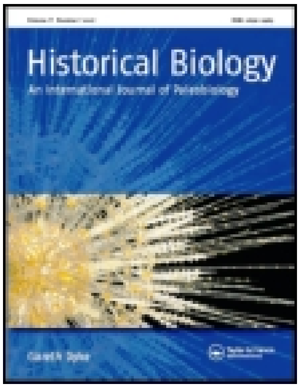

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First record of a complete giant theropod egg clutch from Upper Cretaceous deposits, South Korea

Min Huh[a], Bo Seong Kim[b], Yeon Woo[a], D. Jade Simon[c], In Sung Paik[d] & Hyun Joo Kim[d]

[a] Korea Dinosaur Research Center and Faculty of Earth Systems and Environmental Sciences, Chonnam National University, Gwangju 500-757, Republic of Korea

[b] Mokpo Natural History Museum, Mokpo 530-839, Republic of Korea

[c] Department of Earth Sciences, Montana State University, Bozeman, MT 59717, USA

[d] Department of Earth Environmental Sciences, Pukyong National University, Busan 608-737, Republic of Korea

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Min Huh[a]*, Bo Seong Kim[b], Yeon Woo[a], D. Jade Simon[c], In Sung Paik[d] and Hyun Joo Kim[d]

[a]*Korea Dinosaur Research Center and Faculty of Earth Systems and Environmental Sciences, Chonnam National University, Gwangju 500-757, Republic of Korea;* [b]*Mokpo Natural History Museum, Mokpo 530-839, Republic of Korea;* [c]*Department of Earth Sciences, Montana State University, Bozeman, MT 59717, USA;* [d]*Department of Earth Environmental Sciences, Pukyong National University, Busan 608-737, Republic of Korea*

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Here, we report the first occurrence of a complete *Macroelongatoolithus* clutch from outside of China. Excavated from Upper Cretaceous strata of Aphae-do in Shinan-gun, Jeollanam-do Province, South Korea, the clutch of 19 eggs is characterised by large, elongate, symmetrical eggs arranged in a single-layered ring-shaped clutch. Eggs are inclined towards the centre of the 2.3-m diameter clutch, and average 41.17 cm long and 15.58 cm wide. Of the 19 eggs, 8 clearly retain a paired configuration. This specimen represents only the second report of large theropod eggs from South Korea and is the most complete *Macroelongatoolithus* clutch known from the region to date. Eggshell microstructural features are consistent with *Macroelongatoolithus xixiaensis* (oofamily Elongatoolithidae), previously known only from Cenomanian strata of southeastern China. This first record of a giant theropod egg clutch, here assigned to *M. xixiaensis*, extends the stratigraphic and paleogeographic range of *Macroelongatoolithus* eggs and parent animals to include the Campanian of South Korea.

Keywords: giant theropod clutch; Aphae-do, Korea; Upper Cretaceous; *Macroelongatoolithus xixiaensis*; Elongatoolithidae; oviraptorid; dinosaur eggs

Introduction

Eggshell fragments discovered in 1972 from deposits in the Hasandong Formation, South Gyeongsang Province, were the first dinosaurian remains of any type found in Korea (Lee et al. 2001). Intact fossil eggs were not discovered in the country until 1996, when at least six elongate specimens were excavated from mudstones only 50 m from the 1972 eggshell find (Yun and Yang 1997). Subsequent authors reported dinosaur eggs and clutches, including massive nesting grounds in Gyeonggi Province (Lee et al. 2000), from several sites within and nearby the Gyeongsang basin; Hasandong (Paik et al. 2012), Sinsu-do (Yun et al. 2004), Goseong (Paik et al. 2006) and Tongyeong (Kim, Yang, et al. 2011). In addition, dinosaur eggs and eggshell have been reported from regions outside of the western portion of the Gyeongsang basin including deposits within Boseong (Huh and Zelenitsky 2002; Paik et al. 2004; Huh et al. 2006) and Shiwha basin (Lee et al. 2000; Lee 2003).

While the frequency of dinosaur egg discoveries has increased in recent years, most of those formally described from Korean localities belong to the oofamilies Faveoloolithidae (Huh and Zelenitsky 2002; Paik et al. 2012) and Spheroolithidae (Huh and Zelenitsky 2002) – ootaxa circumstantially linked to members of the Sauropoda or Ornithopoda, respectively (Huh et al. 2006). Faveoloolithid eggs are presumed to belong to sauropods due to the co-occurrence of bones and eggshell within the same formation (Mikhailov 1991); however, this egg-to-parent assignment is in suspect, as faveoloolithid eggs containing sauropod embryos remain undiscovered. North American spheroolithid eggs, conversely, are strongly linked to hadrosaurid dinosaurs through embryo–egg associations (Horner 1999), suggesting that Korean spheroolithid eggs may also be referable to hadrosaurids.

An additional oofamily, the Dendroolithidae, is also represented in Korean strata (Lee et al. 2000; Lee 2003) and may be referable to theropod dinosaurs. Dendroolithid eggs have been described in association with both *Torvosarus* and therizinosauroid embryos; however, questions about the similarity of therizinosauroid eggshell to that of other dendroolithids (Zelenitsky 2004; Barta et al. Forthcoming) prevent a definite assignment of Korean dendroolithid specimens to *Torvosaurus* or a therizinosaur. Small elongate eggs (possibly theropod) and elongatoolithid (theropod) eggshell fragments have also been reported from the Shiwha Formation (Yun and Yang 1997; Lee 2003); however, the paucity of whole eggs and the lack of formal descriptions of the few found prevent a more specific assignment of this material. Intact eggs of the famously large oogenus *Macroelongatoolithus* were unknown from Korean strata until recently, when a partial clutch of large theropod eggs, assigned to the oospecies *Macroelongatoolithus goseongensis*, was described from the Upper Cretaceous (Campanian) Goseong Formation (Kim, Yang, et al. 2011).

