

Reconstruction of oviraptorid clutches illuminates their unique nesting biology

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Oviraptorosaurs, a group of non-avian theropod dinosaurs from the Cretaceous of Asia and North America, left behind the most abundant and informative fossil evidence of dinosaur reproductive biology. Previous studies had suggested that oviraptorosaur reproductive biology represents an intermediate stage and exhibited unique modern avian traits. For instance, the adult-associated clutches were predominantly considered as evidence for brooding/thermoregulatory contact incubation (TCI) behaviors, whereas the hypotheses of laying or protection were neglected. Despite numerous oviraptorid egg clutches uncovered from China and Mongolia, their nest architecture and clutch arrangement were rarely investigated in detail. Here we present a comprehensive reconstruction of an oviraptorid clutch based on five new oviraptorid clutches from Jiangxi Province, China. A detailed examination of the new clutches reveals a partially-open oviraptorid nest that contains 3–4 rings of paired eggs (more than 15 pairs total) whose blunt end points toward the center devoid of eggs at an angle of 35–40°. Our detailed three-dimensional reconstruction indicates that the oviraptorid clutch has a unique architecture unknown from extant bird clutches, implying an apomorphic nesting mode. Such a unique nest architecture further contradicts the TCI hypothesis in oviraptorids, hindering sufficient heat transfer to the inner (lower) ring(s) of eggs. Moreover, the size of the new oviraptorid clutches (>30 eggs) is significantly larger than that of the adult-associated clutches (<22 eggs), raising the alternative hypothesis that the adult-associated clutches were uncompleted. This clue thus supports the hypothesis that the clutch-associated oviraptorid adults possibly represent females after an oviposition before a catastrophic sandstorm/flooding burial.

Key words: Dinosauria, *Oviraptor*, clutches, nest, thermoregulatory contact incubation, Cretaceous, China.

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Introduction and historical background

From a thief to a loving mom.—*Oviraptor*, which means “egg thief”, was named by Osborn in 1924 based on the *Oviraptor philoceratops* specimen (AMNH FARB 6517)

and an associated clutch (AMNH FARB 6508) from the Late Cretaceous (Campanian) Djadokhta Formation of Bayn Dzak (= The Flaming Cliffs = Shabarakh Usu), Mongolia (Osborn 1924). This was the first time that this kind of adult-clutch association was reported. Osborn (1924) assigned the associated clutch to protoceratopsian dinosaurs and hypothesized that oviraptors preyed on proceratopsian

eggs. Seventy years later, Norell et al. (1994) described an embryo-containing egg (IGM100/971) from the Djadokhta Formation of Ukhaa Tolgod, Mongolia, that exhibited striking morphological similarity to the putative protoceratopsian eggs of the 1924 clutch. However, the embryonic cranial remains showed features diagnostic of oviraptorids and not of *Protoceratops*, falsifying the hypothesis that the adult oviraptor AMNH FARB 6517 was preying on the egg clutch AMNH FARB 6508 and questioning the hypothesis that oviraptors were egg thieves. Subsequently, Norell et al. (1995) reported another oviraptor adult-clutch association (IGM 100/979) from Ukhaa Tolgod and interpreted the fossil as evidence for bird-like “brooding” behavior.

In the 1990s, two more adult-clutch associations were discovered and interpreted as representing brooding behavior as well: IVPP V9608 from the Djadokhta Formation of Bayan Mandahu, Inner Mongolia, China (Dong and Currie 1996; Longrich et al. 2010), and IGM 100/1004, again from Ukhaa Tolgod (first reported by Clark et al. 1999 and re-described by Norell et al. 2018). The specimens IGM 100/979 and IGM 100/1004 were used to erect the new taxon *Citipati osmolskae* in 2001 (Clark et al. 2001). Subsequently, Fanti et al. (2012) described yet another adult-clutch association consisting of a clutch of 18 eggs from the Baruungoyot Formation of the Nemegt Basin of southern Mongolia (MPC-D 107/15). The specimen lacks a clear clutch patterning due to poor preservation but sports a partial skeleton in brooding position on top of the clutch. Fanti et al. (2012) erected the new taxon *Nemegtomaia barsboldi* based on MPC-D 107/15. Most recently, oviraptor adult-clutch associations were discovered in southern China. Two specimens (AGM 4990 and an uncatalogued specimen) were excavated from the fluvial deposits of the Nanxiong Formation in Jiangxi Province, and the uncatalogued specimen was preliminarily described by Bi and Xu (2017).

Thus, to date at least seven oviraptorid clutches topped by an adult individual have been discovered, including five from the sand-dune deposits in Mongolia and Inner Mongolia, China, and two from the fluvial Nanxiong Formation of southern China (Table 1 and references therein). The ones from the sand-dune deposits in Mongolia and

Inner Mongolia, China, represent four different taxa of oviraptorosaurs (Table 1 and references therein).

Brooding and incubation: clarification of terms.—In modern birds, the term “brooding” covers the two categories “prehatching brooding” and “posthatching brooding” (Mandal 2012). For dinosaurs, previous studies mainly discussed “prehatching brooding” (Norell et al. 1995; Dong and Currie 1996; Clark et al. 1999; Fanti et al. 2012), while “posthatching brooding” was rarely discussed. Posthatching brooding comprises protecting and taking care of the young after hatching, and also includes body heat transfer from the adult to the hatched offspring (Mandal 2012; see also Norell et al. 2018). Prehatching brooding involves incubation behavior, which means the adult is sitting on the eggs to keep them warm and to bring them to hatching, also known as thermoregulatory contact incubation (TCI). TCI implies an open nest because the body heat is transferred by contact between adult and eggs and generally involves heat generated by the endothermic metabolism of the adult. In altricial birds, endothermy develops in the chicks only after hatching, which is why they are thermally dependent on brooding adults for the first days after hatching (Dawson et al. 1976; Whittow and Tazawa 1991; Hohtola and Visser 1998). In superprecocial and precocial birds, endothermy is gained even before hatching (Whittow and Tazawa 1991). Since altricial bird embryos and hatchlings show a strong allometry of skull, wing, and hindlimb proportions, freshly hatched chicks are rather immobile, which forces them to remain in their nest at least for some time (Whittow and Tazawa 1991). More precocial birds have already well developed walking legs and musculature and are thus not that limited in their locomotion (Whittow and Tazawa 1991). Precocial birds do not need as much “post-hatching” parental care as altricial birds do. Furthermore, adults usually “brood” their hatchlings during the first days after hatching also to protect them from predation (Dial 2003; McLennan et al. 2004). These observations on modern birds contribute to possible explanations for the common occurrences of oviraptorid adult-associated clutches (Table 1 and references therein).

Table 1. Characteristics of previously reported oviraptorid adult-associated clutches. The question mark means number of rings is still uncertain.

Specimen number	Taxonomic assignment	Clutch size	Number of rings	Locality information	Stratigraphic horizon	References
AMNH 6508/AMNH 6517	<i>Oviraptor philoceratops</i>	15	2	Bayn Dzak (The Flaming Cliffs = Shabarakh Usu), Mongolia	Djadokhta Formation	Osborn 1924
IGM 100/979 (Big Mamma)	<i>Citipati osmolskae</i>	15 (visible), 22 (estimated)	2	Ukhaa Tolgod, Mongolia	Djadokhta Formation	Norell et al. 1995
IGM 100/1004 (Big Auntie)	<i>Citipati osmolskae</i>	12	2	Ukhaa Tolgod, Mongolia	Djadokhta Formation	Clark et al. 1999; Norell et al. 2018
IVPP V9608	cf. <i>Machairasaurus</i>	6	1	Bayan Mandahu, Inner Mongolia, China	Djadokhta Formation	Dong and Currie 1996; Longrich et al. 2010
MPC-D 107/15	<i>Nemegtomaia barsboldi</i>	18	2?	Nemegt, Mongolia	Baruungoyot Formation	Fanti et al. 2012

Review of hypotheses explaining adult-clutch associations.—Norell et al. (1995) made it clear that the usage of the term “brooding” did not imply heat transfer from adult to eggs by stating “brooding behaviour (by which we only refer to the behaviour of sitting on nests)”. Norell et al. (1995) offered an alternative hypothesis, i.e., that of the female having been killed while laying her eggs, to explain the adult-clutch associations in oviraptorid dinosaurs. However, they found the evidence preserved by IGM100/971 to be “strongly suggestive” of TCI. The notion of preserved brooding behavior gave rise to the hypothesis that bird-like incubation originated in basal maniraptoran dinosaurs and predated the origin of birds. The TCI hypothesis for explaining oviraptor adult-clutch associations appears to have progressively gained more acceptance over the egg-laying hypothesis, following a surge of discoveries of feathered dinosaurs in northeastern China and Canada, which traced more avian features back to their dinosaur ancestors (Ji et al. 1998; Zelenitsky et al. 2012).

