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New material of a derived ornithomimosaur from the Upper Cretaceous Nemegt Formation of Mongolia

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New material of an ornithomimid from the Late Cretaceous deposits of Tsagan Khushu (Gobi Desert, Mongolia) is described. The material includes a partial axial skeleton, and hind and forelimb elements. The specimen is similar to *Anserimimus planinychus* from nearby Bugin Tsav locality in having ventrally flat, long, almost straight manual unguals. The new specimen differs from *A. planinychus* in the length of the penultimate manual phalanx II-2, which is only slightly shorter than Ph III-3, in a considerably lesser alae of the manual unguals, and in the height/width ratio of the proximal articular surfaces. The material suggests presence of third, hitherto unknown ornithomimid from the Nemegt Formation.

Key words: Dinosauria, Ornithomimidae, *Anserimimus*, Cretaceous, Nemegt, Mongolia.

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Introduction

The Late Cretaceous formations of Mongolia, especially the Nemegt Formation, are among the richest fossil-bearing land sediments in Asia. Since the expeditions of the 1920s led by Roy Chapman Andrews, which unearthed few important representatives of major dinosaurian clades (Granger and Gregory 1923; Osborn 1924), numerous other excavations have been conducted in Mongolia and surrounding areas. Between 1963 and 1971 several Polish-Mongolian Paleontological Expeditions (PMPEs) to the Gobi Desert (see e.g., Kielan-Jaworowska 2004 and a review of the Gobi paleoecosystem in Sabath 2004) unearthed Late Cretaceous faunas including mammals, dinosaurian representatives of Ceratopsia, Ankylosauria, Sauropoda, and Theropoda, as well as crocodiles, lizards, amphibians, and invertebrates. The theropod material includes, among others, members of moderately large, edentulous, cursorial coelurosaurs, namely Ornithomimosauria (see Makovicky et al. 2004 for a revision of the group) represented by the ornithomimid *Gallimimus bullatus* Osmólska, Roniewicz, and Barsbold, 1972, a putative ornithomimosaur *Deinocheirus mirificus* Osmólska and Roniewicz, 1970 (this taxon has also been placed outside ornithomimosaur clade, e.g., Barsbold 1976, 1983, but see Makovicky et al. 2004; Kobayashi and Barsbold 2006; Senter 2007), and a peculiar ornithomimid specimen which is the subject of the present paper.

The first mentioned species, *Gallimimus bullatus* is represented by a few specimens including juveniles, and is so far the best-known ostrich-mimic dinosaur from the Cretaceous deposits of Mongolia. In the years following the PMPEs, ad-

ditional specimens of *Gallimimus* and other ornithomimosaur from Mongolia and China have been described (Gilmore 1933; Barsbold 1981, 1988; Barsbold and Perle 1984; Ji et al. 2003; Kobayashi and Lü 2003). Though poorly known, the most peculiar among these species is *Anserimimus planinychus* Barsbold, 1988 which differs from all other members of Ornithomimosauria in having a well elaborated deltopectoral crest, a large biceps tubercle on the coracoid and straight manual unguals that are flat ventrally. In this paper the new material from the Tsagan Khushu locality is described (Fig. 1). Some remarks on its possible phylogenetic position are given, resulting from the characters present in the forelimb. The new form from the Nemegt deposits of the Gobi Desert is found to have similarities with *Ornithomimus* from North America and *Anserimimus* from Asia.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; GIN, Paleontological Center of the Mongolian Academy of Sciences, Ulaanbaatar, Mongolia; NMC, National Museum of Canada, Ottawa, Canada; WGUW, Faculty of Geology, University of Warsaw, Warsaw, Poland; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Anatomical abbreviations.—C, cervical; Ca, caudal; D, dorsal; Mtc, metacarpal; Ph, phalanx; S, sacral; U, ungual.

Material and methods

The material labeled ZPAL MgD-I/65 has been disarticulated, but the configuration of the bones in one piece of rock

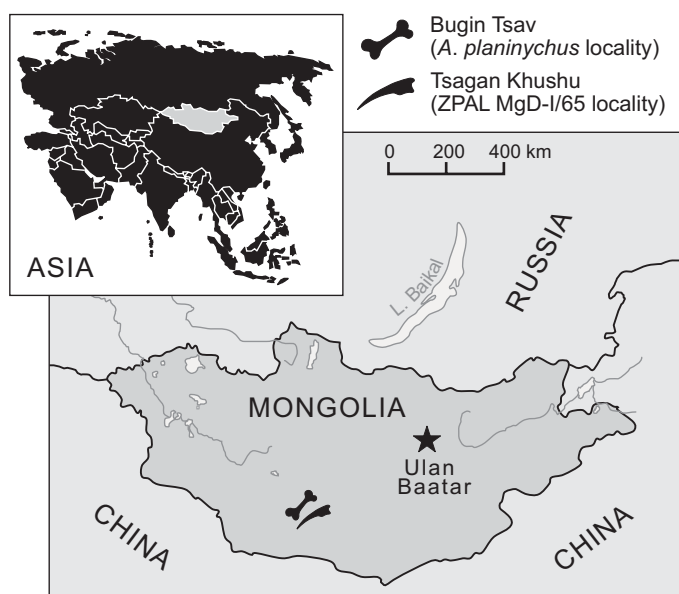


Fig. 1. Geographical location of the Tsagan Khushu (referred material locality) and Bugin Tsav (*Anserimimus planinychus* locality) sites in the Gobi Desert, Mongolia (Upper Cretaceous).

suggests they belong to one individual. The specimen includes: 7 cervical, 3 dorsal, 2 sacral, and 7 caudal centra; scapulae; both left and right manual bones (fragmentary left Mtc I, complete left Mtc II and fragmentary right Mtc II; phalanges of the left manual digits [I-1, II-1 and II-2, III-3], fragmentary ungual phalanx of the second digit (II-3), almost complete ungual phalanx of the first digit (I-2), two complete phalanges of the second (II-2) and third (III-3) digits of the right manus; proximal part of the left pubis, lesser trochanter and distal end of the left femur, fragmentary phalanges of the second (II-1, II-2) and third (III-1, III-3) digits and complete fourth digit (IV-1, IV-2, IV-3, IV-4, IV-5) of the right pes, fragmentary phalanges of the second (II-1) and third (III-1) digits and complete second phalanx of the third digit (III-2) of the left pes.

Additional specimens which supplement the description include: ZPAL MgD-I/66 ?third phalanx (III-3) of the third manual digit and ungual phalanx of the ?first (I-2) manual digit; ZPAL MgD-I/23, ZPAL MgD-I/231, ZPAL MgD-I-233, manual ungual phalanges.

Systematic paleontology

Dinosauria Owen, 1842

Theropoda Marsh, 1881

Coelurosauria von Huene, 1914

Maniraptoriformes Holtz, 1996

Ornithomimosauria Barsbold, 1976

Genus *Anserimimus* Barsbold, 1988

Type species: SPS GIN AN MPR 100/300, Bugin-Tsav, Upper Senonian (all according to Barsbold (1988); in the present text it is referred as GIN 100/300).

aff. *Anserimimus planinychus* Barsbold, 1988

Figs. 2–9.

Material.—ZPAL MgD-I/65, associated partial axial skeleton with hind- and forelimb elements; ZPAL MgD-I/66, forelimb elements; ZPAL MgD-I/23, ZPAL MgD-I/231, ZPAL MgD-I/233, unguals of the manus.

Stratigraphic and geographic range.— The specimen was collected in Tsagan Khushu locality (near Bugin Tsav which is the type locality of *Anserimimus planinychus*) in the Nemegt Formation, Ömnögöv Province, Mongolia (Fig. 1). Additional specimens were collected in the vicinity of the ZPAL MgD-I/65 but were not directly associated with the skeleton.

