

A new theropod dinosaur from the Lower Cretaceous Longjiang Formation of Inner Mongolia (China)

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ABSTRACT

A new small-bodied theropod dinosaur, *Migmanychion laiyang* gen. et sp. nov., is erected based on appendicular skeletal material from the Lower Cretaceous of the Pigeon Hill locality, Inner Mongolia, China. This theropod shows a peculiar combination of features in the hand, in part shared with therizinosaurs, oviraptorosaurs and with the enigmatic *Fukuivenator paradoxus* from Japan. Phylogenetic analysis supports the closest affinity of *Migmanychion* with *Fukuivenator*, yet alternative placements among Oviraptorosauria or among the non-avian paravians result suboptimal descriptions of the character distribution. Although this new taxon is confidently referred to Maniraptora, this result is based uniquely on derived features of the hand: only additional material could substantiate its precise placement among the bird-like theropods. Fragmentary appendicular material from the same locality cannot be unambiguously referred to *Migmanychion*. One specimen, including associated partial pelvis and hindlimbs, is tentatively referred to a paravian maniraptoran.

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1. Introduction

In the last decade, a new Lower Cretaceous freshwater fossil locality, the Pigeon Hill locality from Morin Dawa Daur Autonomous Banner, Hulunbuir City, Inner Mongolia Autonomous Region, China, has drawn extensive attention for yielding exceptionally preserved fossils of the Jehol Biota (Jia and Gao, 2016; Gao and Chen, 2017; Wang et al., 2017, 2019, 2021, 2022a, 2022b; Wang et al., 2017; Xing et al., 2019, 2022a, 2022b). Although this new locality is far from the famous core area containing the Jehol Biota in western Liaoning, the uncovered fossils are similar and closely related in the two areas. *Cretadromus khinganensis* from the Pigeon Hill locality provided a well-documented case of inter-basinal

correlation at genus level with *Cretadromus liaoningensis* from western Liaoning (Wang et al., 2017). In the recent years, new theropod dinosaurs have been collected from the Pigeon Hill Locality. The ornithuromorph *Khinganornis* shows morphological similarity with the *Gansus*-like birds of the Jehol Biota (Wang et al., 2021). Furthermore, the enantiornithine *Beiguornis* shares derived features with *Sulcavis* and *Zhouornis*, which support its referral within Bohaiornithidae (Wang et al., 2022a). The dromaeosaurid *Daurilong* is most closely related to the short-armed taxa *Tianyuraptor* and *Zhenyuanlong* than to the long-armed Microraptorinae (Wang et al., 2022b). Here, we describe additional theropod material from the Pigeon Hill locality, including a complete hand showing a peculiar combination of features supporting the erection of a new taxon.

1.1. Geological background

The Pigeon Hill locality, located in Morin Dawa Daur Autonomous Banner ('Moqi' for short), Hulunbuir City, Inner Mongolia

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Autonomous Region, China (Fig. 1), belongs to the Dayangshu Basin of the Great Khingan Range fold belt (Liu et al., 2008). The Lower Cretaceous exposed in the Dayangshu Basin includes the Longjiang Formation, the Jiufengshan Formation, and the Ganhe Formation from bottom to top (Sun et al., 2018). The upper part of the Longjiang Formation is composed of intermediate-acid lava and clastic rocks, and the lower part is composed of intermediate lava mixed with clastic rocks and thin acidic lava. The Jiufengshan Formation is mainly composed of intermediate-basic lava, volcanic clastic rocks with conglomerate, sandstone, mudstone and coal seam. The Ganhe Formation is mainly composed of intermediate-basic volcanic rocks with a small amount of clastic rocks. The fossils of the Jehol Biota in Moqi occur in the upper part of the Longjiang Formation, mainly in a set of gray tuffaceous siltstone with mudstone, tuffaceous shale and sedimentary tuff (Fig. 2). The geochronologic age of the fossiliferous layers in Moqi is the Early Cretaceous (Wang

et al., 2019, 2021a, 2021b, 2022a, 2022b; Yu et al., 2021), but the stratigraphic unit is still controversial. The fossiliferous layers in Moqi have been referred in the Guanghua Formation (Heilongjiang Bureau of Geology and Mineral Resources, 1993; Jia and Gao, 2016; Zhang et al., 2016, 2017; Gao and Chen, 2017), Longjiang Formation (Li et al., 2013; Ding et al., 2013, 2014; Tan et al., 2018), and “Moqi fossil bed” (Yu et al., 2021; Dong et al., 2022). This paper agrees that the Guanghua Formation is the volcanic clastic rock section overlying the Longjiang Formation.

2. Material and methods

The material here described is represented by incompletely preserved skeletal material belonging to small-bodied theropod dinosaurs (Figs. 3–6). The material was collected at the Pigeon Hill locality, near Baoshan town. The Pigeon Hill fossil locality is