The ambiguities of the term “brooding” induced a number of discussions about the correct interpretation of the brooding oviraptorids for the last 20 years (Carpenter 1999; Horner 2000; Zhao 2000; Deeming 2002, 2006; Ruben et al. 2003; Jones and Geist 2012). For instance, Deeming (2002) doubted the viability of TCI in oviraptors, noting that the eggs in the lower egg layer(s) (actually the inner ring(s), see below) would not have had sufficient contact with the brooding adult and thus would not have benefited from the parent’s body heat. A brooding bird arranges its eggs in a single layer to place all the eggs below its brood patch, ensuring efficient heat transfer to all eggs, and periodically manipulates them in order to equably distribute the heat (Deeming 2002). Alternative interpretations, grounded in behavior observed in extant non-avian archosaurs such as crocodylians were published such as that the parent or adult oviraptorid might have been sitting or lying atop its clutch mainly to protect it (Ferguson 1985; Webb and Cooperpreston 1989; Norell et al. 1995; Dong and Currie 1996; Clark et al. 1999; Deeming 2002).

The regular multiple-ring clutch arrangement of paired oviraptorid eggs described in the current and previous studies (referred to as superposed layers by Clark et al. 1999 and Grellet-Tinner et al. 2006) and a pair of eggs preserved in the pelvic region of an oviraptorosaur specimen (Sato et al. 2005) indicate that the fossilized clutches record the arrangement of the eggs as they were laid. The highly regular clutch architecture thus appears inconsistent with egg manipulation during avian brooding (Varricchio et al. 1997; Varricchio and Jackson 2016). Such manipulation had been hypothesized by Norell et al. (1995)

Some studies had offered different perspectives on the sitting oviraptors. Martin and Simmons (1995) and Carpenter (1999) suggested that oviraptorids sat in the center of their semi-exposed egg rings around a mound: in other words, they built partially open nests. These authors also proposed that the oviraptors were sitting on their clutches to

protect them from predators, a hypothesis also considered by Norell et al. (1995). Their suggestions were challenged by Paul (2002), who argued that the predation risk for eggs is lower in a buried nest than in an open nest.

All the hypotheses reviewed above are closely linked to the clutch architecture of an oviraptorid clutch and are potentially falsified by features of clutch architecture. Clutch architecture has been discussed in several previous studies (Sabath 1991; Norell et al. 1995; Dong and Currie 1996; Deeming 2002; Fanti et al. 2012; Varricchio and Jackson 2016; Wiemann et al. 2017; Tanaka et al. 2018). Thus, we would like to present a short review that presents different hypotheses regarding the architecture of an oviraptorid clutch for highlighting the aims of this study.

Architecture of an oviraptorid clutch.—Clarification of terminology is in order to distinguish between a clutch, a cluster, and a nest. A clutch refers to all the eggs laid by one or several archosaurs (monogamous or polygamous), at a single time or in a single reproductive season, particularly in a nest (Lack 1948). In fossils, it is sometimes difficult to determine if all the eggs found in close proximity to each other were laid at the same time or within the same reproductive season; hence, the term “cluster” is used to describe an accumulation of eggs found in close proximity, but which cannot be assigned to a single clutch with certainty (Vila et al. 2010). One reason for identifying clutches in the fossil record is the nearly ubiquitous lack of a nesting trace associated with a cluster of eggs (Chiappe et al. 2004). Werner and Griebeler (2013) and Ruxton et al. (2014) concurred with Vila et al.’s (2010) usage.

In accordance with Hechenleitner et al. (2015), herein we define that a nest consists of a clutch of eggs and its associated shelter; however, the latter is often poorly preserved in the fossil record or destroyed during excavation (Chiappe et al. 2004). Varricchio et al. (1997) discovered a *Troodon* nest (MOR 963) comprising a 24-egg clutch within a shallow depression bordered by a distinct rim. No distinct sedimentological nest structures have been reported in association with oviraptorid clutches before. However, we are confident that oviraptorid egg clusters generally represent clutches because of the uniform arrangements of the eggs in the cluster.

As we will describe in detail below based on multiple well-preserved specimens, oviraptorid clutches show the following features: partial burial of the eggs, multiple (up to four) superimposed rings of paired eggs, center devoid of eggs, blunt end of the eggs pointing upwards and slightly inwards (i.e., egg long axis leaning towards the clutch center at a high angle).

Inaccuracies and controversy have surrounded the history of research on oviraptorid clutch architecture. Illustrations played an important role in earlier papers and expressed hypothetical reconstructions often in more detail than the text (e.g., Sabath 1991; Norell et al. 1995; Dong and Currie 1996; Deeming 2002; Fanti et al. 2012; Tanaka et al. 2018). Sabath (1991) first reconstructed oviraptorid clutch

architecture and proposed the first taphonomic scenario describing how the oviraptorid clutch architecture changed during fossilization. The eggs are shown within a mound nest and are completely buried (Sabath 1991: fig. 5). At least some of the eggs are paired and their blunt end points upward but the eggs are inclined outwards instead of inwards. The center is devoid of eggs, but the multi-ringed architecture is not apparent. Instead, the observable overlap of eggs was interpreted by Sabath (1991) as resulting from oviposition in a spiral (see also Jones and Geist 2012). Sabath (1991) also realized that the angle of inclination of the eggs decreased because of sediment compaction.

Four years later, Norell et al. (1995) visualized another interpretation of clutch architecture, in an illustration showing an oviraptorid individual sitting on a randomly arranged egg clutch (Norell et al. 1995: fig. 2). The illustration depicts the eggs in a shallow pit surrounded by a raised rim of the nest. Dong and Currie (1996) corrected some flaws in the Norell et al. (1995) reconstruction based on the oviraptorid clutch IGM 100/1008 (Dong and Currie 1996: fig. 3). This sketch of the IGM 100/1008 specimen showed a highly organized and paired egg arrangement with the blunt ends of the eggs pointing to a center devoid of eggs. However, it was left open whether the eggs were buried or exposed to the air. Dong and Currie (1996) also proposed that the oviraptorid nest should be reconstructed as a mound rather than as a pit as described in Norell et al. (1995), since they observed that the eggs are inclined to the ground at gentle angles (13–16°) and slope away from the clutch center.

Deeming (2002) reconstructed the oviraptorid clutch based on the literature published at the time. He shows two superimposed rings of eggs with the eggs lying on the side of a mound, thus sloping away from the center (Deeming 2002: figs. 1, 2). However, the reconstruction lacks the paired arrangement and has the acute ends pointing to the center. Finally, Fanti et al. (2012) reconstructed the clutch in an inverted position without egg pairing and egg polarity, but with two superimposed layers of eggs. Based on sedimentological evidence, Fanti et al. (2012) suggest that the upper layer of the clutch was not buried (or was only partially buried). Fanti et al. (2012) partly echoed Wang and Jan's (1963), Martin and Simmons's (1995), and Carpenter's (1999) speculation that the oviraptorid dinosaur laid eggs on a mound.

Varrichio and Jackson (2016) briefly review oviraptorid clutch architecture, emphasizing egg pairing, and note superimposed rings (1–3) but not the orientation of the blunt end. They also conclude that the eggs differ from those of *Troodon* in their low angle of inclination. Most recently and based on new finds from Southern China, Tanaka et al.

(2018) visually reconstruct the clutch with the eggs openly lying in superimposed rings on the slope of a mound, the blunt end pointing inwards. However, egg pairing is neither mentioned nor illustrated.

Oviraptorid dinosaur nests were initially considered to belong to the covered nest type based on the high water vapor conductance of the eggshell calculated from the porosity of single eggshell fragments (Sabath 1991; Mou 1992; Deeming 2006; Tanaka et al. 2015). However, estimating the total water vapor conductance based on isolated fragments of eggshell may be misleading because of the heterogeneous pore distribution and shell thickness variation across the whole egg (see Varrichio et al. 2013; Simon 2014; Yang et al. 2015; Wiemann et al. 2017). Finally, Wiemann et al. (2017) suggested that the oviraptorid clutch was partially open to the air based on detected pigments (reddish-brown protoporphyrin and blue-green biliverdin) and heterogeneous distribution of water vapor conductance.

