

Anatomy of *Mahakala omnogovae* (Theropoda: Dromaeosauridae), Tögrögiin Shiree, Mongolia

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ABSTRACT

The dromaeosaurid *Mahakala omnogovae* is known from a unique specimen from the Late Cretaceous deposits of the Djadokhta Formation at Tögrögiin Shiree, Ömnögov Aimag, Mongolia. The holotype specimen is comprised of a well-preserved but partial skull and a nearly complete postcranial skeleton. *Mahakala omnogovae* is included in a comprehensive phylogenetic analysis of Coelurosauria using a dataset, which reflects a greatly expanded character set and taxon-sampling regime. Several interesting features of *Mahakala omnogovae* have implications for deinonychosaurian and avialan character evolution and for understanding patterns of size variation and size change within paravian theropods. These morphologies include the shape of the iliac blade, the triangular obturator process of the ischium, and the evolution of the subarctometatarsalian condition. We present an expanded diagnosis of *Mahakala omnogovae*, which included following unique combination of characters (autapomorphies noted by *): a ledgelike depression at the confluence of metotic strut and posterior tympanic recess on the anterior face of the paroccipital process*, a posteriorly tapering scapula; a shortened forelimb (humerus 50% femur length); a strongly compressed and anteroposteriorly broad ulna tapering posteriorly to a narrow edge*; elongate lateral crest on the posterodistal femur*; anterior caudal vertebrae with subhorizontal, laterally directed prezygapophyses*; a prominent supratrochanteric process; and the absence of a cuppedicus fossa.

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FIGURE 1. View of the discovery site looking west. Picture was taken 100 m east of “3” in Norell and Makovicky (1997: fig. 3).

INTRODUCTION

Although small theropod dinosaurs are generally extremely rare, they are common in the Upper Cretaceous rocks of the Djadokhta Formation of Mongolia and northern China (Jerzykiewicz and Russell, 1991; Norell and Makovicky, 1997; Norell et al., 1995). Here we provide a detailed description of *Mahakala omnogovae*, a dromaeosaurid from the Late Cretaceous that was named and briefly described by Turner et al. (2007a). This skeleton was discovered during the 1992 year of the joint American Museum of Natural History–Mongolian Academy of Sciences expeditions by M.A. Norell. The specimen was in a series of associated limonitic concretions in a small gully at the northern end of the Tögrögiin Shiree (fig. 1).

Although the number of valid dromaeosaurid species has increased dramatically in the past decade, this taxon is only the third dromaeosaurid reported from the Djadokhta Formation (a possible fourth taxon may be present if *Velociraptor osmolskae* (Godefroit et al., 2008) proves to be valid). In light of its basal phylogenetic position, *Mahakala* has bearing on character evolution within deinonychosaurs and basal avialans. Furthermore, in the preliminary description it was shown that *Mahakala* provides critical information on estimating the ancestral body sizes among dromaeosaurid theropods.

INSTITUTIONAL ACRONYMS

The following acronyms are used throughout this work:

- AMNH-FARB American Museum of Natural History, New York, collection of fossil reptiles, amphibians and birds
- BMNH Natural History Museum, London, UK
- FMNH Field Museum of Natural History, Chicago
- IGM Mongolian Institute of Geology, Ulaan Bataar, Mongolia
- IVPP Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China
- MCF Museo Carmen Funes, Plaza Huinacul, Neuquén Province, Argentina
- MCZ Museum of Comparative Zoology, Harvard University, Cambridge
- MPCA Museo Carlos Ameghino, Cipolletti, Río Negro Province, Argentina
- TMP Royal Tyrell Museum of Paleontology, Alberta, Canada
- UA University of Antananarivo, Madagascar
- UCMP University of California Museum of Paleontology, Berkeley
- YPM Yale Peabody Museum, New Haven, CT

PREPARATION MATERIAL AND METHODS

Most of the IGM 100/1033 was prepared by Amy Davidson (AMNH), with additional preparation carried out by William Amaral (Harvard, MCZ) and Ana Balcarcel (AMNH). The specimen was collected in nodules and Davidson prepared these by embedding in Carbowax[®] 4600 (Union Carbide) polyethylene glycol, tinted with blue dry pigment for visibility. The matrix was prepared by softening with ethanol and removing with a hand-held needle. After preparation the Carbowax[®] was removed with a needle by melting and brief submersion in hot water. Adhesives and consolidants present on the specimen include ethyl cyanoacrylates and Paraloid[®] B-72 (Rohm and Haas), an ethyl methacrylate and methyl acrylate copolymer. Other adhesives may also be present. A preparation record is held at the AMNH Division of Paleontology.

