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An articulated pes from a small parvicursorine alvarezsauroid dinosaur from Inner Mongolia, China

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A near complete and articulated parvicursorine pes from the Campanian Wulansuhai Formation is described. This pes is referred to the genus *Linhenykus* and is one of the first foot skeletons to be described for a derived alvarezsaur, providing new information on the first digit of the pes. The evolution of a laterally directed flange of the anterior face of the distal third metatarsal in arctometatarsalian taxa is described and discussed. This flange may have increased stability of the foot during cursorial locomotion and may also provide useful taxonomic and systematic data.

Key words: Dinosauria, Theropoda, maniraptoran, arctometatarsal, Cretaceous, Inner Mongolia.

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Introduction

Alvarezsauroidea is an extinct clade of small-bodied maniraptoran theropod dinosaurs. The first fossil alvarezsauroids were only recognised in the 1990s (Bonaparte 1991), although recent discoveries, particularly from China, have dramatically increased the known diversity of the group. Alvarezsauroids are now known from North America (Hutchinson and Chiappe 1998; Longrich and Currie 2009), South America (Bonaparte 1991; Novas 1996; Martinelli and Vera 2007), Europe (Naish and Dyke 2004; Kessler et al. 2005), and especially Asia (Chiappe et al. 2002; Suzuki et al. 2002; Nesbitt et al. 2011). Among Chinese alvarezsaurs, the basalmost and oldest alvarezsauroid is known from the earliest Late Jurassic of the Shishugou Formation in Xinjiang (Choiniere et al. 2010) and two derived members of the derived alvarezsaur group Parvicursorinae are known from the Late Cretaceous of Inner Mongolia (Xu et al. 2011, inpress) and Henan (Xu et al. 2010b), respectively.

Despite the many new taxa and specimens, alvarezsaur fossils remain relatively rare. Here we describe a specimen (IVPP V 17608) of an alvarezsaur pes from the Late Cretaceous of China (Fig. 1). Despite the small size, it is relatively well preserved and includes a complete digit I. Based on its size, morphology and provenance, this specimen is referred to the Chinese parvicursorine *Linhenykus monodactylus* (Xu et al. 2011). This specimen provides new information on the parvicursorine pes, and we present a possible functional adaptation for the parasagittal "flange" of the otherwise constricted third metatarsal.

Institutional abbreviations.—GIN, Paleontological Center, Ulaanbaatar, Mongolia; IGM, Institute of Geology, Ulaanbaata, Mongolia; IVPP, Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, China; LH, Long Hao Institute of Geology and Paleontology, Hohhot, China; MOR, Museum of the Rockies, Bozeman, Montana, USA; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Other abbreviations.—mt, metatarsal.

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Geographical and geological setting

The specimen was found on the surface sand at Bayan Mandahu, "The Gate" locality, in the province of Inner Mongolia, China in June 2009, with GPS coordinates: N41° 44'31.3", E106°44'42.4". Exposures of sedimentary rock at this locality are identified as part of the Wulansuhai Formation (Xu et al. 2010a) and are probably lateral equivalents of the Djadokhta strata in Mongolia, which are dated as Campanian (Jerzykiewicz et al. 1993). The bones were preserved in a small sandstone nodule which was partially eroded. The quality of preservation and the fact that the material is articulated suggests that the specimen may have originally been complete, or at least far more extensive. The nodule was found in association with numerous other undiagnostic bone fragments from a far larger animal, probably a neoceratopsian, although these were not preserved in nodules. The point of discovery was very close to the location of the holotypes of both the parvicursorine *Linhenykus* (Xu et al. 2011, 2013) and the dromaeosaurid *Linheraptor* (Xu et al. 2010a).

Systematic paleontology

Theropoda Marsh, 1881

Coelurosauria Huene, 1926

Maniraptora Gauthier, 1986

Alvarezsauroidea Bonaparte, 1991

Parvicursorinae Karhu and Rautian, 1996

Genus *Linhenykus* Xu, Sullivan, Pittman, Choiniere, Hone, Upchurch, Tan, Xiao, Lin, and Han, 2011

Type species: *Linhenykus monodactylus* Xu, Sullivan, Pittman, Choiniere, Hone, Upchurch, Tan, Xiao, Lin, and Han, 2011; Wulansuhai Formation, Campanian, Upper Cretaceous.

