

A NEW ORNITHOMIMOSAURIAN MATERIAL FROM THE KHOK KRUAT FORMATION, LOWER CRETACEOUS OF THAILAND

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ABSTRACT

The Aptian–Albian Khok Kruat Formation is composed of sediments rich in dinosaur remains occur in Nakhon Ratchasima, Thailand. Here, we report a distal part of right metatarsal III of an ornithomimosaur (NRRU-F01020052) found at the Ban Krok Duean Ha dinosaur locality in 2017. Notable characteristics of this specimen are the subtle mediolateral expansion, the almost triangular cross-section with an extremely narrow posterior plane in distal diaphysis, and the concave posterior surface neighboring to the distal condyle. The combination of these characters indicates that NRRU-F01020052 is attributable to an ornithomimosaur with an incomplete arctometatarsalian pes. This discovery indicates that Thailand had a great diversity of ornithomimosaurs in the early to late Early Cretaceous, corresponds to the Asian ornithomimosaurian diversity.

Key words: Ornithomimosauria, arctometatarsalian metatarsus, Khok Kruat Formation

INTRODUCTION

Ornithomimosauria is a clade comprising medium to large dinosaurs usually interpreted as ostrich-mimic, having a better cursorial ability and herbivorous diet indicated by slender hindlimbs and a small head with teeth-reduced jaws. The earliest definitive ornithomimosaur is known from the Lower Cretaceous (Berriasian–Valanginian) Kirkwood Formation of South Africa (de Klerk et al., 2000), whereas a possible ornithomimosaurian occurrence from the Upper Jurassic (Kimmeridgian) Alcobaça Formation of Portugal has recently been suggested (Hattori et al., 2023). There are two major clades within Ornithomimosauria, which are Ornithomimidae and Deinocheiridae (Choiniere et al., 2012; Lee et al., 2014). These two clades can be hypothesized to have diverged earlier in the Early Cretaceous due to the presence of an oldest deinocheirid *Tyrannomimus fukuiensis* from the Aptian Kitadani Formation of Fukui, Japan (Hattori et al., 2023), as well as a possible deinocheirid *Kinnareemimus khonkaenensis* from the Barremian Sao Khua Formation (Samathi, 2024), which is the first-reported ornithomimosaur in Thailand (Buffetaut et al., 2009).

The ornithomimosaur material reported here is from the Khok Kruat Formation, the uppermost of the Khorat Group in Nakhon Ratchasima Province, northeast Thailand (Fig. 1). Since 2007, the Northeastern Research Institute of Petrified Wood and Mineral Resources, Rajabhat University (NRRU) and the Fukui Prefectural Dinosaur Museum (FPDM) have intensively surveyed for the fossil vertebrate fauna from the Khok Kruat Formation as Japan–Thailand Dinosaur Project (JTDP), which discovered numerous disarticulated vertebrate fossils to the present. The dinosaur fossils have been reported from a number of sites where the Khok Kruat Formation is distributed, and in our research, we have been excavating at two main sites, Ban Saphan Hin (BSH) and Ban Krok Duean Ha (KDH) (Fig. 1C). The BSH site has yielded fossils of various vertebrates as well as dinosaurs such as *Sirindhorna* and *Siamraptor*, providing important information for understanding the fauna of the Khok Kruat Formation (Shibata et al., 2015; Kubo et al., 2018; Chokchaloemwong et al., 2019; Sekiya et al., 2023). The KDH site (Fig. 1E) has been excavated during 2017–2018. In addition to dinosaur fossils, including the incomplete right metatarsal III of an ornithomimosaur (NRRU-F01020052) reported here, crocodilians, turtles, and fishes were found, including well-preserved sinamiin fish fossils, which were reported as a new genus and species *Khoratamia phattharajani* (Deesri et al., 2023). There were also three different taxa of pterosaurs (Nakamura et al., 2022). These fossils of ornithomimosaur, fish,

Received July 15, 2024. Accepted November 24, 2024.

