

ORNITHOMIMIDS FROM THE NEMEGT FORMATION OF MONGOLIA

Yoshitsugu Kobayashi¹ and Rinchen Barsbold²

¹Hokkaido University Museum, Hokkaido University, Sapporo, Hokkaido, 060-0810 Japan, ykobayashi@museum.hokudai.ac.jp

²Paleontological Center of Mongolian Academy of Sciences, PO Box 260, Ulaan Bataar 210351, Mongolia, barsgeodin@magicnet.mn

Abstract: Two ornithomimids (*Gallimimus bullatus* and *Anserimimus planinychus*) and an enigmatic ornithomimid (*Deinocheirus mirificus*) from the Nemegt Formation (Maastrichtian) of Mongolia are reviewed in this study. *Gallimimus bullatus* is one of the best-known ornithomimids, but its diagnoses need to be revised. The length ratio of the manus/humerus in *Gallimimus bullatus* is 0.61. This is the smallest value in ornithomimosaur (approximately 0.8 or more in other ornithomimosaur) and may be a good character to diagnose *Gallimimus bullatus* as suggested by previous studies. *Anserimimus planinychus* is a unique ornithomimosaur in having strong deltopectoral crest of the humerus, dorsoventrally flat and nearly straight manual unguals, and long forelimbs. *Anserimimus planinychus* shares two characters (position of the biceps tubercle and alignment of the glenoid) with *Gallimimus bullatus* and has a long metacarpal I as in *Ornithomimus edmontonicus* (derived ornithomimosaur) and a long metacarpal III as in *Harpymimus okladnikovi* (primitive ornithomimosaur). The phylogenetic position of *Deinocheirus mirificus* has been problematic since its discovery. Preliminary phylogenetic analyses are tested in this study based on three large data matrices of Theropoda from previous studies. In two of the data matrices results indicate that *Deinocheirus mirificus* is a possible ornithomimosaur because it has some ornithomimosaur-like features (e.g., subequal metacarpals and weak deltopectoral crest of humerus), but the phylogenetic status of *Deinocheirus mirificus* as an ornithomimosaur is not confirmed because results using the other character matrix placed this taxon outside of the clade Ornithomimosauria.

Key words: Ornithomimids, Nemeget Formation, Late Cretaceous, Mongolia

INTRODUCTION

The Nemegt Formation is Maastrichtian in age, the youngest unit among the Upper Cretaceous formations in the Gobi region of Mongolia (Fig. 1B), and is rich in dinosaurs. Theropod dinosaurs from the Nemegt Formation include tyrannosaurids, ornithomimids, a therizinosaurid, oviraptorosaurs, a dromaeosaurid, troodontids, and birds (Currie, 2000). Ornithomimids from the Nemegt Formation are *Gallimimus bullatus*, *Anserimimus planinychus*, and *Deinocheirus mirificus* (Currie, 2000). Nemegt ornithomimids are known from various localities in Omnogov', southern part of Mongolia, (Fig. 1A).

Gallimimus bullatus, described by Osmólska *et al.* (1972), is the most common ornithomimid from the deposits and is the best-known among the Nemegt ornithomimids (Fig. 2A). The original description is based on three nearly complete skeletons and some fragmentary specimens, found during the Polish-Mongolian Expeditions, and revealed its anatomy in detail, allowing us to compare with North American ornithomimids (Osmólska *et al.*, 1972; Russell, 1972). Since the first discovery of *Gallimimus bullatus*, additional specimens of this animal have been discovered from the Nemegt Formation by Mongolian expeditions accompanied by other countries (e.g., American, Canadian, and Japanese colleagues). Barsbold has recognized the morphological variation among the new specimens of *Gallimimus*, but the variation has not been described in the literature.

Anserimimus planinychus, named by Barsbold in 1988, is similar to *Gallimimus bullatus* but differs in having a strong deltopectoral crest on the humerus and flat manual unguals (Barsbold, 1988) (Fig. 2B). Because the original description of *Anserimimus planinychus* emphasized these characteristic features

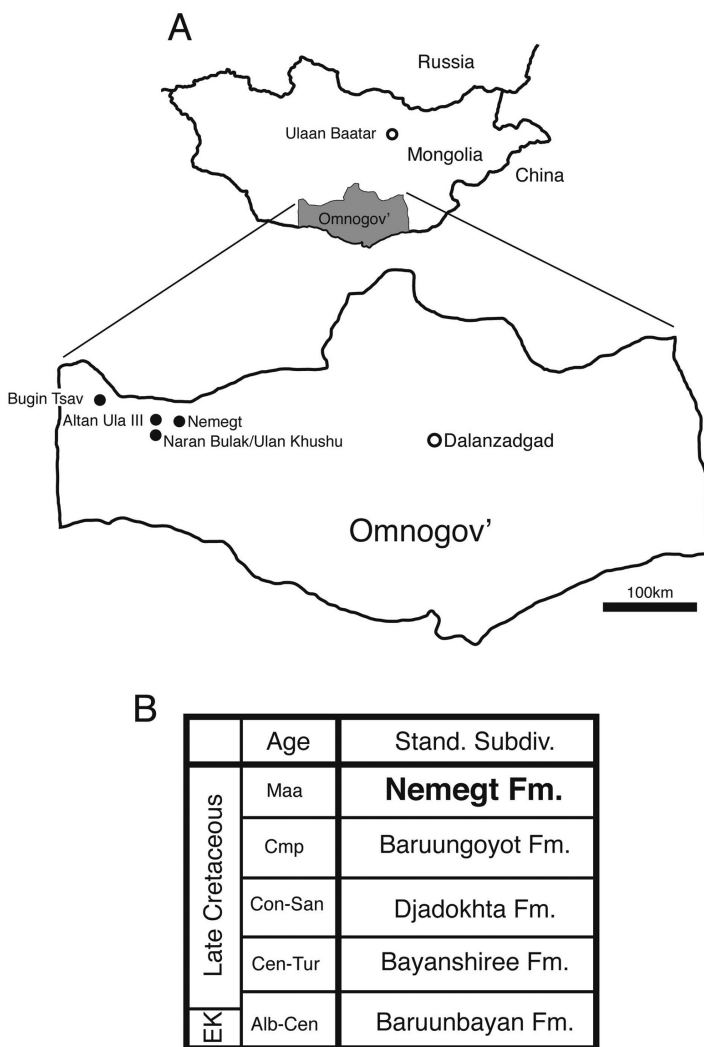


Fig. 1. Map of localities of *Gallimimus bullatus* (Nemegt, Bugin Tsav, Naran Bulak, and Ulan Khushu), *Anserimimus planinychus* (Bugin Tsav), and *Deinocheirus mirificus* (Altan Ula III) in Omnogov', Mongolia (A) (from Watabe and Suzuki, 2000) and stratigraphic position of the Nemegt Formation (from Khand *et al.*, 2000). EK, Early Cretaceous.

and provided a brief description of the animal, detailed knowledge of this taxon and comparisons with *Gallimimus* have been limited so far. Some phylogenetic studies show that it has a close relationship with *Gallimimus bullatus* (Kobayashi and Lü, 2003; Kobayashi and Barsbold, 2004).

