

A new troodontid from the Upper Cretaceous Gobi Basin of inner Mongolia, China

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ARTICLE INFO

Article history:

Received 23 April 2021

Received in revised form

15 August 2021

Accepted in revised form 26 September 2021

Available online 1 October 2021

Keywords:

Dinosauria
Troodontidae
Late Cretaceous
Phylogeny
Osteohistology

ABSTRACT

A new troodontid dinosaur, *Papilovenator neimengguensis* gen. et sp. nov., from the Upper Cretaceous (Campanian) Wulansuhai Formation at Bayan Manduhu, Inner Mongolia, China, is described here. The holotype (BNMNH-PV030) consists of a nearly complete cranium and fragmentary postcranial bones in semi-articulation and this specimen is inferred as a subadult based on the osteohistological information and the fusion of bones. *Papilovenator neimengguensis* is distinguishable from other troodontids based on a suite of features such as the lateral groove of the dentary not posteriorly expanded, a deep surangular fossa anteroventral to the glenoid fossa and hosting the surangular foramen, the ventral ridge of the surangular fossa mainly on the surangular, and a unique anterolaterally broadened and butterfly-shaped neural arch of the anteriormost dorsal vertebrae in dorsal view. Our phylogenetic analysis recovered *Papilovenator neimengguensis* at the earliest-diverging branch of a clade including all other Late Cretaceous troodontids except *Almas*. The discovery of *Papilovenator neimengguensis* allows for an improved understanding of troodontid anatomy, as well as the regional variation of troodontids from the Upper Cretaceous of the Gobi Basin.

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1. Introduction

Troodontidae is a clade of lightly built theropod dinosaurs. As one of the most bird-like dinosaurian lineages, troodontids closely resemble avialans in both morphology and behavior (Makovicky and Norell, 2004; Xu and Norell, 2004; Turner et al., 2012; Xu et al., 2017). Fossil remains of troodontids are relatively rare but widely distributed, mostly known from the Cretaceous of Asia and North America. Fragmentary or dubious troodontid specimens are also reported across Asia, North America and Europe since the Late Jurassic (Makovicky and Norell, 2004; Hartman et al., 2019). The Upper Cretaceous of eastern Asia, namely the Gobi Basin in China

and Mongolia has yielded the most diverse troodontid records up to this point (Barsbold, 1974; Barsbold et al., 1987; Norell et al., 2000; Makovicky and Norell, 2004; Bever and Norell, 2009; Xu et al., 2011, 2012; Tsuihiji et al., 2014; Pei et al., 2017a). Nine species of troodontids have been named in this region from the Nemegt and the Djadokhta formations and the Djadokhta Formation equivalent fossil beds (*Almas ukhaa*, *Borogovia gracilicrus*, *Byronosaurus jaffei*, *Gobivenator mongoliensis*, *Linhevenator tani*, *Philovenator curriei*, *Saurornithoides mongoliensis*, *Tochisaurus nemegtensis* and *Zanabazar junior*). The Djadokhta Formation and its equivalent fossil beds have been referred as the Campanian (Jerzykiewicz and Russell 1991; Jerzykiewicz 2000; Dashzeveg et al., 2005; Dingus et al., 2008; Xu et al., 2015). Six troodontid taxa have been named from the Djadokhta-equivalent formations of the Gobi Desert in China and Mongolia, five of which, *Saurornithoides*, *Byronosaurus*, *Gobivenator*, *Linhevenator* and *Almas*, are preserved with most cranial bones and partial postcranial skeletons, while *Philovenator* only has

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a hindlimb preserved (Barsbold, 1974; Norell et al., 2000; Xu et al., 2011, 2012; Tsuihiji et al., 2014; Pei et al., 2017a). Most of the Gobi troodontids have low cranial profiles with an elongate rostrum, with the exception of *Almas*, in which the skull has a high and triangular profile in lateral view, resembling most Early Cretaceous troodontids from the Jehol Biota (Norell et al., 2000, 2009; Xu et al., 2002, 2011, 2012, 2017; Tsuihiji et al., 2014; Pei et al., 2017a). Here we report a second short-snouted troodontid taxon from the Late Cretaceous and also the third troodontid taxon from the Djadokhta equivalent Wulansuhai Formation at Bayan Manduhu, Inner Mongolia, China (Fig. 1), after the discoveries of *Philovenator* and *Linhevenator* (Xu et al., 2011; 2012).

2. Systematic paleontology

Theropoda Marsh, 1881
Coelurosauria Huene, 1920
Maniraptora Gauthier, 1986
Troodontidae Gilmore, 1924

Papiliovenator neimengguensis gen. et sp. nov.

ZooBank LSID urn:lsid:zoobank.org:pub:6018ADAA-FAEC-4552-835E-07E4E0368137.

Etymology. The generic name derives from ‘papilio’ (Latin for butterfly, referring to the unique shape of the neural arches of anteriormost dorsal vertebrae) and ‘venator’ (Latin for hunter); the specific name refers to Inner Mongolia, the autonomous region that produced the type specimen.

Locality and horizon. Bayan Manduhu Fossil Preserve, Bayan Manduhu, Wulatehouqi, Bayannur, Inner Mongolia (Fig. 1); Wulansuhai Formation, Campanian, Upper Cretaceous (Jerzykiewicz et al., 1993; Xu et al., 2015).

Holotype. The type specimen BNMNH-PV030 was collected in the Bayan Manduhu Fossil Preserve by the expedition of Inner Mongolia Geological Environment Monitoring in 2017. This specimen is now housed at the Bayannur Museum of Natural History.

BNMNH-PV030 is a semi-articulated skeleton comprising most of the cranial bones, most cervical vertebrae, the anterior dorsal vertebrae, partial scapulae, a partial right coracoid, a fragmentary pelvic girdle and fragmentary limb bones (including partial humeri, left ulna, left radius, partial manus, left femur, left tibia, left fibula, left pes and a right pedal phalanx II-3) (Figs. 2–6). The skull of BNMNH-PV030 is articulated and nearly complete, but the limb bones are heavily eroded and therefore unmeasurable. The neural arches of the dorsal vertebrae are fused to the centra in BNMNH-PV030. In addition to the fusion of the neurocentral suture, osteohistological information indicates this specimen probably at a subadult ontogenetic stage.

Diagnosis. *Papiliovenator neimengguensis* can be distinguished from all other troodontids by a unique combination of the following features: lateral groove of the dentary not posteriorly expanded (Figs. 2, 3), deep surangular fossa hosting the surangular foramen anteroventral to the glenoid fossa (Figs. 2, 3), ventral ridge of the surangular fossa mainly on surangular (Figs. 2, 3), anterolaterally broadened and butterfly-shaped neural arches of the first and second dorsal vertebrae in dorsal view (Fig. 4).

Among the troodontids from the Wulansuhai Formation at Bayan Manduhu, *Papiliovenator neimengguensis* can be additionally differentiated from *Linhevenator* in the presence of unserrated teeth and the proportionally longer humeri (humerus more than half the length of the skull in BNMNH-PV030). *Papiliovenator neimengguensis* can be differentiated from *Philovenator* in having a less mediolaterally compressed metatarsus and the mid-shaft of metatarsal II significantly narrower mediolaterally than metatarsal IV in anterior view.