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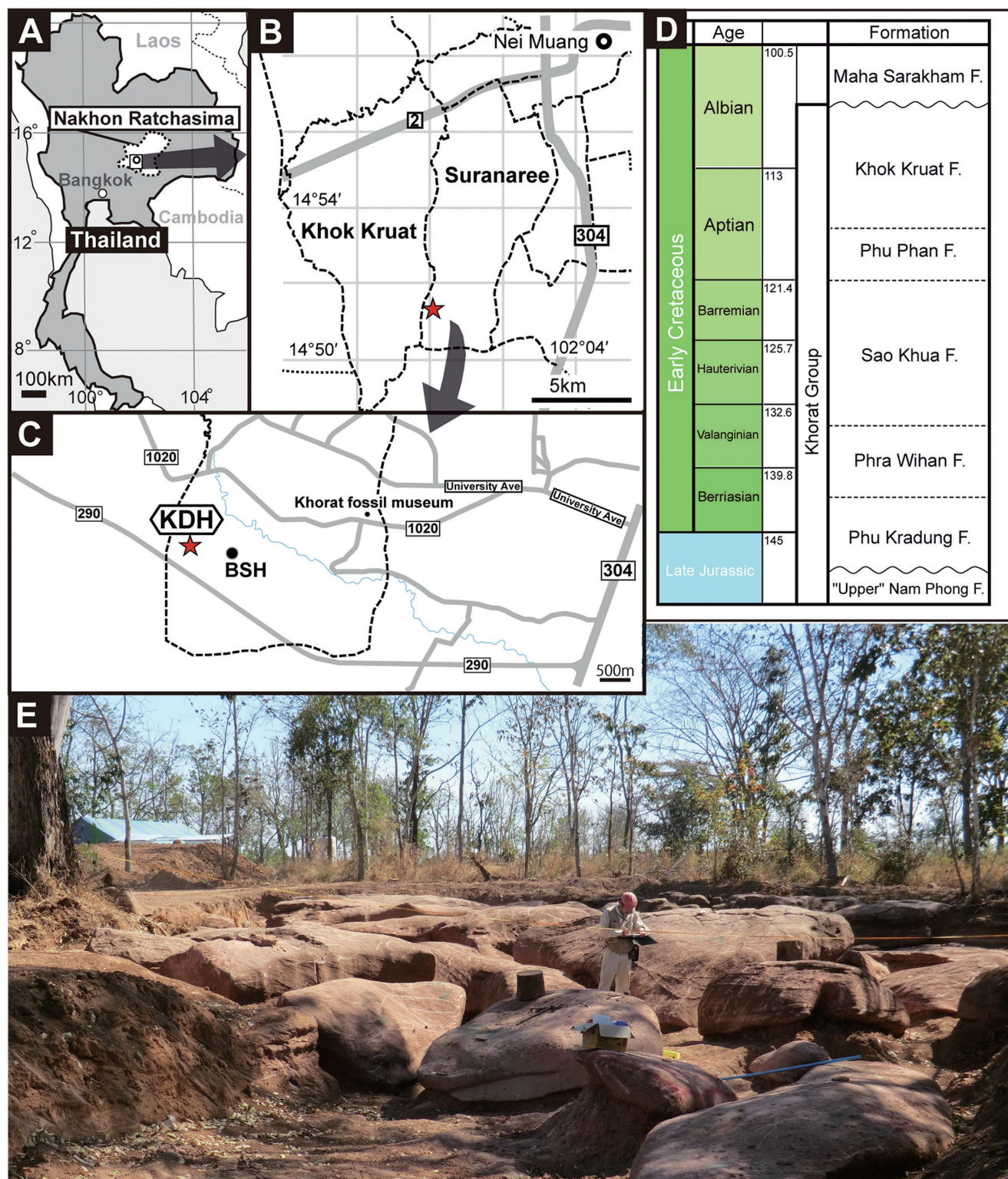


FIGURE 1. Locality map and stratigraphy of Khorat Group. **A**, map of Nakhon Ratchasima Province, Thailand; **B**, locality map of Suranaree and Khok Kruat subdistricts with the subdistrict boundaries (Modified from Chokchaloemwong et al., 2019); **C**, enlarged locality map of the Ban Krok Duean Ha (KDH) and Ban Saphan Hin (BSH), Suranaree Subdistrict; **D**, stratigraphic column of the Khorat Group (modified from Booth and Sattayarak, 2011; Chowchuvech et al., 2024); **E**, a photograph of the Ban Krok Duean Ha excavation site. Red-colored stars in B–C indicate the locality described in this study and the grey-colored lines in B–C indicate capital roads.

