First find of an ornithomimid theropod dinosaur in the Upper Cretaceous of the Russian Far East

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Abstract

A fragmentary tibia of an actively growing sub-adult individual from the Upper Cretaceous (Maastrichtian) Udurchukan Formation at Kundur, Amur oblast, Far East, Russia, is similar to the tibia of *Qiupalong henanensis* from the Maastrichtian of Henan Province, China, in bearing a weak posteromedial ridge at the distal end and equally projecting distal malleoli. *Qiupalong* had a transcontinental distribution and likely originated in North America. Similarly, lambeosaurine hadrosaurids from the Udurchukan Formation have American affinities and their ancestors may had dispersed from North America to East Asia together with a *Qiupalong*-like ornithomimid. *Q. henanensis* and Ornithomimidae indet. from Kundur are the only records of the Maastrichtian Ornithomimidae in Asia outside Gobi Desert.

Keywords: Dinosauria, Theropoda, Ornithomimidae, Late Cretaceous, Far East, Russia

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Introduction

The Kundur locality, situated in Arkhara rayon of Amur oblast, Russia, produce a diverse assemblage of Late Cretaceous dinosaurs including theropods (Tyrannosauridae indet., Dromaeosauridae indet., and *Richardoestesia* sp.), lambeosaurine hadrosaurid *Olorotitan arharensis* Godefroit, Bolotsky et Alifanov, 2003, saurolophine hadrosaurid *Kundurosaurus nagornyi* Godefroit, Bolotsky et Lauters, 2012, and ankylosaurs (Nesov, 1995; Moiseenko, Sorokin, and Bolotsky, 1997; Alifanov and Bolotsky, 2002; Godefroit, Bolotsky, and Alifanov, 2003; Tumanova, Bolotsky, and Alifanov, 2004; Bolotsky, 2011; Godefroit, Bolotsky, and Bolotsky, 2012; Godefroit, Bolotsky, and Lauters, 2012). Although an identification of Ornithomimidae indet. appeared in the faunal lists of Kundur and Blagoveshchensk localities (e.g., Moiseenko, Sorokin, and Bolotsky (1997); Markevich and Bugdaeva (2001)), no actual material was described, and we do not know a source of these identifications. In a review of the theropod dinosaurs from the Upper Cretaceous of Amur Region, it is indicated that there are no remains of ornithomimids in Kundur and Blagoveshchensk localities (Alifanov and Bolotsky, 2002; see also Averianov and Lopatin (2023)). The incomplete tibia from the Kundur locality described in this paper is the first identifiable specimen of Ornithomimidae for the Late Cretaceous of the Russian Far East.

The Kundur locality represents a monodominant hadrosaurid bonebed interpreted as a debris flow / hyperconcentrated flow deposit (Markevich, Bolotsky, and Bugdaeva, 1994; Van Itterbeeck, Bolotsky, Bultynck, and Godefroit, 2005; Godefroit et al., 2011). This bonebed is attributed to the Udurchukan Formation (previously referred to as the Tsagayan Formation or Lower Tsagayan Formation), the age of which is currently estimated as Maastrichtian (Godefroit et al., 2011).

Institutional abbreviation. AEIM, Amur Museum of Natural History, Blagoveshchensk, Russia.

Materials and methods

To describe microanatomical and histological structures and identify the ontogenetic stage of AEIM 2/1045, we sampled the central part of bone (a section taken close to the mid-diaphyseal level). A thin-section was prepared based on the methodology outlined in Chinsamy and Raath (1992). The section was examined under normal and polarized light using an optical microscope (Leica 4500, Leica Microsystems, Wetzlar, Germany) in the Saint Petersburg State University Research Centre for X-ray Diffraction Studies (Saint Petersburg, Russia). Histological terminology follows Francillon-Vieillot et al. (1990).