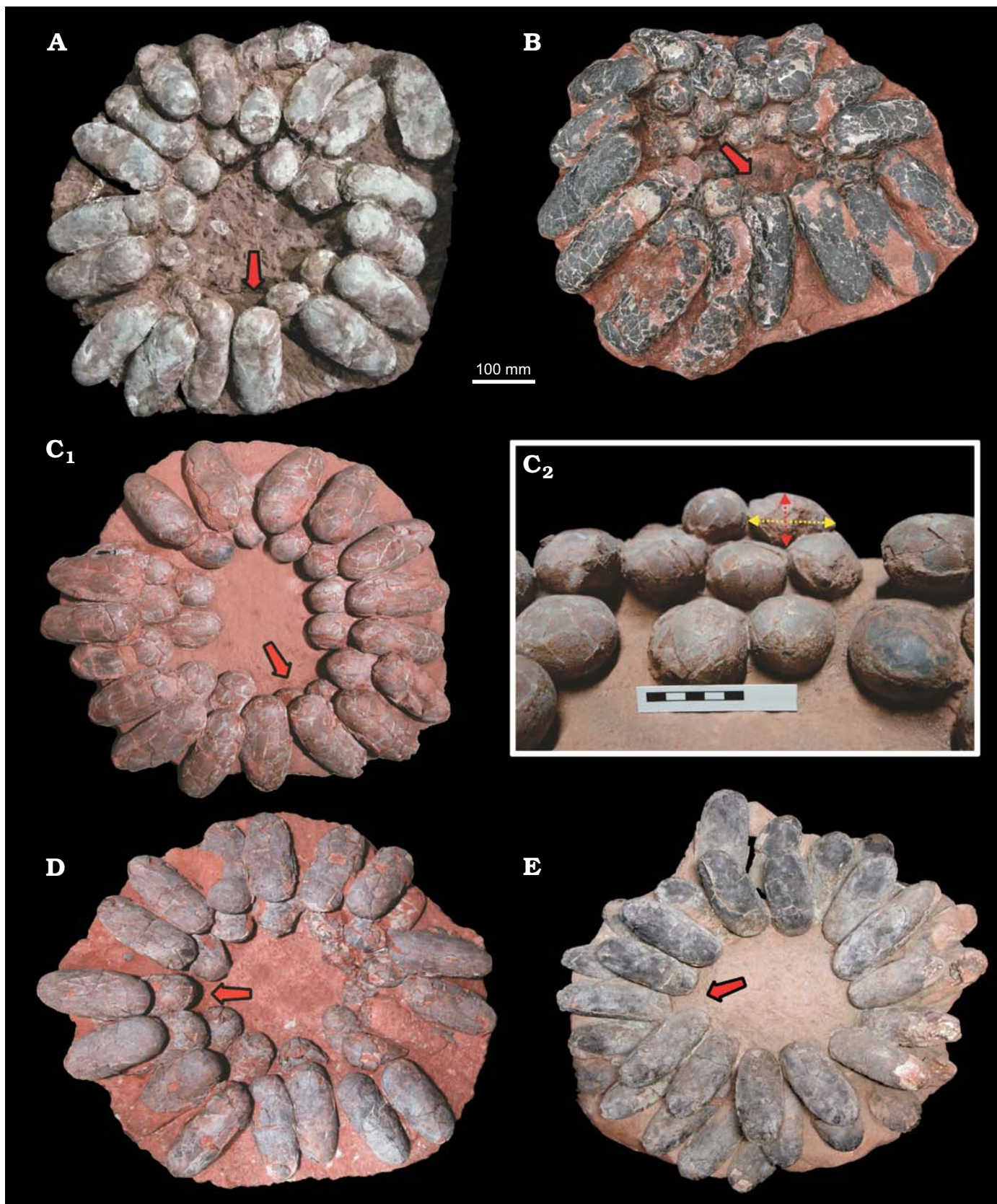
Although focusing on egg coloration, in a previous study, we briefly describe clutch architecture as well (Wiemann et al. 2017) based on new clutches from southern China that, however, lack associated adults. We note that the low eggshell porosity of the blunt end suggest that it was exposed to the air, as does the coloration of the eggshell (Wiemann et al. 2017).

The purpose of this study is to provide a detailed reconstruction of the architecture of the oviraptorid clutch and to re-evaluate the hypothesis of thermoregulatory contact incubation. Our evidence consists of new scientifically prepared and well preserved clutches from Southern China. We also address the effect of diagenetic sediment compaction on clutch architecture which was largely neglected by later studies after the seminal work of Sabath (1991).

Institutional abbreviations.—AGM, Anhui Geological Museum, Hefei, Anhui, China; AMNH FARB, American Museum of Natural History (Fossil Amphibians, Reptiles and Birds), New York, USA; DM, Darwin Fossil Museum, Keelung, Taiwan; HGM, Henan Geological Museum, Zhengzhou, Henan, China; IGM, Institute of Geology, Ulaanbaatar, Mongolia; IVPP: Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; MPC, Mongolian Paleontological Center, Ulaanbaatar, Mongolia; MOR, Museum of the Rockies, Bozeman, USA; NMNS, National Museum of Natural Sciences, Taichung, Taiwan; PFMM, Paleowonders Fossils and Mineral Museum, New Taipei City, Taiwan.

Other abbreviations.—CL, continuous layer; ML, mammillary layer; TCI, thermoregulatory contact incubation.

Fig. 1. The oviraptorid clutches described in this study. All clutches were discovered from the Late Cretaceous Nanxiong Formation at a construction site in Dayu County, Ganzhou City, Jiangxi Province, China (25.386N, 114.369E) and now are repositated at various institutions (Table 2). All eggs are arranged in pairs with their blunt ends pointing towards the clutch center devoid of eggs. **A.** Top view of HGM-41H-V0074, a complete clutch with 30 eggs arranged in three superimposed rings. Two isolated eggs in the upper right might have been pushed away from the uppermost ring before burial. The vacant center is 266 × 213 mm. **B.** Top view of DM-2014-P0154, a complete clutch with 31 eggs arranged in four superimposed rings. The vacant center is comparatively smaller than in the other specimens studied, measuring only 133 × 105 mm. **C.** PFMM-0014002972; C₁, top view of the specimen with 32 eggs arranged in three superimposed rings, the vacant center is 240 × 135 mm; C₂, detail of the lateral view from the center of the specimen; three →



rings of eggs are separated by thin layers of sediments; yellow dashed line, the major axis (46 mm); red dashed line, the minor axis (24 mm); scale bar 50 mm. **D.** Top view of PFMM-0014004392, a complete clutch with 32 eggs arranged in three superimposed rings. The vacant center is 200 × 186 mm. **E.** Bottom view of PFMM-0014003019, a complete clutch with 35 eggs arranged in three superimposed rings. The vacant center is 293 × 280 mm, which is the largest opening among the specimens described in this study. Arrows point to the opening in the lowermost ring.

Geological setting

The new egg clutch specimens were discovered in the Nanxiong Formation (Nanxiong Group) of the Ganzhou Basin in South China. Regional tectonics during the Late Cretaceous–early Paleogene resulted in a series of NE-SW trending extensional basins sharing similar sedimentological and stratigraphic features in southern Jiangxi and northern Guangdong, including the Hongcheng Basin, Ganzhou Basin, Nanxiong Basin, etc. (Bureau of Geology and Mineral Resources of Jiangxi Province 1984). These basins are elongate and filled in by red fluvial-lacustrine clastic sequences, exemplified by the dinosaur-containing Late Cretaceous Nanxiong Group (Dafeng, Zhutian, Zhenshui, and Pingling formations) and the mammal-bearing Loufuzai Group (Shanghu and Nongshan formations) (Bureau of Geology and Mineral Resources of Jiangxi Province 1984).

The Nanxiong Formation in the Ganzhou Basin is composed of brownish red, medium-grained sandstone and sparsely interbedded clay sediments, dated to 66–72 Mya (latest Maastrichtian, Upper Cretaceous; Bureau of Geology and Mineral Resources of Jiangxi Province 1984). Petrographic observation on sediments of the Late Cretaceous Nanxiong Formation indicates an arid to semi-arid climate in southern China during the latest Maastrichtian period (Wang et al. 2015). He et al. (2017) suggested that the dinosaur egg-bearing Nanxiong Formation in the Ganzhou Basin formed in a middle to distal region of an alluvial fan based on the gravel and planar cross beds. All dinosaur egg clutches or skeleton are well-preserved, indicating that the fossils in the Ganzhou Basin were not, or only for a short distance, transported by water currents (He et al. 2017).

The Nanxiong Formation yields a great number of oviraptorid dinosaurs, including *Heyuannia huangi* (Lü 2003), *Shixinggia oblita* (Lü and Zhang 2005), *Banji long* (Xu and Han 2010), *Ganzhousaurus nankangensis* (Wang et al. 2013b), *Nankangia jiangxiensis* (Lü et al. 2013), *Jiangxisaurus ganzhouensis* (Wei et al. 2013), *Huanansaurus ganzhouensis* (Lü et al. 2015), *Tongtianlong limosus* (Lü et al. 2016), and *Corythoraptor jacobsi* (Lü et al. 2017). Five embryo-containing eggs (Cheng et al. 2008; Wang et al. 2016) and the

oviraptorid pelvis with a pair of eggs (Sato et al. 2005) were also discovered in the same group.