3. Description and comparison

The skull of BNMNH-PV030 is articulated and nearly completely preserved, missing the premaxillae and the anterior tips of the maxillae. The anteroposterior length of the preserved portion of the

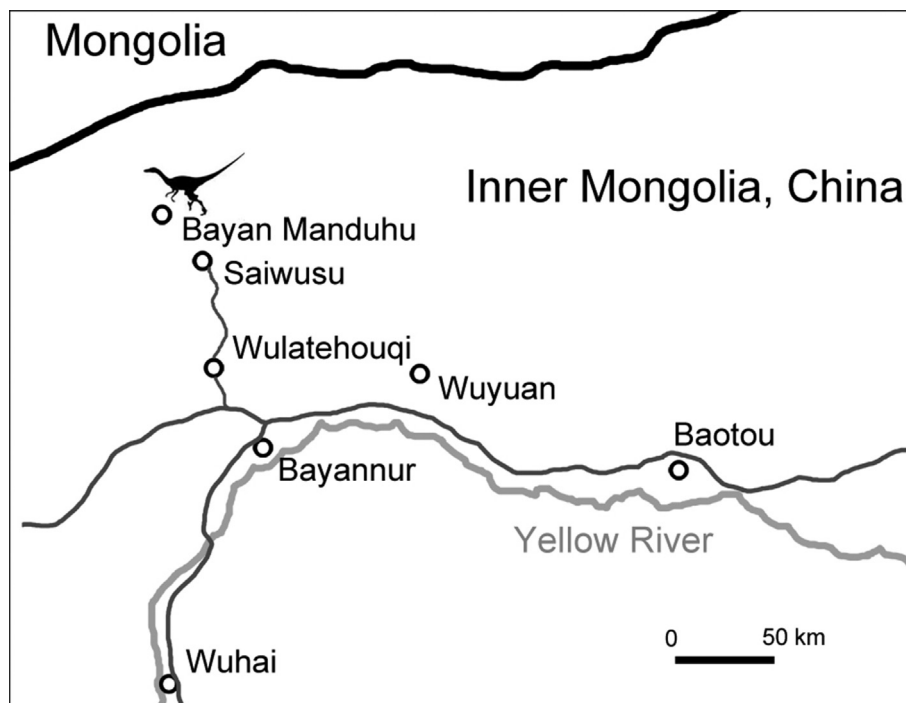


Fig. 1. Locality (E106° 43' 47.76", N41° 47' 33.31") of the holotype (BNMNH-PV030) of *Papiliovenator neimengguensis* gen. et sp. nov., indicated by the theropod icon.

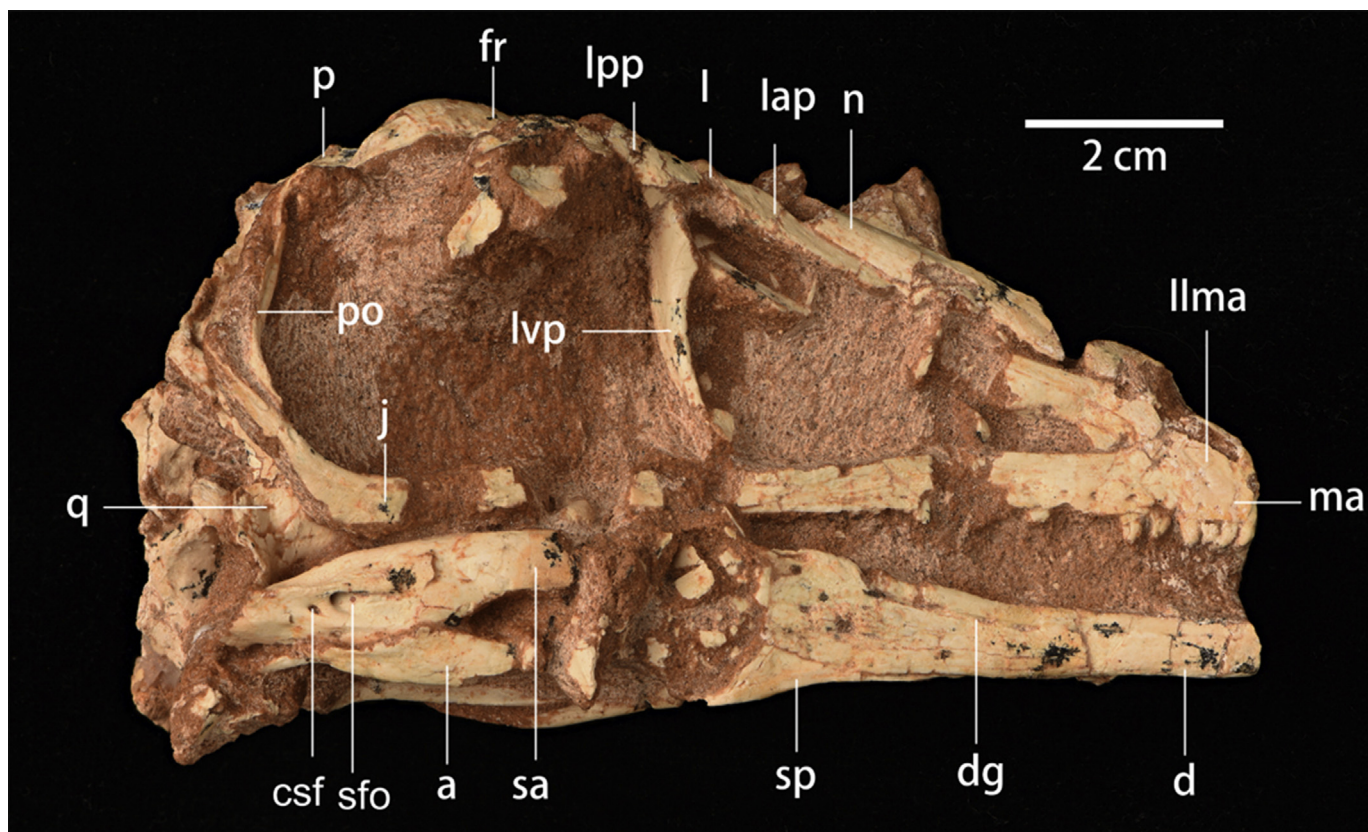


Fig. 2. Skull of *Papiliovenator neimengguensis* gen. et sp. nov., holotype (BNNMH-PV030), in right view. a, angular; csf, caudal surangular foramen; d, dentary; dg, dentary groove; fr, frontal; ma, maxilla; j, jugal; l, lacrimal; lap, anterior process of lacrimal; llma, lateral lamina of maxilla; lpp, posterior process of lacrimal; lvp, ventral process of lacrimal; n, nasal; p, parietal; po, postorbital; q, quadrate; sa, surangular; sfo, surangular fossa; sp, splenial. Scale bar = 2 cm.

skull (from the occipital condyle to the anterior part of the maxilla) is 11 cm, and we estimate the skull with a full length of about 12 cm, shorter than the skulls of most Late Cretaceous troodontid forms except *Almas* (Table 1). The skull of *Papiliovenator neimengguensis* is generally high, with a triangular profile like *Almas* and the Jehol troodontids (Figs. 2, 3), but in contrast to the long and low skulls of other Late Cretaceous troodontids (Xu et al., 2002; Xu and Norell, 2004; Norell et al., 2009; Tsuihiji et al., 2014; Xu et al., 2017; Shen et al., 2017a; Pei et al., 2017a). The orbit of BNNMH-PV030 is large and generally round. The anteroposterior lengths of the antorbital fossa in *Papiliovenator neimengguensis*, *Almas* and the Jehol troodontids are similar to the orbital lengths, unlike *Saurornithoides*, *Zanabazar*, *Gobivenator* and *Linhevenator*, in which the antorbital fossa is anteroposteriorly longer than the orbit.