Systematic paleontology

Dinosauria Owen, 1842
Saurischia Seeley, 1887
Theropoda Marsh, 1881
Coelurosauria Huene, 1914
Ornithomimosauria Barsbold, 1976
Ornithomimidae Marsh, 1890
Ornithomimidae gen. et sp. indet.
Figs. 1, 2

Material — AEIM 2/1045, incomplete left tibia in two pieces.

Locality and horizon — Kundur, Arkhara rayon, Amur oblast, Russia; Udurchukan Formation, Upper Cretaceous (Maastrichtian).

Description

AEIM 2/1045 is an incomplete left tibia consisting of two pieces, proximal and distal (Fig. 1). Both fragments originally had a loose contact but it was removed by taking bone samples for the paleohistological analysis. The proximal end of the bone is missing. The bone is relatively slender, long, and straight. The bone is hollow with thick bone walls. At the preserved proximal end, the bone is triangular in cross section, with anterior side concave between the cnemial and fibular crests, nearly flat posterolateral side, and slightly convex posteromedial side. Only the base of the cnemial crest is preserved (Fig. 1A–C). The fibular crest starts opposite to the distal end of the cnemial crest and extends distally for about 40 mm. The robust fibular crest is incompletely preserved. On the lateral side posterior to the fibular crest there is a large vascular foramen with a vascular groove, which passes outward from a foramen (Fig. 1C). In the region of the fibular crest, the anterior side of the shaft is flat and it becomes slightly convex more distally. At the preserved distal end of the proximal fragment, the shaft is lenticular in cross section, forming convex anterior and posterior sides and acuminate medial and lateral ends. On the distal fragment, the anterior side is flat and slightly depressed with a poorly delimited attachment area for the astragalus and its ascending process. Along the lateral margin of the anterior side, there is a poorly defined transversely narrow depression for the distal fibula and calcaneum. The posterior side of the distal fragment is deeply convex proximally and becomes flat to slightly concave distally. At the distal end, there is a low longitudinal ridge along the medial side of the shaft. The distal end is transversely one and a half times wider than the shaft. Its transverse width is 57.0 mm, anteroposterior diameter is 19.5 mm. The lateral malleolus does not project distally beyond the medial malleolus. The outline of the distal end in distal view is an irregular transversely long parallelogram, with the medial edge longer than the lateral edge.

The mid-diaphyseal level of the tibia AEIM 2/1045 has a thick cortex (minimal cortical thickness about 5.8 mm; maximal cortical thickness about 7.8 mm), composed of primary and secondary bone tissues surrounding a well-defined medullary cavity (Fig. 2A, C). The primary bone organization of the cortex is a fibrolamellar complex. The vascularization of a primary cortex is characterized by reticular and plexiform patterns in the deepest part of the cortex and laminar vascularization in the outer cortex (Fig. 2C). The innermost part of the cortex is lined with endosteal lamellar bone (= inner circumferential layer, ICL) and is partly remodeled with secondary osteons (Fig. 2A, C). Additionally, a large area in the cortex of the lateral side of the bone is highly remodeled and infilled with secondary osteons of two generations, indicative of repaired cracks in the primary cortex (Fig. 2B). Four lines of arrested growths (LAGs) are present in the primary cortex (Fig. 2C). The primary cortex does not have an external fundamental system (EFS).

Ontogenetic age of AEIM 2/1045

The presence of the endosteal lamellar bone (ICL) suggests that the expansion of the medullary cavity had stopped, which indicates that this individual was not a juvenile. The active secondary remodeling (formation of the secondary osteons in the innermost part of the cortex) also suggests the non-juvenile stage of the AEIM 2/1045. On the other hand, the absence of an external fundamental system (EFS) and signs of slowing of the growth rate (appearance of longitudinal vascularization in the outer cortex) indicates that the individual did not

Fig. 1. Ornithomimidae gen. et sp. indet., AEIM 2/1045, left tibia, proximal and distal fragments, in medial (A), anterior (B), lateral (C), posterior (D), and distal (E) views. Kundur, Amur oblast, Russia; Udurchukan Formation, Upper Cretaceous (Maastrichtian). Abbreviations: caf, calcaneum facet; cnc, cnemial crest; fic, fibular crest; fif, fibular facet; fo, vascular foramen; pmr, posteromedial ridge. Scale bar equals 5 cm.