The sediments of the Tsagan Khushu are considered to be Late Cretaceous in age (lower Campanian or ?upper Campanian–?lower Maastrichtian; see Gradziński 1970; Gradziński et al. 1977; Karczewska and Ziemińska-Tworzydło 1983; Jerzykiewicz 2000).

Description

Axial skeleton.—The vertebral column of ZPAL MgD-I/65 is very incomplete (Fig. 2). Available vertebrae are represented by their centra, mainly without anterior articular surfaces. The odontoid of the putative axial vertebra is oval and subtriangular in anterior view, and it has a flat ventral surface. The centrum of this vertebra is slender, antero-posteriorly long, and ventrally flat. The preserved posterior articular surface of the next preserved cervical vertebra is concave, subrectangular and with a gently convex dorsal edge. A preserved part of the centrum indicates that the anterior articular surface has been elevated in relation to the posterior articular surface. The next centrum in the cervical series, preserved with a fragmentary vertebral arch that has a deep posterior ligament scar, demonstrates the same feature, with the same elevation of the anterior articular surface as in the previous one. On the basis of comparisons with *Gallimimus bullatus* Osmólska, Roniewicz, and Barsbold, 1972, the latter two centra should be placed in the region of the 3rd–5th vertebrae in the neck region. The articular surfaces of the following centra, which are also ventrally flat, do not have the elevation. The most complete cervical centrum is the penultimate one. In comparison with the vertebrae of *G. bullatus*, it is the ninth cervical centrum. Its body is antero-posteriorly (ratio of vertebral body height (VBH)/vertebral body length (VBL) equals approximately 0.4) long and it is flat ventrally. The posterior articular surface of the centrum, in contrast to the anterior surface, is dorso-ventrally low. The next preserved centrum, probably the tenth cervical, consists only of its posterior half. The fragment has a small keel on its ventral surface that indicates that it was a transitional vertebra between the cervical and dorsal regions.

The next preserved of the available centra, comparing to *G. bullatus* and GIN 96091KD (Kobayashi 2004: fig. 20), is

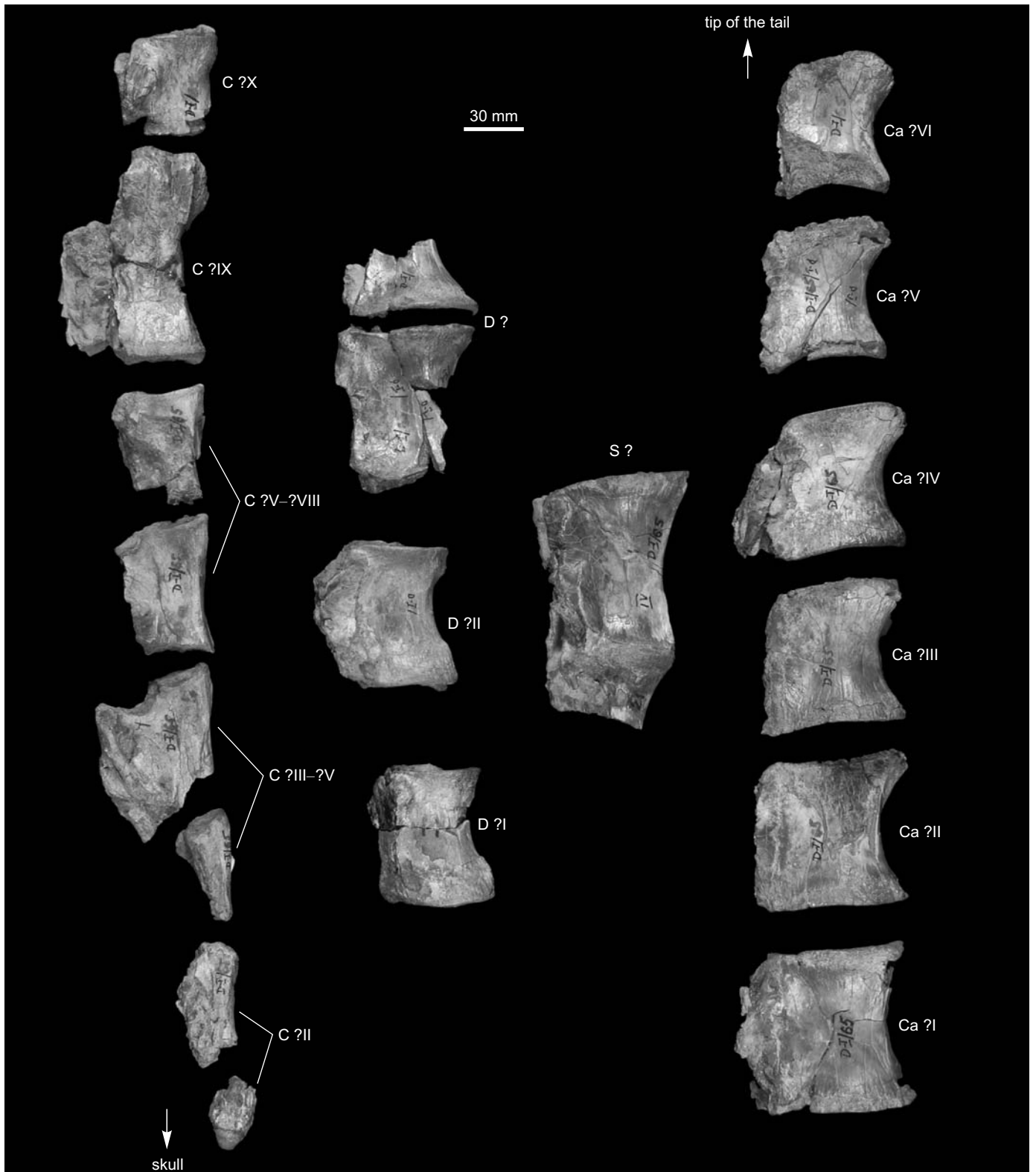


Fig. 2. Vertebral centra available for the ornithomimid ZPAL MgD-I/65 from the Upper Cretaceous Nemegt Formation, Mongolia in left lateral view. Abbreviations: C, cervical; D, dorsal; S, sacral; Ca, caudal.

considered as one of the first dorsals. All dorsal centra are spool shaped, and their articular surfaces tend to be enlarged and become more rounded posteriorly.

The sacrum is represented only by one centrum which is

massive, spool shaped and flat ventrally with the articular surface of the subsequent vertebra firmly attached to it. Its anterior articular surface is rectangular, and posterior one is oval, with the vertical axis being the longest. Along the ven-