Material and methods

Five remarkably complete oviraptorid clutches from the comprehensive collections housed at DM (2014-P0154), HGM (41H-V0074), and PFMM (0014002972, 0014003019, 0010404392) are included in this study (Fig. 1) for comparison with the clutches associated with “brooding” adults (Table 1 and references therein). All of the five clutches were collected from the Upper Cretaceous Nanxiong Group of the Hongcheng Basin near the city of Ganzhou, in southern Jiangxi Province, China. This is the same locality where the gravid oviraptorosaur was discovered and reported in 2005 (Sato et al. 2005).

To avoid problems with fabrication of the clutches, we only studied clutches with a known preparation history. The DM and PFMM specimens were prepared by technicians of the PFMM and by Yen-Nien Cheng of the NMNS, and the HGM specimen was prepared by technicians of the HGM (Fig. 1, Table 2). Except for specimen PFMM-0014003019, all clutches were prepared from the field top as they were found in the field. However, no sedimentological context remains for the clutches that would have aided in the interpretation of clutch architecture. The five clutches were chosen because the eggs in these clutches are well preserved and only slightly compacted. The nearly round egg cross sections indicate that these clutches still retain their original shape and arrangement (Fig. 1) and were not affected much by sediment compaction which would have altered egg cross sections from round to an elliptical.

We also re-examined specimen IVPP V9608 (Dong and Currie 1996) and compared it with IGM 100/979 (Norell et al. 1995). As noted, IVPP V9608 was discovered in the Djadokhta Formation in Bayan Mandahu, Inner Mongolia, China (Dong and Currie 1996). It can be divided into two parts: a partial oviraptorid skeleton and six eggs. The partial skeleton is composed of vertebrae, the pectoral girdle, the right forelimb, and the right hind limb. Before preparation, Dong and Currie (1996) observed that the oviraptorid skel-

Table 2. Characteristics of the complete clutches from the Nanxiong Formation of China described in this study. I, innermost ring; II, second ring.

Catalogue number	Clutch size	Ring no.	Size of vacant center (mm × mm)	Number of rings	Ornamentation type	Prepared by
HGM-41H-V0074	30	I	266 × 213	3	linearituberculate	technicians of HGM
		II	390 × 325			
DM-2014-P0154	31	I	133 × 105	4	linearituberculate	Yen-Nien Cheng of NMNS
		II	275 × 200			
PFMM-0014002972	32	I	240 × 135	3	linearituberculate	technicians of PFMM
		II	325 × 275			
PFMM-0014004392	32	I	200 × 186	3	linearituberculate	technicians of PFMM
		II	305 × 300			
PFMM-0014003019	35	I	393 × 280	3	linearituberculate	technicians of PFMM
		II	350 × 325			

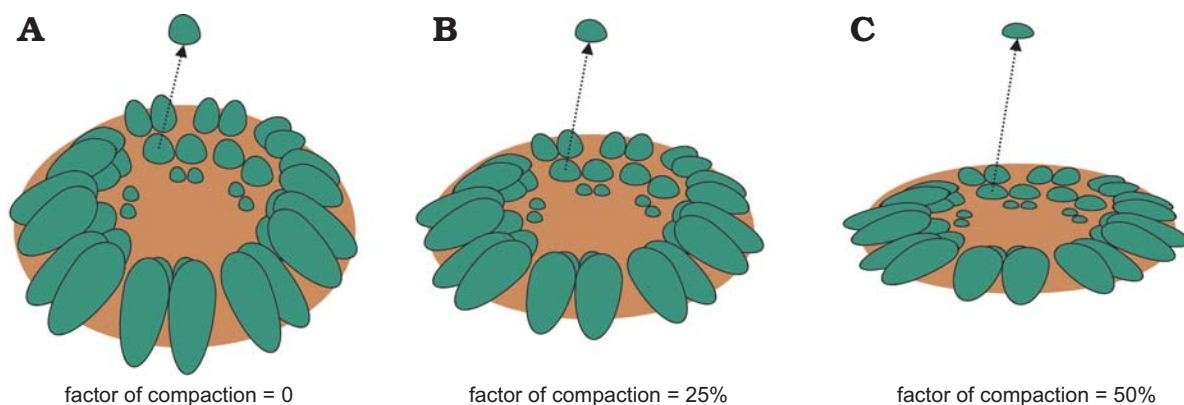


Fig. 2. A schematic illustration of an oviraptorid clutch affected by different degrees of compaction. **A.** Original configuration. **B.** The same configuration affected by a compaction factor of 25%. **C.** The same configuration affected by a compaction factor of 50%. Note the change of inclination angle and shape of the eggs.

eton was lying atop the clutch. We also recorded the clutch sizes of other “brooding” specimens reported in previous studies (Table 1 and references therein).

To reconstruct the original clutch architecture, and potential diagenetic deformation of the clutches, we studied the spatial arrangement of the eggs in the clutches (both with and without associated skeletons) in detail, taking sediment compaction into account. Oviraptorid eggs are generally elongated, with the elongation index (ratio of long axis to girth) exceeding 2.0 (reviewed in Varricchio and Jackson 2016). Based on the principles of egg formation (Romanoff and Romanoff 1949), it is reasonable to assume that the original cross section of the eggs in the clutches was circular. This notion is supported by a pair of eggs preserved inside the pelvis of an oviraptorosaur which show circular cross sections perpendicular to egg long axis (Sato et al. 2005). If we find this circular cross section to have been changed to an ellipse, we have to infer sediment compaction during fossilization as the cause (Sabath 1991). Hence, based on photos taken looking down the egg long axis from the center of the clutch (the polar view from the blunt end of an egg), we are able to estimate the amount of deformation by examining the shape of egg cross sections (Figs. 1C₂, 2).

The factor of sediment compaction (and with it the encased eggs) can be calculated by dividing the difference between the length of the major axis of the egg ellipse (L_{major}) and the length of the minor axis (L_{minor}) (as viewed from the blunt end of the egg) by the restored egg diameter (Figs. 1C₂, 2). Egg diameter equals the length of the major axis (L_{major}) because the egg diameter perpendicular to the compaction force does not increase during compaction since eggs are encased in sediment.

$$\text{Factor of compaction} = \frac{L_{major} - L_{minor}}{L_{major}} \quad (1)$$

Thus, we are able to reconstruct the original inclination of an egg by multiplying the measured angle of inclination with the factor of compaction (Figs. 1C₂, 2; Davison 1987; Sabath 1991). Combined with the measured angle of inclination for the eggs in the different rings, we used the factor of

compaction to geometrically reconstruct the original angle of inclination of the long axis of the eggs towards the center of the clutch (Davison 1987; Sabath 1991; Figs. 1C₂, 2).

The oviraptorid clutch consists of multiple rings of eggs, each two of which enclose a thin layer of sediment (Fig. 1C₂). An egg ring is defined by a line connecting the blunt ends of the eggs, which also denotes the size of the vacant center. Since the egg ring is usually an ellipse rather than a perfect circle, the minor and major axes of the ellipse that fits the egg ring the best are measured for the expression of the size of the egg ring (Table 2). Since the outermost ring of the studied clutches consists of only two to seven eggs and thus fails to form a complete ring, we measured only the ring size of the innermost ring (I) and second ring (II) (Table 2). Besides, we also measured the maximum vertical topographical distance between two egg rings by viewing the blunt ends from the clutch center (Fig. 1C₂).

To determine the developmental stage of the eggs of the sitting specimens, we sampled the eggshell of specimen IVPP V9608 for thin sectioning. The eggshell thin sections were examined with a Leica DMLP Polarizing Microscope. Normal and polarized light images were acquired with a Leica DFC420 camera by using the Leica ImageAccess EasyLab 7 software. The calcium of the eggshell is a predominant resource for eggshell formation so that the ML is eroded during embryogenesis, which provides information on the developmental stage of the eggs (Weishampel et al. 2008; Cheng et al. 2008).

Systematic palaeontology

Oofamily Elongatoolithidae Zhao, 1975

Oogenus *Macroolithus* Zhao, 1975

Type oospecies: *Macroolithus rugustus* Young, 1965, Nanxiang, Guangdong, China, Late Cretaceous.

Macroolithus sp.

Figs. 1, 3.