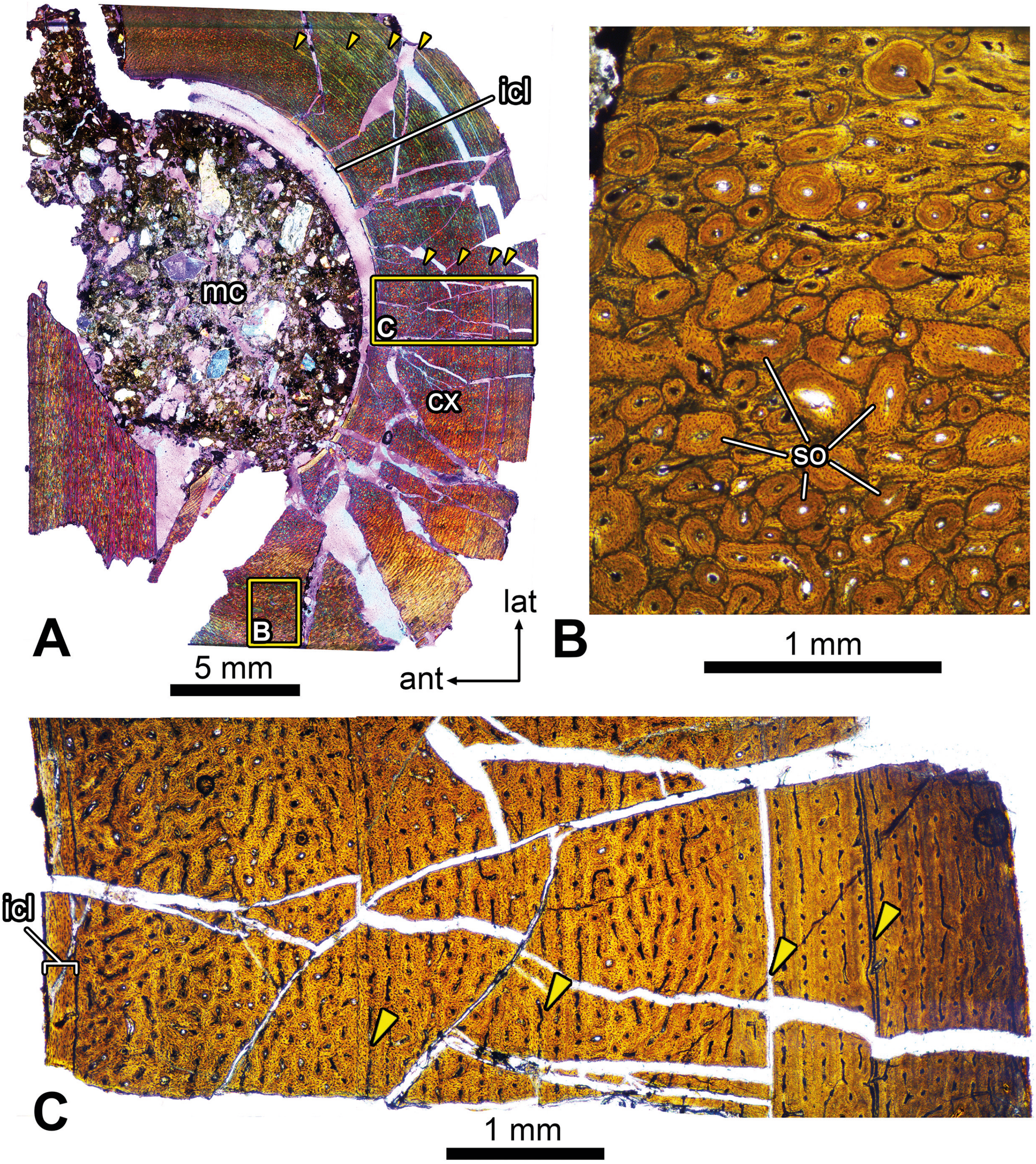

Fig. 2. Ornithomimidae gen. et sp. indet., AEIM 2/1045, left tibia, histological sections under polarized light with lambda waveplate (A), and under normal light (B–C). (A) Microanatomical overview. (B) Close-up of the cortex of the lateral side of the bone showing the secondary osteons of two generations, indicative of repaired cracks in the primary cortex. (C) A close-up view of the cortex. Note the presence of ICL, LAGs (yellow arrows), and the different vascularization patterns of the primary cortex (reticular and plexiform in the inner cortex, and laminar in the outer cortex). Abbreviations: cx, cortex; mc, medullary cavity; icl, inner circumferential layer; ol, osteocyte lacuna; so, secondary osteons.

reach adult size and was still actively growing at the time of death. As a result, we suggest that the AEIM 2/1045 derives from a skeletally immature individual of a subadult growth stage.

Comparison

Tibia proportions. AEIM 2/1045 is a very long and straight bone, suggesting hind limb proportions typical for cursorial animals. Among Coelurosauria, such proportions of tibia are present in Ornithomimosauria, Alvarezsauridae, and some Oviraptorosauria (*Avimimus*). In alvarezsaurids, the cnemial and fibular crests of tibia are more reduced compared with AEIM 2/1045 and all known alvarezsaurids are much smaller in size (Perle et al., 1994; Chiappe, Norell, and Clark, 2002; Averianov and Lopatin, 2021). In parvicursorine alvarezsaurids the fibula is reduced distally