SYSTEMATIC PALEONTOLOGY

Theropoda Marsh, 1881

Coelurosauria Huene, 1920

Maniraptora Gauthier, 1986

Dromaeosauridae Matthew and Brown, 1922

MAHAKALA OMNOGOVAE TURNER ET AL., 2007

HOLOTYPE: IGM 100/1033, a nearly complete skeleton comprised of paired frontals, partial left maxilla, partial right dentary and splenial, left ectopterygoid, right partial pterygoid, left partial quadrate, and braincase region of the skull with a single isolated tooth, associated with partially articulated postcranial elements. These postcranial remains include portions of both

TABLE 1. Select Measurements of *Mahakala omnogaovae* (in mm)

	IGM 100/1033
Frontal: length	25.2
Occiput: width	22.0
Caudal vertebrae series: length	171.0
Humerus (right): length	26*/35–40 ^a
Radius (left): length	36*
Ulna (left): proximal transverse width	32*/40 ^a
Metacarpal II (left): length	18.0
Metacarpal II (left): length	15*
Ilium (left): length	52.5
Femur (left): length	79.0
Tibia (left): length	110.0
Metatarsus (right): length	82.0
Pedal ungual, digit II (right): anteroposterior length	17.0
Pedal ungual, digit II (right): length of outside curve	19.0

*Partial element.

^aEstimated total length.

forelimbs (right and left scapulae, humeri, ulnae, radii, and portions of the metacarpals and phalanges) and both hind limbs (left femur, left and right tibia, and fibula and metatarsals). The pedal phalanges are best represented from the left pes, which preserves a trenchant second pedal ungual (table 1).

LOCALITY AND HORIZON: Tugrugyin Member of the Djadokhta Formation (Campanian), Tögrögiin Shiree, Ömnögov Mongolia (fig. 1).

EMENDED DIAGNOSIS: A small maniraptoran diagnosed by the following unique combination of characters: a ledgelike depression at the confluence of metotic strut and posterior tympanic recess on the anterior face of the paroccipital process*; a posteriorly tapering scapula; a short forelimb (humerus 50% femur length); a strongly compressed and anteroposteriorly broad ulna tapering posteriorly to a narrow edge*; elongate lateral crest on the posterodistal femur*; anterior caudal vertebrae with subhorizontal, laterally directed prezygapophyses*; a prominent supratrochanteric process; and the absence of a cuppedicus fossa.

DESCRIPTION

The specimen is an adult or near adult as can be determined by the degree of neurocentral suture and astragalocalcaneal fusion, braincase coossification and histological analysis (see Turner et al., 2007a). Only a few skull bones are known for *Mahakala*, predominately from the braincase, although a small portion of the left maxilla, right dentary and right splenial are also preserved. A single dentary tooth and the right ectopterygoid were recovered. Four fragmentary elements are also present. These may represent portions of the left pterygoid, quadrate, right ectopterygoid and articular respectively.