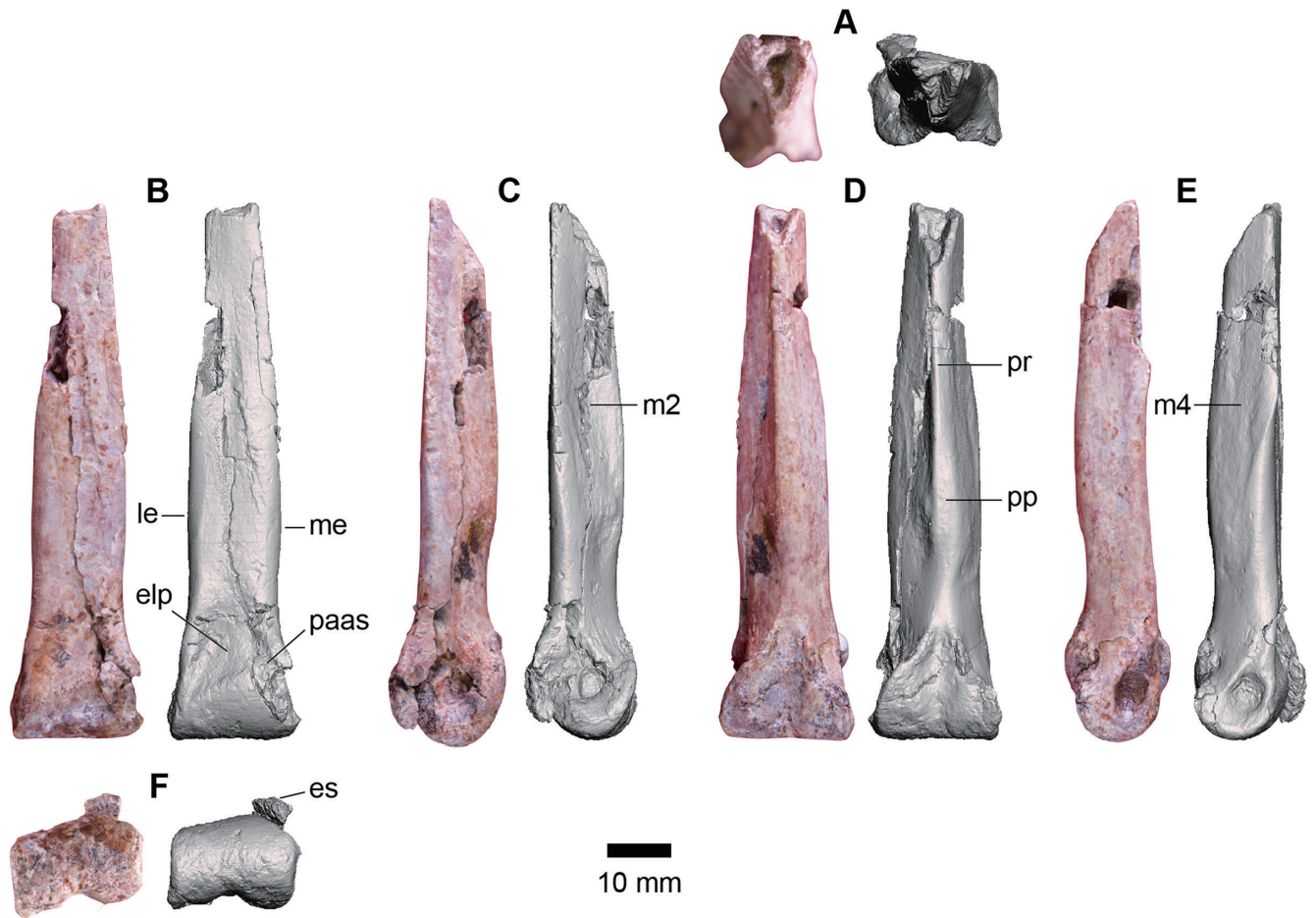


FIGURE 2. Photographs (left) and 3-D rendered images (right) of the distal part of the right metatarsal (NRRU-F01020052). **A**, proximal; **B**, anterior; **C**, medial; **D**, posterior; **E**, lateral; **F**, distal views. Abbreviations: elp, extensor ligament pit; es, surface elevated by a fracture; le, lateral expansion; m2, articular facet for metatarsal II; m4, articular facet for metatarsal IV; me, medial expansion; paas, proximal apex of the articular surface; pr, posteromedial ridge; pp, posterior plane. Scale bar equals to 10 mm.