The lateral lamina of the ascending process of the maxilla is penetrated by small foramina (Fig. 2). The lateral lamina is a broad plate with a convex anterodorsal edge in lateral view (Fig. 2), like that of late-diverging troodontids such as *Gobivenator*, *Saurornithoides*, *Zanabazar*, *Byronosaurus*, *Xixiasaurus* and dromaeosaurids (Makovicky et al., 2003; Norell et al., 2009; Lü et al., 2010; Turner et al., 2012; Tsuihiji et al., 2014), but different from the Early Cretaceous troodontids, especially those from the Jehol Biota, in which the lateral lamina is reduced to a triangular plate with a straight or concave anterodorsal edge (Xu et al., 2002; Xu and Norell, 2004; Ji et al., 2005). The ventral ramus of the maxilla is band-like with almost parallel dorsal and ventral edges, which is a typical troodontid condition in contrast to the distinctly posteriorly tapering ventral ramus in dromaeosaurids (Figs. 2, 3). A shallow horizontal groove runs along the lateral surface of the ventral ramus of the maxilla, like other troodontids from the Djadokhta

Formation and its equivalent fossil beds, such as *Saurornithoides*, *Byronosaurus*, *Gobivenator*, *Almas* and the Ukhaa Tolgod perinates (Bever and Norell, 2009; Pei et al., 2017a). The antorbital fossa is triangular. A small and irregular opening is located at the anterior tip of the right antorbital fossa (Fig. 2) but is absent on the left side (Fig. 3). This opening possibly represents the promaxillary fenestra or simply a breakage, as no laterally exposed promaxillary fenestra has been reported in Late Cretaceous troodontids. The maxillary fenestra is situated along the ventral margin of the antorbital fossa, as found in all troodontids in contrast to the dorsally shifted maxillary fenestra in dromaeosaurids (Norell and Makovicky, 2004; Turner et al., 2012; Pei et al., 2014). The maxillary fenestra is anteroposteriorly elongate and low, similar to those of other troodontids from Djadokhta-equivalent fossil beds, *Zanabazar*, *Sinornithoides* and *Sinuso nasus* (Russell and Dong, 1993; Makovicky et al., 2003; Xu and Wang, 2004; Norell et al., 2009; Tsuihiji et al., 2014), but different from those of *Sinovenator*, *Mei*, *Jianianhualong* and *Hesperornithoides* (Xu et al., 2002; Xu and Norell, 2004; Xu et al., 2017; Pei et al., 2017a; Hartman et al., 2019). Unlike *Byronosaurus*, the interfenestral bar of *Papiliovenator neimengguensis* is inset from the lateral surface of the ventral ramus similar to other troodontids (Makovicky et al., 2003).

The maxillary teeth are ziphodont and relatively smaller than those in dromaeosaurids. Six teeth are preserved on the left side while seven on the right. The tooth row extends to a point just posterior to the interfenestral bar. Estimated around 20 tooth positions are developed on each side, comparable to most troodontids except *Byronosaurus* who probably bears 30–40 maxillary teeth on each side (Makovicky et al., 2003). The preserved maxillary teeth are slightly eroded, and no serrations are developed, resembling

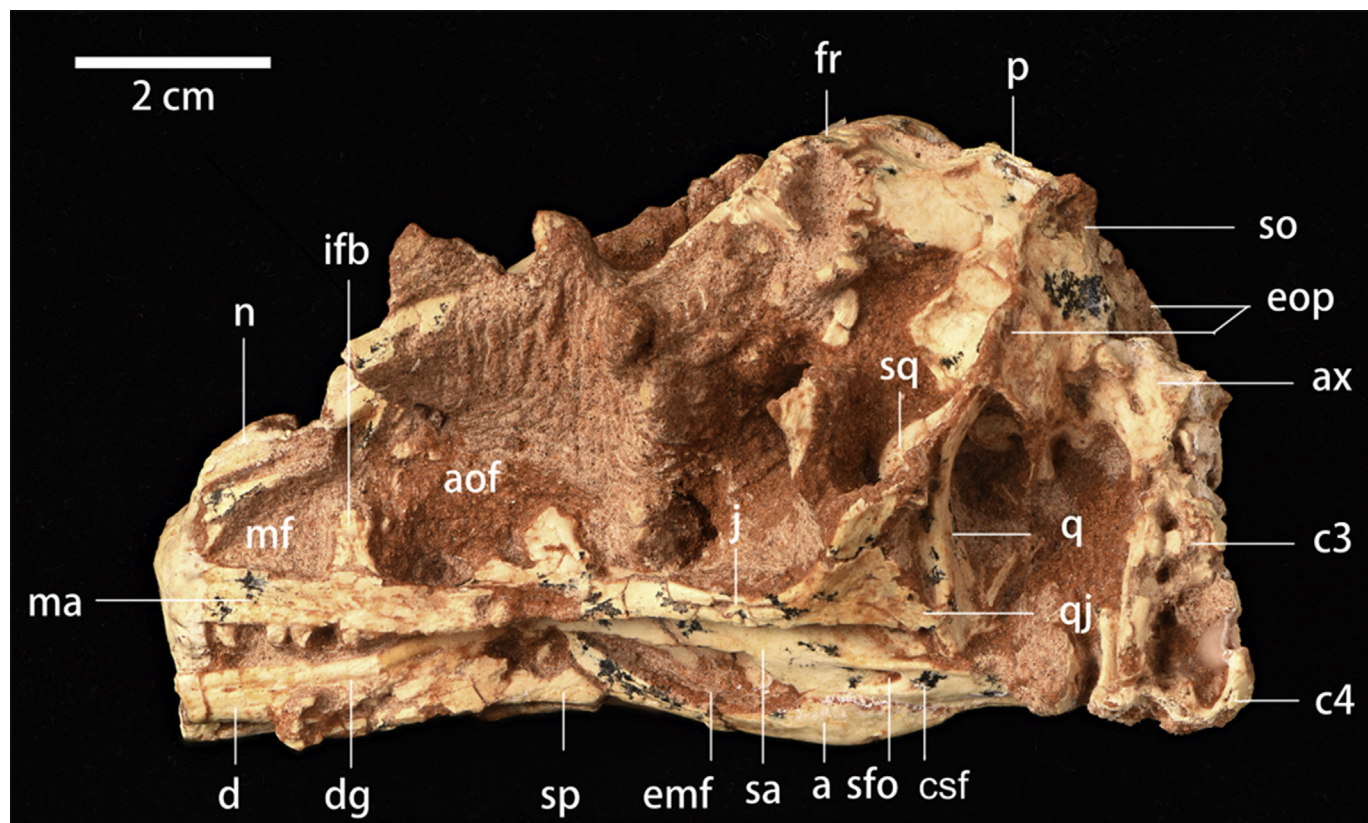


Fig. 3. Skull of BNMNH-PV030 in left view. a, angular; aof, antorbital fenestra; ax, axis; c3-4, cervical vertebrae 3-4; csf, caudal surangular foramen; d, dentary; dg, dentary groove; emf, external mandibular fenestra; eop, exoccipital-opisthotic process; fr, frontal; ifb, interfenestral bar; j, jugal; ma, maxilla; mf, maxillary fenestra; n, nasal; p, parietal; q, quadrate; qj, quadratojugal; sa, surangular; sfo, surangular fossa; so, supraoccipital; sp, splenial; sq, squamosal. Scale bar = 2 cm.

Gobivenator, *Almas*, *Byronosaurus*, *Xixiasaurus* and *Mei*, but different from other troodontids (Makovicky et al., 2003; Makovicky and Norell, 2004; Xu and Norell, 2004; Gao et al., 2012; Tsuihiji et al., 2014; Pei et al., 2017a; Hartman et al., 2019). The middle teeth are only slightly larger than the closely packed anterior teeth. Unlike *Sinovenator*, *Sinornithoides*, *Almas*, most maxillary teeth of *Papiliovenator* do not show distinct constrictions between the tooth crown and the root in lateral view (Currie and Dong, 2001; Xu et al., 2002; Pei et al., 2017a).