Deinocheirus mirificus was described by Osmólska and Roniewicz (1970) based on pectoral girdle and forelimb elements with some other associated material (Fig. 2C). The relationship of this taxon to Ornithomimidae is contentious (Currie, 2000; Makovicky *et al.*, 2004). Previous studies mentioned ornithomimid features in *Deinocheirus mirificus* (weak deltopectoral crest of the humerus and long metacarpal I) (Osmólska and Roniewicz, 1970; Currie, 2000; Makovicky *et al.*, 2004). Makovicky *et al.* (2004) suggested the possibility that *Deinocheirus mirificus* is a primitive ornithomimosaur because of the lack of some features seen in ornithomimids. Currie (2000) also mentioned that the long arm might

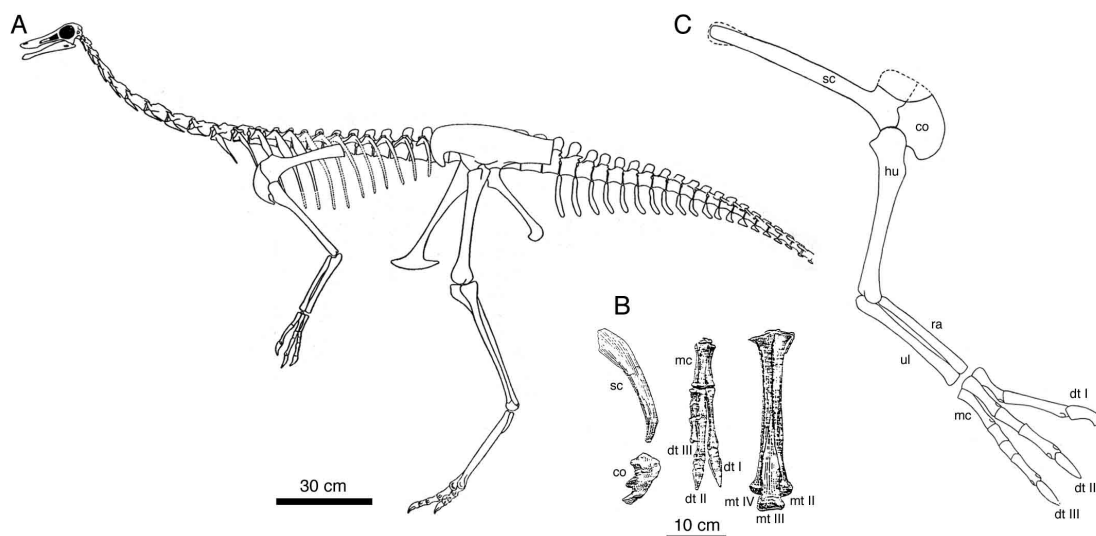


Fig. 2. Materials discussed in this study. (A) Complete skeletons of *Gallimimus bullatus* (from Osmólska, *et al.*, 1972), (B) a partial skeleton of *Anserimimus planinychus* (from Barsbold, 1988), and (C) pectoral girdle and forelimb of *Deinocheirus mirificus* (from Osmólska and Roniewicz, 1970). Scale below the reconstruction of *Gallimimus bullatus* for (A) and (C). Abbreviations: co, coracoid; dt, digit; hu, humerus; mc, metacarpal; mt, metatarsal; ra, radius; sc, scapula; ul, ulna.

suggest a close relationship with therizinosaurids. The problem of taxonomic and phylogenetic assignment of *Deinocheirus mirificus* is largely because of the fragmentary nature of the holotype specimen.

The three main goals for this study are: (1) to review previous studies on *Gallimimus*, (2) to provide more comparisons between *Anserimimus planinychus* and *Gallimimus bullatus*, and (3) to utilize preliminary phylogenetic analysis to test affinities of *Deinocheirus mirificus* with Ornithomimosauria.

Institutional abbreviations - MPD, Mongolian Paleontology Dinosaur, Paleontological Center of Mongolia, Ulaan Baatar, Mongolia; ROM, Royal Ontario Museum, Toronto, Ontario, Canada; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

REVIEWS AND DISCUSSIONS ON NEMEGT ORNITHOMIMIDS

Gallimimus bullatus Osmólska, Roniewicz et Barsbold, 1972

Gallimimus bullatus, discovered from at least four different localities of the Nemegt Formation in Omnogov' during the Polish-Mongolian Expeditions, was well described by Osmólska *et al.* (1972) (Fig. 2A). The original description is based on three nearly complete skeletons (MPD 100/10, MPD 100/11, and ZPAL MgD-I/94) and some fragmentary specimens. MPD 100/11 is the type specimen and is the largest individual (roughly 2 m high at the hip), and MPD 100/10 is a juvenile individual and is the smallest (roughly 0.5 m high at the hip) (Osmólska *et al.*, 1972; Currie, 2000).

Most of the diagnosis of *Gallimimus bullatus* in the original paper by Osmólska *et al.* (1972) is focused on skull structures (long and dorsoventrally flat snout, subtriangular infratemporal fossa, jugal excluded from the infratemporal fenestra, common exit for third and fourth nerve, shovel-like lower jaw, and elongated external mandibular fenestra) and limb proportions (humerus longer than scapula, manus