and not contacting the calcaneum. In *Avimimus*, the tibia is fused with the proximal tarsals into the tibiotarsus (Kurzanov, 1987). By proportions and other characters, discussed below, AEIM 2/1045 can be safely attributed to Ornithomimidae.

Vascular foramen posterior to fibular crest. A large vascular foramen on the lateral side posterior to the fibular crest (= tibial foramen of Naish, 1999) besides AEIM 2/1045 is also present in the Bissekty ornithomimid (Sues and Averianov, 2016: fig. 18G), *Gallimimus bullatus* (Osmólska, Roniewicz, and Barsbold, 1972), and *Qiupalong henanensis* (Xu et al., 2011: fig. 4c). This foramen predates the development of fibular crest in basal theropod *Herrerasaurus ischigualastensis* (Novas, 1993: fig. 8B). Although this foramen is present in a variety of theropods, it is possibly one of the potential common features of ornithomimosaurs.

Curvature of the distal end of the tibia. In AEIM 2/1045, the distal end of the tibia is straight in medial/lateral view. This condition is present in most ornithomimosaurs. However, it is distinctly deflected anteriorly in *Ornithomimus velox* (Claessens and Loewen, 2015: fig. 7C, D).

Fibular facet. In AEIM 2/1045, the fibular facet is poorly delimited at the articulation with the calcaneum, being more or less noticeable only at its distal end, as in most other ornithomimosaurs. The fibular facet bears a marked groove in *Ornithomimus velox* (Claessens and Loewen, 2015: fig. 7A), and *Qiupalong henanensis* (Xu et al., 2011: fig. 4a).