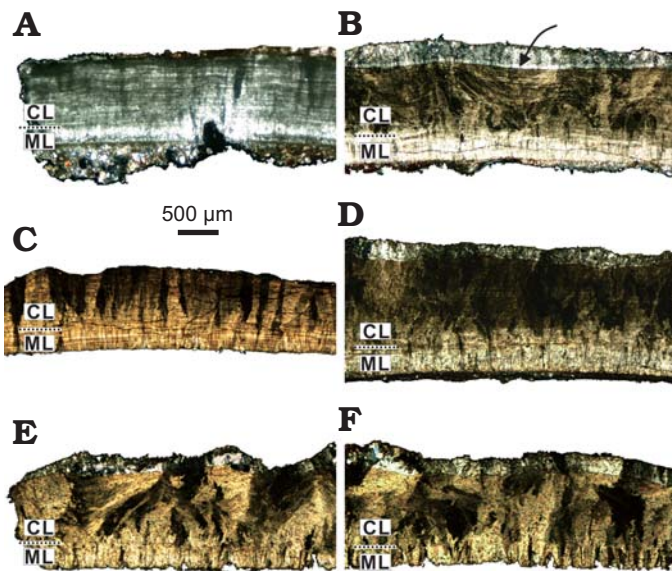


Fig. 3. Radial petrographic thin sections of eggshells from an adult-associated clutch (A) from the Late Cretaceous of Bayan Mandahu, Inner Mongolia, China (Dong and Currie 1996) and the studied clutches (B–F) from the Late Cretaceous Nanxiong Formation of a construction site in Dayu County, Ganzhou City, Jiangxi Province, China. A. HGM-41H-V0074. B. DM-2014-P0154. C. PFMM-0014002972. D. PFMM-0014004392. E. PFMM-0014003019. F. IVPP V9608. Dashed line, the ML/CL boundary; arrow, the calcite layer. CL, continuous layer; ML, mammillary layer.

Material.—Five egg clutches (HGM-41H-V0074, DM-2014-P0154; PFMM-0014002972, PFMM-0014004392, PFMM-0014003019) from the Late Cretaceous, Nanxiong Group of Dayu County, Ganzhou, Jiangxi, China

Description.—All eggs in the five clutches (HGM-41H-V0074, DM-2014-P0154; PFMM-0014002972, PFMM-0014004392, PFMM-0014003019) display elongate egg shape and linearituberculate surficial ornamentations (Fig. 2). Eggs are arranged in three or four rings (Fig. 2). While the length and width of the eggs in the inner rings are not measurable, the eggs in the outermost ring of the five studied clutches present similar gross morphology (length: 152–197 mm and width: 58–86 mm). The eggshell thickness of the studied egg clutches varies from 1.0–1.5 mm (Fig. 3). In some eggs, a layer of secondary calcite is observed on the calcitic eggshell layer (see Fig. 3B, D–F). The secondary calcite layer is distinguishable based on its different extinction pattern from the eggshell layer under the polarized microscope, thus indicating a lack of diagenetic replacement in the eggshell layer that may lead to overestimation of shell thickness. The ML thickness varies from 0.2–0.3 mm and the CL thickness ranges from 0.8–1.0 mm; therefore, the CL:ML ratio is from 2:1–3.4:1. The ML/CL boundary is apparent and wavy.

Remarks.—The elongate egg shape presented by the studied egg indicates the assignment to Elongatoolithidae (Zhao 1975), which is laid by oviraptorosaurians as evidenced by several reports of oviraptorosaurian embryo-containing eggs (Cheng et al. 2008; Wang et al. 2016; Pu et al. 2017). The oofamily Elongatoolithidae contains *Elongatoolithus*,

Macroolithus, *Macroelongatoolithus*, *Nanhsiungoolithus*, *Heishanoolithus*, *Paraelongatoolithus*, *Undulatoolithus*, and *Megafusoolithus*. Based on the egg length (152–197 mm; Fig. 2), *Macroelongatoolithus* and *Megafusoolithus* (usually more than 400 mm; Table 3; Zhao et al. 2015) are excluded. The eggshell thickness of the studied egg (1.3–1.5 mm; Fig. 3) is significantly greater than that of *Elongatoolithus* (usually less than 1.2 mm; Table 3; Wang et al. 2016), *Nanhsiungoolithus* (Zhao, 1975), *Paraelongatoolithus* (0.5–0.8 mm; Table 3; Wang et al. 2010) and *Undulatoolithus* (0.75–1.46 mm; Table 3; Wang et al. 2013a). Although *Heishanoolithus* eggs present similar eggshell thickness (1.2–1.5 mm; Table 3; Zhao and Zhao 1999), the studied eggs display distinctive eggshell surface ornamentation (linearituberculate), thus further constraining the studied egg clutches to *Macroolithus*. While the wavy ML/CL boundary present in the studied egg clutches is indicative of *Macroolithus yaotunensis* (Fig. 3), we do not assign the clutches to a specific ootaxon because of ootaxonomic ambiguity. Moreover, despite the report of an *Heyuannia huangi* embryo inside a *Macroolithus yaotunensis* egg (Cheng et al. 2008), *Macroolithus* eggs could possibly pertain to any similar sized oviraptorid dinosaur because many elongatoolithid eggs are microstructurally similar to each other. We therefore refer to all studied eggs simply as “oviraptorid eggs.”

Results

Clutch HGM-41H-V0074.—Twenty-eight eggs arranged in two rings are visible in HGM-41H-V0074; however, two eggs in the innermost ring only expose a small region of their blunt pole and were left unprepared in order not to disturb the eggs of the second ring. Two eggs are slightly offset from the outer ring, but still overlap with eggs of the second ring (Fig. 1A). The innermost ring contains twelve eggs and has a longer diameter of 266 mm and a shorter diameter of 200 mm, while the outer ring has 16 eggs and has a long diameter of 390 mm and a short diameter of 325 mm (Table 2). The inclination angle of the eggs ranges approximately from 27–33° (Table 2).

Clutch DM-2014-P0154.—DM-2014-P0154 has 31 eggs arranged in four rings but the smallest ring size among the studied egg clutches (Fig. 1B, Table 2). The first, innermost ring has eight eggs and has a longer diameter of 133 mm and a shorter diameter of 105 mm, and the second ring with 13 eggs has a longer diameter of 275 mm and a shorter diameter of 200 mm (Fig. 1B, Table 2). Both the third (four eggs) and fourth rings (six eggs) do not form a complete ring, being restricted to one side of the clutch; hence, no ring size can be measured (Fig. 1B). DM-2014-P0154 also has the highest inclination angle among the studied clutches, ranging from 35–40° (Fig. 1B). The egg inclination angle in DM-2014-P0154 might be close to the original angle since the egg shape, when viewed from the blunt pole, is nearly circular (Fig. 1B).

Table 3. An overview of the egg gross morphology and microstructural features of elongatoolithid eggs for ootaxonomic identification of the studied clutches; * specimens in this paper include HGM-41H-V0074, DM-2014-P0154, PFMM-0014002972, PFMM-0014004392, and PFMM-0014003019. Abbreviations: CL, continuous layer; ML, mammillary layer.

Ootaxonomic assignment	Egg length (mm)	Egg width (mm)	Eggshell thickness (mm)	Ornamentation type	ML thickness (mm)	CL thickness (mm)	CL:ML ratio	ML-CL boundary type	Pore shape	References
<i>Macroolithus rugustus</i>	165–180	75–85	1.44–1.7	sagenotuberculate in the polar regions and ramotuberculate near the middle	0.41 (average)	1.2 (average)	3:1	flat	angusticanalicate	Young 1965; Zhao 1975
<i>Macroolithus yaotumensis</i>	175–210 190–210	67–94 70–90	1.4–1.9 1.4–1.85	linearituberculate	0.29–0.51 0.4–0.7	–	3:1	wavy	angusticanalicate	Zhao 1975; Zhao et al. 2015
<i>Macroolithus mutabilis</i>	~170	–	1.3–2.0, up to 2.3 mm in the ornamented area	rimocanalicate	–	–	–	–	angusticanalicate	Mikhailov 1994
<i>Macroolithus lanshutuanensis</i>	–	–	2.3–2.7	–	–	–	1.5:1–2:1	gradual transition	tubocanalicate	Fang et al. 2009
<i>Elongatoolithus</i>	70–170 110–170	58–82	0.3–1.5	variable	–	–	2:1–3:1 1:1–6:1	sharp separation	angusticanalicate to tubocanalicate	Zhao 1975; Simon 2014; Zhao et al. 2015
<i>Nanxiongoolithus</i>	131–145	68 55–75	0.8 0.6–1.3	no ornamentation	–	–	–	gradual transition	irregular	Zhao 1975; Zhao et al. 2015
<i>Macroolithus</i> sp.	152–197	58–86	1.0–1.2	linearituberculate	0.2–0.3	0.8–1.0	2:1–3.4:1	wavy	angusticanalicate	this paper*

Clutch PFMM-0014002972.—PFMM-0014002972 has 32 eggs arranged in three rings (Fig. 1C₁, Table 2). The innermost ring (ten eggs) has a longer diameter of 240 mm and a shorter diameter of 135 mm, and the outer ring (16 eggs) has a longer diameter of 325 mm and a shorter diameter of 300 mm (Fig. 1C₁, Table 2). Six eggs rest upon the outer ring without forming a ring (Fig. 1C₁, Table 2). The inclination angle of the eggs ranges from 25–30°. The longer and shorter axes of the egg cross section from the view of the blunt pole, which are 46 and 24 mm, respectively. The factor of compaction is hence 47.8%. Hence, the original inclination angle would have been approximately 37–44°.