Linhenykus monodactylus Xu, Sullivan, Pittman, Choiniere, Hone, Upchurch, Tan, Xiao, Lin, and Han, 2011

Holotype: IVPP V 17608, a partial postcranial skeleton containing elements from all of the axial column, partial limb girdles, most of the forelimbs and hindlimbs.

Type locality: Bayan Mandahu "gate area", Inner Mongolia, China.

Type horizon: Nodular sandstone layer above a bioturbated layer, Wulansuhai Formation, Upper Cretaceous.

Referred specimen.—IVPP V 18190, a partial distal left pes, including a complete pedal digit I, the distal ends of mts (metatarsals) II, III, and IV, and pedal phalanges II-1, II-2, partial II-3, III-1, and IV-1 to 3. Referred to *Linhenykus* based on the size of the specimen and the general proportions, which are a close match. It was found at the same locality as the holotype of *Linhenykus monodactylus*.

Description.—IVPP V 18190 is an incomplete distal left hindlimb consisting of the distal ends of mts II–IV, a complete pedal digit I, a nearly complete digit II, and phalanges for digits III and IV (see Fig. 1 and Table 1). mt I and phalanges II-3, III-2 to 4, and IV-3 to 5 are missing. The preserved bones are in articulation although mts III and III-1 are slightly separated from one another by matrix. A transverse break filled with matrix extends across metatarsals II–IV, between the metatarsal shafts and the condylar portions and phalanges. This break offsets the distal end of the metatarsals slightly medially from the proximal portion. This suggests that the elements had suffered from some erosion and that the break occurred before burial. The bone cortex of the posterior surface of the proximal preserved half of mt II and the anterior surface of the proximal tip of the preserved portion of mt III is missing.

The shafts of metatarsals II and IV are subcircular in cross section and contact each other medially in proximal view, completely excluding mt III from the proximal end of the metatarsus, as in parvicursorines generally (Chiappe et al. 2002). This suggests that mt III is complete. As in the parvicursorines *Linhenykus* (IVPP V17608) and a specimen referred to *Shuvuuia* (IGM 100/1304), the posterolateral margin of the shaft of mt II has a small flange projecting laterally and overlapping the medial margin of mt IV. This flange also appears to be present in *Parvicursor* (Karhu and Rautian 1996), but we were unable to examine this specimen first hand. This flange is positioned close to the proximal end of mt III (a similar feature is seen in some dromaeosaurs such as *Velociraptor*, but on mt II rather than mt IV). The distal condyles of mt II are asymmetrical, with the medial condyle being mediolaterally narrower and located proximal to the lateral condyle. The intercondylar sulcus is U-shaped and displaced medially so that its midline is medial to the midline of the metatarsal shaft. Breakage makes it hard to determine, if the distal end of mt II angles medially from the shaft, as it does in *Shuvuuia*, but this seems likely as there is greater separation between the distal ends of mts II and III than between mts III and IV. The proximal end of mt III tapers to a sharp point and is wedged between II and IV. The shaft is triangular in cross section, with the base of the triangle forming a broad anterior face and the apex of the triangle pointed posteriorly. The anterior surface of

Table 1. Measurements of major elements of IVPP V 18190. Asterisked elements are incomplete.

Element	Length [in mm]
mt II	18.7
mt III	21.1 (as visible)
mt IV	17.7*
I-1	5.9
I-2	5.5
II-1	11.7
III-1	9.8
IV-1	7.3
IV-2	7.3
IV-3	5.3*