The articular contact to the fibula. In *Allosaurus fragilis*, the entire fibular contact is positioned on the lateral side of the tibia (Gilmore, 1920: fig. 48). Among Ornithomimosauria, this plesiomorphic condition is retained in *Hexing qingyi* (Jin, Jun, and Godefroit, 2012), *Harpymimus okladnikovi* (Kobayashi and Barsbold, 2005a: figs. 6.9E–H), and *Dromiceiomimus brevitertius* (Macdonald and Currie, 2019: p. 139, fig. 17). In AEIM 2/1045, according to the fibular facet, the distal end of fibula was placed on the anterior side of the tibia (Fig. 1B). Such a derived condition is characteristic for *Garudimimus brevipes* (Kobayashi and Barsbold, 2005b: fig. 14A, C), the Bissekty ornithomimid (Sues and Averianov, 2016: fig. 18I), *Sinornithomimus dongi* (Kobayashi and Lü, 2003), *Gallimimus bullatus* (Osmólska, Roniewicz, and Barsbold, 1972: pl. 58, fig. 3), *Ornithomimus velox* (Claessens and Loewen, 2015: fig. 7A, D), *Qiupalong henanensis* (Xu et al., 2011: fig. 4a), and *Rativates evadens* (McFeeters, Ryan, Schröder-Adams, and Cullen, 2016: fig. 9O).

Posteromedial ridge at distal end. This ridge is located at the distal end of the tibia and is very low in AEIM 2/1045, like *Quipalong henanensis* (Xu et al., 2011: fig. 4f), but it is much higher in those of the Bissekty ornithomimid (Sues and Averianov, 2016: fig. 18J).

Ridge on posterolateral corner of distal end. This ridge (= pronounced rounded flange of McFeeters, Ryan, Schröder-Adams, and Cullen (2016)) is located at the distal end of the tibia and also present in *Harpymimus okladnikovi*, *Garudimimus brevipes*, and *Archaeornithomimus asiaticus* (Smith and Galton, 1990: fig. 3O, Q; Kobayashi and Barsbold, 2005b, 2005a). However, it is absent in the Bissekty ornithomimid (Sues and Averianov, 2016), *Sinornithomimus dongi* (Kobayashi and Lü, 2003) and in more derived ornithomimids, including AEIM 2/1045.

Lateral malleolus distal projection. In AEIM 2/1045, the medial and lateral malleoli of the tibia project equally distally. A similar condition is present in *Qiupalong henanensis* (Xu et al., 2011: fig. 4a, b). The lateral malleolus projects distinctly more distally, compared with the medial malleolus in *Beishanlong grandis* (Makovicky et al., 2010: fig. 3d), in *Garudimimus brevipes* (Kobayashi and Barsbold, 2005b: fig. 14B), and in the Bissekty ornithomimid (Sues and Averianov, 2016: fig. 18I). Outside Ornithomimidae, the lateral malleolus extends much further distally than the medial malleolus in most tyrannosauroids (Brusatte et al., 2010).

Microanatomical and histological structures. The tibia AEIM 2/1045 is characterized by the presence of highly vascularized primary cortex with a combination of reticular, plexiform, and laminar vascularization, the number of lines of arrested growths (LAGs), the endosteal lamellar bone (inner circumferential layer, ICL), and partly remodeled inner part of the cortex with secondary osteons formation. A similar structure of the tibial cortex is present in a large-bodied ornithomimid, *Ornithomimus edmontonicus* (Zelenitsky et al., 2012: fig. S6B), and in an ornithomimid theropod from the Maastrichtian Horseshoe Canyon Formation in Alberta (Cullen et al., 2014: fig. 3A). The Bissekty ornithomimid has no laminar and plexiform vascularization in the primary cortex of the long bones (only longitudinal pattern is present; Skutschas, Boitsova, Averianov, and Sues, 2017). The presence of LAGs, the inner circumferential layer, and the secondary remodeling of the inner part of the cortex are general features for the ornithomimid theropods (Skutschas, Boitsova, Averianov, and Sues, 2017; Chinzorig et al., 2022).