*Corresponding author. Email: minhuh@chonnam.ac.kr

Here, we describe a complete clutch of eggs belonging to *Macroelongatoolithus*, excavated from the island of Aphae-do, Shinan-gun, Jeollanam-do province of South Korea. Only four intact clutches of these large eggs have been reported worldwide, and previous reports have typically been restricted to clutch diameter and cursory examination of egg attributes (Li et al. 1995; Wang and Zhou 1995; Grellet-Tinner et al. 2006; Wang, Zhao, et al. 2010). The Aphae-do specimen provides a widely available, thorough description of a *Macroelongatoolithus* clutch, including microstructural examination of the eggs. Given the previously demonstrated link between elongatoolithid eggs and oviraptorids (Norell et al. 1994; Dong and Currie 1996; Clark et al. 1999; Norell et al. 2001; Grellet-Tinner 2005; Sato et al. 2005; Cheng et al. 2008; Weishampel et al. 2008), the Aphae-do and Goseong *Macroelongatoolithus* clutches suggest the presence of a large oviraptorid in South Korea during the Late Cretaceous.

Institutional abbreviations

MNHM, Mokpo Natural History Museum; KDRC, Korea Dinosaur Research Center.

Geologic setting

The Gyeongsang basin is one of many transtensional sedimentary basins formed on the Korean Peninsula by subduction of the Paleo-Pacific Izanaga Plate during the Cretaceous (Chun and Chough 1992; Lee 1999; Chough et al. 2000). Within the Gyeongsang basin, extensive portions of the 9000-m-thick Gyeongsang Supergroup are exposed in Gyeonsannam-do and Jeollanam-do Provinces. The Gyeongsang Supergroup is divided into the alluvial and fluvial Sindong and Hayang Groups, and the volcanic deposits of the Yucheon Group (Choi 1986; Lee 2003; Paik et al. 2004). These strata reflect a suite of diverse fluvial paleoenvironments, including meandering stream systems, floodplain environments and alluvial plains (Paik et al. 2012). Dinosaurian taxa are primarily known from fragmentary bones and teeth throughout the Hasadong Formation and fossil egg sites within the Seonso and Shiwha formations (Lee et al. 2000; Huh and Zelenitsky 2002; Paik et al. 2004, 2012).

The Upper Cretaceous Aphae-do site is located in the southwestern portion of the Okcheon fold belt in a small, isolated basin that extends across several districts, including Haenamgun, Jindogun, Najusi-Muangun-Shinan-gun and Hampyeonggun-Yeonggwanggun (Figure 1). Deposits are predominantly red mudstones with lenticular-bedded conglomerates intercalated with calcic and vertic

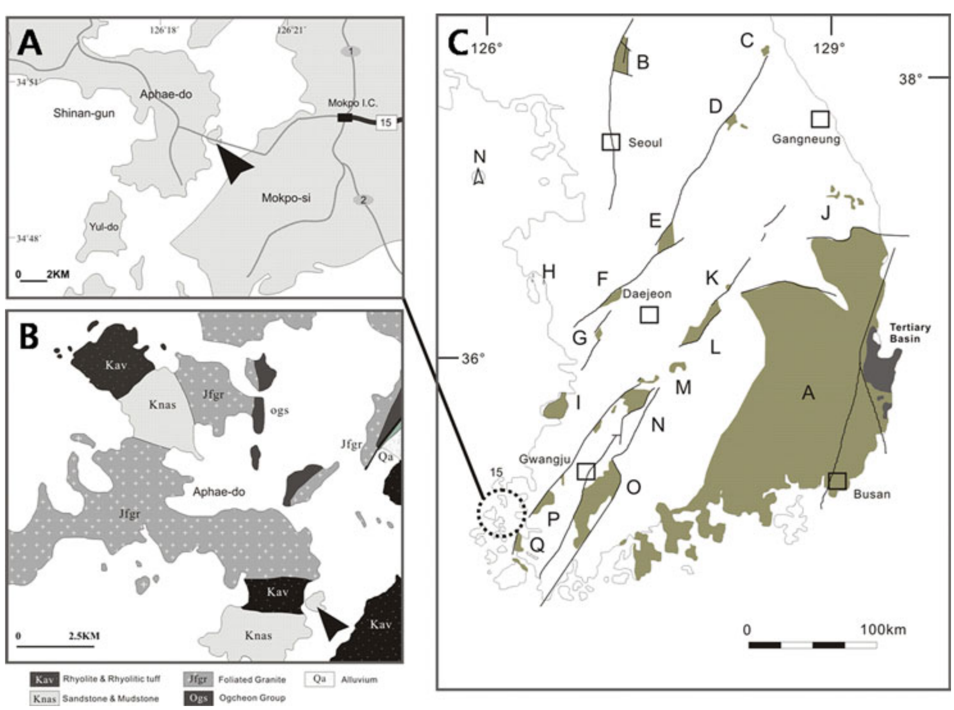

Figure 1. (Colour online) (A) Locality map and (B) geological map (modified from Choi et al. 2002) of the Aphae-do study area, arrows indicate location of the Aphae-do theropod clutch site. (C) Distribution of the Cretaceous sedimentary basins in southern Korea, indicated by shading. Open dashed circle represents the study area (modified from Kang et al. 1995). A: Gyeongsang basin; B: Chenonwon basin; C: Misiryeong basin; D: Pungam basin; E: Eumseong basin; F: Gongju basin; G: Puyeon basin; H: Cheonsuman basin; I: Kyokpo basin; J: Tongni basin; K: Jungsori basin; L: Yongdong basin; M: Muju basin; N: Chinan basin; O: Neungju basin; P: Hampyoeng basin; Q: Haenam basin.

paleosols (Figure 2) (Paik et al. 2004). Recent Ar/K dating of the strata indicates that the Aphae-do site is 77–83 Ma (Rhee et al. 2012) and therefore temporally correlated with the nearby egg-bearing Seonso Formation (81 Ma) of Boseong and the Uhangri Formation (79–81 Ma), which contains abundant track way sites of pterosaurs, non-avian dinosaurs and birds (Hwang et al. 2008).