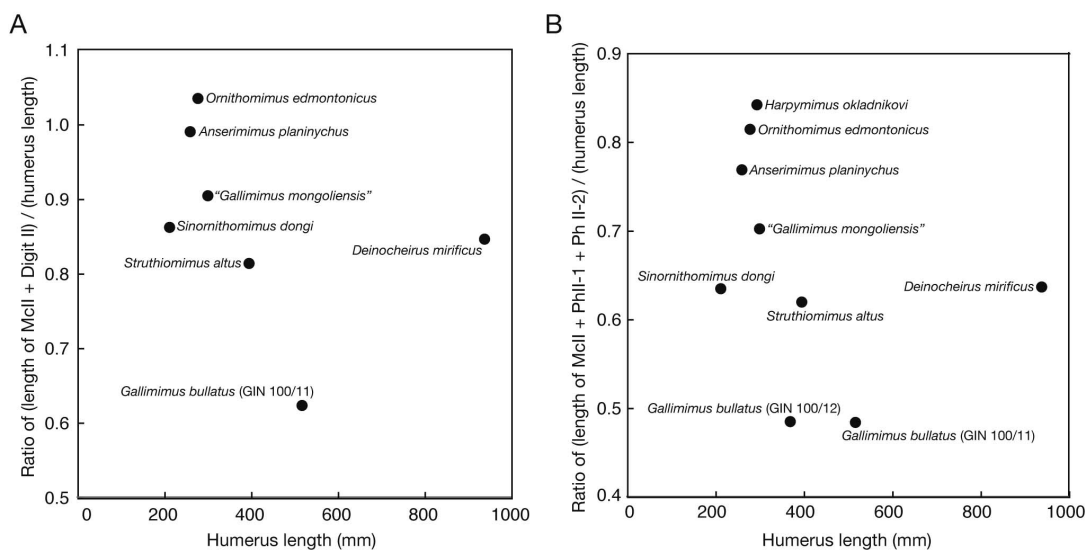


Fig. 3. Scatter plot graphs, showing distinctively short manus of *Gallimimus bullatus* among ornithomimosaur.

equal to a quarter of total forelimb, manual ungual of digit III (III-4) shorter than penultimate phalanx of the same digit (III-3), metatarsus more than 70% of crural length, metatarsal II equal 97% of metatarsal IV, and pedal digit III equal a third of crural length). Nicholls and Russell (1981) made comparisons of the proportions of the forelimb elements in *Gallimimus bullatus* and North American taxa and showed that *Gallimimus bullatus* had a long humerus and short manus. They also suggested that in *Gallimimus bullatus* a manual ungual III-4 is longer than a penultimate phalanx III-3 and the humerus is longer than scapula in *Ornithomimus edmontonicus* (fig. 2 in Nicholls and Russell, 1981) as well. Makovicky *et al.* (2004) mentioned some possible diagnostic characters of this taxon, including reduced external mandibular fenestra, short manus, expanded flange bordering the extensor groove on the craniodistal face of the femur, and an additional foramen of unknown function on the braincase wall bordering the metotic strut lateral to the vagus foramen. But they also suggested that further studies are needed to confirm if these are diagnostic for this taxon. The short manus of *Gallimimus bullatus* has been discussed by all of the previous studies. The length ratio of manus/humerus is 0.61 in *Gallimimus bullatus* (MPD 100/11), whereas the ratio in other ornithomimosaur is roughly 0.8 or more (Fig. 3A). The length ratios of manus (excluding ungual)/humerus are compared and shown in Fig. 3B. This ratio is used because some specimens have poor preservation of unguals. The graph shows that a short manus is not an ontogenetic character and is a good diagnostic feature of *Gallimimus bullatus* because a low ratio (roughly 0.5) is found in the largest individual (MPD 100/11; holotype) and in a smaller individual (MPD 100/12).

A nearly complete skeleton of ornithomimid (MPD 100/14) was found from the Baishin Tsav of south-eastern Mongolia (where a primitive but toothless ornithomimosaur, *Garudimimus brevipes*, was discovered) and was informally called "*Gallimimus mongoliensis*" by Barsbold. It possesses derived features (e.g., lack of teeth, subequal metacarpals, and arctometatarsalian condition of metatarsals) of Ornithomimidae. It also differs from *Gallimimus bullatus* in having a small skull, more proximally positioned medial divergence of metacarpal I, nearly straight manual unguals, and shorter metatarsals (Figs. 4C, 5B). The length ratio of manus/humerus is 0.91, greater than *Gallimimus bullatus*, but a common ratio for ornithomimosaur (Fig. 3). These suggest that this ornithomimid (MPD 100/14) is not *Gallimimus* but belong to another genus, perhaps a new taxon.

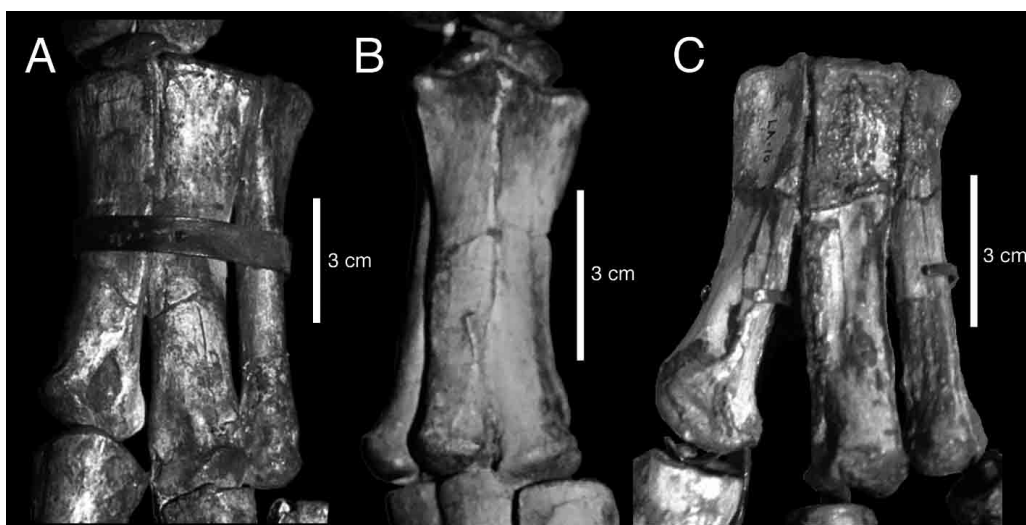


Fig. 4. Metacarpals of *Gallimimus bullatus* (left) (MPD 100/11) (A), *Anserimimus planinychus* (right) (MPD 100/300) (B), and “*Gallimimus mongoliensis*” (left) (MPD 100/14) (C).

***Anserimimus planinychus* Barsbold, 1988**

Anserimimus planinychus (MPD 100/300) was described and named by Barsbold (1988) (Fig. 2B). The type specimen preserves posterania and is missing the skull. It is known only from the type specimen from the Nemegt Formation at Bugin Tsav in Omnogov’.