The nasals of *Papiliovenator neimengguensis* are elongate and narrow, with a vaulted dorsal surface. One vague foramen is present on the lateral side of the left nasal, while the preserved portion of the right nasal appears generally smooth. In contrast, a continuous series of foramina is developed on the lateral side of the nasal in other troodontids like *Gobivenator*, *Almas* and *Linhevenator*. The anterior end of the nasal extends more anterior than the anterior end of the antorbital fossa, indicating that the external naris of *Papiliovenator* should be located entirely anterior to the antorbital fossa, which is a condition common to all reported Late Cretaceous troodontids (Pei et al., 2017a).

The lacrimal is T-shaped, and the anterior process is much longer than the posterior process (Fig. 2), as typical of troodontids (Makovicky et al., 2003; Makovicky and Norell, 2004). The anterior process of the lacrimal is attached to the posterolateral side of the nasal, roofing the antorbital fenestra. The ventral process of the lacrimal is anteroposteriorly flat. Its upper portion is vertical in lateral view but its lower portion curves anteriorly like in *Gobivenator*, *Saurornithoides* and *Byronosaurus* (Makovicky et al., 2003; Norell et al., 2009; Tsuihiji et al., 2014), in contrast to *Almas*, *Jianianhualong*, *Mei*, *Sinovenator*, *Hesperornithoides* and the *Uhkaa*

Tolgod perinates, in which the ventral process either is vertical or leans anterodorsally (Xu and Norell, 2004; Bever and Norell, 2009; Xu et al., 2017; Pei et al., 2017a; Yin et al., 2018). A narrow groove runs close to the medial edge on the posterior surface of the ventral process. The posterior process of the lacrimal is short and laterally expanded, forming an iconic supraorbital crest of troodontids (Pei et al., 2017a).

The suborbital process of the jugal has a twisted lateral surface, with the anterior half slightly everted dorsally and the posterior half everted ventrally. The suborbital process of the jugal is slightly shallower than the maxillary ventral ramus. The postorbital process of the left jugal is broken off, while the postorbital process of the right jugal seems have a smooth orbital margin like in most troodontids (Figs. 2, 3), but different from *Gobivenator*, in which the orbital margin of the postorbital process of the jugal is anterodorsally convex. The right postorbital is partially preserved with a slender and sinusoid ventral process that loosely attaches onto the anterior side of the postorbital process of the jugal. The quadrate is partially exposed with the posterior surface hosting a pneumatic groove, which is also present in other troodontids such as *Sinovenator* and *Gobivenator* (Xu et al., 2002; Tsuihiji et al., 2014; Yin et al., 2018).

The frontal has a smooth dorsal surface. Both frontals meet along a straight suture. A groove is developed medial to the lateral edge of the frontal. The two parietals are fused and the suture between the bones is ridged into a well-developed sagittal crest, similar to *Zanabazar*, *Gobivenator*, *Latenivenatrix* and *Sinovenator* (Norell et al., 2009; Tsuihiji et al., 2014; van der Reest and Currie, 2017; Yin et al., 2018). The dorsal ridge of the parietal wing slopes lateroventrally.

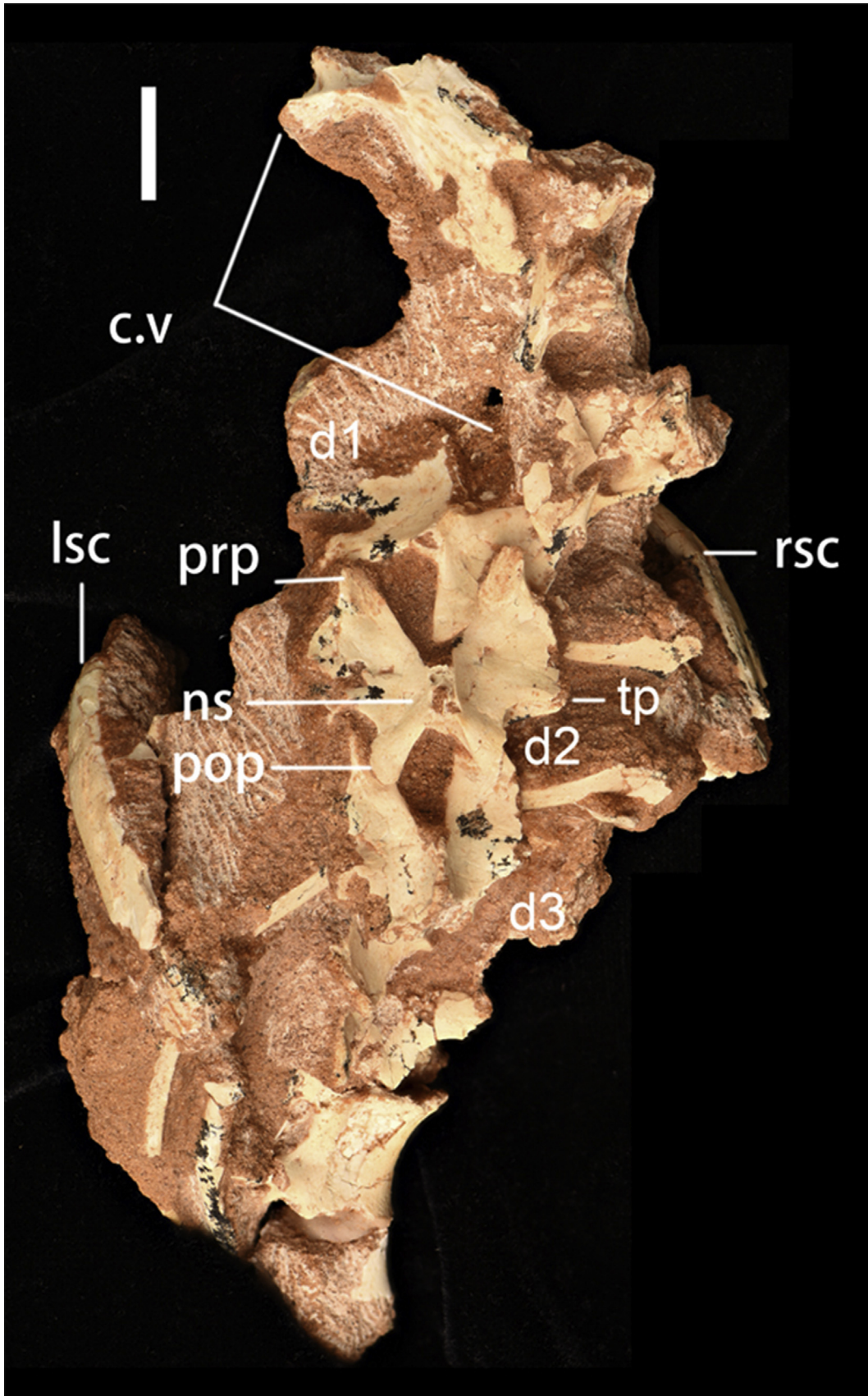


Fig. 4. Posterior cervical vertebrae and anterior dorsal vertebrae of BNMNH-PV030 in dorsal view. c.v, cervical vertebrae; d1-d3, dorsal vertebrae 1–3; lsc, left scapula; ns, neural spine; pop; postzygapophysis; prp, prezygapophysis; rsc, right scapula; tp, transverse process. Scale bar = 1 cm.



Fig. 5. Forelimb bones of BNMNH-PV030. A, left radius and ulna in posterior view; B, left humerus in anterior view; C, right humerus in anterior view. dpc, deltapectoral crest; ra, radius; u, ulna. Scale bar = 1 cm.