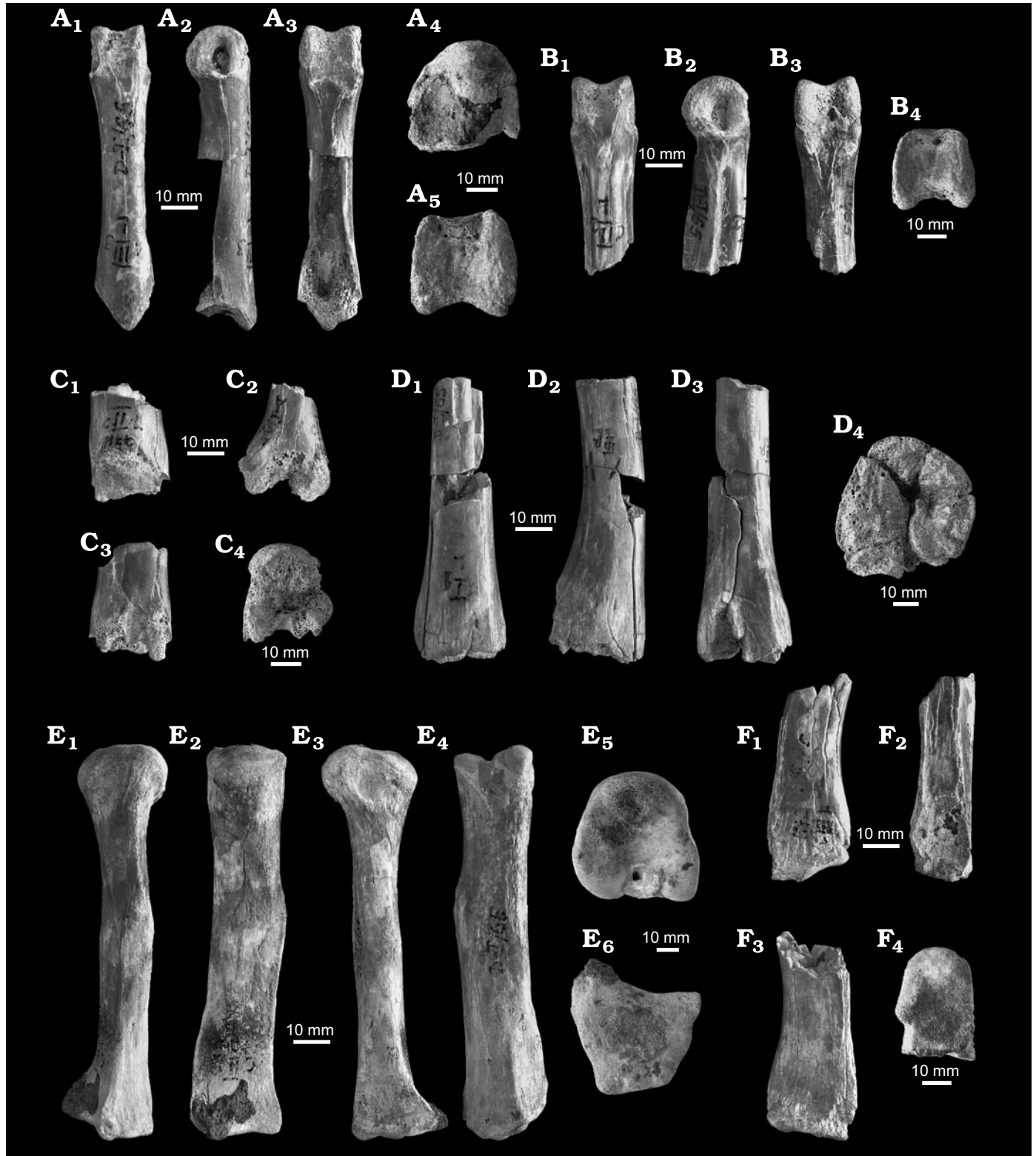


Fig. 3. Manual bones of the ornithomimid ZPAL MgD-I/65 from the Upper Cretaceous Nemegt Formation, Mongolia shown in multiple views. **A.** Ph III-3 in dorsal (A₁), lateral (A₂), ventral (A₃), proximal (A₄), and distal (A₅) views. **B.** Ph II-2 in dorsal (B₁), lateral (B₂), ventral (B₃), and distal (B₄) views. **C.** Ph II-1 in dorsal (C₁), lateral (C₂), ventral (C₃), and proximal (C₄) views. **D.** Ph I-1 in dorsal (D₁), lateral (D₂), ventral (D₃), and proximal (D₄) views. **E.** Mtc II in medial (E₁), dorsal (E₂), lateral (E₃), ventral (E₄), distal (E₅), and proximal (E₆) views. **F.** Mtc I in dorsal (F₁), lateral (F₂), ventral (F₃), and proximal (F₄) views.

tral side of the centrum there is a scar that is widest at the contact with the subsequent vertebra. The dorsal side of the

centrum is abraded and it is unclear whether or not the neurocentral suture was fully closed.

The caudals are similar to those in *Gallimimus bullatus*. Their centra are spool shaped with oval articular surfaces and with a ventral oblong scar, which widens and deepens towards both ends of the vertebrae. The scar is restricted laterally (at the contact of the centra) with processes that end with articular surfaces for the hemal arches.

Forelimb.—The preserved portion of the Mtc I (Fig. 3F) is dorso-ventrally flat, and it is subtriangular in cross-section. On its lateral side there is a concave surface to contact with Mtc II.

Mtc II is the best preserved among available metacarpal bones (Fig. 3E). It is dorso-ventrally flat, subrectangular in cross-section at its midpoint, and subtriangular at the proximal and distal end. On its medial side there is a flat surface to contact Mtc I (it occupies approximately 62% of the medial side). The distal half of Mtc II extends laterally at an angle of about 23°. The lateral side of Mtc II has a concavity to contact Mtc III, that is shallower than is seen in *G. bullatus*. The proximal articular surface of Mtc II is triangular in shape. The distal joint surface is ball shaped, constituting ball and socket articulation between the metacarpal and the first phalanx—a feature characteristic of Ornithomimidae (Kobayashi and Lü 2003). The distal articular surface is twisted clockwise at an angle of about 26° in relation to the proximal joint surface. The proximal articular surface of Ph I-1 (Fig. 3C) is oval in outline, slightly laterally flattened with a wide ventral scar. Both proximal and distal articular surfaces of Ph II-2 (Fig. 3B) have a hinge joint with Ph II-1 and Ph II-3, a feature typical for interphalangeal joints of the manus and pes. On the ventral side of the distal half of Ph II-2 there is a transversely oval cavity. Ph III-3 (Fig. 3A) is similar to Ph II-2, but its articular surfaces are smaller. Both phalanges, contrary to the holotype of *Anserimimus planinychus*, are almost equal in length.

The manual ungual of the referred material is almost straight (curvature is slight), and have flat ventral surfaces similar to the condition seen in *A. planinychus* (see Barsbold 1988) (Fig. 5). The flexor tubercle is low with a coarse ventral surface, and is set far distally relative to the joint surface. At the lateral and medial sides there are deep grooves, these are sometimes penetrated by vascular foramina.

Pelvic girdle and hind limb.—The proximal part of the left pubis is preserved (Fig. 6). Despite the lack of some portions of the bone it displays the typical configuration for ornithomimids with a larger ischial peduncle. On the medial side of the ischial peduncle there is a concavity that is shallower than is seen in *Gallimimus bullatus*. On the anterior edge of the pubis, slightly laterally, a rugosity is present, developed almost throughout the length of the specimen. It is abraded just below the attachment surface for the pubic peduncle of the ilium. The remaining part of the structure, which is identified as the origin of *M. ambiens* (Osmólska et al. 1972), is rough, indicating a well developed muscle. Only two fragments of the right femur have been collected from the Tsagan Khushu; the blade of the lesser trochanter (Fig. 7A) and the distal region with deep depression on the anterior side that is eroded, but it has a sharp crest on its medial side above the distal