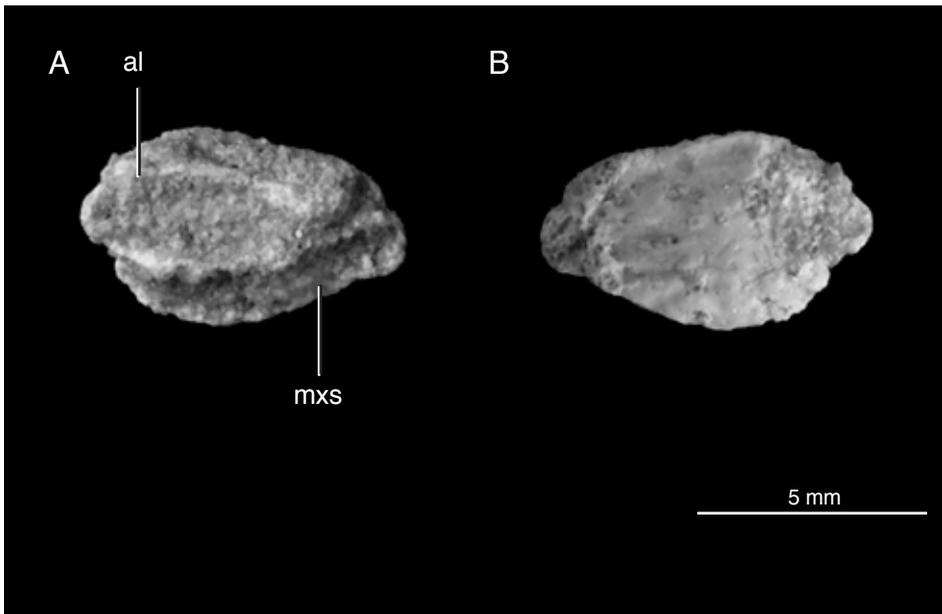


FIGURE 2. Left maxilla of *Mahakala omnogovae* in medial view (A) and lateral view (B).

SKULL

MAXILLA: Only a partial left maxilla was recovered in IGM 100/1033, the holotype and only known specimen of *Mahakala omnogovae* (fig. 2). In lateral view, the preserved maxilla is triangular and tapers anteriorly. The ventral margin, near the tooth row, is marked with three nutrient foramina and possesses a subtle wavy sculpturing. The posteriorly slanting dorsal margin is straight sided and smooth. The surface looks natural and not the result of breakage and erosion and is interpreted as the contact surface for either of the unpreserved premaxilla or nasal. The dentigerous margin is very weakly arcuate in outline. The posterior portion of the maxilla is damaged and little can be said regarding its morphology save that no indication of an antorbital fossa or fenestra is present.

No interdental plates are present and the interalveolar plates are not preserved. Therefore, the exact number and size of the maxillary alveoli cannot be determined. It appears, however, that the alveoli would have been small and numerous as in basal troodontids (Makovicky et al., 2003) and dromaeosaurids such as *Microraptor zhaoianus* (Hwang et al., 2002) and *Buitreraptor gonzalezorum* (Makovicky et al., 2005).

The medial surface of the maxilla is smooth dorsal to the tooth row. A horizontal ridge runs the preserved length of the maxilla near the dorsal margin of the bone. This ridge corresponds with the palatal shelf of the maxilla that forms the floor of the nasal passage.

FRONTAL: The frontals are paired as in most coelurosaurs (fig. 3). Each frontal is vaulted dorsoventrally, similar to the condition seen in *Mei long* (Xu and Norell, 2004), indicating a proportionally large orbit for an animal of this size. In dorsal view, the combined frontals are