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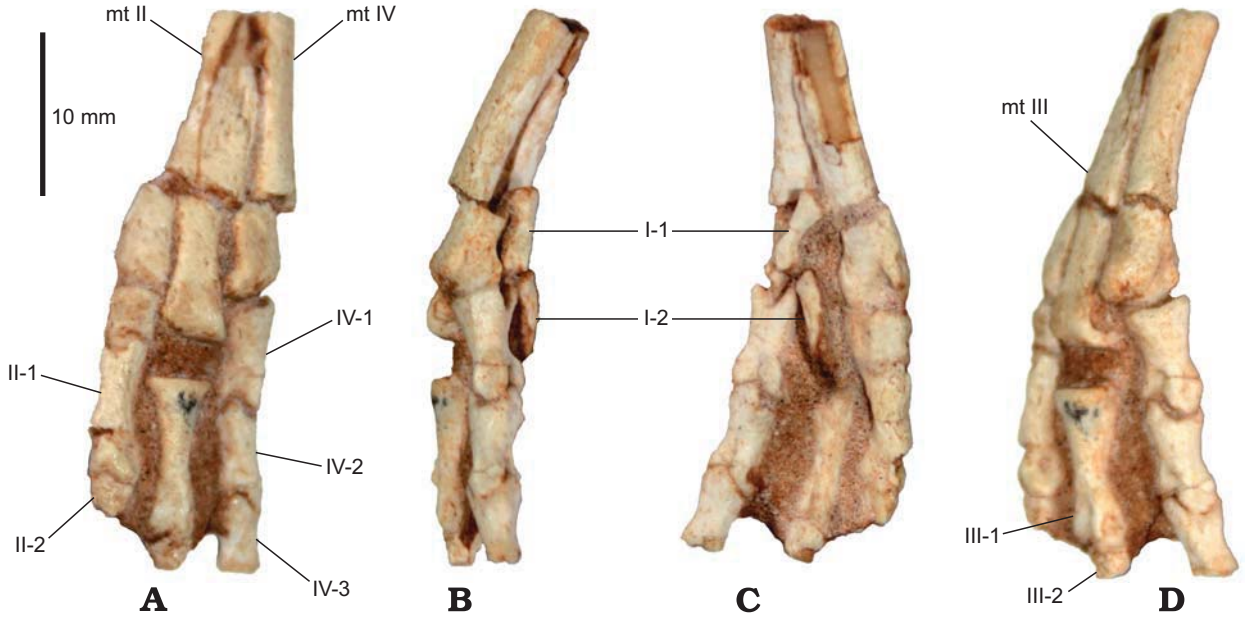


Fig. 1. Parvicursorine left pes IVPP V 18190 referred to *Linhenykus* sp. in anterior (**A**), medial (**B**), posterior (**C**), and lateral (**D**) views. Abbreviations: mt, metatarsal; I–IV, digits; 1–3, phalanges of a given digit.

mt III has a grainy texture on its cortical surface, more so than any other bones on the foot. The anterior surface is mediolaterally expanded at the midshaft and it overlies the anterior faces of mts II and IV. The degree of overlap is greater on mt II, where the shaft of mt III forms a thin, anteromedially projecting ridge. This overlap is common in arctometatarsalian taxa, including tyrannosaurids, ornithomimosaurs, troodontids, and in parvircursorine alvarezsaurs such as *Mononykus* (IGM 107/6), but appears to be absent in *Albertonykus* (Longrich and Currie 2009). In ornithomimosaurs such as *Gallimimus* (ZPAL MgD-I-32; Makovicky et al. 2004; Snively et al. 2004), the expansion of mt III is more evenly distributed over both mt II and IV, whereas in tyrannosaurids and parvicursorines the overlap is primarily on mt II (Snively et al. 2004). In troodontids, the overlap is different, being primarily over mt IV, although mt II is mediolaterally much thinner than mt IV (Makovicky and Norell 2004). Also in contrast with the current specimen and other arctometatarsalian morphologies, in troodontids the anteriorly overlapping portion of mt III on mt II is straight proximodistally, yet the overlap of mt IV angles medially (Snively et al. 2004).