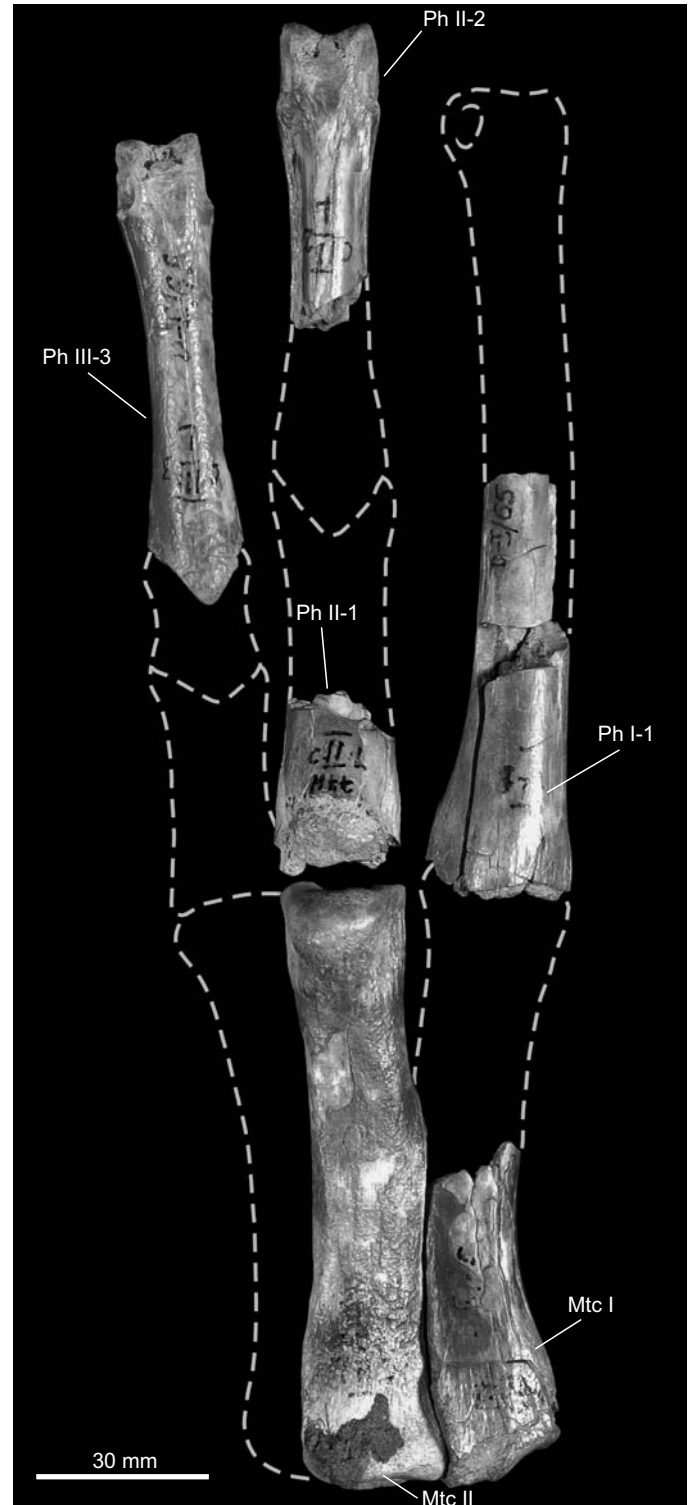


Fig. 4. Left manual bones of the ornithomimid ZPAL MgD-I/65 from the Upper Cretaceous Nemegt Formation, Mongolia shown without unguals, in dorsal view. Dashed lines indicate missing bones. Abbreviations: Mtc, metacarpal; Ph, phalanx.

condyle (Fig. 7B). Ph II-1 is laterally flattened (Fig. 8B). On its ventral surface there is a deep scar. The distal articular surface of Ph II-1 firmly attaches to Ph II-2 (Fig. 8A). Both phalanges indicate a presence of the typical hinge joint.

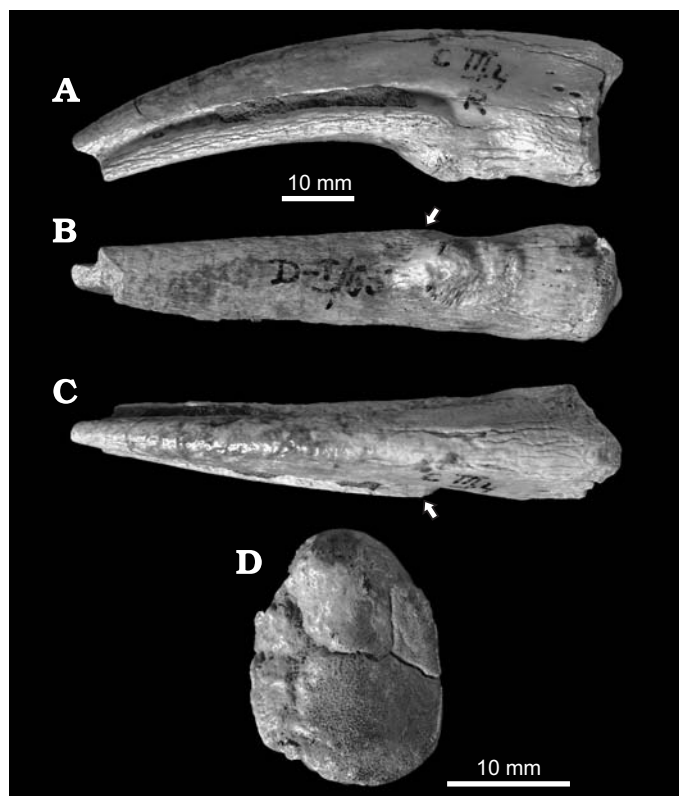


Fig. 5. Manual ungual of the ornithomimid ZPAL MgD-I/65 from the Upper Cretaceous Nemegt Formation, Mongolia collected at Tsagan Khushu locality. In lateral (A), ventral (B), and dorsal (C) views, articular surface (D). Arrows point at the alae.

Ph III-1 is dorso-ventrally flat (Fig. 8D). Its proximal articular surface is concave, subrectangular with a convex dorsal edge. Ventrally there is a scar surrounded by crests, like those present on Ph II-1. Nevertheless, both scar and crests are smaller than in Ph II-1. The distal articular surface of the Ph III-1 is transversely wide with deep ligament pits. Both proximal and distal articular surfaces of the Ph III-2 represent hinge joints. Digit four is the most complete (Fig. 9). The lateral condyles of all the phalanges are taller than medial ones. The ungual is short, ventrally flat, subtriangular in cross-section, and slightly curved, with grooves laterally. The state of preservation of the rest of the ZPAL MgD-I material does not provide any additional anatomical information.

Discussion

On the basis of ball and socket articulation between metacarpals and phalanges, found also in *Gallimimus bullatus* (Osmólska et al. 1972) and *Struthiomimus altus* (Nicholls and Russell 1985), see also Kobayashi and Lü (2003: 255), the referred material is considered to represent a member of Ornithomimidae.

The ZPAL specimen shows similarities with the holotype of *Anserimimus planinychus*, an incomplete taxon from the same formation (the holotype comprises scapulocoracoid

fragments, humerus, manus, and carpal, metacarpal, and metatarsal elements; see Barsbold 1988; the data regarding *A. planinychus* have been obtained from the literature). Both specimens have long, almost straight manual unguals that have flat ventral surfaces. There are three major differences between the referred material and *A. planinychus*. First, the length of the penultimate phalanges of digits II and III (Ph II-2 and Ph III-3, respectively); according to Barsbold (1988: fig. 1), Ph II-2 is distinctively longer than Ph III-3. Contrary to Barsbold's specimen (GIN 100/300), the ZPAL MgD-I/65 has both phalanges almost equal—Ph III-2 is only slightly longer than Ph II-3. The difference itself could be considered an intraspecific heterogeneity which has been reported in theropod dinosaurs (in *Allosaurus fragilis* Marsh, 1877, Chure, and Madsen 1996; in *G. bullatus* Kobayashi and Barsbold, 2006: 195).

A second difference concerns the degree of dorso-ventral flattening of the manual unguals. The height/width ratio in digit I of *Anserimimus planinychus* equals 0.52 (Kobayashi and Barsbold 2006: 199). In ZPAL specimens the ratio equals between 1.16 and 1.26, which falls in the range of other ornithomimosaurs (e.g., for *Archeornithomimus asiaticus* the ratio equals 1.15 and for *Sinornithomimus dongi* it is 2.10; Kobayashi and Barsbold 2006: 199). Lastly, development of the alae of the manual unguals differs with the ZPAL specimen. The alae in the referred material, and thus the flat ventral surfaces of manual digits, are distinctively less developed medially and laterally (i.e., are narrower) than those of the holotype of *Anserimimus planinychus*.