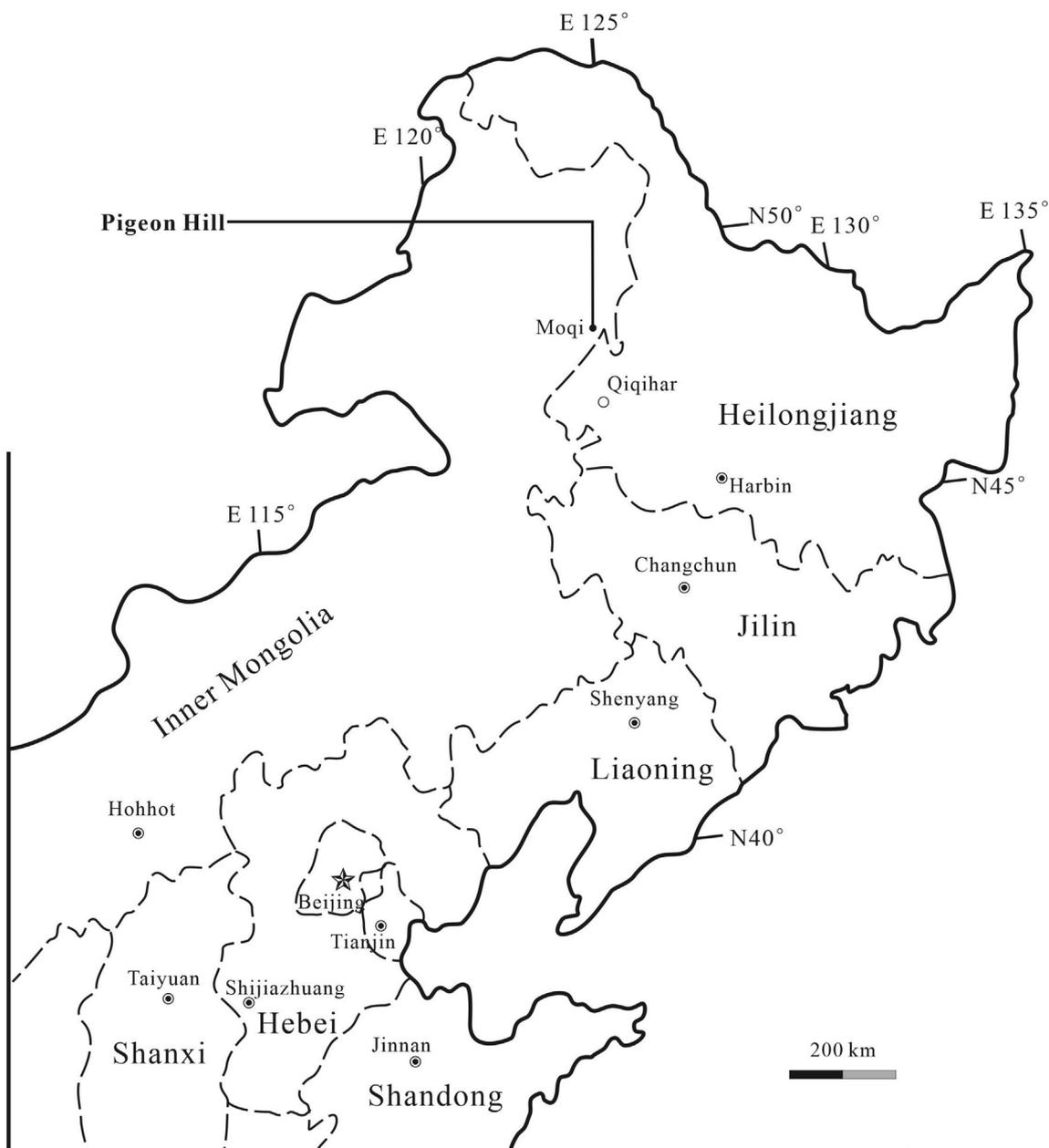


Fig. 1. The geographic location of *Migmanychion laiyang* gen. et sp. nov. (LY 2022JZ3001) type locality.



For.	bed	thick. (m)	lithology
Longjiang Formation	17	0.15	[Symbol] tuffaceous pebbly siltstone
	16	0.68	[Symbol] tuffaceous pebbly siltstone
			[Symbol] tuffaceous pebbly siltstone
	15	0.40	[Symbol] tuffaceous pebbly siltstone
	14	0.37	[Symbol] tuffaceous pebbly siltstone
	13	0.06	[Symbol] mudstone
	12	0.12	[Symbol] mudstone
	11	0.12	[Symbol] sedimentary tuff
	10	0.20	[Symbol] tuffaceous shale
	9	0.04	[Symbol] silty shale
	8	0.22	[Symbol] tuffaceous siltstone
	7	0.10	[Symbol] tuffaceous siltstone
	6	0.10	[Symbol] tuffaceous siltstone
	5	0.09	[Symbol] tuffaceous siltstone
	4	0.05	[Symbol] tuffaceous siltstone
	3	0.12	[Symbol] tuffaceous siltstone
	2	0.11	[Symbol] tuffaceous siltstone
1	0.50	[Symbol] tuff	

Migmanychion laiyang gen. et sp. nov.

Fig. 2. Outcrop and stratigraphic description of the Pigeon Hill locality in the Great Khingan Range. A, outcrop; B, stratigraphic description.

chronostratigraphically dated at about 121 Ma based on Zircon U–Pb dating of volcanic tuff samples (Wang et al., 2019). The most diagnostic material here introduced includes a complete and articulated hand (Figs. 3 and 4): the specimen is housed at the Shandong Laiyang Cretaceous National Geological Park under accession number LY 2022JZ3001. Additional material collected in this locality includes an incomplete yet articulated pelvis including part of the hindlimb (Fig. 5): although the material is comparable in size to LY 2022JZ3001, the lack of evidence supporting their direct association prevents the referral of this material to the same individual. The hindlimb and associated pelvic material is catalogued under the accession number LY 2022JZ3004. Two associated metatarsi are catalogued under the accession number LY 2022JZ3005 (Fig. 6).

2.1. Phylogenetic analysis

We tested the affinities of LY 2022JZ3001 scoring it into an updated version of the phylogenetic analysis of Cau and Madzia (2021) focusing on maniraptoromorphs (i.e., all theropods closer to birds than tyrannosauroids; Cau, 2018). Analysis protocol followed Cau and Madzia (2021) and was performed in TNT (Goloboff et al., 2008) running 100 “New Technology” analyses followed by a second run of “Traditional Search” analyses sampling among the tree islands identified during the first run. Nodal support was calculated sampling 20,000 trees up to ten steps longer than the shortest topologies and using the “Bremer support” function in TNT. Alternative suboptimal topologies relevant for discussing the

affinities of the new theropod were enforced: the step difference from the unenforced shortest topologies was used as quantitative measure of their support. The fragmentary status of LY 2022JZ3004 and LY 2022JZ3005 prevents their inclusion in the numerical analysis (i.e., they could be scored for less than 1.5% of the character statements included in the character list): their affinities were discussed based on the presence of synapomorphic features of key theropod clades identified in the material.

2.2. Nomenclatural act

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This publication LSID: urn:lsid:zoobank.org:pub:F9774BD1-A959-46E0-84CD-4FA46A4CE7DC.

Genus name *Migmanychion* LSID: urn:lsid:zoobank.org:act:C1274284-3B15-410A-9FCA-E20152BC1DCC.

Species name *Migmanychion laiyang* LSID: urn:lsid:zoobank.org:act:158D9158-284E-4A35-9C7A-1587F904CB3F.



Fig. 3. Holotype of *Migmanychion laiyang* gen. et sp. nov. (LY 2022JZ3001). A, counterslab; B, slab. Scale bar = 2 cm.