The distal end of mt III projects distally beyond the ends of mts II and IV, although not to the same extent as in *Mononykus* (IGM 107/6). Its distal condylar surface is flat, and the visible lateral face of the distal end has a deep and sub-circular ligamentous pit. The shaft of mt IV is approximately the same thickness as in mt II, unlike in troodontids. The lateral surface of the distal condyle bears a deep sulcus between the lateral condyle and the dorsal margin that extends distally onto the distal condylar surface, as in *Shuvuuia* (IGM 100/1304), *Albinykus* (Nesbitt et al. 2011), *Mononykus* (IGM 107/6), *Linhenykus* (IVPP V17608), and *Parvicursor* (Karhu and Rautian 1996). This sulcus is not present in *Kol* (IGM 100/2011), in ornithomimosaurs (e.g., *Garudimimus* GIN 100/13), in troodontids (e.g., *Troodon* MOR 748), or in dromaeosaurs (e.g., *Saurornitholestes* MOR 660).

Pedal digit I is preserved on the posterior face of mt II, in what is probably life position. Phalanx I-1 lies such that the proximal end touches mt II with the ungual (I-2) angled to lie alongside mt III. Phalanx I-1 is gracile and elongate compared to the corresponding element in *Mononykus* (IGM 107/6). The ungual is displaced both anteriorly and slightly distally from contact with mt III by invading matrix. The ventral surface of the ungual is straight in lateral view and the dorsal surface is only weakly curved. It lacks a flexor tubercle and bears a deep claw groove at mid-height on its medial surface. This digit is similar to those of *Albinykus* (Nesbitt et al. 2011) and *Kol* (Turner et al. 2009).

Pedal digit II bears a complete phalanx II-1 and the proximal part of II-2. The former is the longest in the foot at nearly 12 mm. It has an enlarged proximal end and then gradually tapers along its length before expanding distally into a ginglymoid articulation with II-2. Pedal digit III is very similar to II with a long proximal digit of similar size and shape and only the proximalmost part of III-2 being preserved. Moderately deep ligament pits are preserved on the distal part of the proximal phalanx though these are likely only missing on II-1 because of erosion. Pedal digit IV preserves the complete first two phalanges and most of IV-3. All three are relatively short (around 7 mm) and have large ligament pits on the lateral and medial faces of the distal ends, which are strongly ginglymoid. Unlike the anteroposteriorly shortened phalanges of pedal digit IV in *Mononykus* (IGM 107/6) and *Kol* (IGM 100/2011), the phalanges of IVPP V 18190 are relatively long, and the dorsal surfaces do not bear the same proximally invasive,

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mediolaterally narrow extensor grooves. The proximal dorsal parts of phalanges IV-2 and IV-3 are elongated into a subtriangular process that extends posteriorly to overlap the dorsal surface of the previous phalanx in the series.

Discussion

Identity.—IVPP V 18190 can be identified as belonging to an alvarezsaur based on the limited morphology available. The arctometatarsalian nature of metatarsals II–IV show that this must be an alvarezsaur, tyrannosaur, ornithomimosaur or troodontid theropod (Holtz 2000), or perhaps a derived oviraptorosaur such as *Avimimus* (Vickers-Rich et al. 2002). All of these, bar the ornithomimosaurs, have representatives at Bayan Mandahu (Jerzykiewicz et al. 1993; Xu et al. 2011), although ornithomimosaurians are known from correlative Djadokhta beds at Ukhaa Tolgod (Ksepka and Norell 2004; Makovicky and Norell 1998). As is common with almost all other arctometatarsalian taxa, the metatarsus is not fused in adults (there is proximal fusion in the arctometatarsalian oviraptorosaurs; Vickers-Rich et al. 2002), and thus the lack of fusion does not indicate ontogenetic status of the material presented here.