and pterosaurs are found in the clasts of clay rip-up pebbles-rich sediments with conglomerates and were found in the same layer. Although there are some differences in fauna between the sites, such as the large number of teeth of hybodont shark found in BSH but almost none in KDH, there is almost no difference in the lithofacies of both sites, which are composed of medium-to coarse-grained sandstone and conglomerate with cross lamination. A hybodont shark *Thaiodus ruchae* has been found in the Takena Formation of the Lhasa block of Tibet, and the same species was found in the Khok Kruat Formation (Cappetta et al., 1990). Compared with the Takena Formation as Aptian–Albian age on the basis of foraminifera, the Khok Kruat Formation is considered to be Aptian–Albian in age (Meesook, 2011), while palynological study suggests that it is Aptian in age (Sattayarak et al., 1991), indicating that Ornithomimosauria existed in at least the Aptian age of the Khorat Group in Thailand.

MATERIAL AND METHOD

NRRU-F01020052 is housed at the Northeastern

Research Institute of Petrified Wood and Mineral Resources and is reported for the first time in the present study. NRRU-F01020052 was analyzed using a veterinary X-ray computed tomography (CT) scanner, Latheta LCT-200 (Hitachi, Ltd, Tokyo, Japan), with the following parameters: voltage of 80 kV, current of 500 μ A, and voxel size of 0.048–0.080 mm (x- and y-axis) and 0.096–0.160 mm (z-axis) at the Institute of Dinosaur Research, Fukui Prefectural University. NRRU-F01020052 was then rendered and exported using VGSTUDIO (v2.2, Volume Graphics; Heidelberg, Germany). The polygon meshes were then imported into Meshmixer (v3.5, Autodesk, San Rafael, USA) to observe, measure, and capture images for Figure 2 under the orthographic projection view.

SYSTEMATIC PALEONTOLOGY

Dinosauria Owen, 1842.

Theropoda Marsh, 1881.

Tetanurae Gauthier, 1986.

Coelurosauria von Huene, 1914.

Ornithomimosauria Barsbold, 1976.

Ornithomimosauria gen. et sp. indet.

Referred material.—NRRU-F01020052, distal part of the right metatarsal III.

Locality and horizon.—Ban Krok Duean Ha, Suranaree subdistrict, Mueang, Nakhon Ratchasima Province (Fig. 1).

DESCRIPTION

NRRU-F01020052 is an incomplete metatarsal III, missing the proximal to middle part but preserving the distal part (Fig. 2). The anterolateral margin of the distal condyle is fractured and the adjacent surface is elevated anteriorly (Fig. 2F). The preserved length is 84.37 mm, and the width is 14.86 mm. The preserved portion of the diaphysis is straight and slender that is mostly composed of flat anterior, posteromedial and posterolateral surfaces, making its cross-section almost triangular (Fig. 2A), indicating the development of the arctometatarsalian condition (Holtz, 1995) but unlike those of caenagnathids, in which the cross-section is trapezoidal with the concave posterior surface (Tsujimura et al., 2021). The triangular cross-section is nearly symmetrical, unlike those with a medially-deflected posterior apex seen in derived troodontids with arctometatarsalian condition (Holtz, 1995).

In anterior view, the middle part of the preserved diaphysis is expanded slightly mediolaterally, exhibiting a medial expansion (Fig. 2B) seen in ornithomimosaurs, eutyranosaurs, *Avimimus* and some dromaeosaurids (Brusatte et al., 2014). However, the degree of expansion is subtle as in *Kinnareemimus*, *Aepyornithomimus* and *Avimimus* (Fig. 3B, D, E), as well as *Gallimimus* and *Deinocoelurus* (Fig. 5 of Chinzorig et al., 2017), but unlike the pronounced expansion of eutyranosaurs and some dromaeosaurids (Fig. 3A, F). The lateral expansion is also subtle like ornithomimids and *Kinnareemimus* (Fig. 3B, D) than that of *Avimimus* (Fig. 3E).