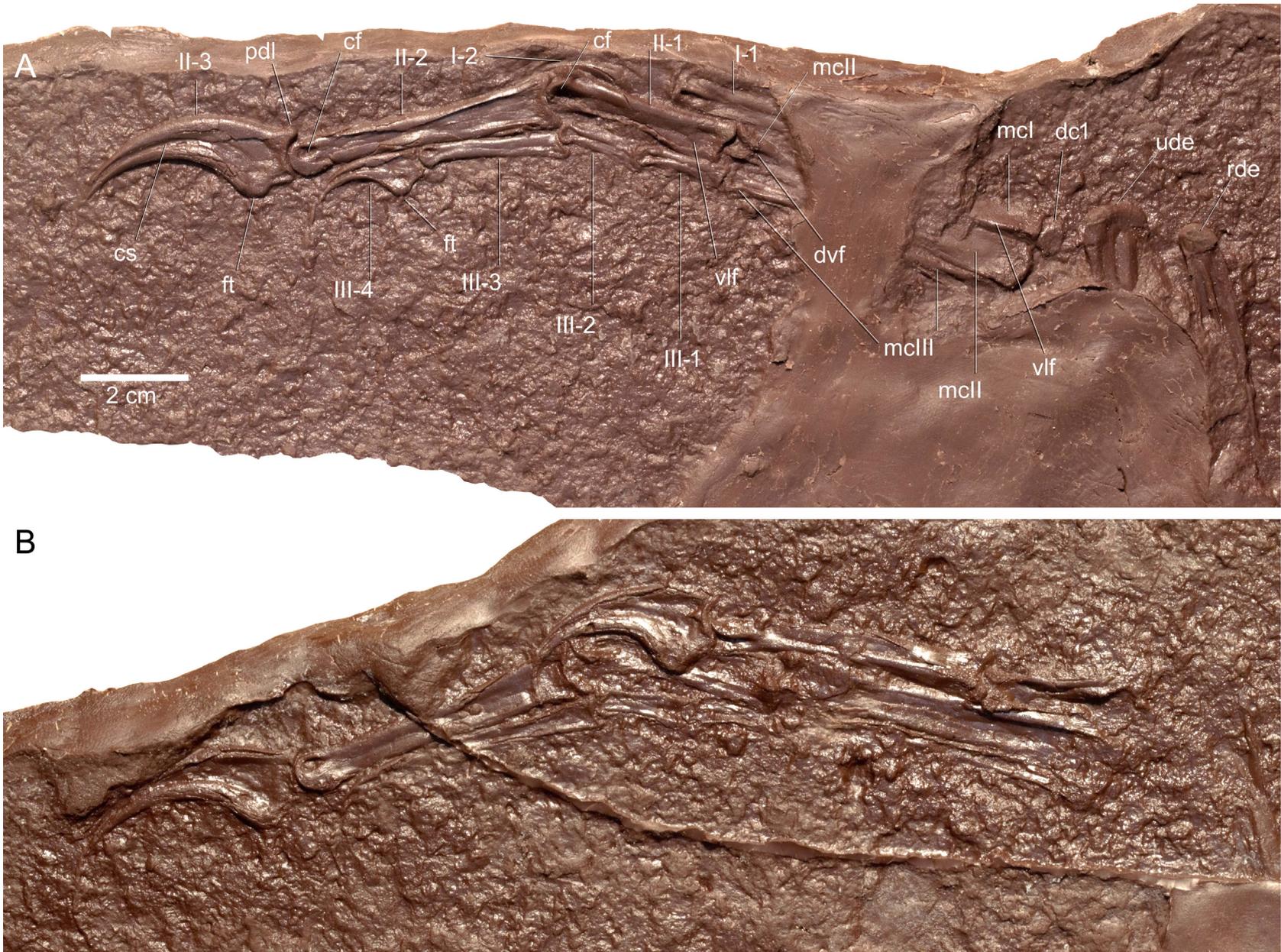


Fig. 4. Cast of holotype hand of *Migmanychion laiyang* gen. et sp. nov. (LY 2022JZ3001). A, counterslab (reversed for comparison); B, slab. Abbreviations: I/II/III, phalanx I/II/III; cf, collateral fossa; cs, collateral sulcus; dc, distal carpal; dvf, distal ventral fossa; ft, flexor tubercle; mc, metacarpal; pdl, posterodorsal lip; rde, radius distal end; ude, ulna distal end; vlf, ventrolateral flange.

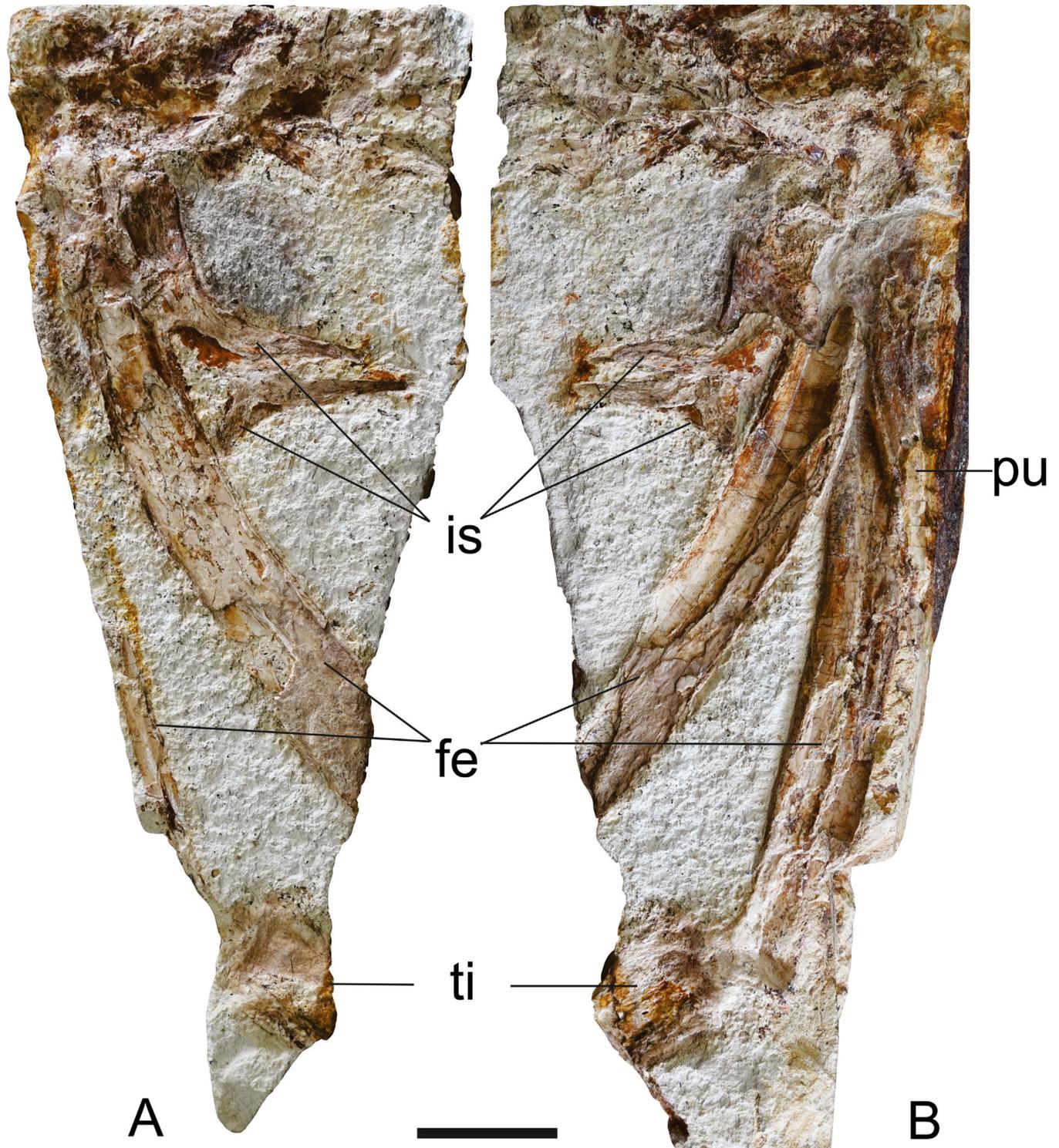


Fig. 5. Indeterminate paravian (LY 2022JZ3004) from Pigeon Hill. A, slab; B, counterslab. Abbreviation: fe, femur; is, ischium; pu, pubis; ti, tibia. Scale bar = 2 cm.

Institutional abbreviations: LY, Shandong Laiyang Cretaceous National Geological Park.

3. Systematic palaeontology

Dinosauria [Owen, 1842](#)
 Theropoda [Marsh, 1884](#)
 Coelurosauria Huene, 1914 *sensu* [Gauthier, 1986](#)

Migmanyction laiyang gen. et sp. nov.
 (Figs. 3 and 4, Table 1)

Etymology. The genus name is from Greek words "μείγμα νυχιών" ("claw mixture"), in reference to the marked heterogeneity in size and shape of the three manual unguals. The species name refers that the holotype is housed at the Shandong Laiyang Cretaceous National Geological Park.