Discussion

Ornithomimids were lightly built cursorial animals with large eyes and brain, edentulous jaws with keratinous beak, elongate forelimbs, and long hindlimbs (Russell, 1972; Makovicky, Kobayashi, and Currie, 2004). The Late Cretaceous ornithomimids are known exclusively from Asia and North America. They are among the most common theropods collected in the Campanian strata of Alberta, Canada (Russell, 1972; Currie and Koppelhus, 2015). However, ornithomimids are rare in the Maastrichtian faunas of western North America (DeCourten and Russell, 1985; Claessens and Loewen, 2015). In Asia, ornithomimids were common in pre-Campanian strata of Uzbekistan and China (Gilmore, 1933; Smith and Galton, 1990; Kobayashi and Lü, 2003; Sues and Averianov, 2016; Yao, Sullivan, Tan, and Xu, 2022), but are rare in the Campanian of Mongolia (Chinzorig et al., 2017). However, the greatest taxonomic diversity of ornithomimosaurs is known from the Maastrichtian Nemegt Formation of Mongolia (Osmólska and Roniewicz, 1970; Osmólska, Roniewicz, and Barsbold, 1972; Barsbold, 1988; Kobayashi and Barsbold, 2006; Bronowicz, 2011; Lee et al., 2014; Chinzorig et al., 2018). Another ornithomimid taxon is present from the contemporary Qiupa Formation in Henan Province, China (Xu et al., 2011).

The rarity of ornithomimids in the Maastrichtian Udurchukan Formation of Russian Far East echoes the Maastrichtian of North America and contrasts with the Maastrichtian of nearby Mongolia. Similarly, the dinosaur assemblages from the Udurchukan Formation are dominated by lambeosaurines with North American affinities (Godefroit, Bolotsky, and Alifanov, 2003; Godefroit, Bolotsky, and Van Itterbeeck, 2004; Godefroit et al., 2011; Godefroit, Bolotsky, and Bolotsky, 2012), while lambeosaurines are not known from the Mongolian Nemegt Formation. The dominant hadrosaurid in that stratigraphic unit is *Saurolophus angustirostris* (Rozhdestvensky, 1952; Maryańska and Osmólska, 1981, 1984; Bell, 2011), while saurolophines are rare in Udurchukan Formation (Bolotsky and Godefroit, 2004).

The comparison of AEIM 2/1045 with tibiae of North American ornithomimids is hampered by the paucity of adequate descriptions of the latter. In most cases, as in the case of *Gallimimus bullatus* (Osmólska, Roniewicz, and Barsbold, 1972), the distal part of the tibia is covered by the proximal tarsal bones that obscure details of distal tibial morphologies. According to the above comparison with all available published tibiae of ornithomimosaurs, AEIM 2/1045 is most similar to the tibia of *Quipalong henanesis* (Xu et al., 2011: fig. 4), having a weak posteromedial ridge at the distal end and equally projecting distal malleoli. McFeeters, Ryan, Schröder-Adams, and Currie (2017) attributed to *Qiupalong* sp. several fragmentary ornithomimid specimens from the Campanian Dinosaur Park Formation of Alberta, Canada, and concluded that it is the first ornithomimid genus with a transcontinental distribution. In addition, they assumed a North American origin for *Qiupalong* and its subsequent dispersal to Asia. If AEIM 2/1045 really belongs to *Qiupalong*, it may be dispersed from North America to East Asia together with the American ancestors of the lambeosaurines of the Udurchukan Formation.

The dinosaur assemblage from the Qiupa Formation is similar in composition to that of Udurchukan Formation. It includes a tyrannosaurid, an ornithomimid *Qiupalong henanensis*, an alvarezsaurid *Qiupanykus zhangi*, an oviraptorid *Yulong mini*, a troodontid, a dromaeosaurid *Luanchuanraptor henanensis*, an ankylosaurid, and an ornithopod (Lü et al., 2007, 2018; Xu et al., 2011; Lü, Yi, Zhong, and Wei, 2013). The alvarezsaurids and oviraptorids have not yet been recorded in the Udurchukan Formation. *Q. henanensis* and Ornithomimidae indet. from Kundur are the only records of Maastrichtian Ornithomimidae in Asia outside Gobi Desert.

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