The supraoccipital has a convex posterior surface (Fig. 3). Like *Sinovenator* and *Almas*, a pair of crescentic fossae hosting the openings of cerebral veins are developed on each side of the midline (Pei et al., 2017a; Yin et al., 2018). The foramen magnum is slightly elliptical along the dorsoventral axis, like in *Byronosaurus*, *Zanabazar*, *Latenivenatrix* and *Sinovenator* (Currie, 1985; Xu et al., 2002; Makovicky et al., 2003; Norell et al., 2009; Yin et al., 2018), but in contrast to the more widened foramen magnum in *Gobivenator* as well as non-troodontid taxa such as *Anchiornis*, *Archaeopteryx*, and dromaeosaurids (Norell and Makovicky, 2004; Alonso et al., 2004; Pei et al., 2017b).

The dentary of *Papiliovenator neimengguensis* bears a lateral groove ventral to the tooth row as typical of troodontids and some paravians like *Buitreraptor* and *Anchiornithids* (Figs. 2, 3) (Makovicky and Norell, 2004; Makovicky et al., 2005; Hu et al., 2009; Pei et al., 2017b). Unlike other troodontids but similar to *Byronosaurus*, the posterior portion of the groove appears dorsoventrally narrow and does not broaden posteriorly (Xu et al., 2002; Makovicky et al., 2003; Norell et al., 2009; Tsuihiji et al., 2014). The splenial attaches onto the posteroventral margin of the dentary and

is exposed as a triangular plate in lateral view, which is typical of deinonychosaurs (Makovicky et al., 2003; Pei et al., 2017b). The surangular has an anterior blade overhanging a large external mandibular fenestra that is absent in *Archaeopteryx* and *Anchiornithids* (Pei et al., 2017b). Like *Gobivenator* but different from *Almas* and Early Cretaceous troodontids, a deep surangular fossa is located immediately anteroventral to the elongate glenoid fossa (Tsuihiji et al., 2014; Pei et al., 2017a; Yin et al., 2018). This fossa is dorsally defined by the laterodorsal flange of the surangular and ventrally by a short horizontal lateral ridge that merged posteriorly into the lateral surface of the surangular (Figs. 2, 3). In *Papiliovenator*, this ventral ridge is mainly developed on the surangular, but in *Gobivenator* this ridge is mainly developed on the angular and has a very limited extension on the surangular. Notably, this surangular fossa is missing in Early Cretaceous troodontids and *Almas* (Pei et al., 2017a), and is unpreserved or unexposed in other known Late Cretaceous troodontid taxa. A similar fossa is also seen in other theropods, such as the tyrannosauroid *Albertosaurus*. The surangular foramen is probably represented by a small opening located inside the surangular fossa like in *Gobivenator*. On the right

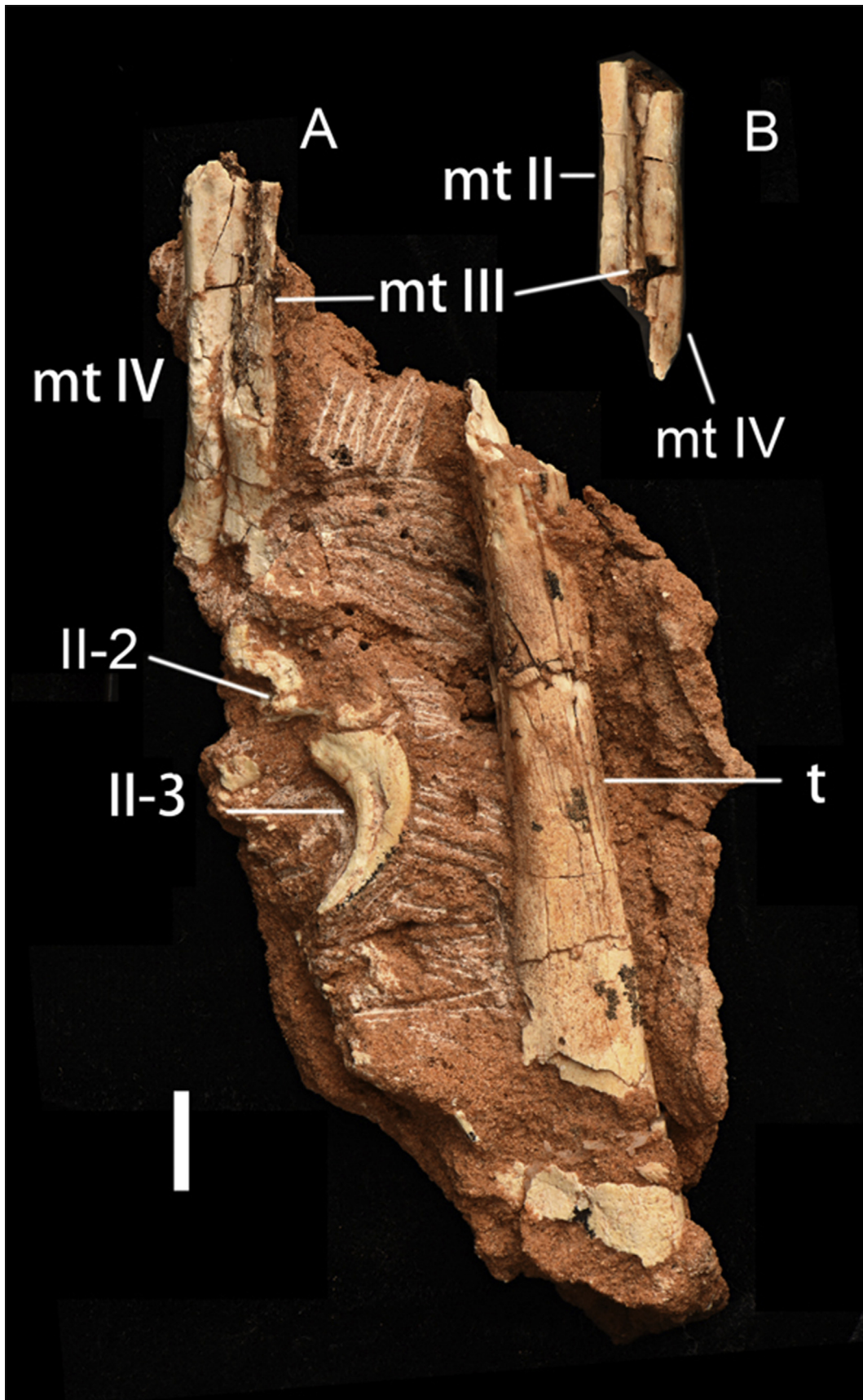


Fig. 6. A, left tibia in medial view and distal section of left pes in posterior view; B, middle section of left metatarsal in anterior view. The osteohistological section was sampled from the distal breakage of the tibia. II-2. Pedal phalanx II-2; II-3 pedal phalanx II-3; mt II-IV, metatarsal II-IV; t, tibia. Scale bar = 1 cm.

Table 1
Skull lengths and related ratios of selected troodontids.

Taxon (specimen)	Skull length (mm)	Skull height/ Skull length	Humeral length/ Skull length
<i>Mei</i> (DNHM D2514)	49	0.43	0.73
<i>Almas</i> (MPC-D 100/1323)	82	0.43	–
<i>Papiliovenator</i> (BNMNH-PV030)	*120	0.36	0.75
<i>Gobivenator</i> (MPC-D 100/86)	*186	0.26	0.58
<i>Linhevenator</i> (LH V0021)	220	–	0.43
<i>Zanabazar</i> (MPC-D 100/1)	280.6	0.30	–
<i>Sauromithoides</i> (AMNH FR 6516)	192	0.28	–

(*including the length of the missing anterior tip, which is estimated based on the proportions of the rostrum in other Late Cretaceous troodontids).

side, one caudal surangular foramen is present immediately posterior to the surangular fossa like in *Gobivenator* (Tsuihiji et al., 2014), while this caudal surangular foramen is represented only by a small recess at the same position on the left side (Figs. 2, 3). The prearticular attaches onto the angular medially, and is exposed through the external mandibular fenestra. A pair of hyoids are present, but only the anterior tips are preserved.