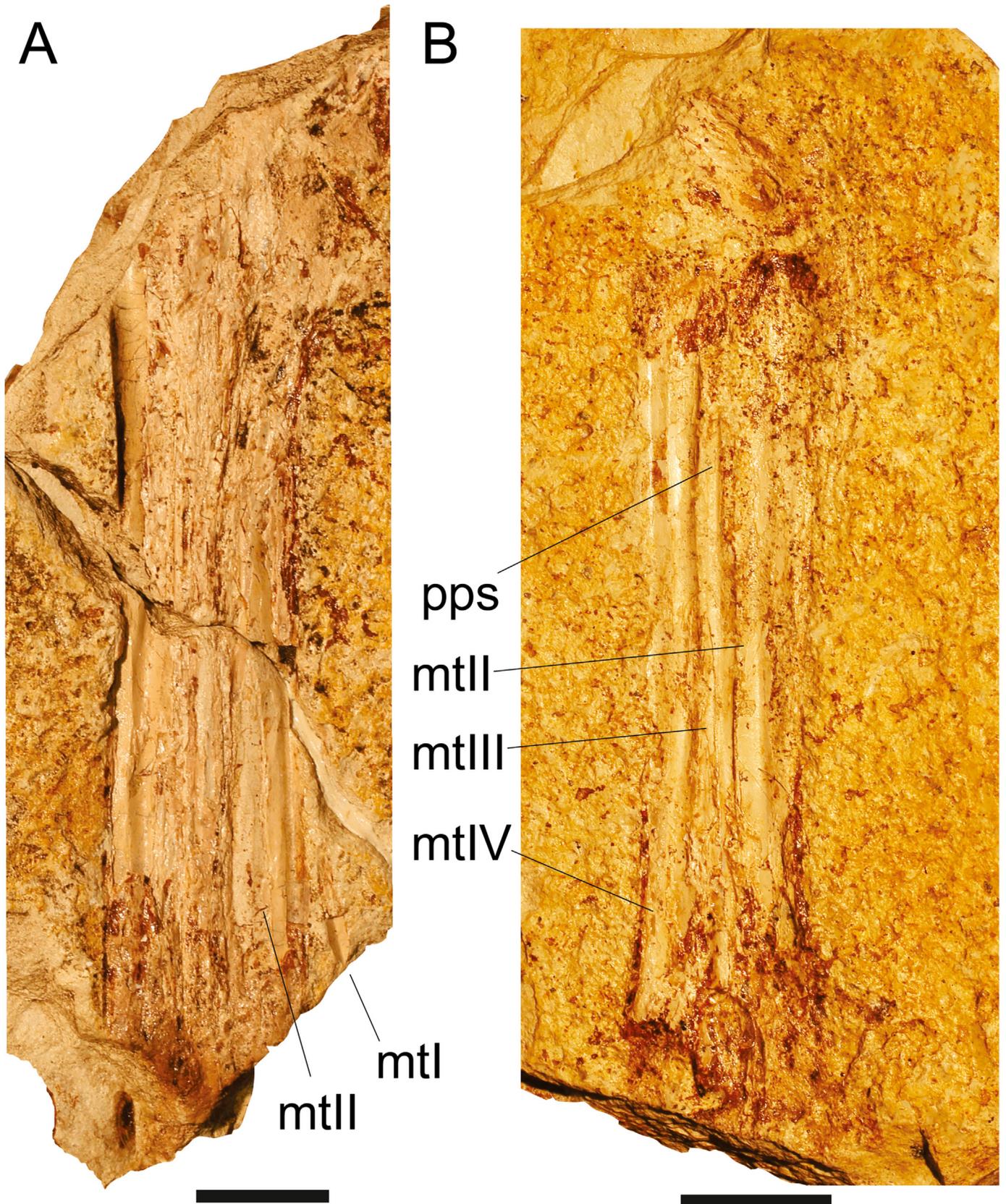


Fig. 6. Indeterminate coelurosaurian metatarsus (LY 2022JZ3005) from Pigeon Hill. A, right metatarsus in dorsal view; B, left metatarsus in ventral view. Abbreviations: mt, metatarsus; pps, pinched proximal shaft of metatarsal III. Scale bar = 2 cm.

Table 1
Measurements (mm) of the preserved materials of *Migmanychion laiyang* gen. et sp. nov. (LY 2022JZ3001).

mc-I	23.1	II-2	43.7
mc-II	52.8	II-3	35.8
mc-III	52.7	III-1	15.1
I-1	41.8	III-2	15.0
I-2	28.6	III-3	24.9
II-1	31.6	III-4	18.5

Holotype. LY 2022JZ3001, an incomplete skeleton including a partial left forelimb with complete hand preserved as slab and counterslab (Fig. 3, Table 1).

Locality and horizon. Pigeon Hill, Morin Dawa Daur Autonomous Banner, Inner Mongolia Autonomous Region (N 48°39′40.76″/E 123°52′41.15″); Longjiang Formation (Wang et al., 2019), Lower Cretaceous (Figs. 1 and 2).

Diagnosis. Maniraptoran theropod differing from other taxa except *Fukuivenator paradoxus* in having a discoidal distal carpal 1 capping exclusively metacarpal I (unknown in *F. paradoxus*); a sharp proximolateral flange on the ventral surface of metacarpal I, a manual phalanx II-1 with a lateroventral ridge (convergent with some paravians); manual ungual II dorsoventrally shallower but proximodistally longer than manual ungual I, and distinct from manual unguals I and III in having a prominent proximodorsal lip and the dorsal margin arched well above the level of the articular facet when the latter is oriented vertically. *Migmanychion* differs from *Fukuivenator* in having: gracile metacarpal I more than four times longer than distally wide and narrower than metacarpal II (it is the most robust metacarpal in *F. paradoxus*); very gracile metacarpal III being no more than 40% of metacarpal II at mid-shaft (55% in *F. paradoxus*); flexor tubercles of all manual unguals distally displaced relative to proximal articular facet of ungual (in *F. paradoxus*, the flexor tubercle of ungual I is confluent with the ungual proximal end); manual ungual II with the dorsal margin arched well above the level of the articular facet when the latter is oriented vertically; manual ungual III half the size of manual ungual II (in *F. paradoxus*, ungual III is >80% the size of ungual II).

Description and comparison. The holotype material of *Migmanychion laiyang* includes fragments of ribs, the distal end of one forearm, and a complete hand. Some dorsal ribs are preserved as middle shaft portions. No uncinat processes can be recognized.

The imprint of the distal ends of two associated ulna and radius is preserved close to the hand, but little details can be determined (Fig. 3). The shaft of the radius is slightly more gracile than that of the ulna, as in most theropods (e.g., Khaan, Balanoff and Norell, 2012). In some paravians, the radius is significantly more gracile than the ulna (e.g., Microraptor, Hwang et al., 2002).

The manual elements are preserved in two counterslabs (Fig. 4). We follow the “traditional” homology pattern for the tridactyl theropod hand (Gauthier, 1986), with the fingers homologous to the medialmost three fingers of the tetrapod pentadactyl condition. The metacarpals and manual digits are all preserved in articulation. The distal carpal 1 is preserved in one slab. The bone caps only the proximal end of metacarpal I, and is thus interpreted as being not fused to distal carpal 2, different from *Falcarius*, which bears distal carpals 1 and 2 fused and capping both metacarpals I and II (Zanno, 2006), and from pennaraptorans, in which the semilunate carpal is a single, larger bone which covers the proximal ends of both metacarpal I and metacarpal II (e.g., Ji et al., 1998; Hwang et al., 2002; Balanoff and Norell, 2012; Lefèvre et al., 2017; Qiu et al., 2019). No carpals of *Fukuivenator* are known.