Materials and methods

Sedimentological data were recorded from stratigraphic sections made in the field by authors I.S. Paik and H.J. Kim. Eggshell fragments were removed from the two-most complete eggs (MNHM-nat201153-6 and MNHM-nat201153-7) of clutch MNHM-nat201153 and numbered according to their position with respect to other eggs within the clutch. Twenty-nine samples were prepared as 30-μm-thick standard petrographic thin sections and studied using transmitted and polarised light microscopy.

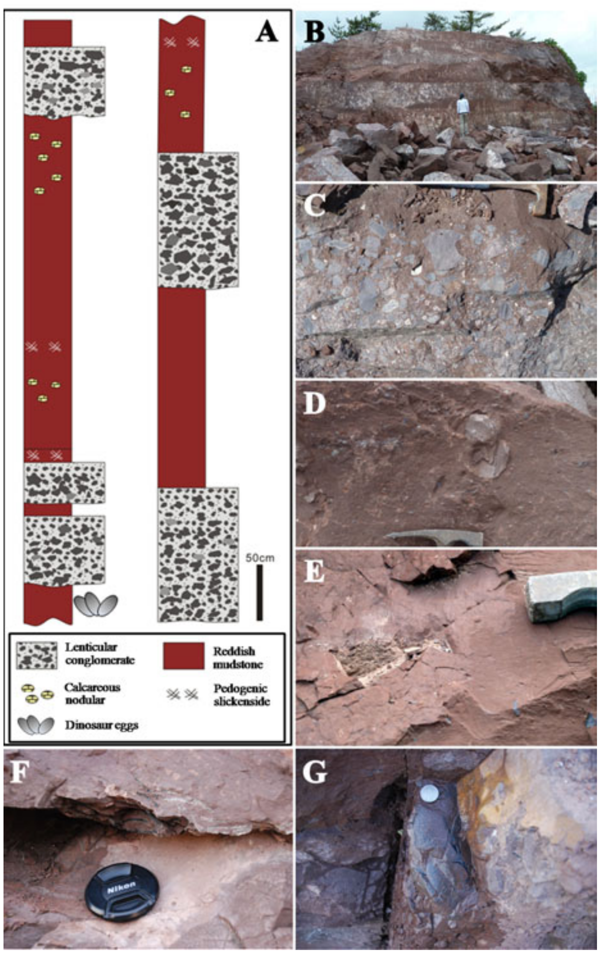

Figure 2. (Colour online) Stratigraphic section of Aphae-do dinosaur egg-bearing deposits. (A) Generalised stratigraphic section of study area. (B) Overall view of the outcrops including nesting site, figure for scale. (C) Detail view of the outcrop. (D) Calcareous nodules. (E) Pedogenic slickenside. (F) Field photograph of dinosaur eggs in Aphae-do outcrop. (G) Field photograph of dinosaur eggs in Aphae-do outcrop.

Systematic paleontology

Oofamily **Elongatoolithidae** Zhao, 1975

Included oogenera

Elongatoolithus (= *Oolithes*) Zhao and Jiang, 1974 (originally *Oolithes elongatus* Young, 1954); *Macroolithus* (= *Oolithes*) Zhao, 1975 (Originally *Oolithes rugustus* Young, 1965); *Nanhsiungoolithus* (= *Oolithes nanhsiungensis* Young, 1965); *Ellipsoolithus* Mohabey, 1998; *Trachoolithus* Mikhailov, 1994a; *Macroelongatoolithus* Li et al., 1995 [see Wang and Zhou (1995) for use of oofamily Macroelongatoolithidae. Refer to Wang et al. (2010) for assignment of oogenus *Macroelongatoolithus* to the oofamily Macroelongatoolithidae, and introduction of the oogenus *Megafusoolithus*]; *Heishanoolithus* Zhao and Zhao, 1999; *Paraelongatoolithus* Wang, Wang, et al., 2010; *Undulatoolithus* Wang et al., 2013.

Oogenus ***Macroelongatoolithus*** Li, Yin and Liu, 1995

Oolithes Young, 1965; Jensen, 1970, pp. 62–63, pl. 1, figs. 1, 2, 4, 6; pl. 2, figs. 3, 5, 6; pl. 3, figs. 4, 7, 8, text fig. 5.

Macroolithus Zhao, 1975, in part, p. 108.

Boletuoolithus Bray, 1998, in part, pp. 221–222, figs. 1–3, 4A, 4B.

Type oospecies

Macroelongatoolithus carlylei (Jensen, 1970).

Other oospecies

Macroelongatoolithus xixiaensis Li et al., 1995; *Macroelongatoolithus zhangi* Fang et al., 2000; *M. goseongensis* Kim, Yang, et al., 2011 (see Kim, Yang, et al. 2011 for placement of *M. goseongensis* within oofamily Macroelongatoolithidae).

Oospecies ***Macroelongatoolithus xixiaensis*** Li et al., 1995

M. xixiaensis Li et al., 1995, pl. 1; Fang et al., 1998, pl. 17, fig. 10, Grellet-Tinner et al., 2006, fig. 6D–F, fig. 7A–F, Jin et al., 2007, figs. 1, 2, Wang et al., 2008, fig. 4-7, 4-8, Wang, Zhao, et al. 2010, figs. 3, 4.