The exact number of cervical vertebrae is unknown. The first four cervical vertebrae including the atlas and the axis are associated with the skull (Fig. 3), two isolated and fragmentary cervical vertebrae might represent the middle cervical vertebrae, and three fragmentary cervical vertebrae are attached to the dorsal column (Fig. 4). The neural arches of the first and second dorsal vertebrae of *Papiliovenator neimengguensis* are anterolaterally broadened and butterfly-like in dorsal view (Fig. 4). The horizontal lamina between the prezygapophysis and the transverse process has an anterolaterally convex margin. In contrast, this margin of the lamina is posteromedially concave between the prezygapophysis and the transverse process in the anteriormost dorsal vertebrae of *Mei* and *Daliansaurus* (Xu and Norell, 2004; Shen et al., 2017a). The prezygapophyses are more laterally spread than the postzygapophyses. The neural spine of the anterior dorsal vertebra is posteriorly located on the centrum and the transverse processes are posterolaterally directed. The transverse processes are elongate and sweep posterolaterally, making acute angles with the postzygapophyses. All preserved dorsal neural arches are completely fused with the centra.

The scapula and coracoid are unfused and separated. The humerus of *Papiliovenator neimengguensis* bears a well-developed deltapectoral crest. Like *Gobivenator*, the lateral edge of the deltapectoral crest forms a low angle with the humeral shaft (Fig. 5B, C), in contrast to the relatively high angle in *Linhevenator* (Xu et al., 2011). The preserved portion of the left humerus of BNMNH-PV030 is 9.0 cm long, close to the real length of this bone. The humerus of *Papiliovenator neimengguensis* is proportionally longer than the humeri of both *Gobivenator* and *Linhevenator* (Table 1). The ulna and the radius have similar diameters in BNMNH-PV030, and the shaft of the ulna is slightly curved as in most troodontids (Fig. 5A), but different from the straight ulna of anchiornithids (Pei et al., 2017b). The shafts of metacarpals I-1 and II-1 are cylindrical. Metacarpal I-2 is strongly curved, with a well-developed flexor tubercle, typical of maniraptorans. Metacarpal I-2 of *Papiliovenator* lacks a clearly defined proximal dorsal lip, which is similar to *Sinornithoides* but different from *Mei* and *Jianianhualong* (Currie and Dong, 2001).

The femur of *Papiliovenator neimengguensis* is bowed, the tibia is straight and the fibula has an expanded proximal section. However, the lengths of these bones are unknown as both ends of the bones are missing. The metatarsus of BNMNH-PV030 is partially preserved and broken into two isolated sections. At the middle portion of the metatarsus of BNMNH-PV030, metatarsal III is extremely mediolaterally compressed, and is offset between metatarsals II

and IV in anterior view (Fig. 6B), like many Late Cretaceous troodontids (Kurzanov and Osmólska, 1991; Zanno et al., 2011; Tsuihiji et al., 2014; Pei et al., 2017a). Metatarsal II of *Papiliovenator neimengguensis* is much narrower mediolaterally than metatarsal IV, resembling those of other Late Cretaceous troodontids with the exception of *Philovenator*, in which metatarsal II has a similar width as metatarsal IV in anterior view (Xu et al., 2012). The distal end of metatarsal III is almost as wide as that of metatarsal IV in posterior view (Fig. 6A). Metatarsal III has a slightly further distal extension than metatarsal IV like *Tochisaurus*, *Borgovia*, *Latenivenatrix* and *Talos* (Kurzanov and Osmólska, 1991; Zanno et al., 2011; van der Reest and Currie, 2017), but different from *Sinovenator*, *Mei*, *Jianianhualong* and *Sinornithoides* where metatarsal IV does not reach distally to the level of the ligament pits of metatarsal III (Currie and Dong, 2001; Xu et al., 2002, 2017; Xu and Norell 2004). Metatarsal II-2 has a typical late-diverging troodontid profile with a strongly abbreviated shaft, and a strongly curved ungual is preserved representing the iconic deinonychosaurian pedal ungual II (Fig. 6A) (Makovicky and Norell, 2004).

4. Phylogenetic analysis

To test the phylogenetic affiliation of *Papiliovenator neimengguensis* we expanded the data matrix from Pei et al. (2020) by including this new taxon and other relatively late-diverging troodontids, such as *Jianianhualong*, *Almas*, *Gobivenator* and *Linhevenator*. A total of 168 coelurosaurian taxa and 853 characters were used in the analysis, with *Allosaurus fragilis* as the outgroup. The dataset was analyzed with equally weighted parsimony with TNT v. 1.5 (Goloboff and Catalano, 2016). A heuristic tree search strategy was performed with 1000 replicates of Wagner trees followed by TBR branch swapping, holding 10 trees per replicate. The best trees obtained at the end of the replicates were subjected to a second round of TBR branch swapping. A strict consensus tree was generated from the 99,999 most parsimonious trees (Fig. 7).

All major coelurosaurian lineages that have traditionally been considered monophyletic are also confirmed to be monophyletic in these results. The general phylogenetic pattern within Troodontidae remains similar as traditionally recognized (Xu et al., 2002; Makovicky et al., 2003; Tsuihiji et al., 2014; Pei et al., 2020). However, with the new taxa added, the positions of several troodontid taxa are changed. Notably, all Late Cretaceous troodontids are recovered as a monophyletic group, and *Almas* is recovered as the earliest-diverging taxon of this clade (Fig. 7), as suggested in our previous study (Pei et al., 2017a). *Papiliovenator neimengguensis* is also found to be a member of this Late Cretaceous troodontid clade, at the second earliest-diverging branch, as the sister taxon to a clade including all other Late Cretaceous troodontids except *Almas*. This placement is supported by the presence of the deep surangular fossa on the mandible hosting the surangular foramen in *Papiliovenator* and all other Late Cretaceous troodontids except *Almas*. The other Bayan Manduhu troodontid, *Linhevenator*, is recovered as

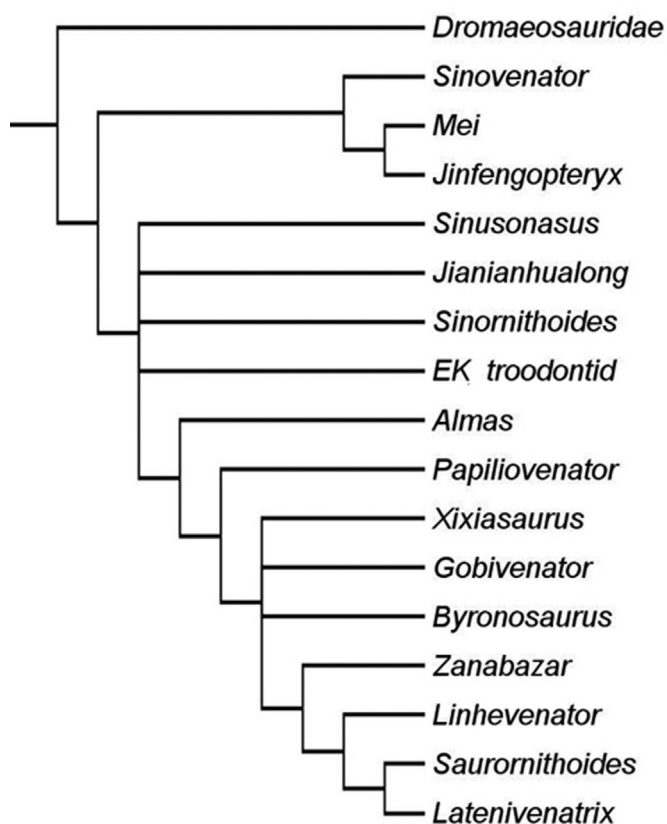


Fig. 7. Phylogenetic relationship of *Papiliovenator*. Reduced strict consensus of 99,999 most parsimonious trees (TL = 3497 steps, CI = 0.321, RI = 0.782).

the sister taxon to a clade of *Saurornithoides*, *Zanabazar* and *Latenivenatrix*.