Clutch PFMM-0014004392.—PFMM-0014004392 has 32 eggs arranged in three rings. There are ten eggs in the innermost ring and 18 eggs in the second ring. The third, outermost ring is composed of two separate pairs of eggs (Fig. 1D, Table 2). The first, innermost ring has a longer diameter of 200 mm and a shorter diameter of 186 mm (Fig. 1D, Table 2). The second ring has a longer diameter of 305 mm and a shorter diameter of 300 mm (Fig. 1D, Table 2). The measured inclination angle of the eggs ranges from 28–35°.

Clutch PFMM-0014003019.—PFMM-0014003019 was prepared from field bottom. It has 35 eggs arranged in three rings (Fig. 1E). The innermost ring containing five pairs of eggs has a longer diameter of 293 mm and a shorter diameter of 280 mm. The second ring consisting of nine pairs of eggs has a longer diameter of 350 mm and a shorter diameter of 325 mm (Fig. 1E, Table 2). The third ring has seven eggs

(three pairs and one single egg) distributed predominantly at the upper left side (Fig. 1E). The measured inclination angle of the eggs ranges from 30–34°.

Developmental stage inferred from eggshell microstructure.—The radial sections of the eggshell from the adult-associated clutch (IVPP V9608, Fig. 3A) and new clutches (Fig. 3B–F) show intact mammillary layers, representing the absence of embryo-induced erosion. The absence of embryo-induced erosion indicates that the eggs would have not started development yet or were at an early stage of development.

General description of studied oviraptorid clutches.—The eggs in all studied oviraptorid clutches were arranged in pairs with their blunt ends pointing to the center devoid of eggs, and stacked in two to four concentric, nearly circular to elliptic rings with sediment in between (Fig. 1C₂). The lowermost, or innermost, ring has the smallest diameter and the lowest number of eggs, and both parameters increase towards the top and perimeter of the clutch. The innermost ring size of the five complete clutches ranges from 133 × 105 mm to 293 × 280 mm, and the second ring ranges from 275 × 200 mm to 350 × 325 mm (Table 2). All clutches contain only unhatched eggs as indicated by the intact blunt end of all eggs (Fig. 2) and show a distinct paired arrangement (Sato et al. 2005). Our observation of the studied clutches suggests an in situ and undisturbed preservation mode, echoing He et al.'s (2017) taphonomic observation in the Ganzhou area. (He et al. 2017).

The clutch size varies from 30 to 35 eggs (Fig. 1A, B, C₁, D, E, Table 2) and have similar inclination angles (27–40° from the horizontal) towards the center of the clutch (Fig. 1). The vertical distance between the highest and lowest ring ranges from eight to ten cm (Fig. 1C₂). The inclination angle does not vary between the rings of a single clutch. The lower egg ring in all of the complete clutches in this study has a gap devoid of eggs (Fig. 1A, B, C₁, D, E). The gap in HGM-41H-V0074 is around 110 mm and could have accommodated another pair of eggs (Fig. 1A). However, the gap in the other specimens is smaller than the width of a pair of eggs (Fig. 1B, C₁, D, E).

Discussion

Clutch size.—The adult-associated clutches, which were discovered in the Gobi Desert, yield various numbers of eggs per of clutch size, ranging 6–22 (Norell et al. 1995, 2018; Dong and Currie 1996; Clark et al. 1999; Fanti et al. 2012), all of which are lower than the previous estimate of 30 (Varricchio et al. 2008; Weishampel et al. 2008). These clutch sizes were obtained from scientifically excavated specimens, unlike the southern Chinese specimens that are typically excavated by non-scientists. The new oviraptorid clutches from southern China described in this study, however, have a clutch size beyond 30, significantly larger than the adult-associated clutches. Here we proposed four hypotheses to explain the difference in clutch size between the adult-associated and the new oviraptorid clutches: (i) clutch size increases with body size; (ii) clutch size decreases with latitude; (iii) the clutches from the Gobi Desert were not completed at the time of burial; (iv) the Gobi Desert clutches were laid by a different oviraptor species than the southern Chinese ones; (v) the Gobi Desert the clutches are incomplete because of taphonomic processes such as incomplete burial or loss to weathering.

The first hypothesis can be rejected because *Citipati osmolskae* from the Gobi Desert and oviraptorids from southern China have a similar estimated body mass (50 kg vs. 42.4 kg, see the Varricchio et al. 2008: supplement and Lü 2003) but differ significantly in clutch size (12–15 vs. 30–35, see Table 1 and references therein, Table 2).

The third hypothesis was briefly mentioned by Dong and Currie (2006) but not further discussed by later workers. The significantly smaller clutch size of the adult-associated clutches could be interpreted as evidence that the clutch-associated adults were in the period of, or shortly after, an oviposition. However, the third hypothesis can only be supported if the interspecific variation (the fourth hypothesis) in clutch size can be rejected, which is currently not possible.

The fourth hypothesis discusses whether the observed maximum clutch sizes (30–35) are an original biological signal or a taphonomic signal. The intact appearance of the studied clutches indicates that all clutches are completely preserved as suggested by He et al. (2017). Therefore, the

observed clutch sizes are very likely original biological signals instead of taphonomic signals. The single egg in the outermost ring of specimen PFMM-0014003019, however, is suggestive of incomplete preservation or collecting and indicates that original clutch size could have been larger. Because of the shelter of the sitting adult and the excavation by trained scientists, the adult-associated clutches very likely represent the original clutch size. Thus, we conclude that the adult-associated clutches from the Gobi Desert were significantly smaller than the egg clutches from South China in our study. We are thus unable to falsify the fourth hypothesis and thus support the second (latitudinal decrease) and third (uncompleted clutch) hypothesis. In the later discussion, we will put emphasis on the evidence arising from the new oviraptorid clutches and their implication for oviraptorid nesting biology.

Paired and highly organized clutch arrangement of oviraptorids: paleobiological implications.—The paired arrangement in oviraptor clutches implies monoautochronic ovulation, which means two functional oviducts, each producing one egg per oviposition. Monoautochronic ovulation is an extinct mode of reproduction that was first proposed by Varricchio et al. (1997) for oviraptorids. The concept was supported by the paired egg-containing oviraptorosaurian pelvis (Sato et al. 2005) and numerous reports of egg pairing in oviraptorid clutches (Norell et al. 1995, 2018; Dong and Currie 1996; Clark et al. 1999; Deeming 2002; Fanti et al. 2012; Tanaka et al. 2018). As noted above, Grellet-Tinner et al. (2006) had doubted that the pairing in *Troodon* clutches is statistically significant, and this question also applies to oviraptor clutches. However, the paired arrangement is unequivocal both from the top view and from the bottom view of the new clutches (Fig. 1). Based on the highly-organized and paired clutch arrangement, it has been argued that oviraptorid eggs were not manipulated after being laid, suggesting that they had no chalazae, similar to *Troodon* eggs (Varricchio et al. 1997; Varricchio and Jackson 2003, 2016). While eggs in a *Troodon* clutch are also highly organized and paired, they present two features different from oviraptorid eggs, including a nearly vertical egg inclination and the absence of a center devoid of eggs (Varricchio et al. 1997; Zhao 2003; Zelenitsky et al. 2012; Varricchio and Jackson 2016).

Some modern birds such as blackbirds (*Turdus merula*) also arrange their clutch in a specific pattern, possibly for recognition of foreign eggs (Polačiková et al. 2013; Hanley et al. 2015). Such a specific egg arrangement in blackbirds, however, is a result of post-laying parental manipulation rather than an original arrangement. On the other hand, the specific highly organized arrangement pattern of oviraptorid clutches must represent an original pattern without later disturbance by parental manipulation (Varricchio et al. 1997; Varricchio and Jackson 2003, 2016). Besides, some avian clutches show a recognizable center (Boulton and Cassey 2012; Šálek and Zárbynická 2015), yet it is not devoid of eggs, a distinctive feature in oviraptorid clutches. Oviraptorid clutches thus

present a unique arrangement that is not analogous to any extant or extinct clades of egg-laying amniotes.