The original paper stated that the diagnostic characters of this taxon are strong deltopectoral crest of the humerus and dorsoventrally flat manual unguals. Makovicky *et al* (2004) added the large epicondyles of the humerus as another unique feature among ornithomimosaur. Comparisons with other ornithomimosaur in this study confirm that the diagnoses in the original paper are still valid although Currie (2000) suggested the possibility of *Anserimimus planinychus* as a junior synonym of *Gallimimus bullatus*. The deltopectoral crest of the humerus is strong in *Anserimimus planinychus*, and the ratio of (proximal width)/(shaft width) is greatest in *Anserimimus planinychus* (2.75) among ornithomimosaur (e.g., *Gallimimus bullatus* (MPD 100/11, 2.23; MPD 100/12, 2.01)) (Fig. 6). In *Anserimimus planinychus*, manual unguals are flat unlike any other ornithomimosaur, and the height/width ratio in the manual ungual of digit I is 0.52 (Fig. 5D, E). In other ornithomimosaur, the ratios range from 1.15 (an ungual of *Archaeornithomimus asiaticus*) to 2.10 (ungual of digit I of *Sinornithomimus dongi*). Additionally, the ratio of (manual ungual length)/(manual ungual proximal height) in *Anserimimus planinychus* is 9.12, the largest in ornithomimosaur.

As discussed earlier, the short manus may be a diagnostic feature of *Gallimimus bullatus* (the length ratio of manus/humerus is 0.61). *Anserimimus planinychus* has a long manus (the above ratio is 0.91), indicating that it is different from *Gallimimus bullatus* (Fig. 3).

Further examination of the original specimens has revealed additional possible unique features of *Anserimimus planinychus*, which are concentrated in forelimb features. *Anserimimus planinychus* has relatively long forelimb elements among ornithomimosaur. These features are expressed in the ratio of (forelimb length)/(hindlimb length), long radius, and long manual phalanges. The ratio (forelimb length)/(hindlimb length) in *Anserimimus planinychus* is 0.69, which is greater value than most ornithomimosaur (*Gallimimus bullatus* (MPD 100/11), 0.55; *Sinornithomimus dongi*, 0.53; *Ornithomimus edmontonicus* (ROM 851), 0.65; *Struthiomimus* sp. (TMP 90.26.1), 0.60). *Anserimimus planinychus* has

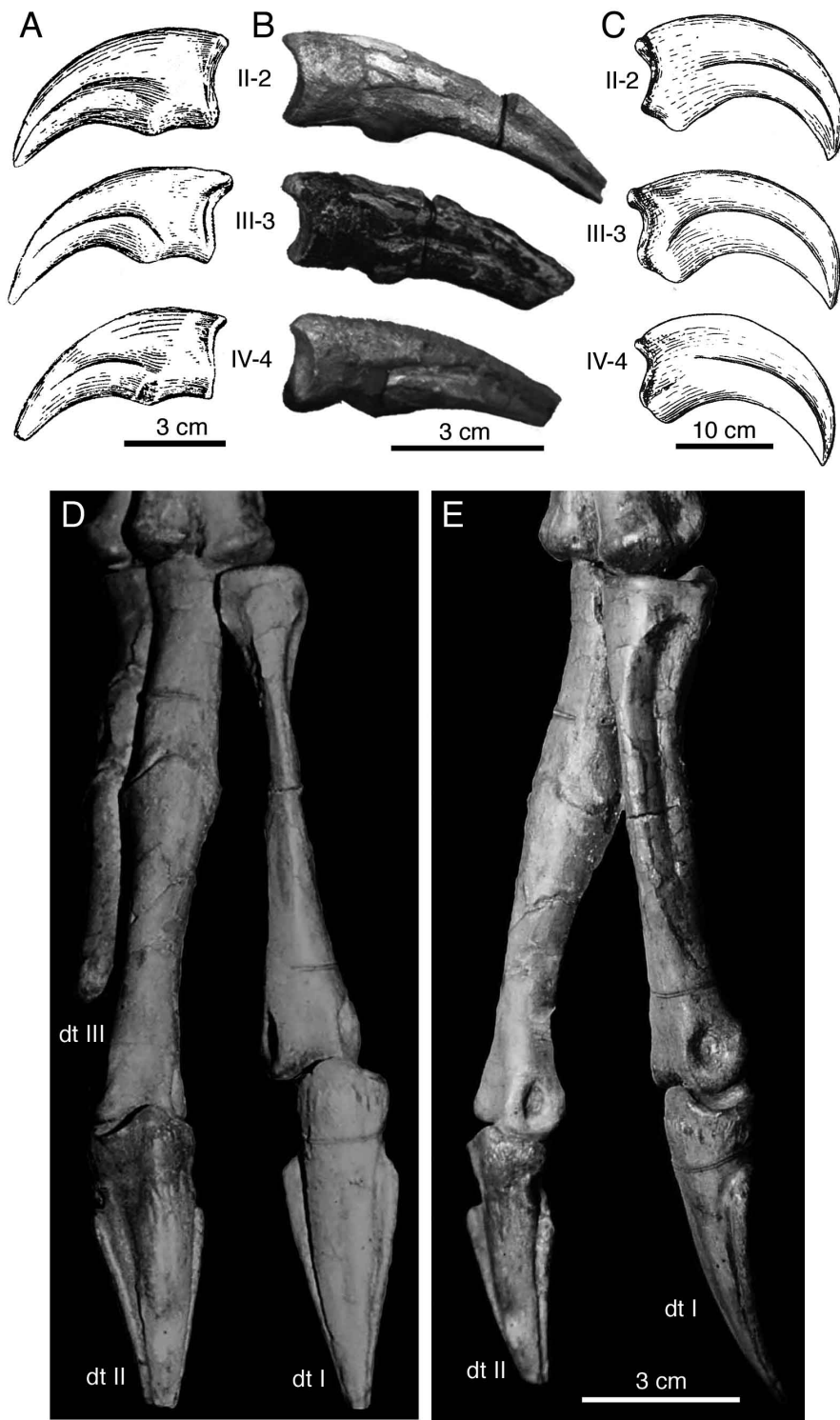


Fig. 5. Manual ungual phalanges of *Gallinimus bullatus* (from Osmólska, et al., 1972) (A), “*Gallinimus mongoliensis*” (MPD 100/14) (B), and *Deinocheirus mirificus* (from Osmólska and Roniewicz, 1970) (C) and right hand of *Anserimimus planinychus* (MPD 100/300) (D and E). Abbreviations: dt, digit; II-2, manual phalanx II-2 (ungual); II-3, manual phalanx III-3 (ungual); IV-4, manual phalanx IV-4 (ungual).