The differences in the development of the manual unguals between *A. planinychus* and ZPAL MgD-I/65 could be interpreted as intraspecific variations, and thus imply that both

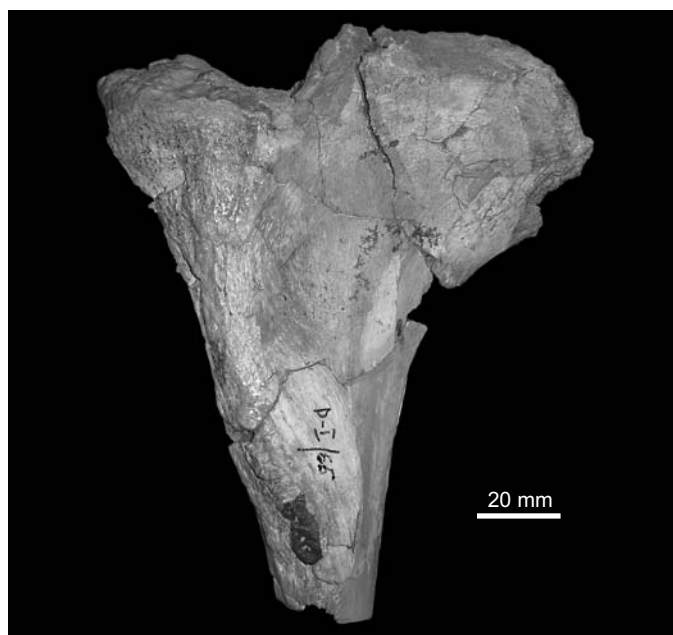


Fig. 6. Proximal part of the left pubis of the ornithomimid ZPAL MgD-I/65 from the Upper Cretaceous Nemegt Formation, Mongolia shown in lateral view.

morphotypes belong to the same taxon (*Anserimimus planinychus* in this case). Smith and Galton (1990: 260) described two different morphotypes for unguals of the other ornithomimosaur *Archaeornithomimus asiaticus* (Gilmore, 1933). Given that the material from the Iren Dabasu Formation is mostly represented by isolated, disarticulated specimens and on the basis of its apparent variability Currie and Eberth (1993: 137) suggested “high probability that more than one ornithomimid species was present at Iren Dabasu”. The same refers to ZPAL MgD-I/65 and *Anserimimus planinychus*. The three above-described differences taken together suggest the presence of an other ornithomimid, similar to *A. planinychus* at Nemegt. It is therefore likely that the referred specimen represents a new species of *Anserimimus* or even a new genus of the Late Cretaceous ornithomimid from the Nemegt Formation, but a firm conclusion is limited by the available data.

Phylogenetic relationships within Ornithomimidae remain problematic (Makovicky et al. 2004). Presumable solutions for that question have been illustrated by the cladograms presented by Norell et al. (2006), Senter (2007) and Turner et al. (2007) in which *Anserimimus* and *Ornithomimus* are sister taxa. Characters that unite these ornithomimids are straight manual unguals with distally placed flexor tubercles, manual phalanx II-1 equal or longer than twice the length of manual phalanx III-1, manual phalanx II-2 equal or longer than twice the length of manual phalanx II-1, metacarpals II and III appressed for their entire lengths and distal expansion of the scapula. Moreover, ZPAL MgD-I/65 seems to share some characters between *Ornithomimus edmontonicus* Sternberg, 1933 from the Late Cretaceous of North America and *Anserimimus planinychus* from the Late Cretaceous of Asia. Casts of the NMC 8632 specimen of *O. edmontonicus*, housed at ZPAL, displays long and straight manual unguals (as coded in the above-mentioned phylogenetic analyses). The NMC specimen also seems to have incipient alae on the manual unguals. These two characters (long, straight manual unguals with alae developed on the lateral and medial side of each ungual) are shared between the referred material and the holotype of *A. planinychus* (in the ZPAL specimen and especially in *A. planinychus* the alae are more elaborated on the medial and lateral side of each ungual expanding the extent of the flat ventral surface). Unfortunately insufficient extraction from the surrounding rock before making a cast disables exact comparisons of the ventral surface of the NMC 8632.

On the basis of other descriptions of *Ornithomimus edmontonicus* (e.g., Parks 1933, see also Kobayashi 2004: fig. 87), the general structure of the manus of that taxon also demonstrates similarities to the ZPAL MgD-I/65 and GIN 100/300 material (Fig. 10); the whole metacarpus is narrower in its mid-length (Kobayashi 2004: fig. 87). Digits I of the ZPAL MgD-I/65, *Anserimimus planinychus*, and *O. edmontonicus* contrary to e.g., *Struthiomimus altus* (Lambe, 1902) or *Gallimimus bullatus* Osmólska, Roniewicz, and Barsbold, 1972, are rotated only slightly medially from digits II and III, resulting in a narrow manus. The three taxa could have had a common ancestor with a narrow manus and digits ending

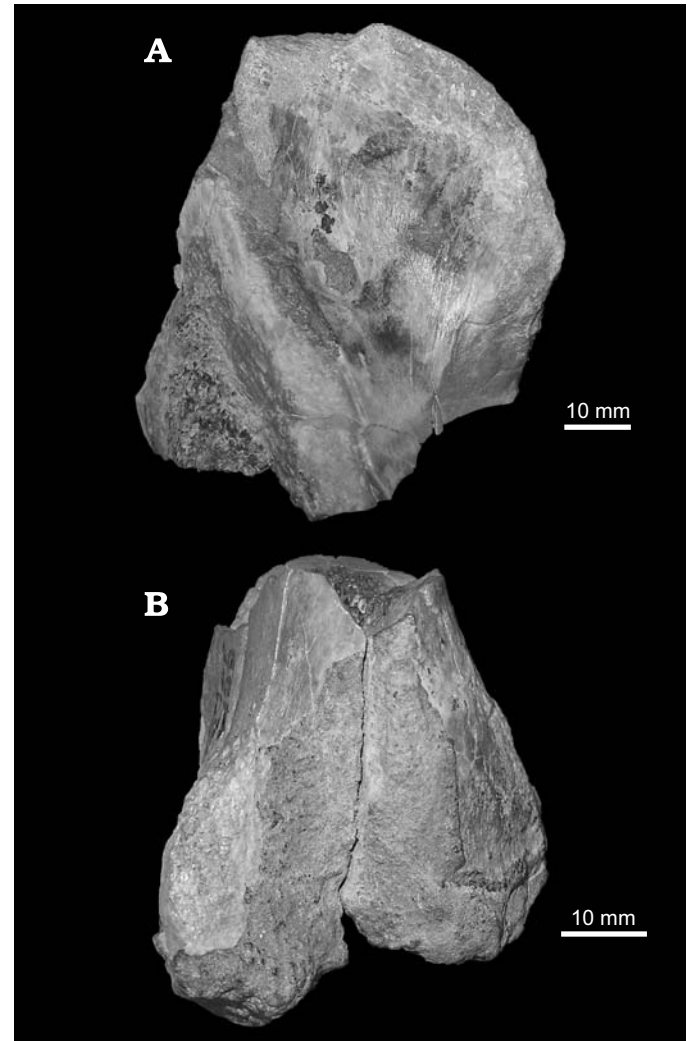


Fig. 7. Bone fragments referred to the left femur of the ornithomimid ZPAL MgD-I/65 from the Upper Cretaceous Nemegt Formation, Mongolia. **A.** Lesser trochanter in posterior view. **B.** Distal condylar process in anterior view.

with long, straight unguals. The referred material would then be closer to the divergence point of *Ornithomimus* and *Anserimimus* lineages than *Anserimimus planinychus*, and should probably be considered an intermediate form between these two taxa.