A review by Varricchio and Jackson (2016) proposed five stages in the evolution of reproduction from basal theropods to neornithines, namely (i) pre-maniraptoran theropods, (ii) oviraptor-grade maniraptorans, (iii) troodontid-grade paravians, (iv) Enantiornithes, and (v) basal Neornithes. The highly organized and paired arrangement is only present in the oviraptor-grade maniraptorans and troodontid-grade paravians.

Notable, some seemingly complete oviraptorid clutches have an odd number of eggs in the clutch, for instance clutch DM-2014-P0154 (Fig. 1B). Assuming dual oviducts, an oviraptorid clutch should always comprise an even number of eggs. The first possible explanation is that the oviraptorid dinosaur might have laid only one egg because of insufficient calcium supply, which is commonly observed in modern birds (Chambers et al. 1966). Second, it is also possible that the oviraptorid dinosaur pushed some eggs out of the nest in order to save the remaining eggs from predators, as ostriches do (Bertram 1992a). HGM-41H-V0074 supports the second hypothesis, since two eggs are notably further away from the clutch center than the remaining eggs (Fig. 1A).

The gap devoid of eggs in the inner ring can be explained by two hypotheses: (i) The gap is the female's exit after completion of the first ring for intermittent rest during protection or incubation; (ii) the gap is simply a larger space between two pairs of eggs resulting from ring geometry and egg laying behaviour. The first hypothesis was hinted at by Sato et al. (2005) who suggested that females came to the center of the nest to lay neat, multilayered, ring-shaped clutches. This would be consistent with the communal nesting behavior inferred from chemical evidence (Yang et al. 2016). If oviraptorid dinosaur exhibited similar sexual and communal nesting behaviors to modern ostriches, oviraptorid dinosaurs might have intermittently left their nests as modern ostriches do. To leave the nest without destroying the highly organized clutch, the female might have to leave a gap as an exit. The "exit" hypothesis would be testable by trackway evidence but no tracks have so far been discovered near any of the studied clutches. The "exit" hypothesis also fails to explain the lack of gaps in the second and third rings.

Our measurements show that most of the gaps are too small to have accommodated another pair of eggs. Without the female being able to exactly calculate the radius of a circle for a given egg size (which appears unlikely), the sequential laying of egg pairs in the ring (by one or more females) inevitably would result in an improper fit as the last pair was deposited. This effect would be more pronounced in a smaller circle with fewer eggs, i.e., the first one, because each pair takes up a larger segment of the circle.

Reconstruction of mound nest architecture and laying process.—As reviewed above, previous studies had suggested that the oviraptorid dinosaur laid eggs in a pit (Norell et al. 1995), on an open mound (Dong and Currie 1996), in

a covered mound (Mou 1992; Deeming 2002, 2006), or in a partially open mound (Martin and Simmons 1995; Carpenter 1999; Fanti et al. 2012). Some of these previous studies, however, failed to consider the original egg inclination angle and illustrated a clutch of horizontally positioned eggs. Our estimation of the inclination of eggs in an oviraptorid clutch of 35–40° supports the idea that oviraptors built a nesting mound, as already posited by Sabath (1991). However, porosity distribution suggests a partially open nest (Yang et al. 2015; Wiemann et al. 2017) and not a covered one, supported by the presence of shell pigmentation (Wiemann et al. 2017), with the blunt end of the eggs exposed to the air.

Combining these facts, including the nest type, shell porosity data, shell pigmentation, and geometry of an oviraptorid clutch, we suggest that the eggs were laid leaning on the flanks around a mound. After finishing the first (or innermost) ring, the female(s) partially covered the first ring of eggs with soil but leaving the blunt end exposed before continuing with the second ring of eggs. Finally, all blunt ends of the eggs were exposed to the air, while the acute ends were buried in soil or sediment, as suggested by shell porosity data (Yang et al. 2015; Wiemann et al. 2017). However, we do not know if the last ring of eggs also was partially buried or left open as depicted, e.g., in Tanaka et al. (2018).

This nest architecture described above raises questions about the exact behavioral program of the females producing it, which is the next research focus, requiring the collection of more data. However, at this time hypotheses can be formulated and ways to test them are offered. Any one of the rings could have been produced by laying one pair after the other in a clockwise or counterclockwise direction until the ring was complete. Next, this pattern would be repeated twice until the animals involved deemed the clutch completed. Alternatively, the pairs in a ring could have been deposited randomly or in opposed locations on a ring structure, for which there also is some evidence because incomplete upper rings show sometimes pairs in opposite locations and nothing in between (e.g., Fig. 1D). There is no evidence, however, for an upper ring having been started before the lower ring was completed. These hypotheses could be tested in a clutches that preserves embryos of different developmental stages, as seen in the fragmentary clutch described by Yang (2018). Relative internal shell resorption observed in samples from homologous locations in each egg of a clutch could also provide this relative time information. Finally, the careful architectural analysis of a sample of clutches significantly larger than covered in this study will shed light on these hypotheses.

Although mound-building in megapodes has been used as analog for oviraptor mound nests in the past (e.g., Coombs 1989), current phylogenetic hypotheses for birds make it clear that mound nesting is an apomorphic character in megapodes which form a monophyletic group of galliform birds (Hansell 2000). In addition, megapode nests are very different from those of oviraptors and make a poor analog. Megapodes bury all eggs in the mound without exposing

them to the air, and the eggs are distributed in the mound in an irregular fashion, having been laid into the finished mound (Jones et al. 1995).

A reevaluation of the meaning of the adult-associated oviraptor clutches.—Four hypotheses have been proposed for explaining the unique oviraptorid adult-associated clutch specimens: (i) egg stealing, (ii) brooding/TCI, (iii) protection, and (iv) egg laying, as reviewed in the introduction. Although the hypothesis of brooding/TCI is now commonly accepted, criticism has been offered from the perspectives of biology and ornithology (see Introduction). In the following discussion, we put emphasis on reevaluating the TCI hypothesis based on reviewing previous arguments and evidence arising from this study in various aspects.

Based on our re-examinations of the IVPP and IGM specimens and the comparison with complete clutches, we concur with Deeming (2002) in that it appears unlikely that the oviraptorid skeleton-clutch associations represent TCI behavior. Using the definition from avian biology, the act of incubation comprises an adult's behavior of sitting atop its eggs with direct body-egg contact to transfer body heat from the adult to the eggs. The multi-ring clutch must have prevented sufficient heat transfer to the inner rings of eggs because of their topographically lower position in the clutch and an overburden consisting of sediment and eggs in the outer rings, as already noted by Deeming (2002). The steep angle of the eggs arranged in the nest would also have hindered the heat transfer because the contact surface between any one egg in the clutch and the warm parent body would have been rather small and insufficient for incubation. A multidimensional heat transfer model developed for chicken eggs also showed that the heat transfer is more efficient in horizontal direction than in vertical direction (Turner 2002), which explained why birds arrange their eggs at a gentle angle to the ground, increasing the body-egg contact. An important part of avian TCI is the manipulation of the eggs in a clutch to provide them with heat evenly. However, a fixed clutch architecture of the kind seen in oviraptors certainly would have precluded this behavior, again arguing against TCI.

Another line of evidence from clutch architecture also contradicts the TCI hypothesis; this is the center devoid of eggs. Birds incubate their eggs under their brood patch. This is a feather-less region on an incubating bird's belly that allows for efficient heat transfer to the incubated eggs. Any heat generated by the brooding oviraptor would have heated the sediment, not the eggs. An incubating bird keeps its eggs close to its body (brooding patch) by building the nest as small as possible, allowing for efficient heat transfer and equal covering of the eggs. Hopp and Orsen (2004) suggested that the supposedly incubating oviraptorids used their feathered wings to cover the whole clutch. Nevertheless, the skeletal reconstruction by Fanti et al. (2012) showed that *Nemegtomaia* would not have covered the whole clutch because it was too large. Our re-examination of specimen IVPP

V9608 also shows that the eggs are not completely covered by the sitting adult's heat-generating abdominal region.

Furthermore, in a modern avian paternal care system such as in ostriches (Bertram 1992b), the male comes to start incubating after the clutch is completed and thus initiates development of the eggs. Therefore, if oviraptor males did incubate the clutch after the completion of the clutch, as suggested by Varricchio et al. (2008), all eggs would have been at a similar developmental stage. However, a recent study has shown this not to be the case (Yang 2018). Oviraptorid embryos at various developmental stages in the same clutch thus indicate that the incubation behavior of oviraptorids might be not as well-developed as of modern birds (Weishampel et al. 2008). Within-clutch variation of development in some modern birds, resulting in hatching asynchrony, however, is related to environmental conditions or sexual dimorphism (Cook and Monaghan 2004; Barrientos et al. 2016).