In the proximal part of the preserved diaphysis, although the posterior side of the bone is strongly pinched, there is a very narrow surface (Fig. 2D). Proximally, this surface is continuous with the posterolateral surface but is distinguished from the posteromedial surface by a posteromedial ridge. Distally, the posterolateral ridge emerges in the middle part of the preserved diaphysis to form a narrow posterior plane. This plane disappears more distally to form a D-shaped cross-section of the diaphysis. Just proximal to the distal condyle, the posteromedial and posterolateral ridges reappear and diverge to merge with the medial and lateral hemicondyles. The non-articular surface between these ridges is notably concave, in contrast to the raised subtriangular platform seen in eutyranosaurs (Serenó et al., 2009).

The anterior and distal margins of the distal condyle are flat while its posterior margin has a concavity (Fig. 2B, F) as in some ornithomimosaurs (e.g., Osmólska et al., 1972; Kobayashi and Barsbold, 2005; Samathi, 2024), but unlike the flat posterior margin seen in *Rativates* (McFeeters et al., 2016)

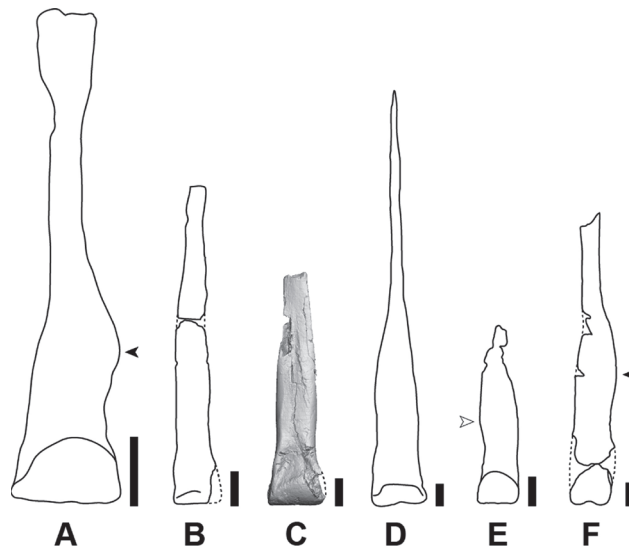


FIGURE 3. Comparison of the third metatarsal in anterior view.

A, mirrored left MT III of *Tyrannosaurus rex* (adapted from Brochu, 2003); B, mirrored left MT III of *Kinnareemimus khonkaenensis* (adapted from Samathi et al., 2024); C, right MT III of NRRU-F01020052; D, mirrored left MT III of *Aepyornithomimus tugrikensis* (adapted from Chinzorig et al., 2017); E, right MT III of *Avimimus portentosus* (adapted from Vickers-Rich et al., 2002); F, mirrored left MT III of *Neuquenraptor argentinus* (adapted from Brissón Egli et al., 2017). Scale bars are 100 mm for A and 10 mm for B–F. Black arrowheads indicate pronounced medial expansion, while white arrowheads indicate pronounced lateral expansion.

and *Aepyornithomimus* (Chinzorig et al., 2017). In anterior view, the proximal apex of the articular surface of the distal condyle is located close to the medial margin (Fig. 2B) as in the Bissekty ornithomimid (Fig. 22 of Sues and Averianov, 2016), as well as *Garudimimus* and *Gallimimus* (Fig. 5 of Chinzorig et al., 2017) but unlike *Aepyornithomimus*, in which the apex is close to the lateral margin (Fig. 3D).

DISCUSSION

NRRU-F01020052 can be identified as an ornithomimosaur metatarsal III due to the presence of triangular cross-section of the diaphysis indicating the development of arctometatarsalian condition in some degree, and the subtle mediolateral expansion of the anterior surface in the distal diaphysis. Although the medial expansion is also known in eutyranosaurs and some dromaeosaurids (Brusatte et al., 2014), they are more distinct than that of NRRU-F01020052 (e.g., Brochu, 2003; Fig. 33 of Turner et al., 2011; Brissón Egli et al., 2017). In addition, NRRU-F01020052 can be distinguished from eutyranosaurs by the absence of a raised subtriangular platform neighboring to the distal condyle (Serenó et al., 2009). Although *Avimimus* shares above-mentioned characters with NRRU-F01020052, they can be distinguished by the developmental degree of lateral expansion, which is much more distinctive in *Avimimus* (Fig. 3E).