Contrary to this hypothesis Kobayashi (2004), the study of the structure of the pectoral girdles suggests close affinity of *A. planinychus* (and thus the unnamed taxon allegedly related to *Anserimimus*) to *Gallimimus bullatus*. In this case similarities of the structure of the manus would be the result of convergent evolution, triggered by similar use of the forelimbs. However, as noted by Kobayashi and Barsbold (2006: 202): “...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 Mtc I and III longer than Mtc II...”. The first character, as noted by the authors, is common in North American taxa, e.g., *Ornithomimus*. Such similarity is another link uniting *A.*

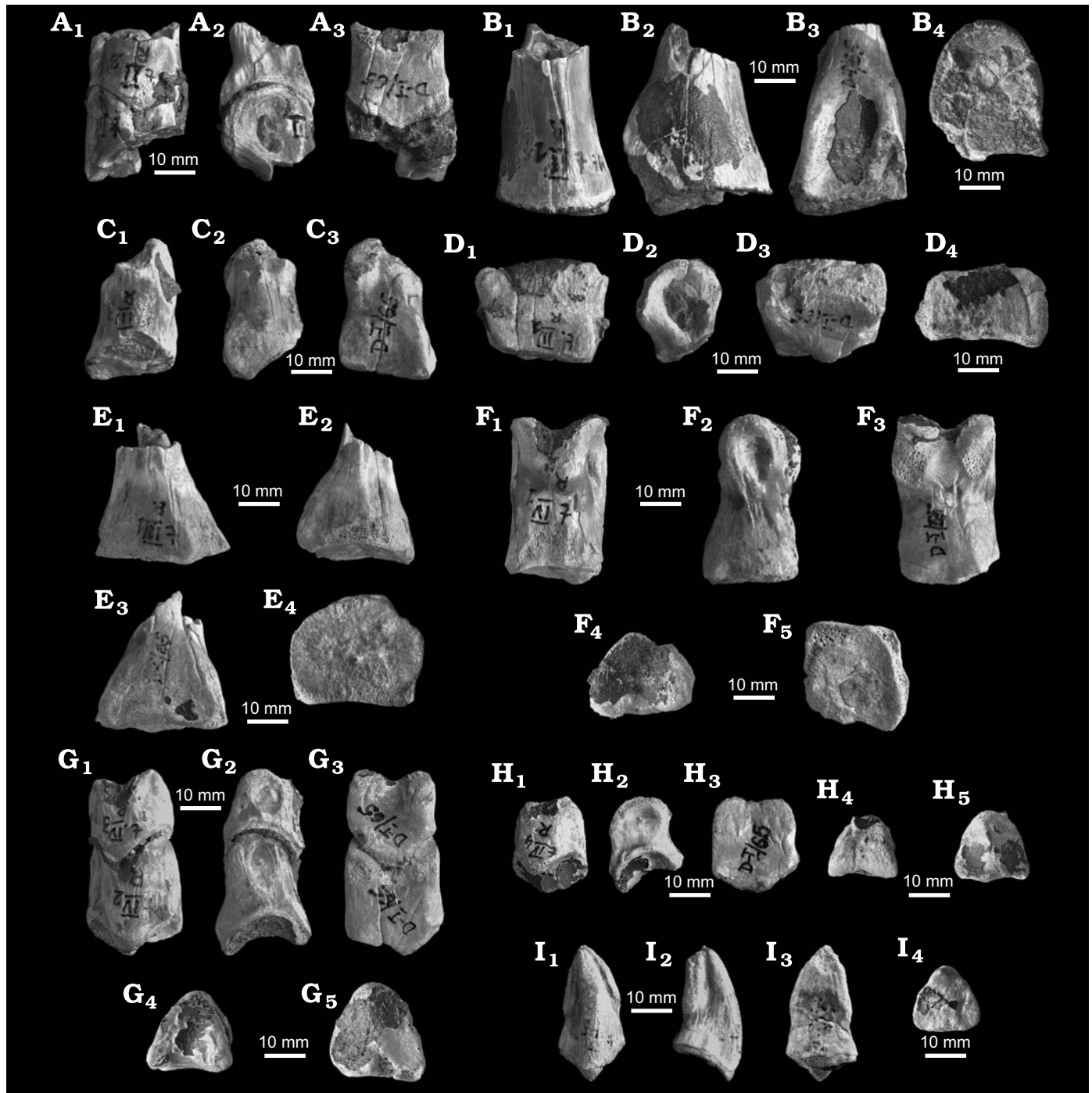


Fig. 8. Pedal bones of the ornithomimid ZPAL MgD-I/65 from the Upper Cretaceous Nemegt Formation, Mongolia shown in multiple views. Explanations: A. Ph II-1 (distal part) + Ph II-2 in dorsal (A₁), medial (A₂), and ventral (A₃) views. B. Ph II-2 (proximal part) in dorsal (B₁), medial (B₂), ventral (B₃), and proximal (B₄) views. C. Ph III-3 in dorsal (C₁), medial (C₂), and ventral (C₃) views. D. Ph III-1 (distal part) in dorsal (D₁), medial (D₂), ventral (D₃), and distal (D₄) views. E. Ph III-1 (proximal part) in dorsal (E₁), medial (E₂), ventral (E₃), and proximal (E₄) views. F. Ph IV-1 in dorsal (F₁), medial (F₂), ventral (F₃), distal (F₄), and proximal (F₅) views. G. Ph IV-2 and IV-3 in dorsal (G₁), medial (G₂), ventral (G₃), proximal (G₄), and distal (G₅) views. H. Ph IV-4 in dorsal (H₁), medial (H₂), ventral (H₃), proximal (H₄), and distal (H₅) views. I. U4 in dorsal (I₁), medial (I₂), ventral (I₃), and proximal (I₄) views.

planinychus and North American forms and ZPAL specimen if its affinity to *A. planinychus* is true.

In conclusion, ZPAL MgD-I/65 is a member of the advanced Late Cretaceous Ornithomimidae which are exemplified by the presence of ball and socket articulation be-

tween metacarpals and phalanges. Straight and long manual unguals with flat ventral surfaces and the alae developed on lateral surfaces of each manual ungual are the characters shared by ZPAL MgD-I/65, *A. planinychus*, and *O. edmontonicus*. Metacarpi of these taxa are narrow and com-