The metacarpals contact tightly along their whole length. Metacarpal I is narrower than metacarpal II and about 43% of the length

of the latter. This ratio is similar to those in most oviraptorids (40–60%) (Ji et al., 1998), slightly larger than that of *Protarchaeopteryx* (39%), *Caudipteryx zoui* (39%) and *Xingtianosaurus* (40%) (Ji et al., 1998; Qiu et al., 2019), and approaching that of *Caudipteryx dongi* (45%) (Zhou and Wang, 2000). In most ornithomimosaur, the first metacarpal is proportionally longer, often approaching in length the other two metacarpals (e.g., *Nqwebasaurus*, De Klerk et al., 2000; *Pelecanimimus*, Pérez-Moreno et al., 1994). Metacarpal I in alvarezsaurids (e.g., *Haplocheirus*), *Falcarius* and *Fukuivenator* is proportionally more robust, being wider than metacarpal II at mid-shaft, and about half the length of the latter (Zanno, 2006; Choiniere et al., 2010; Hattori et al., 2021). In ventral view, metacarpal I bears a sharp lateral flange overlapping the proximal end of the second metacarpal (Fig. 4). This feature is shared with *Fukuivenator* (Hattori et al., 2021) and is topographically homologous to the quadrangular buttress widespread among therizinosauroids (Russell and Dong, 1993; Zanno, 2006). In oviraptorosaurs, the ventrolateral margin of metacarpal I extends beneath the adjacent metacarpal, recalling the condition in the above mentioned maniraptorans (Zanno and Sampson, 2005). Metacarpal II is nearly the same length as metacarpal III. This condition differs from those in many non-maniraptoran coelurosaurs (e.g., tyrannosauroids), which usually have metacarpal III shorter than 75% of metacarpal II (e.g., *Tanycolagreus*, Carpenter et al., 2005). In both *Falcarius* and *Fukuivenator*, metacarpal III is distinctly shorter than metacarpal II (the former bone being about 80% the length of the latter, Zanno, 2006; Hattori et al., 2021). In *Protarchaeopteryx*, *Caudipteryx* and *Xingtianosaurus* metacarpal III is slightly shorter than metacarpal II (Ji et al., 1998; Zhou and Wang, 2000; Qiu et al., 2019). *Migmanychion* differs from *Xiaotingia*, scansoriopterygids and halszkaraptorines which have metacarpal III distinctly longer than metacarpal II (Zhang et al., 2002; Xu et al., 2011; Cau et al., 2017). In many early-diverging paravians, the metacarpals II and III are subequal in length, recalling the new Pigeon Hill theropod (e.g., *Deinonychus*, Ostrom, 1969; *Serikornis*, Lefèvre et al., 2017). Metacarpal III is extremely slender (with mid-shaft diameter about 30–35% of that of metacarpal II) and slightly projected laterally toward the distal end. The shaft of this bone differs from those of many avialans (e.g., *Jeholornis*, Zhou and Zhang, 2002) in not being markedly bowed laterally. A very gracile metacarpal III is shared with *Caudipteryx* (Ji et al., 1998), whereas the bone is relatively more robust in most maniraptorans, including *Fukuivenator*, where it is about 50–66% the width of the adjacent metacarpal (e.g., Zanno, 2006; Hattori et al., 2021). Manual digit I extends slightly beyond the distal end of phalanx II-1, which terminates at the middle of phalanx II-2 in *Fukuivenator*, *Protarchaeopteryx* and *Caudipteryx* (Ji et al., 1998; Hattori et al., 2021), and at the middle of phalanx II-1 in *Xingtianosaurus* (Qiu et al., 2019). Phalanx I-1 is straight and slightly shorter than phalanx II-2. This condition differs from *Protarchaeopteryx* (Ji et al., 1998), *Caudipteryx zoui* (Zhou and Wang, 2000) and *Xingtianosaurus* (Qiu et al., 2019), which have phalanx I-1 as the longest manual phalanx, and from *Caudipteryx dongi* (Zhou and Wang, 2000) which shows phalanx I-1 subequal to phalanx II-2 in length. *Migmanychion* differs from the alvarezsaurids, which have phalanx I-1 the most elongate and robust hand phalanx (e.g., *Haplocheirus*, Choiniere et al., 2010), and from microraptorines and most avialans, which have a relatively shorter and more gracile phalanx I-1 (e.g., *Microraptor*, Xu et al., 2003; *Jeholornis*, Zhou and Zhang, 2002). The proximal contact surface of phalanx I-1 is deeply concave, which is a widespread theropod feature also present in late-diverging oviraptorosaurs but different from the weakly concave surface in caudipterids (Qiu et al., 2019). Phalanx II-1 bears a distinct lateral flange along the proximal half of the ventral margin, a morphology absent in other non-paravian coelurosaurs but shared with

Fukuivenator (Hattori et al., 2021). This feature in phalanx II-1 is not a taphonomic artifact, since no evidence of cracking is present in the bone, and no flange-like features are present in the other phalanges, including the comparably large phalanx II-2. A flange-like process topographically equivalent to the ridge in *Fukuivenator* and *Migmanychion* is reported in some dromaeosaurids (e.g., *Deinonychus*, *Sinornithosaurus*, but not in *Velociraptor*; Paul, 2002; Parson and Parson, 2009). The distal end of the phalanx bears large deep collateral ligament pits as in *Caudipteryx* and most theropods, but different from the small and dorsally located pit in *Xingtianosaurus* and some late-diverging oviraptorosaurs (Qiu et al., 2019). Phalanx II-2 is the most robust and longest phalanx. The collateral ligament pits in the distal end of the other phalanges are relatively small and dorsally located, approaching the condition in *Xingtianosaurus* and some oviraptorids (Qiu et al., 2019). Manual digit III possesses four phalanges as in most theropods, different from the only two small phalanges present in *Caudipteryx* (Zhou and Wang, 2000). The third phalanx of the third finger is slightly shorter than the combined length of the two preceding phalanges, as in most oviraptorosaurs, *Falcarius* and *Fukuivenator*, (Zanno, 2006; Balanoff and Norell, 2012), and differing from most paravians which show a proportionally longer penultimate phalanx (e.g., Ostrom, 1969; Hwang et al., 2004; Xu et al., 2013; Godefroit et al., 2014; Lefèvre et al., 2017). All phalanges of manual digit III are much shorter and narrower than the other manual phalanges.