Longiteresoolithus xixiaensis Wang and Zhou, 1995, pl. 1; Zhou et al., 1999, pp. 298–299, fig. 1B, 1D; Zhou et al., 2001, p. 98; Liang et al., 2009.

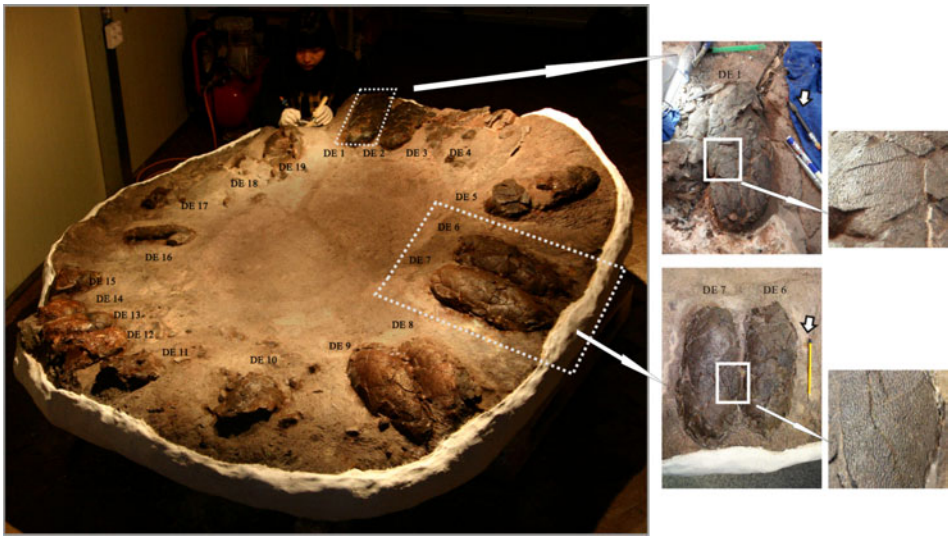

Figure 3. (Colour online) Aphae-do *M. xixiaensis* clutch, MNHM-nat201153. Insets of well-preserved eggs indicating typical elongatoolithid ornamentation grading from ramotuberculate to lineartuberculate.

Macroelongatoolithus xixia Carpenter, 1999, fig. AII.22.
Macroelongatoolithus sp. Carpenter, 1999, fig. 10.12.

Diagnosis

Large, elongate eggs 39–52 cm long and 13–18 cm wide. Elongation index ranges from 2.6 to 3.9. Continuous layer to mammillary layer ratio variable, with a distinct, undulating boundary between layers. Eggshell thickness ranges from 1.5 to 4.45 mm including surface ornamentation. Shell surface covered with coarse lineartuberculate ornamentation at equator grading to dispersituberculate at the poles. Eggs arranged in pairs within single-layered ring-shaped clutch with a central space devoid of eggs (modified after Jin et al. 2007).

Occurrence

Mid-Cretaceous (Cenomanian–Turonian), Liangtoutang Formation, Tiantai County, Zhejiang Province, China; Upper Cretaceous (Campanian), Jeollanam-do Province, Korea; Upper Cretaceous (Maastrichtian) Zoumagang Formation, Xixia County, Henan Province, China.

Material examined

MNHM-nat201153, large egg clutch including 19 eggs (MNHM-nat201153-1–19) and numerous associated fragments. Clutch, eggshell fragments and eggshell thin sections (MNHM-nat201153-5-t2, nat201153-13-t1, nat201153-13-t2, nat201153-15-t1, nat201153-15t1, nat201153-16-t2, nat201153-16-t4 and nat201153-17-t2) were housed in the MNHM, South Korea. Excavated from Aphae-do, Jeollanam-do Province, southwestern Korea (Kim, Huh, et al. 2011).

Age and locality

Upper Cretaceous (Campanian) (77–83 Ma) deposit located on the island of Aphae-do in Shinan-gun, Jeollanam-do Province, southwestern Korea.

Description

The Aphae-do clutch (MNHM-nat201153) consists of 19 eggs in a ring-shaped configuration with a maximum external clutch diameter of 2.3 m (Figures 3 and 4).

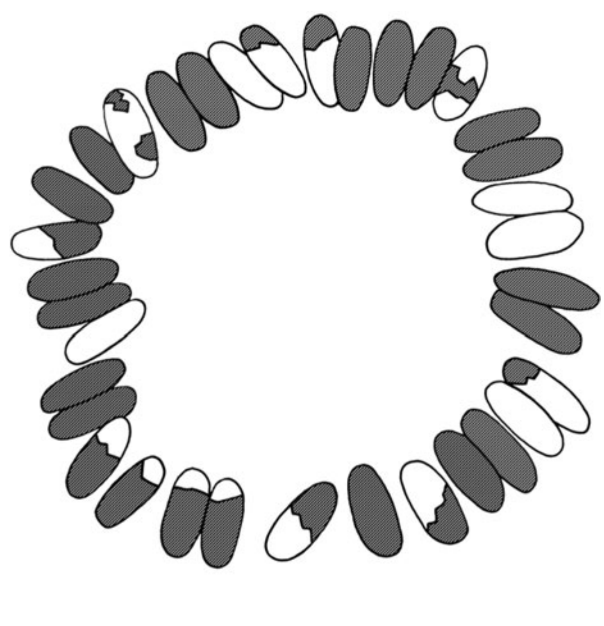

Figure 4. Line reconstruction of clutch in map view. Shading indicates missing or poorly preserved portions. Scale bar is 50 cm.