IVPP V18190 cannot be a troodontid because these have a proportionally short mt II and mediolaterally wide mt IV, lack the expansion of mt III and have a hyperextensible digit I (Makovicky and Norell 2004). IVPP V18190 also cannot be a derived oviraptorosaur because a similar discrepancy between mts II and IV and lack of medial expansion is seen in arctometatarsalian oviraptorosaurs like *Avimimus* (Vickers-Rich et al. 2002) and *Elmisaurus* (Osmólska 1981). It is unlikely that IVPP V18190 is an ornithomimosaur because only the basalmost ornithomimids retain digit I of the pes (Makovicky et al. 2004), and mt III reaches the mesotarsal joint in all known ornithomimosaurs. In the Late Cretaceous, the only tyrannosaurs known are exceptionally large-bodied (Holtz 2004; Hone et al. 2011) and even a hatchling tyrannosaurine would likely have had a pes of significantly greater size than IVPP V 18190 (e.g., Tsuihiji et al. 2011). IVPP V18190 then can be identified as an alvarezsaur, and specifically a parvicursorine based on the apparent lack of a proximal splint to mt III (Snively et al. 2004) and the sulcus on the lateral surface of the distal condyle of mt IV. Furthermore, the proximal end of phalanx IV-1 is deeply notched ventrally, a feature seen only in parvicursorines. Within Parvicursorinae, IVPP V18190 can be excluded from the genus *Mononykus* because it has a long, gracile pedal phalanx I-1 and relatively long pedal phalanges on digit IV.

The specimen is here tentatively referred to *Linhenykus* (Xu et al. 2011). It was found very close to the *Linhenykus* holotype and from approximately the same stratigraphic level. The *L. monodactylus* holotype has parts of both feet preserved, so IVPP V 18190 cannot pertain to IVPP V17608. However, the two are strikingly similar in size and, given the lack of other parvicursorines from Bayan Mandahu, *Linhenykus* is the best candidate. This referral is made, however, in the absence of any diagnostic features of *Linhenykus* (Xu et al. 2011, 2013). The parvicursorine *Shuvuuia* (Chiappe et al. 1998) is known from coeval Djadokhta outcrops at Ukhaa Tolgod, and although the type specimen does not preserve a pes, a specimen referred to this taxon (IGM 100/1304) shows similar pedes.

The holotype of *L. monodactylus* (IVPP V 17608) preserves a near complete left metatarsal block with partial pes. Digit 1 is absent but parts of the toes of digits II–IV are present (Xu et al. 2011, 2013)). In size at least this is very similar to IVPP V 18190, with the phalanges differing in length by only around 1 mm. Metatarsal III is considerably longer in *Linhenykus* than here (31.3 mm versus 21.1 mm) though part of the latter may be missing. The position of the expanded flange of mt III is also different, with the widest part being some 17.6 mm from the distal part of the bone in *Linhenykus*, but only 13.1 mm in IVPP V 18190. Their widths are near identical, however, with a maximum breadth of the flange of 3.8 and 3.6 mm respectively, and a total width of the foot at this point of 6.3 and 6.6 mm.

Evolution and morphology of the arctometatarsus.—In early phylogenetic work on theropods, Holtz (2000) recovered a monophyletic group with an arctometatarsus, termed the Arctometatarsalia, but this has not been supported by subsequent work. Holtz (2000) had noted that many of the characters supporting his group were linked to locomotion, and the arctometatarsalian condition provides a mechanical function in transferring stress and perhaps increasing agility (Snively and Russell 2002; Snively et al. 2004).

Evidence for the convergent evolution of the arctometatarsalian condition is its absence in basal forms of arctometatarsal-bearing clades. The morphology is absent in basal tyrannosaurs (it is lacking in both *Guanlong* [IVPP V 14531] and *Dilong* [IVPP V 11579]), basal ornithomimids (Snively et al. 2004), and basal alvarezsauroids (Bonaparte 1991; Choiniere et al. 2010), basal oviraptorosaurs (Senter 2007) and basal troodontids (Xu et al. 2002; Snively et al. 2004). In addition, it is absent in the intervening clades on the theropod tree, namely compsognathids, therizinosaurs, dromaeosaurs and basal birds. Some taxa do however exhibit a somewhat intermediate condition termed a "subarctometatarsus", but this is distinct from the condition described here (Xu et al. 2002; White 2009).

This independence is reflected in the different morphologies of the arctometatarsus in these lineages. For example, uniquely in parvicursorine alvarezsaurs, mt III is reduced to the point that there is no proximal split of this element (Turner et al. 2009), and the ankle joint is made of mts II and IV alone, whereas troodontids are unique in having asymmetrically sized mts II and IV buttressing mt III. However, in addition to the gross proximal reduction of mt III, a second feature is convergently acquired in a number of arctometatarsus-bearing lineages, a parasagittal flange of bone on the anterior face of mt III that extends both medially and laterally, such that it partly overlaps the anterior faces of mts II and IV.