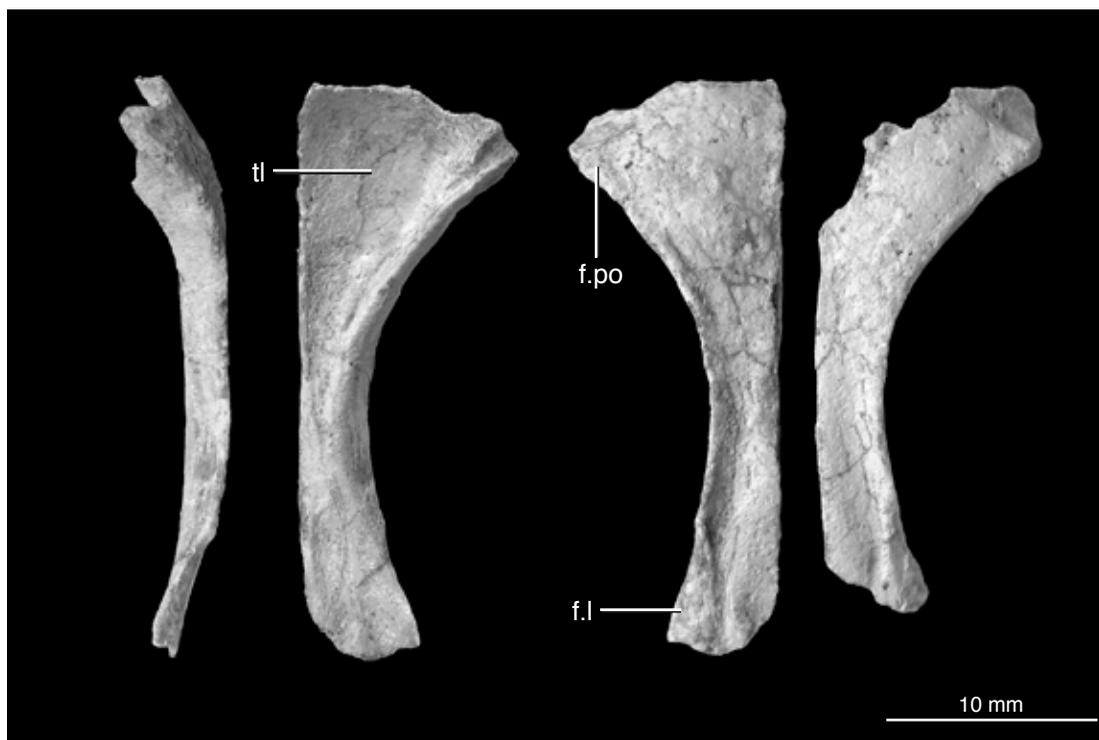


FIGURE 3. Right frontal of *Mahakala omnogovae* in lateral and ventral views (left). Left and right frontals of *Mahakala omnogovae* in dorsal view (right).

weakly hourglass shaped, narrow anteriorly, and widest at the contact with the postorbitals and laterosphenoids. The interorbital region is very narrow, unlike dromaeosaurids but similar to the troodontids *Sinovenator changii* (Xu et al., 2002) and *Mei long* (IVPP V12733). Anteriorly, the frontal remains narrow for roughly two-thirds its length, expanding slightly as in other deinonychosaurs where it forms an abrupt transverse suture with the nasals. On the anterolateral corner of the frontal a small lappet, presumably for articulation with a T-shaped lacrimal, is present, as in other dromaeosaurids. The dorsal surface of the lappet is marked by a posteriorly constricting V-shaped groove. A small, rounded ridge bounds the groove laterally. This ridge as well as the lateral surface of the lappet is smooth, lacking the notch present in the dromaeosaurids *Velociraptor mongoliensis* (IGM 100/985), *Dromaeosaurus albertensis* (AMNH FARB 5356), *Tsaagan mangas* (IGM 100/1015) and *Saurornitholestes langstoni* (Sues, 1977). Ventrally, the lappet is accompanied by a small longitudinal slot just lateral to the depression for the olfactory bulb. In troodontids, this serves as an additional articulation surface for the lacrimal (Makovicky and Norell, 2004). No indication for a prefrontal ossification is present on the frontals, as in most other dromaeosaurids.

The frontals contact along the midline in a straight suture. The suture sits on a rounded slightly raised ridge that is separated from the orbital margin by a shallow longitudinal depression. The orbital rims are everted slightly, beginning at the limit of the lacrimal facet and end-