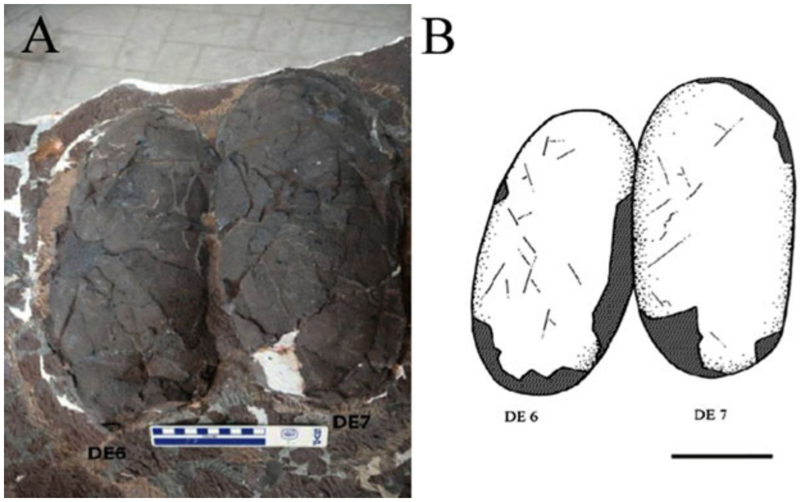

Figure 5. (Colour online) (A) Detail of DE6 and DE7. (B) Line reconstruction of DE6 and DE7. Shading indicates missing or poorly preserved sections. Scale bar is 10 cm.

Four complete and 15 partial eggs are preserved inclined towards the centre of the clutch. Of the four complete eggs, one pair shows parallel alignment; however, the sample size of intact, measurable eggs is inadequate to determine intra-egg angle among egg pairs. The eggs are symmetrical to slightly asymmetrical, elongate and appear to occur in discrete pairs arranged in a single layer (Figures 4 and 5). This contrasts with clutches of elongatoolithid eggs of smaller sizes, such as *Elongatoolithus* (eggs typically 13–17 cm in length), which often show greater asymmetry and may be found with up to three layers of eggs in stacked circular configurations (Carpenter 1999; Clark et al. 1999; Liang et al. 2009). Egg symmetry within Elongatoolithidae is highly variable and may not be a reliable diagnostic feature.

The central void of the clutch has a long axis of 1.29 m and a shorter axis of 1.12 m, giving the clutch an oval appearance. This may be a product of deformation, as previously reported *Macroelongatoolithus* clutches have been depicted as ring-shaped or circular (Li et al. 1995; Wang and Zhou 1995; Grellet-Tinner et al. 2006; Wang, Zhao, et al. 2010). The two well-preserved egg pairs occur on a single side of the clutch. The paucity of intact eggs with two exposed poles is unsuited to a meaningful assessment of some clutch attributes, such as the angle at which the eggs are in contact with the surrounding sediment. The four fully exposed, intact eggs slope away from the central area at an angle of 13°; however, this may vary along the clutch perimeter.

Intact eggs (Figure 5) measure 38.5–43 cm long × 14.5–16.5 cm wide (41.16 cm × 15.58 cm on average) and have a mean elongation index of 2.7 (Table 1). Surface ornamentation is well preserved and grades from lineartuberculate along the long axes to ramotuberculate at the poles of the eggs (Figure 6). Eggshell thickness ranges from 2.99 to 4.75 mm (including ornamentation), with the greatest measurements at the egg poles.

The eggshell consists of two structural layers of calcite, the mammillary layer and the continuous layer, separated by an abrupt and undulating boundary (Figure 7). Mammillary layer thickness ranges from 0.67 to 1.45 mm and continuous layer thickness ranges from 1.68 to 3 mm, excluding surface ornamentation. The continuous layer to mammillary layer thickness ratio (CL:ML) varies from 2.07 to 3.98 (Table 2). The mammillary layer is composed of densely packed cones of radiating calcite crystals that originate from nucleation sites at the inner eggshell surface. Shell units and crystal structure are not visible in the continuous layer in radial thin section. Although rare, crystal splaying occurs across the ML–CL boundary (Figure 7). Densely packed straight accretion lines mark the lower portion of the continuous layer. Towards the outer portion of this layer, the lines begin to conform to the topography of the surface ornamentation, parallel to the surface of the eggshell (Figure 7). The pore system is angusticanaliculate to obliquicanaliculate. In tangential, thin sections pores are distributed sporadically and are round to sub-round in cross-sectional shape (Figure 8).

Table 1. Dimensions of well-preserved eggs from MNHM-nat201153 clutch.

Egg number	Length (mm)	Width (mm)	Elongation index
1	420	155	2.7
5	430	145	3.0
6	420	150	2.8
7	420	165	2.5
9	395	165	2.5
19	385	155	2.5
Averages	411.7	155.8	2.7