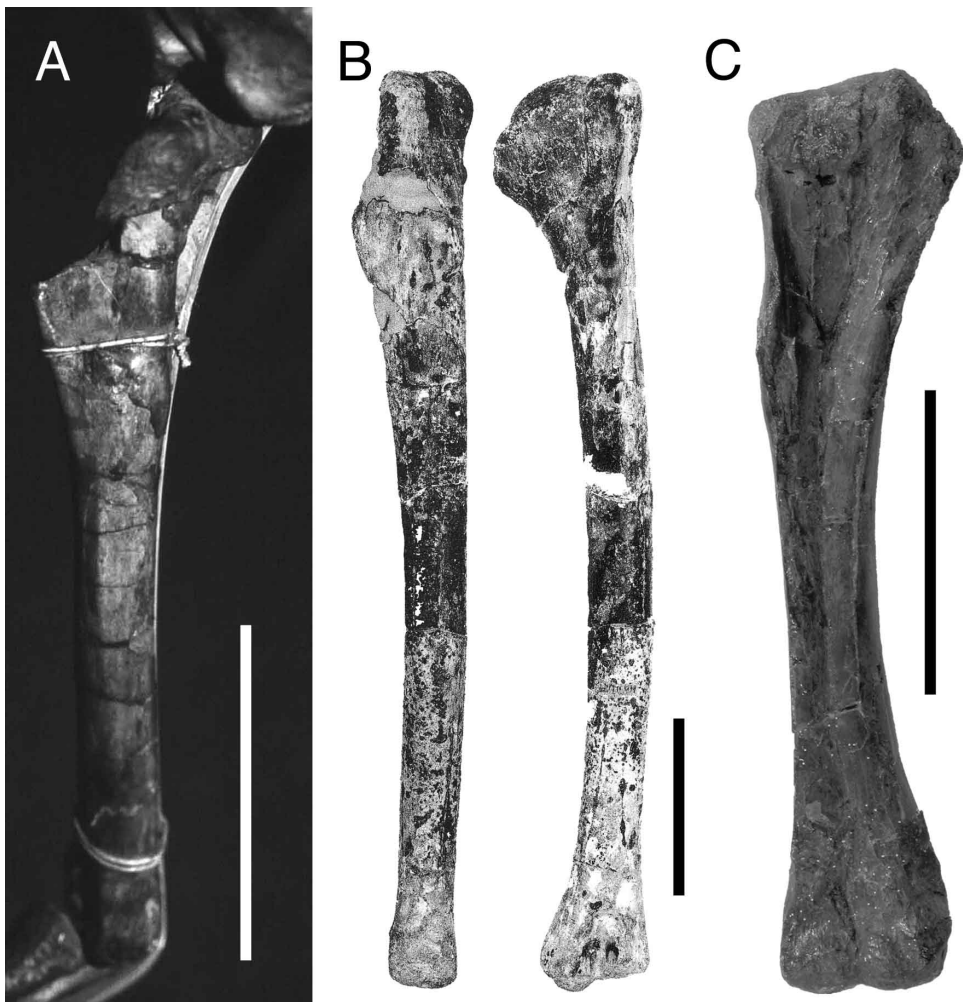


Fig. 6. Humeri of ornithomimosaur. (A) Left humerus of *Anserimimus planinychus* (MPD 100/300) in lateral view, left humerus of *Gallimimus bullatus* (MPD 100/11) (from Osmólska, *et al.*, 1972) in lateral (left) and ventral (right) views (B), and right humerus of *Harpymimus okladnikovii* (MPD 100/29) (from Kobayashi and Barsbold, 2005) in ventral view. Scales are 10 cm.

long radii. The radius/humerus length ratio is 0.80 in this taxon but it is between 0.50 and 0.75 in most of ornithomimosaur, including *Gallimimus bullatus* (MPD 100/11, 0.67 and MPD 100/12, 0.64). The sum of the length of the manual phalanges III-1+III-2 is shorter than manual phalanx III-3 in *Gallimimus* and other ornithomimosaur, but it is longer in *Anserimimus*.

Previous phylogenetic analyses show that *Anserimimus planinychus* is placed within Ornithomimidae, sharing an unambiguous synapomorphy of the clade (proximal end of metatarsal III is covered by metatarsals II and IV in anterior view: arctometatarsalian condition) (Barsbold, 1988; Kobayashi and Lü, 2003; Makovicky *et al.*, 2004). *Anserimimus planinychus* also possesses derived characters among ornithomimosaur such as radial condyle of the humerus smaller than ulnar condyle, long metacarpal I, medially rotated distal end of metacarpal I, and loss of pedal digit I (Kobayashi and Lü, 2003). Two characters in the coracoid (position of the biceps tubercle and alignment of the glenoid) indicate that

Anserimimus planinychus is a sister taxon to *Gallimimus bullatus*. In addition to the diagnostic characters noted for *Anserimimus planinychus*, the phylogenetic analysis by Kobayashi and Lü (2003) showed differences between *Anserimimus planinychus* and *Gallimimus bullatus* in the former having a depression dorsal to the supraglenoid buttress of the scapula and metacarpals I and III longer than metacarpal II (Fig. 7). The presence of the depression on the scapula is common in North American forms (*Ornithomimus*, *Struthiomimus*, and *Dromiceiomimus*). Metacarpals I and III are longer than metacarpal II in *Anserimimus planinychus*. A long metacarpal III is also seen in a toothed primitive ornithomimosaur from the Early Cretaceous, *Harpymimus okladnikovi* (Barsbold and Perle, 1984; Kobayashi and Barsbold, 2005). On the other hand, a long metacarpal I is present in a derived North American ornithomimid, *Ornithomimus* (Nicholls and Russell, 1981), showing mosaic metacarpal features present in primitive and derived ornithomimosaur.