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This anteriorly positioned flange of bone that extends both medially and laterally is well developed in IVPP V 18190. Note that a careful distinction must be made between taxa that simply have a third metatarsal that is constricted posteriorly to give it a sub-triangular cross-section and one that actually has a thin, projecting plate of bone that extends from the anterior surface. A similar flange is also present in other alvarezsaur specimens, including *Xixianykus* (Xu et al. 2010b), *Albinykus* (Nesbitt et al. 2011), and other arctometatarsalian taxa, such as the tyrannosaur *Raptorex* (LH PV 18), *Tarbosaurus* (IGM 107/2), *Gallimimus* (Osmólska et al. 1972), *Struthiomimus* (Makovicky et al. 2004), and some troodontids (Osmólska and Barsbold 1990) such as *Troodon* (MOR 748). This flange is not universal in arctometatarsus-bearing taxa. However, it is absent in *Tyrannosaurus* (Brochu 2003) and in *Albertonykus* (Longrich and Currie 2009) at least. To our knowledge this flange has not been noted before, although White (2009: 9) mentions supporting flanges of bone, but on the plantar face, not the dorsal face, of a troodontid metatarsal group. While there has been some discussion and investigation into the systematic implications and mechanical function of the arctometatarsus, this feature has yet to be explored and there are differences apparent in the exact placement and extent of the flange between IVPP V 18190 and the *Linhenykus* holotype.

The appearance of this flange only on some taxa with a well-developed arctometatarsus—already a specialised morphotype—suggests that it is linked to cursoriality. The position of the flange implies that it provides some resistance to the movement of the metatarsals during the step cycle, either to restrict the posterior motion of mt III, the anterior movement of mts II and IV or some combination of the two. This would also prevent rotation of mt III relative to mts II and IV, but not necessarily restrict dorsoventral movements allowing for energy conservation by intermetatarsal ligaments (Holtz 1995). While these ideas await testing, we therefore hypothesise that the flange would assist in stabilising the foot during running.

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References

Bonaparte, J.F. 1991. Los vertebrados fosiles de la Formacion Rio Colorado, de la ciudad de Neuquen y cercanias, Cretacico Superior, Argentina. *Revista Museo Argentino Ciencias Naturales "Bernardino Rivadavia", Paleontologia* 4: 17–123.

Brochu, C.A. 2003. Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. *Journal of Vertebrate Paleontology, Memoir* 7: 1–138.

Chiappe, L.M., Norell, M.A., and Clark, J.M. 1998. The skull of a relative of the stem-group bird *Mononykus*. *Nature* 392: 275–278.

Chiappe L.M., Norell, M.A., and Clark, J.M. 2002. The Cretaceous, short-armed Alvarezsauridae: *Mononykus* and its kin. *In*: L.M. Chiappe and L.M. Witmer (eds.), *Mesozoic Birds: Above the Heads of Dinosaurs*, 87–120. University of California Press, Berkeley.

Choiniere, J.N., Xu, X., Clark, J.M., Foster, C.A., Guo, Y., and Han, F. 2010. A basal alvarezsauroid theropod from the early Late Jurassic of Xinjiang, China. *Science* 327: 571–574.

Holtz, T.R., Jr. 1995. The arctometatarsalian pes, an unusual structure of the metatarsus of Cretaceous Theropoda (Dinosauria: Saurischia). *Journal of Vertebrate Paleontology* 14: 480–519.

Holtz, T.R., Jr. 2000. A new phylogeny of the carnivorous dinosaurs. *Gaia* 15: 5–61.

Holtz ,T.R., Jr. 2004. Tyrannosauroidea. *In*: D.B. Weishampel, P. Dodson, and H.F. Osmólska (eds.), *The Dinosauria, Second edition*, 111–136. University of California Press, Berkeley.

Hone, D.W.E., Wang, K., Sullivan, C., Zhao, X., Chen, S., Li, D., Ji, S., Ji, Q., and Xu, X. 2011. A new, large tyrannosaurine theropod from the Upper Cretaceous of China. *Cretaceous Research* 32: 495–503.