ing posteriorly halfway along the orbital margin. Everted orbital margins are present in troodontids (Makovicky and Norell, 2004) and the dromaeosaurids *Tsaagan mangas* (IGM 100/1015), *Bambiraptor feinbergorum* (AMNH FARB 30556), and some specimens of *Velociraptor mongoliensis* (e.g., IGM 100/982). In *Troodon formosus* (Currie and Zhao, 1993), *Zanabazar junior* (Barsbold, 1974), *Saurornithoides mongoliensis* (Norell et al., 2009), and *Sinovenator changii* (Xu et al., 2002), the everted orbital margins are more pronounced than in *Mahakala* and persist to the contact with the postorbital. The abbreviated eversion of the orbital rim is more similar to that seen in *Mei long* (IVPP V12733) and the previously mentioned dromaeosaurids. Posteriorly, the frontals expand to more than twice the interorbital width. The expansion is gradual and marks a smooth transition from the orbital margin to the postorbital processes of the frontal. This is similar to the condition seen in troodontids (Makovicky and Norell, 2004) and unlike the abrupt transition and sharply demarcated frontal postorbital processes present in dromaeosaurids (Currie, 1995). The dromaeosaurid *Austroraptor cabazai* also has a gradual transition from the body of the frontal to the postorbital process. However, because of the large size disparity between *Austroraptor* and *Mahakala*, and because the exact extent of the postorbital process in *Austroraptor* is unclear due to breakage there, a more precise comparison between the two taxa is difficult. The posterodorsal surface of the frontals is slightly

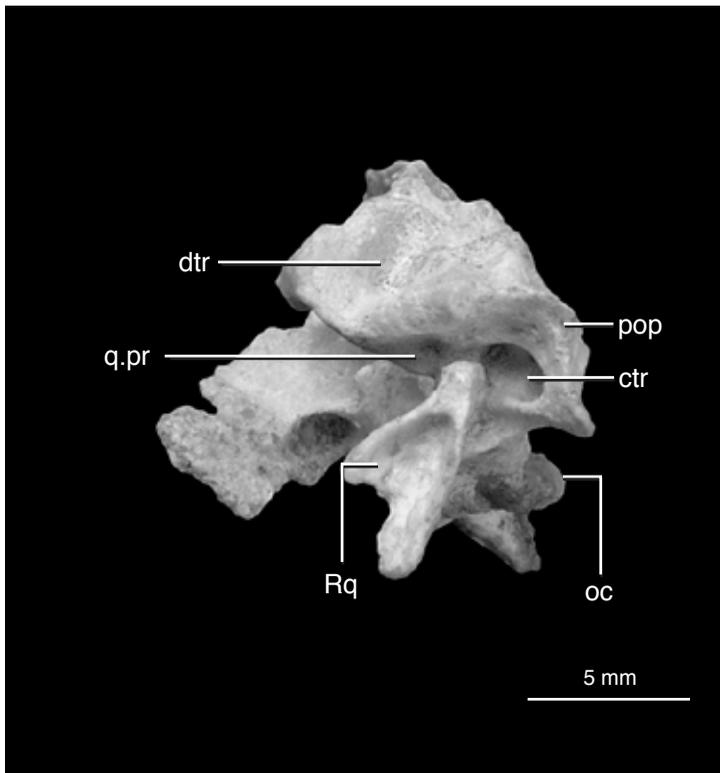


FIGURE 4. Braincase and proximal left quadrate of *Mahakala omnogovae* (IGM100/1033) in left lateral view.

convex, expressing the shape of the tectal lobes of the midbrain. On the dorsal surface of the posterolateral corner a small transverse ridge defines the corner of the supratemporal fenestra, where the frontal projects ventrally to form part of the supratemporal fossa. The fossa margin is weakly curved, not sinuous like that seen in all dromaeosaurids except *Tsaagan mangas* (Norell et al., 2006) and *Austroraptor cabazai* (Novas et al., 2009). The posterior margin of the frontals, which would have bordered the parietal along the frontoparietal suture, is poorly preserved on the left element. However, as can be determined from the right

element, this margin was probably straight and may have had a small anteriorly projecting concave indentation near the lateral margin on the supratemporal fossa.

Ventrally, on the posterolateral corner of each frontal, a small slot, presumably for articulation with the postorbital, lies medial to the crista cranii. The posterior half of the ventral surface bears a deep excavation for the tectal lobe of the mid-brain. The cristae are laterally continuous with the everted orbital rims of the frontal. The deep tectal depression contributes to prominent cristae cranii posteriorly. The tectal depression is connected to the small oval-shaped olfactory depression

by a shallow longitudinal groove. Along the lateral margin of this groove, the cristae cranii are weakly developed and disappear entirely prior to the anterior limit of the olfactory depression.