5. Osteohistological study

An osteohistological analysis was conducted to further determine the ontogenetic stage of BNMNH-PV030. Osteohistological samples were taken from the already broken part of the left tibia and the left fibula, at approximately the mid-shaft of the bones. Based on the transverse sections of the tibia and the fibula, BNMNH-PV030 is inferred to be a subadult.

The section of the tibia shows a thin compacta (about 1.96 mm) surrounding a large central medullary cavity (about 8.86 mm in diameter, Fig. 8A). A very thin layer of endosteal lamellar bone (about 0.14 mm in thickness) is deposited partly around the medullary cavity (Fig. 8A), which probably indicates that the expansion of medullary cavity is nearly complete, as no secondary endosteal bone has been reported in troodontids (Varricchio 1993; Gao et al., 2012; Shen et al., 2017c; Selles et al., 2021). The primary cortex is composed of fibrolamellar bone with longitudinal and reticular vascular canals. Lines of arrested growth (LAGs) are absent in the compacta. No EFS (external fundamental system) is present, and only primary osteons are present. The density of vascular canals and osteocytes slightly decreases from inner to outer cortex (Fig. 8A). All osteohistological evidence shows that the tibia was still actively growing when the animal died but the growth had started to slow down. The histological information of the fibula is similar as it is in the tibia but it appears to be at a more mature stage of development than the tibia (Fig. 8B). In the outermost cortex, a very thin layer of parallel-fibered bone with two tightly packed

LAGs is present in the fibula (Fig. 8B). No endosteal bone is deposited around the medullary cavity in the fibula. Based on the osteohistological information, we interpret BNMNH-PV030 as a young subadult whose growth rate has started to decrease. Similar to the relatively early diverging troodontids such as *Mei* and *Tamarron*, *Papiliovenator* has a high density of vascularization showing a rapid initial growth rate without secondary bone remodelling (Gao et al., 2012; Selles et al., 2021), and attains the subadult ontogenetic stage much earlier than the Late Cretaceous troodontids from North America (Varricchio et al., 2008; Zanno et al., 2011).

6. Discussion

Papiliovenator neimengguensis can be referred to troodontids based on the following suite of features: presence of a lateral groove on the dentary, presence of the supraorbital crest of the lacrimal, anterior process of the lacrimal much longer than the posterior process, maxillary teeth closely packed anteriorly, bowed ulna and radius and an asymmetrical metatarsus. Even though the general shape of the skull of *Papiliovenator neimengguensis* is similar to that of *Almas* and many Early Cretaceous Jehol troodontids, BNMNH-PV030 shows a Late Cretaceous anatomical profile and differs from the early-diverging troodontids in the presence of a broader lateral lamina of the ascending process of the maxilla, a highly asymmetrical metatarsus with metatarsal IV much wider mediolaterally than metatarsal II, and metatarsal IV extending distally almost as far as metatarsal III.

As the seventh named troodontid from the Campanian of eastern Asia, *Papiliovenator neimengguensis* resembles the Late Cretaceous troodontids from Djadokhta Formation and its equivalent deposits in possessing a shallow horizontal groove along the lateral surface of the maxilla ventral ramus (Pei et al., 2017a). However, it could also be easily differentiated from *Saurornithoides*, *Byronosaurus*, *Linhevenator* and *Gobivenator* from the general shape of the skull. Based on the length of the skull (Table 1), *Papiliovenator* is larger than *Almas*, and significantly smaller than *Saurornithoides*, *Linhevenator*, *Gobivenator* and *Byronosaurus* (Makovicky et al., 2003; Norell et al., 2009; Xu et al., 2011; Tsuihiji et al., 2014; Pei et al., 2017a), while the relative size of *Philovenator* and *Papiliovenator* can not be directly compared. Among the only three taxa whose forelimb measurements could be assessed, the forelimb of *Papiliovenator neimengguensis* is proportionally longer than those of *Linhevenator* and *Gobivenator* (Table 1).

As a histologically subadult, BNMNH-PV030 could have potentially acquired a larger size had its ontogenetic trajectory continued, but this size increase would not be substantial as the growth rate of this individual had already started to decrease. The degree of skeletal fusion in BNMNH-PV030 indicates a relatively late ontogenetic stage and this specimen was possibly approaching its adulthood at death. BNMNH-PV030 exhibits complete fusion between the parietals and complete fusion between the neural arches and the centra of all preserved dorsal vertebrae, indicating its skeletal morphology is fairly stable and likely similar to a somatically mature individual. The cranial proportions of BNMNH-PV030 is similar to those of the adult and subadult individuals of the Early Cretaceous troodontids that also show pedomorphic cranial features such as relatively large orbits and short snouts (Gao et al., 2012; Shen et al., 2017a, 2017b, 2017c). No precise ontogenetic series has been established for troodontids due to the lack of materials, but a pedomorphic cranial shape has been suggested in early-diverging eumaniraptorans, and an ontogenetic trajectory of the rostral elongation exists in troodontids like in other theropod groups (Bever and Norell, 2009; Bhullar et al., 2012; Pei et al., 2017a).