Implications of isotope geochemistry for TCI.—Isotope geochemical research potentially contributes to testing the TCI hypothesis. Eagle et al. (2015) determined body temperature of oviraptor females during periods of ovulation based on the clumped isotope analysis of eggshells. Assuming that no alteration of the isotopic signal occurred during diagenesis, the temperature recorded is the one during egg formation which is the same as the mother's body temperature. The results of Eagle et al. (2015) showed a significantly lower body temperature in oviraptors than in modern birds. This would suggest the oviraptors had a thermoregulatory mode not analogous to modern birds and may not have produced the amount of metabolic heat required for TCI. However, another recent study (Amiot et al. 2017) from the field of isotope geochemistry concluded that both the eggshell (formed inside the mother) and the embryonic bone (formed inside the eggs after oviposition) formed at temperatures of 35–40°C. Amiot et al. (2017) then went on to suggest that oviraptors incubated their eggs at this temperature, which is similar to the body and incubation temperature in modern birds (for example, 36–40.5°C in chickens; Lundy 1969). Thus, the results of Eagle et al. (2015) and Amiot et al. (2017) for the temperature of eggshell formation and thus parental body temperature contradict each other, and a solution will require further research. Whereas the high embryonic bone formation temperatures found by Amiot et al. (2017) are consistent with TCI, such high temperatures could have resulted from incubation heat supply from the environment, perhaps enhanced by specific behavior of an attending adult.

Stage of development of eggs from adult-associated clutches.—Incubation temperature plays a critical role in archosaur embryonic development. The embryos of extant birds using TCI (virtually all birds except Megapodidae) show an increased developmental rate after the adult starts incubating (Chaiseha and El Halawani 2015), and embryonic development is inhibited when external heat provided by incubation is lacking. However, no embryonic remains have so far been reported from the eggs of any of the adult-as-

sociated clutches (Osborn 1924; Norell et al. 1995, 2018; Dong and Currie 1996; Clark et al. 1999; Fanti et al. 2012), although many of the eggs reveal their inside in fractures. In addition, embryos from clutches not associated with adults are sufficiently frequent finds in Mongolia, Inner Mongolia and South China to suggest that the general taphonomic conditions would have allowed embryo preservation in adult-associated clutches. Furthermore, embryo-induced shell erosion is absent in adult-associated clutches (see Norell et al. 1995: fig. 2 and the new specimens reported in this study shown in Figs. 1 and 3A), indicate that the eggs of the adult-associated clutches did not start development yet or were at an early stage of development.

Perhaps significantly, none of previously reported oviraptorid embryo-containing eggs were associated with an adult despite a number of discoveries (Norell et al. 1994; Weishampel et al. 2008; Cheng et al. 2008; Wang et al. 2016). Norell et al. (2018) re-examined the first oviraptorid adult-associated clutch (AMNH FARB 6508 and 6517, see Osborn 1924) and reported the remains of a juvenile (perinate) oviraptorid (AMNH FARB 33092) that was found with the adult-associated clutch, yet it is uncertain if this perinate oviraptorid had hatched from the clutch. Eggshell sampling from the eggs in clutch AMNH FARB 6508 could indicate if the eggs were close to hatching at the time of burial. Thus, the lack of evidence for embryo development in the adult-associated clutches argues against TCI, although comprehensive sampling of all adult associated clutches is clearly necessary.

Alternative hypotheses to TCI.—To briefly conclude, the different lines of evidence introduced above questioned the TCI hypothesis as an explanation for the adult-clutch associations. If the clutch-associated adults were not incubating their clutch, their brooding (sitting) posture might correspond to pre-oviposition, the process of oviposition, post-oviposition, or protection. The absence of eggs inside the clutch-associated adults (and their presence in at least one other skeleton) suggests that the clutch-associated adults were not in the stage of pre-oviposition or oviposition, possibly because they were males. These observations and hypotheses are consistent with the lack of medullary bone in several individuals that were sampled histologically (Erickson et al. 2007; Varricchio et al. 2008). If this smaller clutch size was not a result of incomplete recovery of the fossil or interspecific variation of fecundity, the significantly smaller clutch size of the adult-associated clutches compared to isolated clutches (Tables 1, 2, and references therein) is consistent with the hypothesis that clutches were still in the process of production. The female would not have completed laying her eggs when she died, and the clutch thus failed to be completed by other females as it might have been buried by a sandstorm, if this smaller clutch size was not a result of incomplete recovery of the fossil or interspecific variation of fecundity.

Implications for nest architecture in oviraptorosaurs in general.—Caenagnathid and oviraptorid dinosaurs constitute the theropod clade Oviraptorosauria. As noted, and is

the subject of this study, the reproductive biology of oviraptorid dinosaurs was extensively explored based on the paired eggs in an oviraptorosaurian gravis (Sato et al. 2005), oviraptorid adult-associated clutches (Osborn 1924; Norell et al. 1995, 2018; Dong and Currie 1996; Clark et al. 1999; Fanti et al. 2012), and oviraptorid embryo-containing eggs (Norell et al. 1994; Clark et al. 1999; Weishampel et al. 2008; Cheng et al. 2008; Wang et al. 2016). On the other hand, reports of caenagnathid clutches or embryo-containing eggs are rare (Huh et al. 2014; Simon 2014) and were not recognized as such before macroelongatoolithid eggs were associated to caenagnathids based on a *Beibeilong sinensis* perinate (Pu et al. 2017). Based on this association, caenagnathid clutches are also composed of two or more rings of eggs with the blunt ends pointing to the center devoid of eggs, which is comparable to oviraptorid clutches (Pu et al. 2017; Tanaka et al. 2018). These similarities suggest that our interpretation of oviraptorid clutches may also apply to macroelongatoolithid clutches and that this unique clutch architecture was an apomorphic character of oviraptorosaurs, though more studies are required to test this inference.

Open questions pending for more investigations.—The detailed descriptions of five remarkable oviraptorid clutches and the reconstruction of their clutch architecture in our study not only shed lights on the reproductive biology of oviraptorid dinosaurs but also generate more open questions about their bizarre reproductive biology. While Varricchio et al. (2008) provided statistical evidence for communal nesting behavior in oviraptorid dinosaurs, it is still uncertain if an oviraptorid clutch was contributed by several females and if the contributing females mated with the same male. If this is true, then how many females contributed to a clutch and how long did it take to finish a clutch? Was the sitting adult of the adult-associated clutches female or male? Furthermore, why did the oviraptorid dinosaurs built such a highly organized clutch and how did they manage to do so? A valuable start has been made by Tanaka et al. (2018), who proposed that oviraptorosaurian egg rings enlarged allometrically with increasing egg size for accommodating bigger body size. However, such a highly organized clutch arrangement is still mysterious and pending for more investigations of the type outlined above in the section “Reconstruction of mound nest architecture and laying process”.

Conclusions

Varricchio and Jackson (2016) suggested that oviraptor-grade maniraptorans represent one of five evolutionary stages of reproduction from basal theropod dinosaurs to neornithines. The reproductive biology of oviraptorid dinosaurs is therefore crucial for further understanding the evolution of reproduction from dinosaurs to birds. Although a number of previous studies have attempted to investigate oviraptorid clutches, this study aims to rigorously describe

oviraptorid clutch architecture based on evidence from new isolated clutches and reevaluation of clutch-adult associations. We conclude that the oviraptorid nest showed the following features: (i) the nest was a mound with a slope inclination 35–40° on which the eggs were leaning. (ii) Clutch architecture is highly organized: the eggs are arranged in pairs, and these pairs are themselves arranged in three to four elliptical rings with sediments interbedded in between. (iii) The inner ring was the topographically lowest, with successive rings being eight to ten cm higher. (iv) Since egg distance and egg pair distance remained constant, number of eggs per ring increases outwards. (v) The clutch has a center devoid of eggs. (vi) The eggs were pigmented and partially exposed to the air. We note that oviraptorid dinosaur clutches, or even all oviraptorosaur clutches, lack modern analogs and are so unique that they represent an apomorphic nesting trait deviating greatly from the strategies characterizing the bird stem line. Our study also infers the extinct reproductive biology of oviraptorid dinosaurs based on the same fossils. Our results indicate that oviraptorosaur reproductive biology was similarly unique to their clutch architecture and may not inform as much on the evolution of bird reproductive traits as one would wish.

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