been buried before the burrows were created and the eggs had also clearly failed to hatch. The association of the two fossils is still cannot be ruled out completely. The decaying dinosaur eggs might increase the organic content at the burial site (Xing et al., 2017), and this may well have led to an increase in local decomposers and other small arthropods in the nearby area. This might attract crustacean trace makers (Xing et al., 2017).

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