All manual unguals are gently curved in side view, yet they are not particularly deep dorsoventrally (i.e., the tip of the ungual is not markedly ventral to the level of the articular facet when the latter is oriented vertically). All unguals bear a moundlike flexor tubercle moderately projected ventrally which is distinctly separated from the proximal articular surface by a small gap. The distal displacement of the flexor tubercle recalls ornithomimosaurs and some therizinosaurians (e.g., *Falcarius*, Zanno, 2006), whereas the majority of the other maniraptorans have manual unguals bearing a proximally-placed flexor tubercle confluent with the proximal end of the ungual (e.g., Khaan, Balanoff and Norell, 2012), or bear more prominent flexor tubercles, projected proximally, which describe a notch with the articular facet of the ungual (e.g., *Deinonychus*, Ostrom, 1969). *Fukuivenator* shows a combination of conditions, with the first manual ungual bearing a proximally-placed tubercle, and the other two unguals having more distally-placed tubercles (Hattori et al., 2021). In spite of these general similarities, the three manual unguals in *Migmanychion* are markedly heterogeneous, differing each other in size, proportion, and presence/absence of the proximodorsal lip. Although the second manual ungual is the longest ungual, its proximal margin is dorsoventrally shallower than that of the first ungual, a condition shared by *Fukuivenator* (Hattori et al., 2021). In other theropods (e.g., *Falcarius*, Zanno, 2006; Khaan, Balanoff and Norell, 2012), the longest ungual in the hand is usually also the most robust dorsoventrally. As in *Fukuivenator* (Hattori et al., 2021), a prominent proximodorsal lip is present only on manual ungual II, whereas it is absent in the other two unguals, a condition differing from oviraptorosaurs and therizinosaurians, where a distinct proximodorsal lip is usually present in both unguals II and III (e.g., Zanno, 2006). The gently sinusoidal outline of the dorsal margin of the second ungual (i.e., in side view, the proximodorsal lip is separated from the apex of the dorsal surface by a shallow concavity) is a morphology shared with *Fukuivenator*, therizinosaurians and oviraptorosaurs (e.g., Zanno, 2006; Balanoff and Norell, 2012; Hattori et al., 2021). The apex of the dorsal margin of the second ungual is significantly more dorsal than the articular facet when the latter is oriented vertically (Senter et al., 2012): this feature is shared with many dromaeosaurids (e.g., *Microraptor*, Hwang et al., 2002) but is absent in *Fukuivenator*, oviraptorosaurs and therizinosaurians,

which have a more moderate dorsal arching of the manual unguals relative to the articular facet (e.g., Zanno, 2006; Balanoff and Norell, 2012; Hattori et al., 2021). Nevertheless, contrary to dromaeosaurids (Senter et al., 2012), the first and the third manual unguals of *Migmanychion* do not markedly arch dorsally above the level of the articular facet.

?Paraves Sereno, 1998
Gen. et sp. indet. 1

Material. LY 2022JZ3004 (Fig. 5).

Description and comparison. The material includes a partially preserved pelvis articulated with both femora (the latter missing the trochanteric region), the proximal end of one tibia and fibula closely associated to the distal end of the femora. All elements are preserved in articulation, supporting their referral to the same individual.

Some vertebrae, likely pertaining to the proximal caudal series, are preserved as slab impressions, albeit mostly incomplete and fragmentary.

The right pubis shaft is nearly completely preserved in lateral view, missing the distal end (Fig. 5). The pubis is cranioventrally oriented as in *Falcarius*, oviraptorids and most saurischian dinosaurs (e.g., Balanoff and Norell, 2012), but differing from therizinosauroids, late-diverging Alvarezsaurids and most non-troodontid paravians which have the pubis variably oriented posteroventrally (Makovicky et al., 2004; Norell and Makovicky, 2004; Zanno, 2006; Cau, 2018). The proximal end of the pubis is preserved as a fan-shaped impression on the slab. The ischia are well preserved in the counter slab. The tips of the ischia are gently rounded and complete. The ischia are very short, being about 30–35% the length of the femur, a peculiar condition recalling some paravians (e.g., Anchiornithidae, Godefroit et al., 2013; Lefèvre et al., 2017) more than other maniraptorans which usually have ischia being 45–65% of femur length (e.g., Ji et al., 1998; Zhou and Wang, 2000; Balanoff and Norell, 2012). The shaft of the ischium is bent posteriorly, similar to most oviraptorosaurs (e.g., Balanoff and Norell, 2012), but different from the straight plate-like ischium with the shaft anteriorly concave of *Xingtianosaurus* (Qiu et al., 2019). The medially positioned, triangular obturator process is large and pointed as in most coelurosaurians, and differing from the more lobate process present in some oviraptorids (e.g., Balanoff and Norell, 2012) or the more truncated shape, bearing a distinct distal cleft, present in some paravians (e.g., Godefroit et al., 2013). The dorsal margin of the ischial shaft is uniformly concave caudally as in oviraptorids (Balanoff and Norell, 2012), but not strongly curved backward as in *Chirostenotes* and *Nomingia* (Osmolska et al., 2004). The ischia are distinctly separated and lack a medial symphysis: although most pennaraptorans lack a fused ischial symphysis (e.g., Balanoff and Norell, 2012; Godefroit et al., 2013), this feature in LY2022JZ3004 might indicate immaturity of the specimen.

The right femur is preserved in the counter slab, missing most of the distal part. The left femur is preserved in one slab with the proximal part overlapped by the right pubis. The femoral shaft is slightly bowed caudally in lateral view. The proximal end is broken or covered by other bones. The distal end is expanded but little features of the condylar region can be observed. Only the proximal ends of the left tibia and fibula are preserved. One pedal phalanx is preserved close to the right ischium in lateral view. The bone is slightly expanded proximally and compressed in the middle. One pedal ungual is preserved above the right ischium. The bone is slightly curved, without a distinct flexor tubercle proximally and lacks the acuminate outline of the manual unguals: it is interpreted as a pedal ungual. Other pedal phalanges are preserved as impressions, but very few anatomical features can be determined.