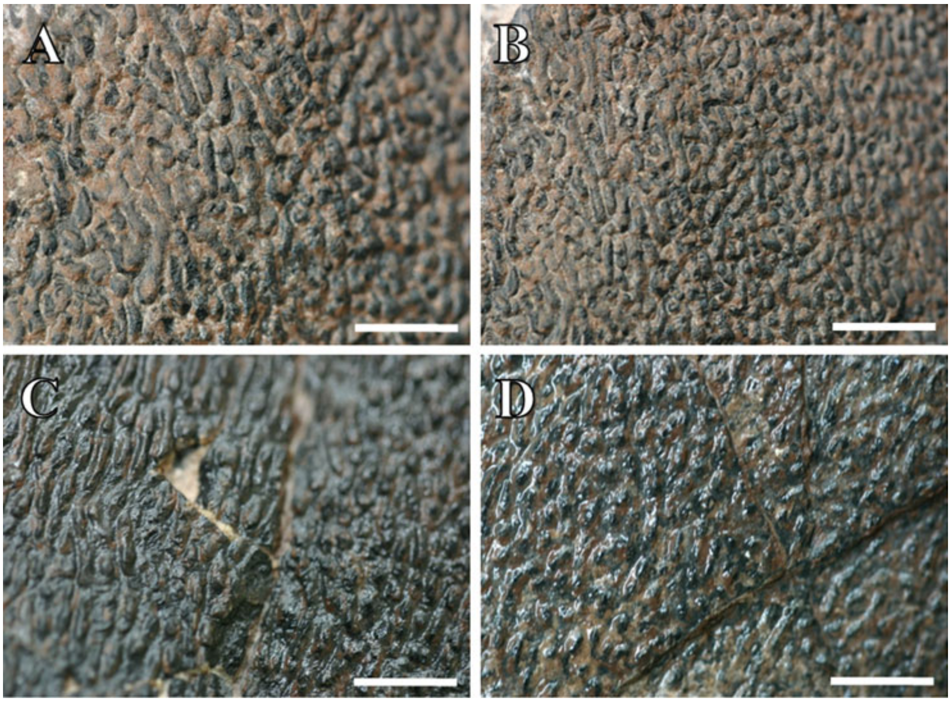

Figure 6. (Colour online) Surface ornamentation of MNHM-nat201153. (A) Gradational lineartuberculate–ramotuberculate ornamentation. (B) Gradational lineartuberculate–ramotuberculate ornamentation. (C) Lineartuberculate ornamentation from equatorial region of egg. (D) Lineartuberculate ornamentation with low relief. Scale bars are 5 mm.

Discussion

Assignment of MNHM-nat201153

The presence of two structural layers separated by an abrupt boundary, well-defined mammillary cones, accretion lines throughout the continuous layer, a straight, narrow pore system, and variable ornamentation ranging from linear ridges to nodes allow assignment of the Aphaedo eggs to the oofamily Elongatoolithidae. Gross morphology – paired elongate eggs arranged in a ring-like clutch – corroborates this assessment. The extremely large size of the eggs and clutch suggest further assignment to the oogenus *Macroelongatoolithus*, which includes oospecies *M. xixiaensis*, *M. carlylei*, *M. zhangi* and *M. goseongensis*.

As *M. carlylei* is known only from fragments and is restricted to North America, it is not used for comparative purposes here. The length, width and ML:CL ratio of eggs within MNHM-nat201153 place them well outside of the known ranges for *M. zhangi*. Rather, the overall size, ornamentation and ML:CL ratio of MNHM-nat201153 are most similar to those of *M. xixiaensis* and *M. goseongensis* (Table 3). Eggs of the MNHM-nat201153 clutch exceed the known length and eggshell thickness of *M. goseongensis*. However, *M. goseongensis* is defined on the basis of four incomplete eggs (Kim, Yang, et al. 2011), and reported measurements may not reflect the full variation of microstructural and gross morphological measurements expected within an oospecies. Due to the

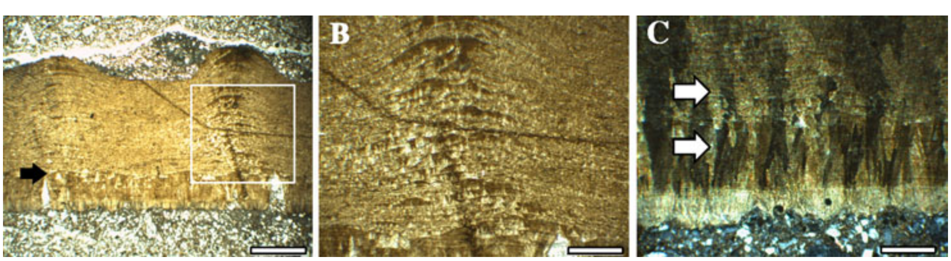

Figure 7. (Colour online) Radial thin sections of MNHM-nat201153. (A) Plane-polarised light image of MNHM-nat201153-16-t1, an eggshell fragment from DE16 (see Figure 5). Black arrow indicates abrupt, undulating boundary between continuous layer and mamillary layer. Cones in mammillary layer are densely packed. As highlighted by white square outline, accretion lines are evident in the continuous layer. Scale bar is 1 mm. (B) MNHM-nat201153-16-t1 (DE16 in Figure 6), enlargement of the box shown in A. Scale bar is 0.4 mm. (C) Cross-polarised light view of eggshell showing crystal splaying across the ML:CL boundary. Scale bar is 0.4 mm.

Table 2. Eggshell microstructure, samples from MNHM-nat201153.

Sample number	Egg number	Shell thickness (mm)	ML (mm)	CL (mm)[a]	CL:ML
MNHM-nat201153-5-t2	5	4.75	1.45	3	2.07:1
MNHM-nat201153-15-t1	15	3.84	0.67	2.67	3.98:1
MNHM-nat201153-16-t1	16	4.1	1.02	2.2	2.16:1
MNHM-nat201153-16-t4	16	2.99	0.67	1.68	2.51:1
MNHM-nat201153-17-t2	17	3.17	0.75	2.03	2.71:1
Averages		3.77	0.912	2.316	2.69:1

[a] Continuous layer measurement does not include eggshell ornamentation.

high variability of the ML:CL ratio documented within *M. xixiaensis* and the overlap of diagnostic features (such as overall size, ornamentation and ML:CL ratio) between *M. xixiaensis* and *M. goseongensis*, we feel that *M. goseongensis* may be synonymous with *M. xixiaensis* and it is therefore most parsimonious to assign MNHM-nat201153 to *M. xixiaensis* at this time (Table 3). Further exploration of overlapping features between these two oospecies is outside the scope of this study; however, a thorough review is needed to ascertain the validity of the two as distinct ootaxa and is underway by one of the authors (D. Simon).