QUADRATE: The proximalmost portion of the left quadrate (the squamosal ramus) is lodged anterior to the paroccipital process of the occiput (fig. 4). The squamosal articulation surface is not a simple ball-shaped process as in dromaeosaurids (e.g., *Velociraptor mongoliensis* IGM 100/982, *Tsaagan mangas* IGM 100/1015, *Sinornithosaurus millenii* [Xu and Wu, 2001]). Instead, it is anteromedially-posterolaterally compressed proximally, quickly becoming triangular in cross section distally (fig. 5). The squamosal articulation is not double headed, but the compressed rectangular profile coupled with the abrupt change to a triangular cross section gives the articular portion of the quadrate a medially directed “head.” It is unclear due to the disarticulated nature of the quadrate, whether this medial “head” would have contacted the lateral wall of the braincase like in *Shuvuuia deserti* (IGM 100/977), *Confuciusornis sanctus* (Chiappe et al., 1999), derived oviraptorosaurs, and derived avialans. A depression on the anterior face of the paroccipital process located proximodorsally, near the dorsal tympanic recess, may correspond to a secondary articulation surface for the quadrate. Furthermore, this depression corresponds topographically to the braincase articulation facet in birds and alvarezsaurids.

The shaft of the quadrate is divided into an anterior (pterygoid) ramus and a lateral (qua-

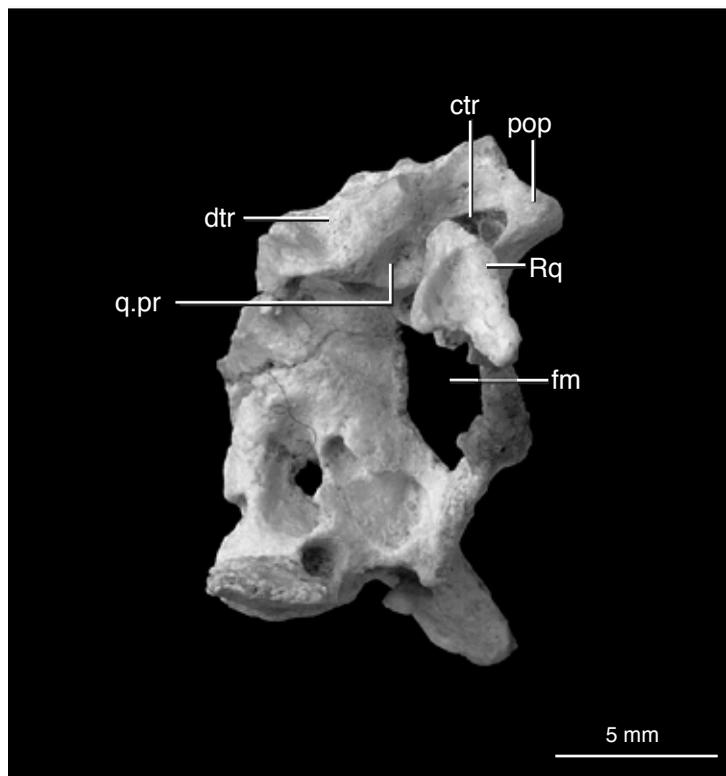


FIGURE 5. Internal surface of braincase and proximal left quadrate of *Mahakala omnogovae* (IGM 100/1033) in left ventrolateral view.