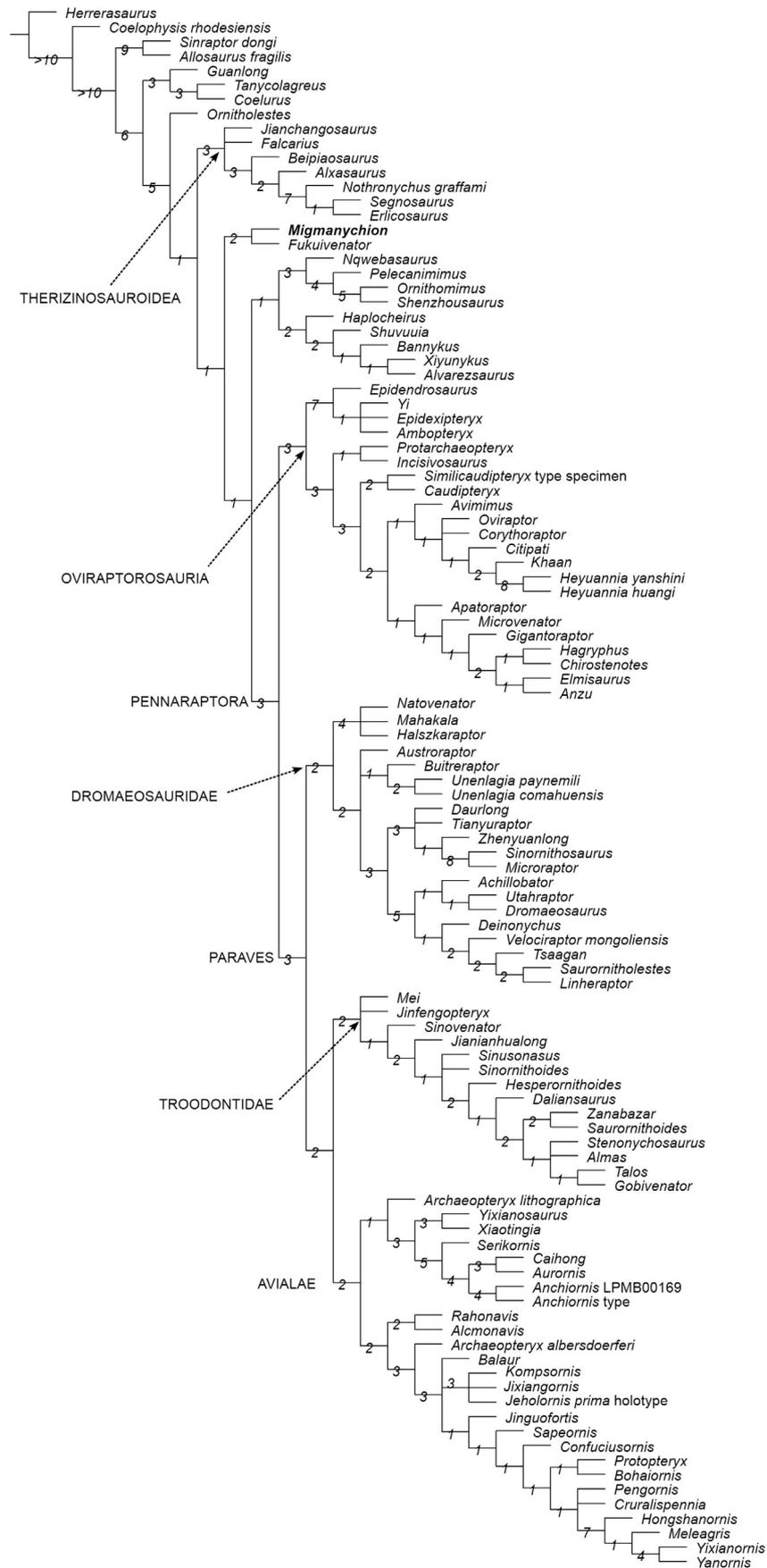


Fig. 7. Phylogenetic affinities of *Migmanychion laiyang* gen. et sp. nov. (LY 2022JZ3001) based on the strict consensus of the shortest trees reconstructed by the phylogenetic analyses. Number at nodes indicate the Bremer support value.

Gen. et sp. indet. 2

Material. LY 2022JZ3005 (Fig. 6). A couple of theropod metatarsi which cannot be unambiguously associated to LY 2022JZ3001 either LY 2022JZ3004.

Description and comparison. Metatarsals I to IV are preserved in both slabs, but the proximal and distal ends are too damaged for determining their morphology (Fig. 6). Metatarsal I is extremely reduced, and located close to the distal end of metatarsal II, a condition recalling several avialans and the scansoriopterygids (e.g., *Epidendrosaurus*, Zhang et al., 2002). Yet, it is unclear if the missing trochlea of metatarsal I was aligned distally with that of metatarsal II as in scansoriopterygids (Zhang et al., 2002). In *Protarchaeopteryx*, metatarsal I is located at the middle shaft of metatarsal II, whereas in *Caudipteryx zoui* the bone is at about a quarter of the way up the posteromedial corner of metatarsal II (Ji et al., 1998). In *Similicaudipteryx* and *Xingtianosaurus*, metatarsal I is located at about one third of the way up the distal end of metatarsal II (He et al., 2008; Qiu et al., 2019). The middle shafts of the three largest metatarsals are straight and tightly appressed. Metatarsal II is the most robust. The middle shaft of metatarsal III is mediolaterally compressed as in several maniraptoriforms, although not to the extreme degree seen in arctometatarsalian taxa (Holtz, 1994).

4. Results

Phylogenetic analysis. All shortest trees found by the phylogenetic analysis place *Migmanychion* as sister taxon of *Fukuivenator*, in a clade which is closer to pennaraptorans than therizinosauroids (tree length = 5212, CI excluding uninformative characters = 0.2433, RI = 0.5140; Fig. 7). Enforcing *Fukuivenator* in Therizinosauria (as suggested in Hattori et al., 2022) and setting *Migmanychion* as a “floater”, the shortest topologies reconstructed are three steps longer than the unenforced shortest topologies: under such constraint, *Migmanychion* keeps being reconstructed as sister taxon of *Fukuivenator*.

Enforcing *Migmanychion* among Pennaraptora and setting *Fukuivenator* as floater, the shortest trees reconstructed are two steps longer than the shortest unenforced topologies: under such constraint, *Migmanychion* is reconstructed as sister taxon of Pennaraptora, with *Fukuiraptor* placed in a more stem-ward position among the maniraptoran clade.

Enforcing *Migmanychion* in Oviraptorosauria and setting *Fukuivenator* as floater, the shortest topologies reconstructed are three steps longer than the shortest unenforced trees: under such constraint, the new Pigeon Hill theropod is reconstructed as a member of the “core oviraptorosaurs” (i.e., closer to oviraptorids than the scansoriopterygids).

Enforcing *Migmanychion* in Paraves, the shortest trees found are three steps longer than the shortest unenforced trees, and reconstruct *Migmanychion* alternatively as a member of the “Microraptorinae + Eudromaeosauria” clade or as sister taxon of *Archaeopteryx*.

The “*Fukuivenator* + *Migmanychion*” node is supported by two unambiguous synapomorphies: the presence of prominent proximodorsal lips in manual unguals II and III (homoplastic among maniraptorans) and the weak ventrolateral projection of the distal condyles of metacarpals II and III. Regardless the possible therizinosauroid affinities of *Fukuivenator* (see Hattori et al., 2021), *Migmanychion* retains the plesiomorphic state for three features optimized as diagnostic of Therizinosauria: the relatively more gracile pollex, the proportionally shorter first manual ungual relative to the preceding phalanx, and the proportionally shorter penultimate phalanx of the third finger. Under the most

parsimonious topology resulted, the new Pigeon Hill taxon is excluded from Pennaraptora because it retains the plesiomorphic state of two features optimized as diagnostic of that clade: a gracile third metacarpal and the presence of a distinct proximoventral process of metacarpal I overlapping the second metacarpal. *Migmanychion* lacks five derived features diagnostic of Scansoriopterygidae (i.e., the ginglymoid distal end of metacarpal III, metacarpal III extended distally to metacarpal II, metacarpal III more robust than metacarpal II, the very elongate first phalanx of the third finger, which is longer than metacarpal III), and one derived feature diagnostic of later-diverging oviraptorosaurs (i.e., a proportionally more robust first metacarpal). One derived feature diagnostic of Paraves is absent in the new Pigeon Hill taxon (i.e., a laterally expanded semilunate carpal capping metacarpal II).