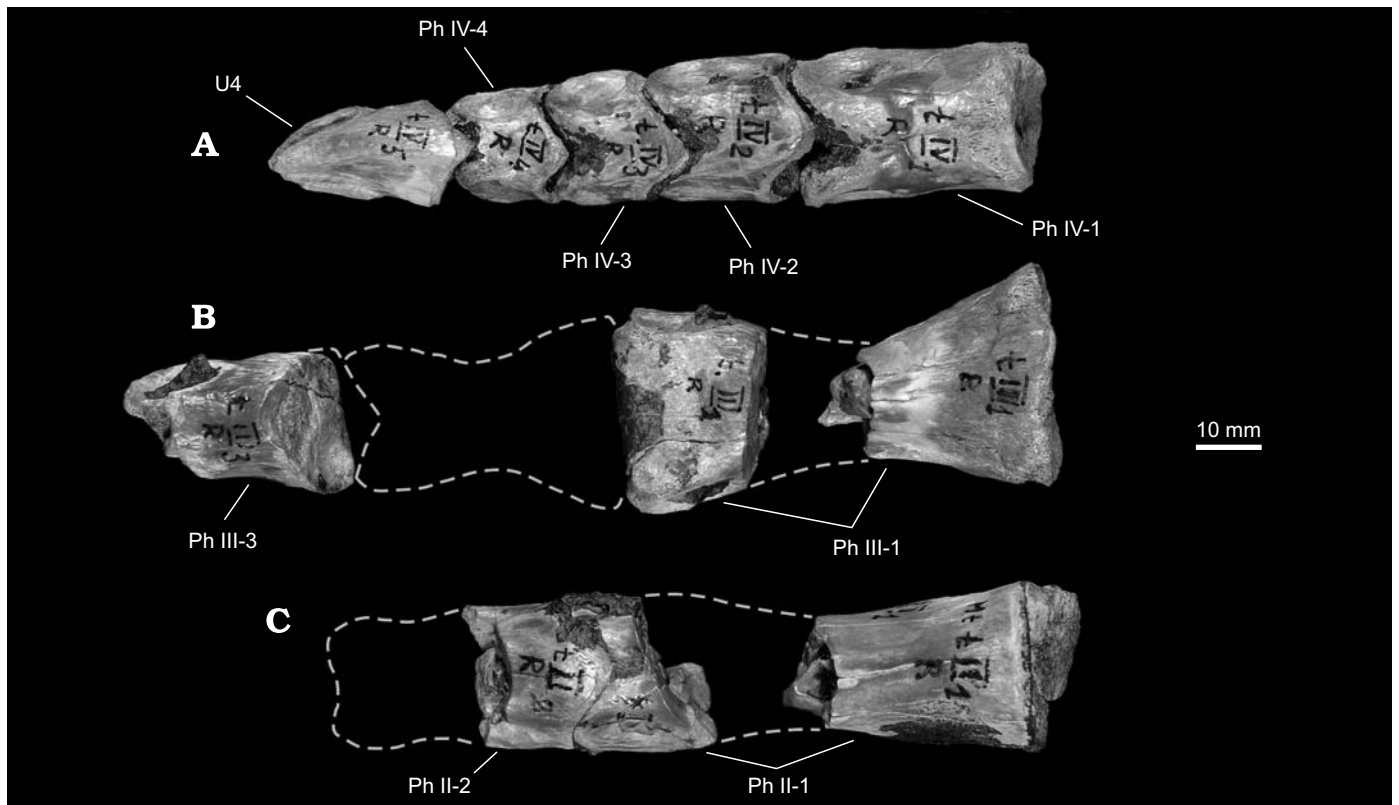


Fig. 9. Right pes of the ornithomimid ZPAL MgD-I/65 from the Upper Cretaceous Nemegt Formation, Mongolia shown in dorsal view. Abbreviations: Ph, phalanx; U, ungual.

pressed. Moreover *A. planinychus* and *O. edmontonicus* share a depression on the scapula (see above). Such anatomical similarities indicate a close relationship between these three taxa. However additional material is needed to provide better data for understanding the phylogenetic position of the ZPAL material.

Recently Longrich (2008) described partial material of a new large ornithomimid from the Late Campanian of the Dinosaur Park Formation (Dinosaur Provincial Park, Alberta, Canada). The degree of the ventral flattening of the manual unguals of the unnamed North American taxon (manual unguals of the ROM 41844 and the TMP 1980.16.1644 have flat ventral surfaces; see Longrich 2008: text-figs. 8, 9A, B) is similar to the new taxon from Mongolia (both differ from unguals of *G. bullatus* which are more rounded ventrally) and could be additional evidence for the closer relationship of the described specimen (and *A. planinychus*) with North American forms.

Phylogenetic analysis

In order to explore a presumable relationships of the ZPAL MgD-I/65 to *Anserimimus planinychus* and *Ornithomimus edmontonicus* a phylogenetic analysis was performed. A total of 42 characters were used, 38 of which are derived from Kobayashi and Lü (2003: appendix 1). An additional 4 new

characters (see Appendix 1) are proposed that might be helpful in resolving the relationships of the ornithomimid genera discussed in this paper. *Allosaurus* has been chosen as an outgroup and eight ornithomimosaur taxa (including ZPAL MgD-I/65) were selected for this analyses. Codings follow Kobayashi and Lü (2003) (Table 1). Characters 24 and 27 of

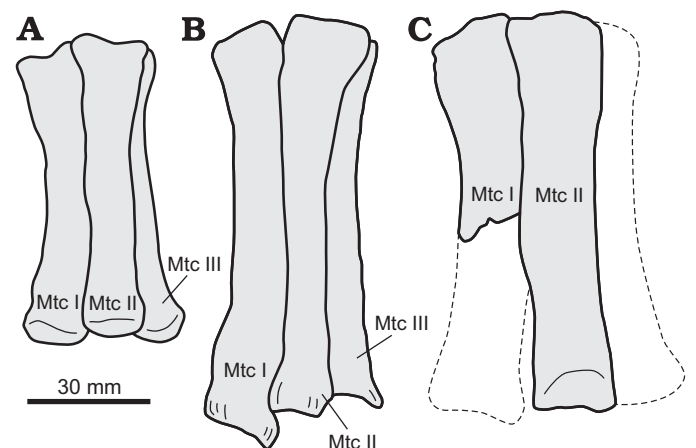


Fig. 10. Metacarpal bones of three ornithomimid taxa shown in articulation. **A.** *Anserimimus planinychus* (Upper Cretaceous Nemegt Formation; after Kobayashi and Barsbold 2006; drawing flipped horizontally). **B.** *Ornithomimus edmontonicus* (Upper Cretaceous Horseshoe Canyon Formation; after Parks 1933). **C.** ZPAL MgD-I/65 (Upper Cretaceous Nemegt Formation; this paper). Abbreviation: Mtc, metacarpal.