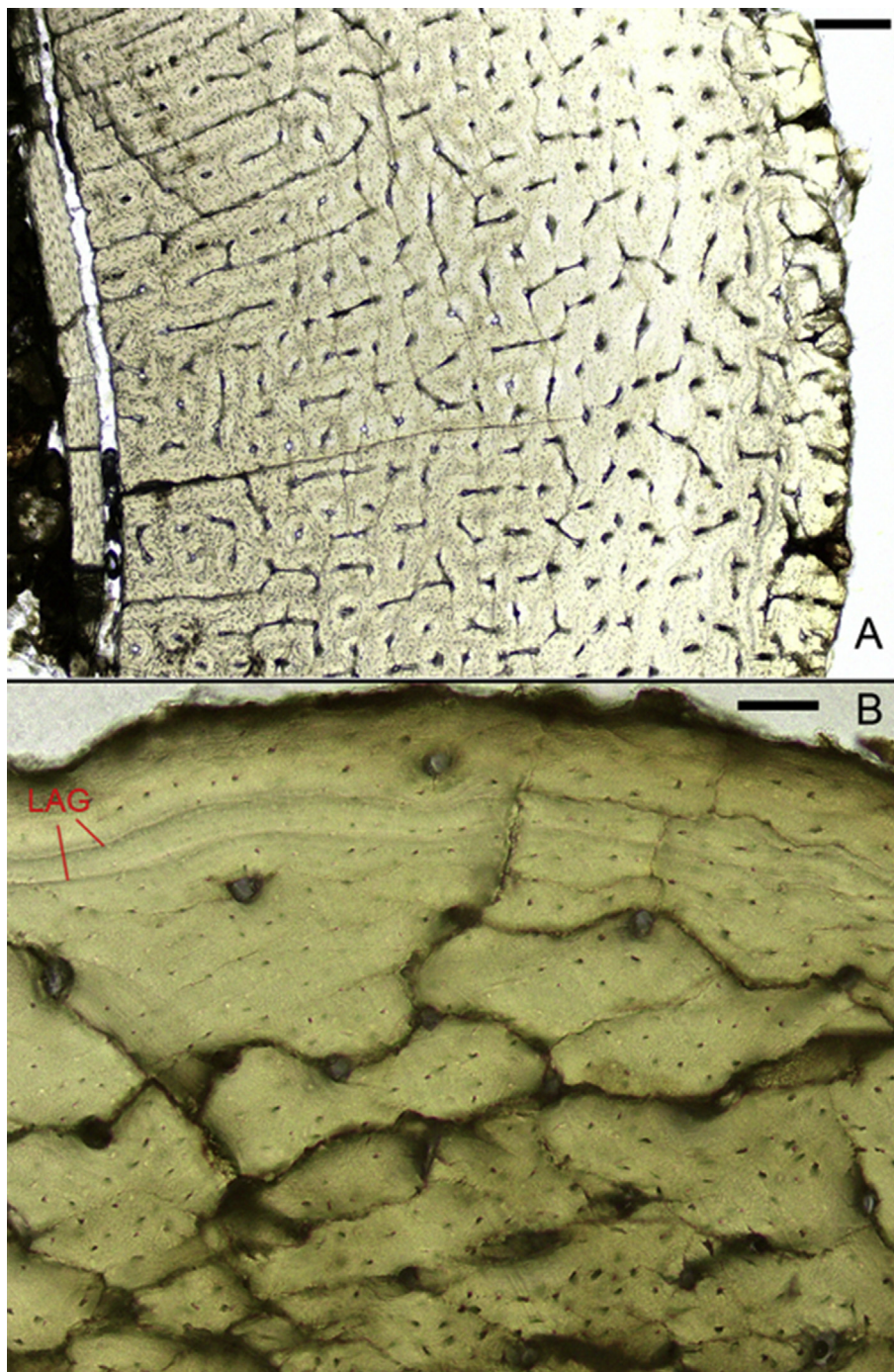


Fig. 8. Bone microstructure in tibia (A) and fibula (B) of BNMNH-PV030 under regular transmitted light. Scale bars = 200 μm (A) and 50 μm (B).

Papiliovenator resembles *Byronosaurus* in having a lateral dentary groove without broadened posterior opening. However, the density of maxillary teeth could differentiate these two taxa, as *Papiliovenator* is estimated to have around 20 maxillary tooth positions, while *Byronosaurus* could easily have 30–40 on each side. Also unlike *Byronosaurus*, the interfenestral bar of *Papiliovenator* is inset from the lateral surface of the maxilla.

Although *Papiliovenator* has a similar cranial proportion to *Almas*, it can be easily distinguished from *Almas* in the anteroventrally curved ventral process of the lacrimal, the presence of the deep surangular fossa, the presence of an additional caudal

surangular foramen, and the absence of a distinct constriction of the maxillary teeth.

Unlike *Papiliovenator*, the metatarsus of *Philovenator* is distinctly mediolaterally compressed, and metatarsals II and IV almost have the same widths in anterior view, while metatarsal III completely vanishes in anterior view at the mid-shaft.

Unlike *Gobivenator*, the lateral groove of the dentary in *Papiliovenator neimengguensis* is not posteriorly broadened and the postorbital process of the jugal does not have an anterodorsally convex margin. Both *Gobivenator* and *Papiliovenator* have the surangular foramen situated in a posterodorsally recessed surangular

fossa, but the ventral ridge of the fossa is mostly restricted on the surangular in *Papiliovenator* whereas it extends onto the angular in *Gobivenator*. Notably, since no well-preserved and/or -exposed surangular of other Late Cretaceous troodontids have been reported, our phylogenetic analysis optimized the presence of this surangular fossa as a synapomorphy for a clade including all Late Cretaceous troodontids except *Almas*.

Apart from the proportional differences from *Papiliovenator* mentioned above, *Linhevenator* and *Saurornithoides* are the only troodontids from the Djadokhta Formation and its equivalent deposits having serrations on teeth. Serrated teeth are common among the troodontids that were reported from the early days, and this feature was optimized to be a plesiomorphy for all troodontids (Makovicky and Norell, 2004). As many new troodontid taxa with unserrated teeth discovered in the last decades (Norell et al., 2000; Xu and Norell, 2004; Lü et al., 2010; Tsuihiji et al., 2014; Pei et al., 2017a), the dental evolution of troodontids appears more complex than previously expected, and the tooth serration may actually be a homoplasy among this family.

Papiliovenator is the second short-snouted troodontid reported from the Late Cretaceous. Earlier-diverging paravians typically have a shortened and angular rostrum. The Early Cretaceous Jehol troodontids (*Sinovenator*, *Sinusoanaxus*, *Mei*, *Jinfengopteryx*, *Jianianhualong*, *Liaoningvenator*, *Daliansaurus*) all have a relatively short and triangular rostrum (Xu et al., 2002; Xu and Wang, 2004; Xu and Norell, 2004; Ji et al., 2005; Shen et al., 2017a; 2017b). In the relatively early-diverging Late Cretaceous troodontids, such as *Almas* and *Papiliovenator*, this rostral proportion of the early-diverging paravians and the Jehol troodontids is retained, while the rest of Late Cretaceous troodontids all adopt a long-snouted cranial profile. Pei et al. (2017a) suggested a series of structural transformations associated with the elongation of the rostrum in most Late Cretaceous troodontid forms, such as the anterior shift of the naris in relative to the antorbital fossa, the elongation of the maxillary fenestra, the antorbital fenestra and the nasal, and the anterior shift of the ventral process of the lacrimal. Interestingly, the ventral process of the lacrimal of the short-snouted *Papiliovenator* also flares anteroventrally like other Late Cretaceous troodontids with an elongate rostrum, which may imply that this feature is not necessarily associated with the changes in shape of the rostrum, but possibly bearing other phylogenetic or functional meanings.

The troodontids from the Djadokhta Formation and its equivalent fossil beds have distinct variations in the cranial and dental forms, as well as the relative lengths of the forelimb. All these features could be linked to foraging behaviors of the animals, and therefore it indicates that these Campanian troodontids from the Gobi Basin may have already adapted to a variety of foraging strategies within a restricted geographical region.

7. Conclusion

BNMNH-PV030 represents a new troodontid taxon, *Papiliovenator neimengguensis*, from the Upper Cretaceous Djadokhta Formation equivalent Wulansuhai Formation at Bayan Manduhu, Inner Mongolia, China. *Papiliovenator neimengguensis* is unique in having a distinguishable combination of osteological features, notably the butterfly-shaped neural arches on the anteriormost dorsal vertebrae in dorsal view. Our phylogenetic analysis placed *Papiliovenator neimengguensis* as the second earliest-diverging branch of a Late Cretaceous troodontid clade after *Almas*. The discovery of this new taxon not only increased the diversity of the Campanian troodontids of the Gobi Basin, but also improved our understanding of their morphological variation.

Acknowledgments

This study was supported financially by the National Natural Science Foundation of China (41972025, 41688103, 42072008), the International Partnership Program of Chinese Academy of Sciences (132311KYSB20190010, 132311KYSB20180016), and the Special Funds for Natural Resources of Inner Mongolia Autonomous Region (C01419399061). We thank the field crew for fossil collection, Z.G. Yang for major preparation and H.L. Zang for photography. We also thank the three anonymous reviewers, whose feedback greatly improved the manuscript.

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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.2021.105052>.