Deinocheirus mirificus Osmólska et Roniewicz, 1970

The pectoral girdle and forelimb elements as well as other fragments (ribs and partial vertebrae) of *Deinocheirus mirificus* (ZPAL MgD-I/6) were found at Altan Ula III of the Nemegt Formation (Omnogov') and described by Osmólska and Roniewicz (1970) (Fig. 2C). *Deinocheirus mirificus* is unique in its large size. Its systematic relationships have been problematic. Originally, Osmólska and Roniewicz (1970) erected Deinocheiridae based on a single taxon, *Deinocheirus mirificus*. Barsbold (1976) coined Deinocheirosauria, which includes *Deinocheirus mirificus* and *Therizinosaurus cheloniformis* both from the Nemegt Formation. Osmólska and Roniewicz (1970) and some previous studies suggested affinities with Ornithomimosauria (Paul 1988; Makovicky *et al.*, 2004). Makovicky *et al.*

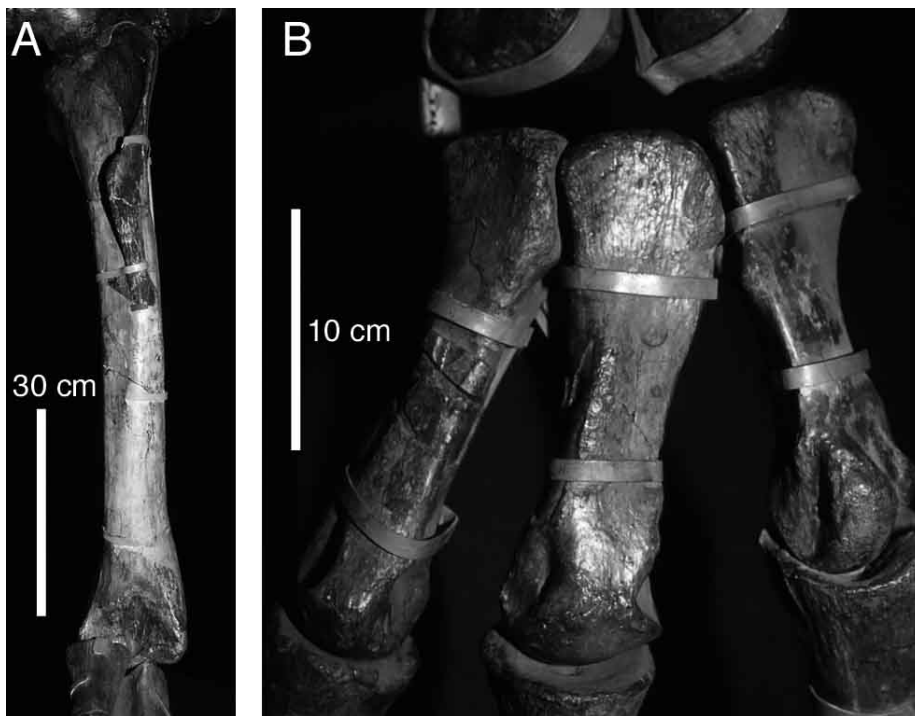


Fig. 7. Left humerus of *Deinocheirus mirificus* (ZPAL MgD-I/6) in lateral view (A) and right metacarpals in anterior view.

(2004) described ornithomimosaur-like characters in *Deinocheirus mirificus* (reduced deltopectoral crest of humerus, a deep acromion process of scapula, and a metacarpal I subequal to metacarpals II and III). On the other hand, they listed non-ornithomimosaur characters (flange on the supraglenoid buttress of scapula absent, strongly curved manual unguals with proximally positioned flexor tubercles, lack of syndesmotical articulation between radius and ulna, and lack of subglenoid shelf of coracoid) (Fig. 5C). Because of the presence of these ornithomimosaur-like and non ornithomimosaur-like characters, the phylogenetic status of *Deinocheirus mirificus* has not been resolved.

In this study, preliminary phylogenetic analyses are used to determine the possible phylogenetic status of *Deinocheirus mirificus* within Theropoda and Ornithomimosauria. Data matrices of previous studies on theropod phylogeny were used (Holtz, 1998; Maryanska *et al.*, 2002; Makovicky *et al.*, 2005). In the data matrices of Holtz (1998) and Maryanska *et al.* (2004), Ornithomimidae/Ornithomimosauria was replaced with twelve taxa (*Pelecanimimus polyodon*, *Harpymimus okladnikovi*, *Shenzhousaurus orientalis*, *Garudimimus brevipes*, *Archaeornithomimus asiaticus*, *Sinornithomimus dongi*, *Gallimimus bullatus*, *Anserimimus planinychus*, *Struthiomimus altus*, *Ornithomimus edmontonicus*, and *Dromiceiomimus brevitertius*), and *Deinocheirus mirificus* was added to the data matrices. For the data matrix of Makovicky *et al.* (2005), *Deinocheirus mirificus* was simply added to their data matrix. Settings for the analyses (outgroups, character weight, search option, and programs) followed the original analyses.

A strict consensus tree of most parsimonious trees obtained based on the data matrix of Holtz (1998) suggested the phylogenetic status of *Deinocheirus mirificus* as a member of Ornithomimosauria and showed that *Pelecanimimus* is a sister taxon to the remaining ornithomimosaur relationships of ornithomimosaur excluding *Pelecanimimus* are unresolved (Fig. 8A). *Deinocheirus mirificus* possesses some unambiguous synapomorphies of Ornithomimosauria from this analysis, and these are reduced acromion of the scapula, metacarpal I subequal to metacarpal II, and non-hyperextensive metacarpal phalangeal joints (Fig. 7B). This analysis also suggests that *Deinocheirus mirificus* is more derived than *Pelecanimimus* because it shares three unambiguous synapomorphies low manus (humerus + radius) ratio, base of metacarpal III along same place as metacarpal I and II, and manual ungual phalanx length greater than three times longer than proximal height).

In the phylogenetic analysis based on the data matrix of Makovicky *et al.* (2005) *Deinocheirus mirificus* is placed within Ornithomimosauria, sharing two unambiguous synapomorphies (fused scapulocoracoid and weak deltopectoral crest of the humerus) with other ornithomimosaur, similar to the conclusions of Makovicky *et al.* (2004) (Figs. 7A, 8B). It also suggested that *Deinocheirus mirificus* is a sister taxon to the remaining taxa (*Pelecanimimus* and higher). *Deinocheirus mirificus* is excluded from the clade of *Pelecanimimus* and higher taxa because it possesses the primitive condition in some forelimb elements (loosely jointed ulna and radius and strongly curved manual unguals with proximally positioned flexor tubercle) (Nicholls and Russell, 1985; Makovicky *et al.*, 2004).

Using the data matrix of Maryanska *et al.* (2002), our phylogenetic analysis suggested that *Deinocheirus mirificus* is placed outside of Ornithomimosauria and Coelurosauria. This is largely because *Deinocheirus mirificus* shows primitive condition in some characters (scapula/humerus length ratio, more than 1.2, short posterior process of the coracoid, total length of manual phalanges III-1 and III-2 greater than III-3) for Ornithomimosauria.