Ootaxonomic considerations

Wang et al. (2010) report a specimen of *M. xixiaensis* that exhibits nodose ornamentation along the entire length of the egg, in contrast to the typical ramotuberculate to lineartuberculate gradational pattern of other *Macroelongatoolithus* specimens. Based on this, Wang et al. (2010) reinstated the previously disregarded oofamily Macroelongatoolithidae Wang and Zhou, 2005, claiming the large size of *Macroelongatoolithus* and predominately nodular ornamentation of some specimens within this group as causes for their removal from Elongatoolithidae. The former oogenus was subsequently placed into Macroelongatoolithidae and split into two oogenera, *M. xixiaensis* and *Megafusoolithus qiaoxiaensis* (the former oogenus and species extrapolated from a partially preserved egg alone). This division was based on variability in ornamentation and minor variation of the ML:CL ratio (Wang, Zhao, et al. 2010).

Extensive weathering of the *Macroelongatoolithus* specimen reported by Wang et al. (2010) and partial preservation of these eggs renders this ootaxonomic revision suspect. Linear ridges are sometimes made up of closely spaced nodes arranged in a straight or faintly undulating line. When weathered or eroded they may resemble isolated nodes. In addition, clutch features used to justify a separate oofamily for *Macroelongatoolithus* specimens include egg size, clutch diameter and the lack of multiple tiers of eggs. These differences may simply reflect the large size of the eggs themselves or the egg-laying animal rather than taxonomic variance of sufficient

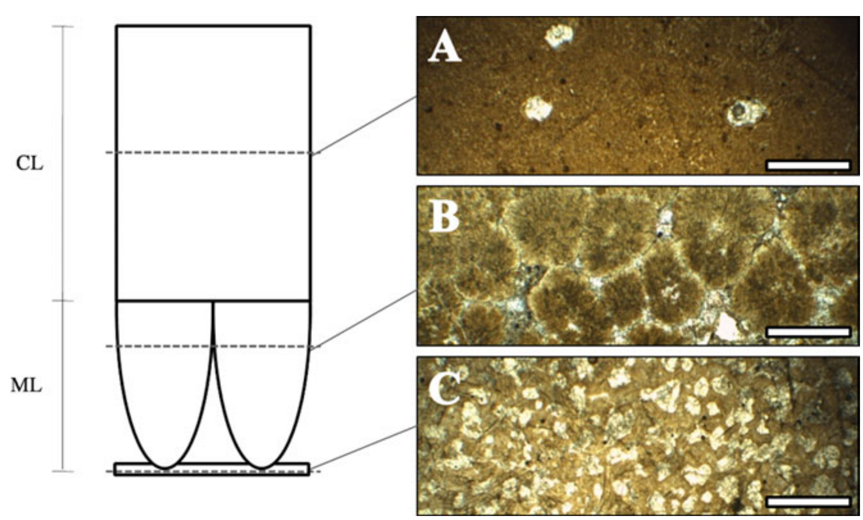

Figure 8. (Colour online) Tangential sections through eggshell at varying heights, viewed under plane-polarised light. (A) MNHM-nat201153-13-t2, section through continuous layer. Pores are irregularly distributed and circular to sub-circular in shape throughout the continuous layer. Scale bar is 1 mm. (B) MNHM-nat201153-13-t2, section through mammillary layer. Note dense arrangement of mammillary cones. Scale bar is 0.4 mm. (C) MNHM-nat201153-13-t2, section through base of mammillary layer. Scale bar is 1 mm.

Table 3. Comparison of oospecies (and synonymous/unresolved taxa) belonging to the oogenus *Macroelongatoolithus*.

Oospecies	Length, width (mm)	Ornamentation	CL:ML	Boundary	Location	Age	Source
M. xixiaensis	393–516, 79–130	Nodular	3.1:1	Abrupt	Zoumagang Fm, Henan Province, China	Mid Cretaceous	Li et al. (1995)
M. xixiaensis	430, 145	Variable	3.0:1	Abrupt	Liangtoutang Fm, Zhejiang Province, China	Mid Cretaceous	Jin et al. (2007)
M. xixiaensis	385–430, 145–165	Variable	2.1:1 to 4:1	Abrupt	Aphae-do, South Korea	Late Cretaceous	This study
L. xixiaensis	340–610, 140–270	Weak Sagenotuberculate	2.5:1 to 2.9:1	Abrupt	Zoumagang Fm, Henan Province, China	Mid Cretaceous	Liang et al. (2009)
M. zhangi	240, 150	Variable	1.8:1	Abrupt	Chichengshan Fm, Zhejiang Province, China	Mid Cretaceous	Fang et al. (2000)
M. carlylei	Unknown	Variable	2.1:1 to 4.1:1	Abrupt	Cedar Mountain Fm, Utah, USA	Early Cretaceous	Zelenitsky et al. (2000)
M. goseongensis	390, 115	Grainy	3.4:1	Abrupt	Tongyeong, South Korea	Late Cretaceous	Kim, Huh, et al. (2011) and Kim, Yang, et al. (2011)
M. Qiaoxiaensis	Unknown	Linear	2:1 to 5:1	Ambiguous	Chichengshan Fm, Zhejiang Province, China	Late Cretaceous	Wang et al. (2010)

significance to warrant splitting the oofamily Elongatoolithidae. Due to the ambiguous nature of the ornamentation reported by Wang et al. (2010), combined with the strong microstructural similarity of *Macroelongatoolithus* to other oogenera within Elongatoolithidae, we recommend that *Macroelongatoolithus* and *Megafusoolithus* remain within Elongatoolithidae.

Temporal and geographic distribution of M. xixiaensis

Macroelongatoolithus specimens have previously been reported from China and North America (Li et al. 1995; Wang and Zhou 1995; Zelenitsky et al. 2000; Grellet-Tinner et al. 2006; Jin et al. 2007; Wang, Zhao, et al. 2010; Simon et al. 2012). The occurrence of elongatoolithid eggs over 40 cm in length indicates the presence of *Macroelongatoolithus* in Mongolia as well (Watabe and Suzuki 1997), however a more detailed description of the Mongolian material is not available. With the addition of a partial clutch from Goseong (Kim, Yang, et al. 2011) and this report of a complete clutch from the Jeolluman-do Province, the geographic range of *Macroelongatoolithus* and the associated egg-laying animal is extended to include South Korea.