Hutchinson, J.R. and Chiappe L.M. 1998. The first known alvarezsaurid (Theropoda: Aves) from North America. *Journal of Vertebrate Paleontology* 18: 447–450.

Jerzykiewicz, T., Currie, P.J., Eberth, D.A., Johnston, P.A., and Zheng, Z.-Z. 1993. Djadokhta Formation correlative strata in Chinese Inner Mongolia: an overview of the stratigraphy, sedimentary geology, and paleontology and comparisons with the type locality in the pre-Altai Gobi. *Canadian Journal of Earth Sciences* 30: 2180–2190.

Karhu, A.A. and Rautian, A.S. 1996. A new family of Maniraptora (Dinosauria: Saurischia) from the Late Cretaceous of Mongolia. *Paleontological Journal* 30: 583–592.

Kessler, E., Grigorescu, D., and Csiki, Z. 2005. *Elopteryx* revisited—a new bird-like specimen from the Maastrichtian of the Haţeg Basin (Romania). *Acta Palaeontologica Romaniae* 5: 249–258.

Ksepka, D.T. and Norell, M.A. 2004. Ornithomimosaur cranial material from Ukhaa Tolgod (Omnogov, Mongolia). *American Museum Novitates* 3448: 1–4.

Longrich, N.R. and Currie, P.J. 2009. *Albertonykus borealis*, a new alvarezsaur (Dinosauria: Theropoda) from the Early Maastrichtian of Alberta, Canada: implications for the systematics and ecology of the Alvarezsauridae. *Cretaceous Research* 30: 239–252.

Makovicky, P.J. and Norell, M.A. 1998. A partial ornithomimid braincase from Ukhaa Tolgod (Upper Cretaceous, Mongolia). *American Museum Novitates* 3427: 1–16.

Makovicky, P.J. and Norell, M.A. 2004. Troodontidae. *In*: D.B. Weishampel, P. Dodson, and H.F. Osmólska (eds.), *The Dinosauria, Second edition*, 184–195. University of California Press, Berkeley.

Makovicky, P.J., Kobayashi, Y., and Currie, P.J. 2004. Ornithomimosauria. *In*: D.B. Weishampel, P. Dodson, and H.F. Osmólska (eds.), *The Dinosauria, Second edition*, 137–150. University of California Press, Berkeley.

Martinelli, A.G. and Vera, E. 2007. *Achillesaurus manazzonei*, a new alvarezsaurid theropod (Dinosauria) from the Late Cretaceous Bajo de la Carpa Formation, Río Negro Province, Argentina. *Zootaxa* 1582: 1–17.

Naish, D. and Dyke, G.J. 2004. *Heptasteornis* was not ornithomimid, troodontid, dromaeosaurid or owl: the first alvarezsaurid (Dinosauria: Theropoda) from Europe. *Neues Jahrbuch für Paläontologie und Geologie, Monatshefte* 2004 (7): 385–401.

Nesbitt, S.J., Clarke, J.A., Turner, A.H., and Norell, M.A. 2011. A small alvarezsaurid from the eastern Gobi Desert offers insight into evolution-

http://dx.doi.org/10.4202/app.2011.0127

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ary patterns in the Alvarezsauroidea. *Journal of Vertebrate Paleontology* 31: 144–153.

Novas, F.E. 1996. Alvarezsauridae, Cretaceous maniraptorans from Patagonia and Mongolia. *Memoirs of the Queensland Museum* 39: 675–702.

Osmólska, H.F. 1981. Coossified tarsometatarsi in theropod dinosaurs and their bearing on the problem of bird origins. *Palaeontologica Polonica* 42: 79–95.

Osmólska, H.F. and Barsbold, R. 1990 Troodontidae. *In*: D.B. Weishampel, P. Dodson, and H.F. Osmólska (eds.), *The Dinosauria, First edition*, 259–268. University of California Press, Berkeley.

Osmólska, H.F., 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.

Senter, P. 2007. A new look at the phylogeny of Coelurosauria (Dinosauria: Theropoda). *Journal of Systematic Palaeontology* 5: 429–463.