Although these preliminary phylogenetic analyses did not resolve the phylogenetic status of *Deinocheirus mirificus*, they summarize the affinities of *Deinocheirus mirificus* with ornithomimosaur, and its non-ornithomimosaur characters. The analyses do not show a close relationship of *Deinocheirus mirificus* with Therizinosauridae. Forelimb elements are important for determining the relationships of derived ornithomimosaur (Ornithomimidae) (Kobayashi and Barsbold, 2005). If *Deinocheirus mirificus* is a primitive ornithomimosaur as suggested by Makovicky *et al.* (2004) and a phylogenetic analysis in this study

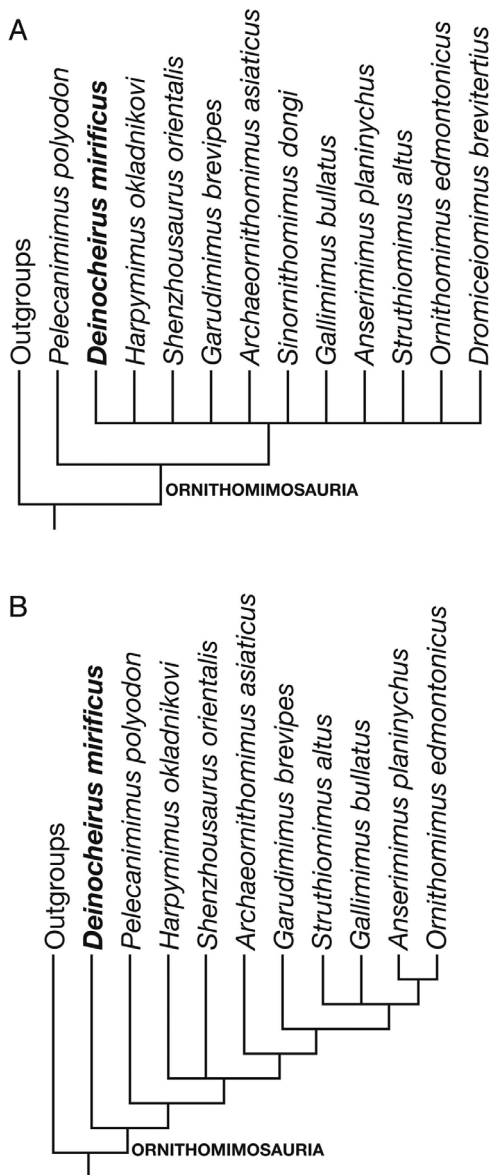


Fig. 8. Strict consensus trees of most parsimonious trees based on the data matrices of Holtz (1998) (A) and Makovicky *et al.* (2005) (B), showing possible phylogenetic status of *Deinocheirus mirificus* within Ornithomimosauria.

based on the data matrix of Makovicky *et al.* (2005), skull and hindlimb elements need to be found in the future because these elements are important for understanding the relationships of basal ornithomimosaurs (Currie, 2000; Makovicky *et al.*, 2004; Kobayashi and Barsbold, 2005).

If *Deinocheirus mirificus* is an ornithomimosaur, three genera of ornithomimosaurs were present during Maastrichtian in southern Mongolia. *Gallimimus bullatus* is characterized by having shorter forelimb, especially the manus, than *Anserimimus planinychus*. *Anserimimus planinychus* had long forelimbs with powerful humerus musculature and flat unguals. *Deinocheirus mirificus* has a large body with large arms. Although some features in the humerus and hand of *Deinocheirus mirificus* are similar to other ornithomimosaurs, it retains primitive features like non-syndesmotically articulated between the ulna and radius and raptorial claws. These differences indicate that *Gallimimus bullatus*, *Anserimimus planinychus*,

and *Deinocheirus mirificus* might have different life styles one from each other.

CONCLUSION

Gallimimus bullatus, *Anserimimus planinychus*, and *Deinocheirus mirificus* are known from the Nemeegt Formation of Mongolia and have been interpreted as definitive and possible ornithomimid dinosaurs. *Gallimimus bullatus* can be diagnosed by its short manus. Other possible diagnostic features need to be studied in the future. *Anserimimus planinychus* is represented by only a single skeleton (whereas *Gallimimus bullatus* is common) from the Nemeegt Formation. It has characteristic features in the arm as well, and these are a strong deltopectoral crest on the humerus, flat and nearly straight manual unguals, and long forelimbs. These two genera are definitive ornithomimosaur and are derived forms, belonging to the Ornithomimidae. Previous studies show that *Gallimimus bullatus* and *Anserimimus planinychus* form a monophyly by sharing two characters (position of the biceps tubercle and alignment of the glenoid of the scapulocoracoid). *Deinocheirus mirificus* is represented by only pectoral girdle and forelimb elements (plus some fragmentary ribs and vertebrae). Preliminary phylogenetic analyses suggested that *Deinocheirus mirificus* has ornithomimosaur-like characters (e.g., weak deltopectoral crest of humerus and subequal metacarpals), but its phylogenetic position as a member of Ornithomimosauria remains unresolved in this study. This study shows that the structures in forelimbs are important for ornithomimosaur, especially for derived ornithomimosaur, but additional materials of *Anserimimus planinychus* and *Deinocheirus mirificus* will help us to better understand the evolution of ornithomimosaur.

ACKNOWLEDGMENTS

We would like to thank Yuong-Nam Lee (Korea Institute of Geoscience and Mineral Resources, Daejeon, South Korea) for giving us an opportunity to present this study. Reviews and suggestions by Dale A. Winkler (Southern Methodist University, Texas, USA) and Junchang Lü (Chinese Academy of Geological Sciences, Beijing, China) greatly improved this manuscript. We are grateful to Isao Takahashi (Gobi Support Japan, Gunma, Japan) for his hospitality during our study in Gunma Prefecture of Japan and Katsuhiro Kubota (Tsukuba University, Tsukuba, Japan) for his discussions. Thanks to Philip J. Currie (University of Alberta, Alberta, Canada), Mark A. Norell (American Museum of Natural History, New York, USA), Peter J. Makovicky (Field Museum of Natural History, Illinois, USA), Kevin Seymour (Royal Ontario Museum, Ontario, Canada) for providing access to specimens.