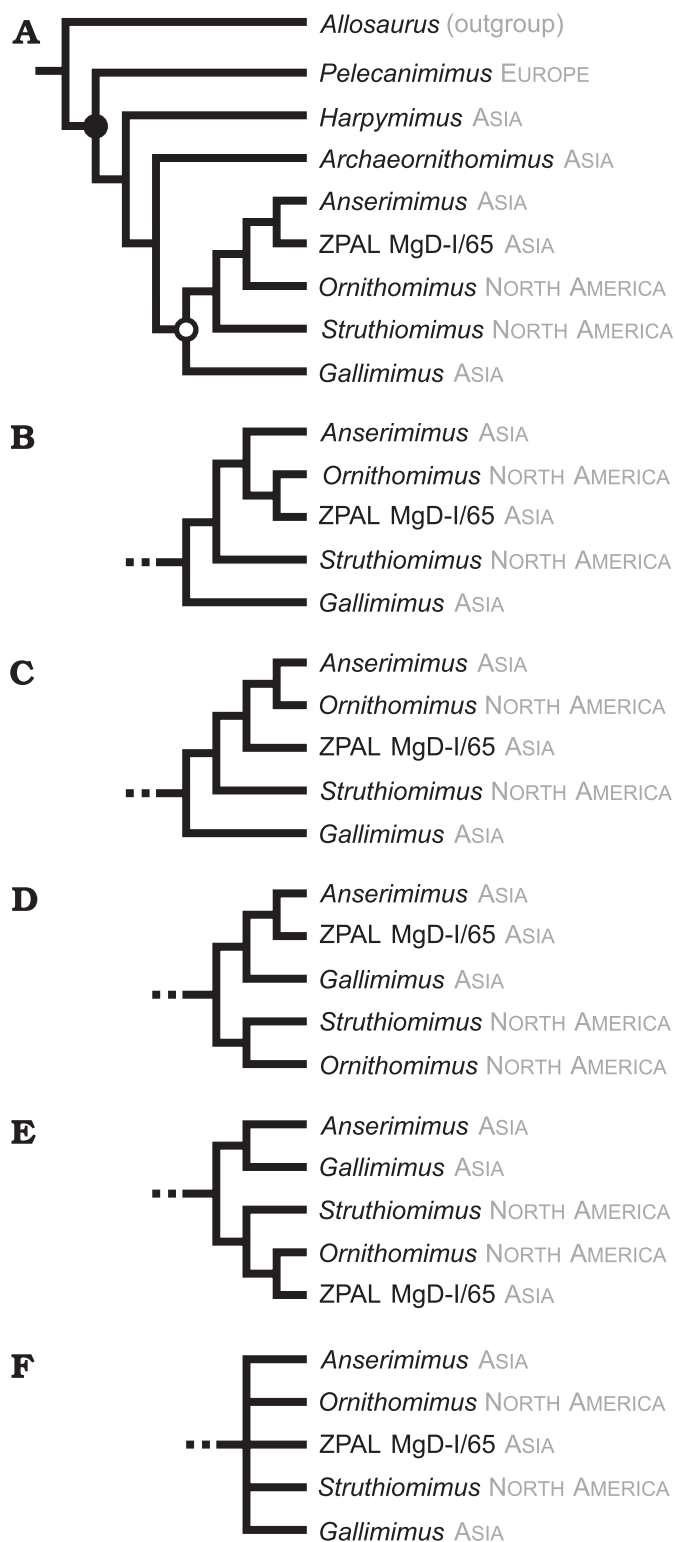


Fig. 11. Results of the phylogenetic analysis performed with PAUP 4.0 Beta 10 and PAST. Solid circle indicates Ornithomimosauria, open circle indicates Ornithomimidae. The tree A shows the full results of the phylogenetic analyses with outgroup taxon and non-ornithomimid ornithomimosaurians plus Ornithomimidae. Topologies of all trees to the level of *Archaeornithomimus* are identical hence the remaining trees (B, C, D, E, F) show only the relationships within Ornithomimidae. The tree F shows the strict consensus tree. To the right of each ornithomimosaurian taxon its geographical provenance has been given.

Gallimimus bullatus were coded by Kobayashi and Lü (2003: appendix 2) as multistate characters (01). In the present analysis only the one state for each character that matches codings of *A. planinychus* has been chosen. Other combinations of character codings have also been tested. In spite of the varying combination used, results regarding the phylogenetic affinities of *A. planinychus*, *O. edmontonicus*, and ZPAL MgD-I/65 remained the same.

Preliminary analysis has been performed using PAST software package (Hammer et al. 2001; it should be noted that the authors treat results obtained using past as preliminary) with Branch-and-Bound search and optimality criteria set to Fitch (all characters unordered and reversible). The main analysis has been performed using PAUP 4.0 beta 10 (Swofford 2000) with Branch-and-Bound search and all characters unordered with equal weights.

Five most parsimonious trees have been produced by both analyses (PAUP tree lengths = 61; C.I. = 0.74; R.I. = 0.60; R.C. = 0.44, PAST tree lengths = 61; C.I. = 0.74; R.I. = 0.89). Trees produced by PAUP and PAST have the same topology. A single strict consensus tree gave the unresolved polytomy of *Anserimimus*, *Gallimimus*, *Struthiomimus*, *Ornithomimus*, and ZPAL MgD-I/65 (Fig. 11F). Three of five shortest trees postulated close relationships between *Anserimimus*, ZPAL MgD-I/65, and *Ornithomimus*: sister taxa relationships of (*Anserimimus* + ZPAL MgD-I/65) + *Ornithomimus* (Fig. 11A) or *Anserimimus* + (ZPAL MgD-I/65 + *Ornithomimus*) (Fig. 11B) or (*Anserimimus* + *Ornithomimus*) + ZPAL MgD-I/65 (Fig. 11C). The remaining shortest trees gave the following results: ((*Anserimimus* + ZPAL MgD-I/65) + *Gallimimus*) + (*Struthiomimus* + *Ornithomimus*) (Fig. 11D) or (*Anserimimus* + *Gallimimus*) + (*Struthiomimus* + (*Ornithomimus* + ZPAL MgD-I/65)) (Fig. 11E). In most cases *Anserimimus*, ZPAL MgD-I/65 and *Ornithomimus* are depicted as closely related taxa (majority consensus tree gave the unresolved polytomy of those three ornithomimids) what would support the hypothesis proposed in this paper. Nevertheless alternative solutions have been proposed by software packages used (Fig. 11D, E) and due to a lack of more complete specimens the exact phylogenetic positions of *Anserimimus* and ZPAL MgD-I/65 remain unresolved.

Conclusions

The new specimen, with ball and socket articulation between metacarpals and phalanges, is found to be a member of Ornithomimidae. The morphology of the unguals, which are almost straight and flat ventrally, suggests its affinities to *Anserimimus planinychus*, but other anatomical differences suggest it represents a different taxon. ZPAL specimen is found to be similar to *Anserimimus* and *Ornithomimus* from the Late Cretaceous of Mongolia and North America, respectively, sharing characters intermediate between these genera. A majority of trees produced by the phylogenetic analysis

Table 1. Data matrix for the phylogenetic analyses performed in this study. Codings 1–38 are after Kobayashi and Lü (2003), codings 39–42 are introduced for the first time.

| | 1–5 | 6–10 | 11–15 | 16–20 | 21–25 | 26–30 | 31–35 | 36–38 | 39–42 |
|---------------------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| <i>Allosaurus</i> | 00000 | 00000 | 00000 | 00000 | 00000 | 00000 | 00000 | 000 | 0000 |
| <i>Pelecanimimus</i> | 0?1?? | 0?100 | 10??? | 0?1?1 | ????1 | ??110 | 111?? | ??? | 0000 |
| <i>Harpymimus</i> | 10111 | 10?10 | 10101 | 1110? | 01001 | 10000 | 0110? | ?00 | 0000 |
| <i>Archaeornithomimus</i> | ????? | ????? | ????? | ???01 | 01001 | 20110 | 1?110 | ?1? | 0000 |
| <i>Anserimimus</i> | ????? | ????? | ????? | ???11 | 10100 | 21211 | 01100 | 111 | 1121 |
| <i>Gallimimus</i> | 11111 | 11111 | 11100 | 00111 | 11101 | 21111 | 11100 | 111 | 0000 |
| <i>Struthiomimus</i> | 11110 | 01?11 | 11110 | 11111 | 01001 | ?0111 | 11101 | 111 | 0000 |
| <i>Ornithomimus</i> | 11110 | 11?11 | 11111 | 11111 | 00011 | 20211 | 11101 | 111 | 1100 |
| ZPAL MgD-I/65 | ????? | ????? | ????? | ????? | ????? | ????? | ??1?? | ??? | 1110 |

new characters

support the author's hypothesis but the fragmentary nature of both *Anserimimus planinychus* and ZPAL MgD-I/65 does not allow certain phylogenetic placement of the referred material. Additional specimens are necessary to clarify its phylogenetic affinities.

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Appendix 1

New characters added to the character list of Kobayashi and Lü (2003).

39. Ratio width of metacarpus (WOM)/length of metacarpus (LOM) equals less than 2 (0) or more than 2 (1).
40. Ventral surface of the manual unguals rounded (0) or flat (1).
41. The lateral and medial extensions of the manual unguals (the alae) slightly laterally elaborated (narrow ventral surface) (0) or moderately laterally elaborated (medium bright ventral surface) (1) or significantly laterally elaborated (bright ventral surface) (2).
42. Articular surface of the manual unguals taller than wide (0) or wider than tall (manual unguals dorso-ventrally flattened) (1).