5. Discussion

The new theropod material collected at Pigeon Hill differs from all the previously named taxa from this locality (e.g., *Khingnormis*, Wang et al., 2021a, 2021b; *Beiguormis*, Wang et al., 2022a; *Daurlong*, Wang et al., 2022b), and supports the presence of at least one new dinosaurian species in the Longjiang Formation. Although based on a fragmentary specimen, the holotype of *Migmanychion laiyang* shows a peculiar hand morphology different from all known theropods, supporting the erection of a new taxon. The larger size, the absence of an ossified carpometacarpus, the phalangeal formula and the overall morphology of the hand clearly differentiate *Migmanychion* from the two avialan genera known from Pigeon Hill (Wang et al., 2021, 2022a). *Migmanychion* differs from the only known non-avian theropod from Pigeon Hill, *Daurlong wangi* (Wang et al., 2022b), in lacking a large semilunate carpal contacting both metacarpals I and II, in having a proportionally shorter and more slender third finger which bears the first two phalanges subequally-elongate (in *Daurlong*, the first phalanx is twice longer than the second), and in having relatively shallower unguals which are less curved ventrally. This new species is referred to the coelurosaurian clade Maniraptoriformes based on the combination of the tridactyl hand (i.e., metacarpals IV and V completely lost), and slender metacarpals with no distinction between proximal end and diaphysis (i.e., the metacarpal mediolateral width is uniform along the whole element) (Makovicky et al., 2004; Osmólska et al., 2004; Cau, 2018). Among maniraptoriforms, *Migmanychion* does not show derived features of Alvarezsauridae and Ornithomimosauria. In particular, *Migmanychion* lacks the robust first metacarpal and corresponding stout pollex widespread among alvarezsaurids (e.g., Choiniere et al., 2010), and differs from ornithomimosaurians in bearing a proportionally shorter and more gracile third finger (e.g., Pérez-Moreno et al., 1994). Among maniraptoriforms, the absence of a large semilunate carpal capping both metacarpals I and II, and the absence of an elongate penultimate phalanx in the third finger (i.e., longer than the combined length of the preceding phalanges) are plesiomorphies which dismiss the referral of this new taxon to Pennaraptora or to Paraves (Hwang et al., 2002; Balanoff and Norell, 2012). The first metacarpal of *Migmanychion* bears a sharp and prominent ventrolateral flange contacting the second metacarpal. This feature is shared with *Fukuivenator* (Hattori et al., 2021), is incipiently developed in oviraptorosaurs (e.g., Zanno and Sampson, 2005), and is topographically equivalent to the prominent quadrangular buttress reported in the first metacarpal of the therizinosauroids and which underlies the second metacarpal (e.g., Falcarius, Zanno, 2006; *Alxasaurus*, Russell and Dong, 1993). The peculiar combination of features in the hand, in particular the presence of a lateroventral flange on phalanx II-1, and the second ungual which is shallower yet longer than the first ungual and is the unique bearing a proximodorsal lip, is shared with the enigmatic

maniraptoran *Fukuivenator*, a taxon recently interpreted as an early-diverging therizinosaurian (Hattori et al., 2021). None of the autapomorphies of *F. paradoxus* (Hattori et al., 2021) could be checked in *Migmanychion* due to the fragmentary condition of the latter, yet the two taxa differ based on several features of their hands (see Diagnosis). The intermetacarpal ratios (i.e., mcl/mcII and mcIII/mcII) in *Migmanychion* are much similar to pennaraptorans than to *Fukuivenator* or early-diverging therizinosaurians (e.g., Zanno, 2006; Godefroit et al., 2013; Lefevre et al., 2017; Hattori et al., 2021). We thus conclude that *M. laiyang* likely belongs to Maniraptora, yet remark that only additional material could corroborate the possible close relationship with *Fukuivenator* – currently based on the peculiar hand morphology shared by the two taxa – or, alternatively, could reinforce a closer affinity with another maniraptoran clade.

The ventrolateral ridge running along the proximal half of manual phalanx II-1 in *Migmanychion* and *Fukuivenator* is topographically equivalent to the flange-like process described in some dromaeosaurids (e.g., *Deinonychus*, *Sinornithosaurus*, Xu et al., 2002; Paul, 2002; Parson and Parson, 2009). In other paravians, the same phalanx is usually the most robust manual element, in particular in their proximal half (e.g., *Microraptor*, Hwang et al., 2002; Xu et al., 2003; Anchiornis, Hu et al., 2009). In more crown-ward taxa, the first phalanx of the second finger is dorsoventrally compressed and transversely expanded proximolaterally resulting in the avian *pila obliqua* (e.g., *Meleagris*, Baumel and Witmer, 1993; Hieronymus, 2016). The patchy distribution of this feature among maniraptorans, and its absence among oviraptorosaurs and therizinosaurids, do not support the homology between the ventrolateral flange present in the first phalanx of the second finger of *Migmanychion* with the condition present in some paravians: under the preferred topology, this feature is optimized as a potential synapomorphy shared by the new theropod and *Fukuivenator*.

The hindlimb material LY 2022JZ3004 is referred to Coelurosauria based mainly on the morphology of the ischium, which shows three derived features found uniquely on the latter clade. The bone 1) bears a subtriangular obturator process (i.e., it lacks a cleft on the distal margin producing a quadrangular outline in side view); 2) the obturator process is placed in the middle of the ventral margin of the bone; and 3) the ischium lacks a distal expansion (ischial foot): this combination of features is widespread among coelurosaurs but is absent in other theropod lineages (e.g., Ostrom, 1969; Gauthier, 1986; Balanoff and Norell, 2012; Lefevre et al., 2017; Cau, 2018). The uniform curvature of the posterodorsal margin of the ischium in LY 2022JZ3004 is homoplastic and shared with many small-bodied theropods, including oviraptorosaurs and some early-diverging paravians (e.g., Balanoff and Norell, 2012; Godefroit et al., 2013; Lefevre et al., 2017), and might support the referral of this specimen to Pennaraptora. Among the mentioned clades, the small size of the ischium compared to the femur (ischium-to-femur ratio < 0.4) is more consistent with some early-diverging paravian clades than with oviraptorosaurs or other theropods (e.g., Anchiornithidae, Godefroit et al., 2013; Lefevre et al., 2017). The slight cranioventral orientation of the pubis is plesiomorphic among maniraptorans and excludes this specimen from late-diverging deinonychosaurs, therizinosaurids, parvicursorines or avialans (Gauthier, 1986; Hwang et al., 2002; Choiniere et al., 2010; Cau, 2018). Based on the available material, LY 2022JZ3004 is tentatively referred to Paraves.

The partial foot material LY 2022JZ3005 is tentatively referred to Coelurosauria based on the constricted proximal end of metatarsal III shaft, which indicates an incipient pinching of the bone as seen in most coelurosaurs but absent in other theropod clades (Holtz, 1994).

6. Conclusion

The specimen LY 2022JZ3001 represents a new taxon of theropod dinosaur, *Migmanychion laiyang* gen. et sp. nov., from the Lower Cretaceous Longjiang Formation in East Inner Mongolia, China. *Migmanychion* possesses a peculiar combination of features in the hand, which is different from all other known theropods. Most of the derived features in *Migmanychion* hand are variably widespread among non-paravian maniraptorans (in particular, among early diverging oviraptorosaurs and therizinosaurids), suggesting that this theropod belongs to this grade and it is not particularly closer to the bird lineage (Avialae). Our phylogenetic analysis supports *Migmanychion* as closely related to the bizarre *Fukuivenator* and places them closer to pennaraptorans than therizinosaurids. Yet, such result has to be considered as provisional. Given the fragmentary nature of the only known specimen of *Migmanychion*, and the alternative suboptimal placements resulted by the constraint analyses, any position of this taxon among Maniraptora is tentative pending additional material.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cretres.2023.105605>.