몽골의 Nemeegt층에서 산출된 ornithomimids

Yoshitsugu Kobayashi¹ and Rinchen Barsbold²

¹Hokkaido University Museum, Hokkaido University, Sapporo, Hokkaido, 060-0810 Japan,
ykobayashi@museum.hokudai.ac.jp

²Paleontological Center of Mongolian Academy of Sciences, PO Box 260, Ulaan Bataar 210351,
Mongolia, barsgeodin@magicnet.mn

요 약: 이 연구에서 몽골의 Nemegt층 (Maastrichtian)에서 산출된 두 ornithomimids (*Gallimimus bullatus* 와 *Anserimimus planinychus*), 그리고 잘 밝혀지지 않은 ornithomimid (*Deinocheirus mirificus*)를 재검토하였다. *Gallimimus bullatus*는 가장 잘 알려진 ornithomimids 중 한 종이지만 그 특징의 정의는 개정할 필요가 있다. *Gallimimus bullatus*의 앞발과 상박골 길이의 비율은 0.61이다. 이 수치는 ornithomimosaur (평균 0.8 이상) 중에서 가장 작으며 이전 연구에서 제안된 것처럼 *Gallimimus bullatus*를 정의하는 좋은 특징이다. *Anserimimus planinychus*는 상박골의 deltopectoral crest가 크게 발달해 있고 긴 앞발과 위아래로 납작하고 거의 똑바른 앞발가락들을 갖고 있다. *Anserimimus planinychus*는 두 가지 특징 (biceps tubercle의 위치와 glenoid의 방향)을 *Gallimimus bullatus*와 공유하며 *Harpymimus okladnikovi* (원시적인 ornithomimosaur)처럼 긴 metacarpal III를 갖고 있다. *Deinocheirus mirificus*는 발견 당시부터 그것의 계통발생학적 위치는 수수께끼였다. 금번 연구에서 이전에 연구되었던 수각류에 대한 3개의 커다란 데이터 조합에 기초해 계통발생학적 기초 분석이 시도되었다. 데이터 중 2개는 *Deinocheirus mirificus*가 ornithomimosaur에 속한 것으로 나타나는데 이는 이 종이 ornithomimosaur 같은 특징들 (즉, 거의 길이가 같은 완골과 두드러지지 않은 상박골의 deltopectoral crest)을 갖고 있지만 *Deinocheirus mirificus*는 계통발생학으로 ornithomimosaur로 확정할 수는 없다. 왜냐하면 다른 특징을 사용한 분석 결과는 이 종이 Ornithomimosauria와는 상관관계가 없게 나타나기 때문이다.

주요어: Ornithomimids, Nemegt층, 후기 백악기, 몽골

REFERENCES

- Barsbold, R. 1976. On the evolution and systematics of the late Mesozoic dinosaurs; pp. 68-75 in Kramarenko, N. N. (ed.), Paleontologîi i biostratigrafiâ Mongolii. Sovmestnaâ Svetsko-Mongolskaâ Paleontologiceskaâ Ekspediciâ, Trudy 3:3.
- Barsbold, R. 1988. A new Late Cretaceous ornithomimid from the Mongolia People's Republic. Paleontologicheskii Zhurnal 122-125.
- Barsbold, R. and Perle, A. 1984. On first new find of a primitive ornithomimosaur from the Cretaceous of the MPR. Paleontologicheskii Zhurnal 121-123.
- Currie, P. J. 2000. Theropods from the Cretaceous of Mongolia; pp. 434-455 in Benton, M. J., Shishkin, M. A., Unwin, D. M. and Kurochkin, E. N. (eds.), The Age of Dinosaurs in Russia and Mongolia. Cambridge University Press, Cambridge.
- Holtz, T. R., Jr. 1998. A new phylogeny of the carnivorous dinosaurs; pp. 5-61 in Pérez-Moreno, B. P., Holtz, T. Jr., Sanz, J. L. and Moratalla, J. (eds.), Aspects of Theropod Paleobiology. GAIA 15.
- Khand, Y., Badamgarav, D., Ariunchimeg, Y. and Barsbold, R. 2000. Cretaceous System in Mongolia and its depositional environments; pp. 49-79 in Okada, H. and Mather, N. J. (eds.), Cretaceous Environments of Asia. Elsevier Science B. V., Amsterdam.
- Kobayashi, Y. and Barsbold, R. 2004. Phylogeny of Ornithomimosauria and its paleobiogeographic implications. Proceedings of the 19th International Congress of Zoology, Beijing, China, 23-27 August 2004. China Zoological Society, Beijing, China. pp. 50-52.
- Kobayashi, Y. and Barsbold, R. 2005. Anatomy of *Harpymimus okladnikovi* Barsbold and Perle, 1984 (Dinosauria; Theropoda) of Mongolia; pp. 97-126 in Carpenter, K. (ed.), Carnivorous Dinosaurs. Bloomington, Indiana University Press.
- Kobayashi, Y. and Lü, J. 2003. A new ornithomimid dinosaur with gregarious habits from the Late Cretaceous of China. Acta Paleontologica Polonica 48:235-259
- Makovicky, P., Kobayashi, Y. and Currie, P. 2004. Ornithomimosauria; pp. 137-150 in Weishampel, D. B., Dodson, P. and Osmólska, H. (eds.), The Dinosauria. 2nd ed. Berkeley, University of California Press.
- Makovicky, P. J., Apesteguia, S. and Agnolin, F. L. 2005. The earliest dromaeosaurids theropod from South America. Nature 437:1007-1011.
- Maryanska, T., Osmólska, H. and Wolsan, M. 2002. Avialan status for Oviraptorosauria. Acta Palaeontologica Polonica 47:97-116.
- Nicholls, E. L. and Russell, A. P. 1981. A new specimen of *Struthiomimus altus* from Alberta, with comments on the

- classificatory characters of Upper Cretaceous ornithomimids. *Canadian Journal of Earth Sciences* 18:518-526.
- Nicholls, E. L. and Russell, A. P. 1985. Structure and function of the pectoral girdle and forelimb of *Struthiomimus altus* (Theropoda: Ornithomimidae). *Palaeontology* 28:643-677.
- Osmólska, H. and Roniewicz, E. 1970. Deinocheiridae, a new family of theropod dinosaurs. *Palaeontologica Polonica* 21:5-19.
- Osmólska, H., Roniewicz, E. and Barsbold, R. 1972. A new dinosaur, *Gallimimus bullatus* n. gen., n. sp. (Ornithomimidae) from the Upper Cretaceous of Mongolia. *Palaeontologica Polonica* 27:103-143.
- Paul, G. S. 1988. *Predatory dinosaurs of the world: a complete illustrated guide*. Simon and Schuster, New York. 464 pp.
- Russell, D. A. 1972. Ostrich dinosaurs from the Late Cretaceous of western Canada. *Canadian Journal of Earth Sciences* 9:375-402.
- Watabe, M. and Suzuki, S. 2000. Cretaceous fossil localities and a list of fossils collected by the Hayashibara Museum of Natural Sciences and Mongolian Paleontological Center Joint Paleontological Expedition (JMPE) from 1993 through 1998. *Hayashibara Museum of Natural Sciences Research Bulletin* 1:99-108.