Snively, E. and Russell, A.P. 2002. The tyrannosaurid metatarsus: bone strain and inferred ligament function. *Senckenbergiana Lethaea* 81: 73–80.

Snively, E., Russell, A.P., and Powell, G.L. 2004. Evolutionary morphology of the coelurosaurian arctometatarsus: descriptive, morphometric and phylogenetic approaches. *Zoological Journal of the Linnean Society* 142: 525–553.

Suzuki, S., Chiappe, L.M., Dyke, G.J., Watabe, M., Barsbold, R., and Tsogtbaatar, K. 2002. A new specimen of *Shuvuuia deserti* Chiappe et al. 1998 from the Mongolian Late Cretaceous with a discussion of the relationships of alvarezsaurids to other theropod dinosaurs. *Contributions in Science, Natural History Museum of Los Angeles County* 494: 1–18.

Tsuihiji, T., Watabe, M., Tsogtbaatar, K., Tsubamoto, T., Barsbold, R., Suzuki, S., Lee, A.H., Ridgely, R.C., Kawahara, Y., and Witmer, L.M. 2011. Cranial osteology of a juvenile specimen of *Tarbosaurus bataar* from the Nemegt Formation (Upper Cretaceous) of Bugin Tsav, Mongolia. *Journal of Vertebrate Paleontology* 31: 497–517.

Turner, A.H., Nesbitt, S.J., and Norell, M.A. 2009. A large alvarezsaurid from the Late Cretaceous of Mongolia. *American Museum Novitates* 3648: 1–14.

Vickers-Rich, P., Chiappe, L.M., and Kurzanov, S. 2002. The enigmatic bird-like dinosaur *Avimimus portntousus*, comments and a pictorial atlas. *In*: L.M. Chiappe and L.M. Witmer (eds.), *Mesozoic Birds: Above the Heads of Dinosaurs*, 65–86. University of California Press, Berkeley.

White, M.A. 2009. The subarctometatarsus: intermediate metatarsus architecture demonstrating the evolution of the arctometatarsus and advanced agility in theropod dinosaurs. *Alcheringa* 33: 1–21.

Wilson, M.C. and Currie, P.J. 1985. *Stenonychosaurus inequalis* (Saurischia: Therepoda) from the Judith River (Oldman) Formation of Alberta: New findings on metatarsal structure. *Canadian Journal of Earth Sciences* 22: 1813–1817.

Xu, X., Norell, M.A., Wang, X.-L, Makovicky, P.J., and Wu, X.-C. 2002. A basal troodontid from the Early Cretaceous of China. *Nature* 415: 780–784.

Xu, X., Choinere, J., Pittman, M., Tan, Q., Xiao, D., Li, Z., Tan, L., Clark, J., Norell, M., Hone, D.W.E., and Sullivan, C. 2010a. A new dromaeosaurid (Dinosauria: Theropoda) from the Upper Cretaceous Wulansuhai Formation of Inner Mongolia, China. *Zootaxa* 2403: 1–9.

Xu, X., Wang, D., Sullivan, C., Hone, D.W.E., Han, F., Yan, R., and Du, F. 2010b. A basal pavicursorine (Theropoda: Alvarezsauridae) from the Upper Cretaceous of China. *Zootaxa* 2413: 1–19.

Xu, X., Sullivan, C., Pittman, M., Choiniere, J., Hone, D.W.E., Upchurch, P., Tan, Q., Xiao, D., Lin, T., and Han, F. 2011. A monodactyl nonavian dinosaur and the complex evolution of alvarezsauroid hand. *Proceedings of the National Academy of Sciences, USA* 108: 2338–2342.

Xu, X., Upchurch, P., Ma, Q., Pittman, M., Choiniere, J., Sullivan, C., Hone, D.W.E., Tan, Q., Tan, L., Xiao, D., and Han, F. 2013. Osteology of the alvarezsauroid *Linhenykus monodactylus* from the Upper Cretaceous Wulansuhai Formation of Inner Mongolia, China, and comments on alvarezsauroid biogeography. *Acta Palaeontologica Polonica* 58: 25–46.

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