Recent zircon dating of tuff beds within the Tiantai basin, China, places *M. xixiaensis* bearing beds at 98–81 Ma (Jin et al. 2007; He et al. 2013). The age of the egg-bearing sediments in this study can be constrained to 83–77 Ma (Rhee et al. 2012), extending the last known occurrence of *M. xixiaensis.* Previously, the range of *M. xixiaensis* was calculated as 109–103 Ma (Jin et al. 2007) to 88–83 Ma (Li et al. 1995).

Identity of egg-laying animal

The microstructural composition of eggs within clutch MNHM-nat201153 is most similar to eggshell types assigned to theropod dinosaurs. The oofamilies Prismatoolithidae and Elongatoolithidae are largely associated with maniraptoran theropods, specifically Troodontidae (Varricchio et al. 1997, 2002; Grellet-Tinner et al. 2006; Erickson et al. 2007; Bever and Norell 2009), *Deinonychus antirrhopus* (Grellet-Tinner and Makovicky 2006) and various oviraptorids (Osborn 1924; Norell et al. 1995; Dong and Currie 1996; Clark et al. 1999, 2001; Grellet-Tinner 2005; Sato et al. 2005; Fanti et al. 2012; He et al. 2012). One ootaxon within Prismatoolithidae has been linked to *Allosaurus fragilis* (Carrano et al. 2013). Egg-pairing within many of these ootaxa suggests that some maniraptoran theropods had two functioning oviducts (Varricchio et al. 1997; Sato et al. 2005; Grellet-Tinner et al. 2006; Jin et al. 2007; Liang et al. 2009), while large clutch size compared with adult body size may suggest paternal care and/or multiple females contributing to a single clutch (Varricchio et al. 2008). The extremely large size of *Macroelongatoolithus* eggs, clutches and the central void within these clutches indicates a large parent animal.

Multiple lines of evidence show a strong link between eggs of the oofamily Elongatoolithidae and oviraptorid theropods. These include skeleton–egg associations (Norell et al. 1995; Clark et al. 1999, 2001; Dong and Currie 1996; Fanti et al. 2012), embryos *in ovo* (Norell et al. 1994; Cheng et al. 2008; Weishampel et al. 2008), *Citipati osmolskae* and *Nemegtomaia barsboldi* specimens in brooding or protective postures over *Elongatoolithus* and *Macroolithus* clutches (Norell et al. 1995; Dong and Currie 1996; Clark et al. 1999, 2001; Fanti et al. 2012), an *Oviraptor philoceratops* specimen in close proximity to an elongatoolithid clutch (Osborn 1924) and eggs within the body cavities of adult oviraptorids (Sato et al. 2005; He et al. 2012).

The gravid females and embryos *in ovo* listed above provide definitive evidence of an oviraptorid–elongatoolithid relationship. Norell et al. (1994) first described oviraptorid embryonic material adhering to the internal surface of an elongatoolithid egg. This elongatoolithid nest contained a single *in ovo* individual as well as the remains of a peri-natal troodontid. Recently, eggs preserved within the body cavities of two individuals have been discovered (Sato et al. 2005; He et al. 2012). Both Sato et al. (2005) and He et al. (2012) describe two eggs in association with a single oviraptorid individual. The former describes a specimen with two eggs within the body cavity, while the individual in the latter paper has a single egg within the body cavity and one in close association with the hips and tail. Both findings support the hypothesis that such animals had two functioning oviducts and were capable of holding two shelled eggs within the body at a time.

Whereas neither skeleton–clutch associations nor gravid females are known for *Macroelongatoolithus* eggs, a single peri-natal specimen, possibly referable as Oviraptorid, preserved in contact with four *M. xixiaensis* eggs has been documented (Grellet-Tinner 2005). The eggs associated with this individual have been thoroughly described; however, a formal description of the peri-natal skeleton has not been published. Contrary to evidence of an oviraptorid–*Macroelongatoolithus* relationship, some researchers have claimed a link between *Macroelongatoolithus* eggs and tyrannosauroid theropods based on egg and clutch size alone (Qian et al. 2007, 2008). In our opinion, the proposed tyrannosauroid–*Macroelongatoolithus* relationship should be disregarded as it lacks concrete supporting evidence. The abundance of evidence indicating an oviraptorid–elongatoolithid relationship, in addition to the lack of any other dinosaurian taxa found intimately associated with elongatoolithid eggs, suggests that a large oviraptorid likely laid *Macroelongatoolithus* eggs.

Conclusion

Descriptions of intact clutches of *Macroelongatoolithus* eggs are exceedingly rare to date, with the Aphae-do specimen increasing the total described in scientific literature to five. Documentation of these clutches provides important insight into intra- and inter-clutch variation as well as nesting habits of the parent animals. This report of a Late Cretaceous (83–77 Ma) clutch, in addition to a previously described partial specimen (Kim, Yang, et al. 2011), extends the geographic and temporal ranges of *Macroelongatoolithus* to include the Campanian of South Korea. In addition, the Aphae-do specimen supports the ring-shaped, single layer arrangement of the clutch, with eggs nearly horizontal to the surrounding sediment. The consistency of this arrangement from mid to Late Cretaceous suggests a biologically real configuration rather than a taphonomically altered one. Further detailed analysis of the eggs within MNHM-nat201153 may provide a better understanding of microstructural and gross morphological variability within a single ootaxon, aiding in our understanding of what constitutes an oospecies.

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