Ornithomimosaurs exhibit various degrees of constriction

in metatarsal III (Makovicky et al., 2004) because the arctometatarsalian condition is not developed to the same extent in all members of the group. The arctometatarsalian metatarsal III shows three features, including (1) a proximal part excluded from the tarsal joint in anterior view by the constriction of itself and the expansion of metatarsals II and IV, (2) a middle part with a simple solid splint bone between metatarsals II and IV, which are more columnar and hollow, and (3) a distal part forming a wedge that abuts the articular facets on the lateral and medial aspects of metatarsals II and IV, respectively (Holtz, 1994; Samathi, 2024). In basal ornithomimosaurs such as *Nqwebasaurus*, metatarsal III is only moderately compressed mediolaterally so that the proximal end is still visible between those of metatarsals II and IV in anterior view and does not show a triangular cross-section in the distal half (Choiniere et al., 2012; Sereno, 2017). On the distal part, Deinocoelidae seems to retain similar condition of the distal diaphysis of metatarsal III, exhibiting a trapezoidal cross-section by broader anterior and narrower posterior surfaces, in contrast to the triangular cross-section seen in Ornithomimidae and *Kinnareemimus* (Buffetaut et al., 2009). Among them, a very narrow posterior plane in the distal diaphysis of metatarsal III seen in NRRU-F01020052 can be referred as an intermediate condition. However, considering *Kinnareemimus* does not represent an ornithomimid taxon (Samathi, 2024), the triangular cross-section seems to be obtained before the divergence of Deinocoelidae and Ornithomimidae, and thus the trapezoidal cross-section was obtained in the former clade independently. In that case, the presence of an intermediate condition with a very narrow posterior plane in the distal diaphysis of metatarsal III indicates that NRRU-F01020052 may belong to a basal ornithomimosaur diverging earlier than *Kinnareemimus*, or a basal deinocoelid diverging later than *Kinnareemimus*.

NRRU-F01020052 is the first ornithomimosaur skeletal remain recovered from the Early Cretaceous Khok Kruat Formation in Nakhon Ratchasima, Thailand. This is not surprising, since the coexistence of ornithomimosaurs with carcharodontosaurian and iguanodontian dinosaurs (Buffetaut and Suteethorn, 2011; Shibata et al., 2011; Shibata et al., 2015; Chokchaloemwong et al., 2019) is common in the Early Aptian–Albian fauna, as seen in East and Southeast Asia (Shibata et al., 2017) and North America (Brownstein, 2018). In addition, the discovery of ornithomimosaurian remains can also be predicted by the presence of footprints referred to cf. *Asianopodus*, which are probably imprinted by ornithomimosaurs (Kozu et al., 2017). Considering that this footprint assemblage also indicates gregarious behavior (Kozu et al., 2017), there may be much additional material from the Khok Kruat Formation to provide more conclusive information on the taxonomy of the KDH ornithomimosaur in the future.

CONCLUSIONS

A new material from the Lower Cretaceous Khok Kruat

Formation of Thailand has been described here as the first ornithomimosaurian remain, although only one metatarsal III was found. The diagnostic characters are the subtle mediolateral expansion of the anterior surface, almost-triangular cross-section with an extremely narrow posterior plane in distal diaphysis, and concave posterior surface neighboring to the distal condyle. Differences against another ornithomimosaur from Thailand implies that ornithomimosaurs were widespread during the Early Cretaceous of Southeastern Asia, as well as Eastern Asia, Europe, South Africa, and North America. This finding shows that Southeast Asia played a role in the early evolutionary history of Ornithomimosauria.

ACKNOWLEDGEMENTS

The authors are grateful to all who contributed to the 2017–2018 JTDP, a collaborative research project between NRRU and FPD. We thank all members who participated in this project, including Yoichi Azuma, Yoshikazu Noda, Teppei Sonoda (FPD), Ryohei Nakagawa (Mie Prefectural Museum), Pratueng Jintasakul, Krongkaew Jenjitpaiboon, Nuntida Yunkratok, Wanida Khonchoho, Praphas Chansom, Mayuree Yosklang (NRRU) for field work and collecting, and Prasert Anankasa and his team for their patient work at the site. We sincerely thank Toru Sekiya (FPD) for editing the manuscript. The authors extend our gratitude to Thomas R. Holtz (University of Maryland) and Rebecca Hunt-Foster (Dinosaur National Monument) for their detailed and insightful reviews, which significantly enhanced this manuscript.

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