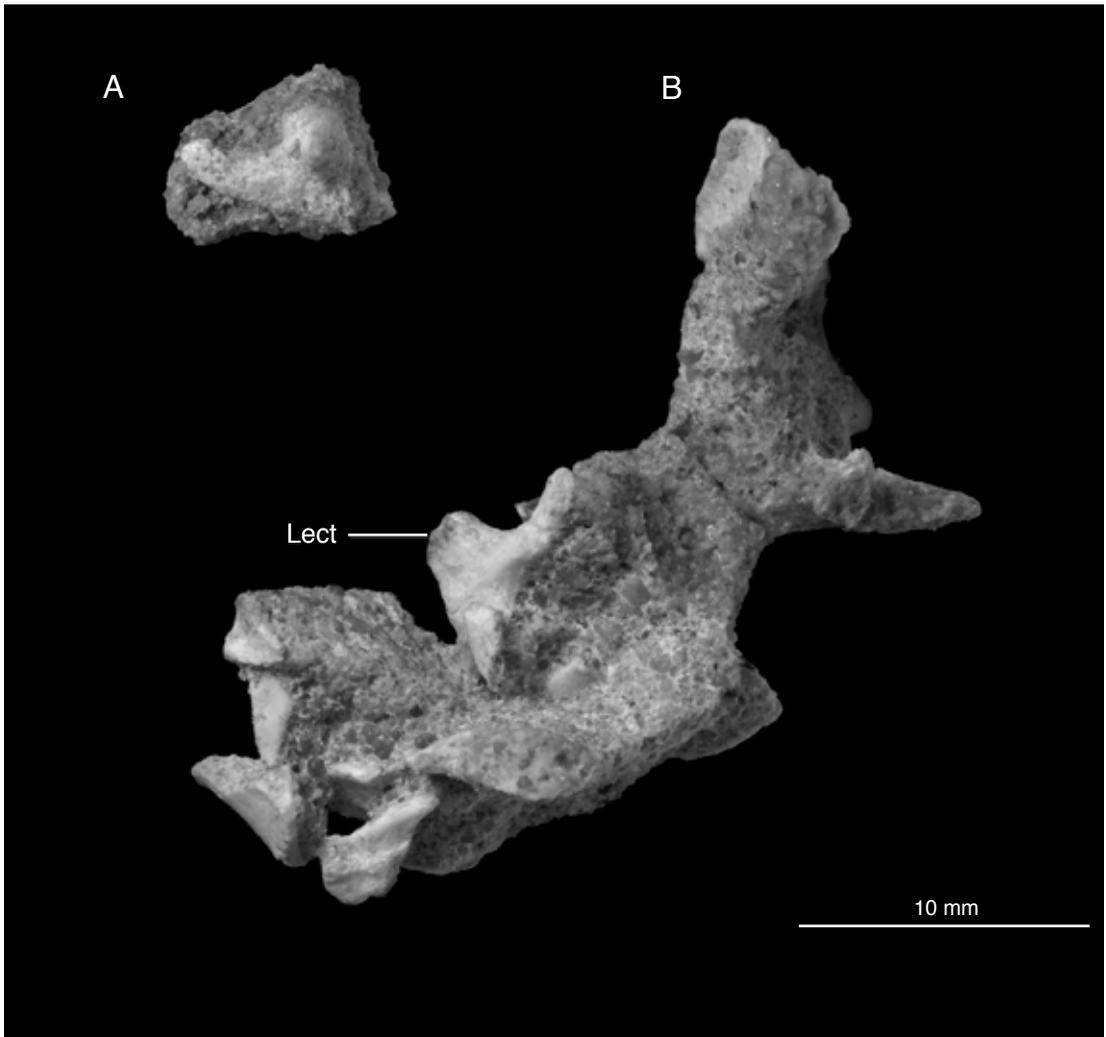


FIGURE 6. IGM 100/1033, *Mahakala omnogovae*. **A**, Possible right ectopterygoid in dorsal view. **B**, Left ectopterygoid in dorsal view.

dratojugal) ramus (figs. 4, 5). The two rami are poorly preserved but apparently were very thin. On the anterior face of the quadrate, a deep, well-defined recess separates the anterior ramus from the lateral one. This recess is distinct from the condition in derived dromaeosaurids (e.g., *Velociraptor mongoliensis* IGM 100/982, *Dromaeosaurus albertensis* AMNH FARB 5356, *Tsaagan mangas* IGM 100/1015, *Sinornithosaurus millenii* [Xu and Wu, 2001]) in which the anterior face of the quadrate is smooth with the lateral flange grading into the anterior ramus without interruption. Given the poor preservation, it is unclear whether the quadrate would have been strongly inclined anteroventrally as in the basal troodontids *Sinovenator changii* (Xu et al., 2002) and *Mei long* (IVPP V12733). Also, unknown for *Mahakala* is whether the quadrate was

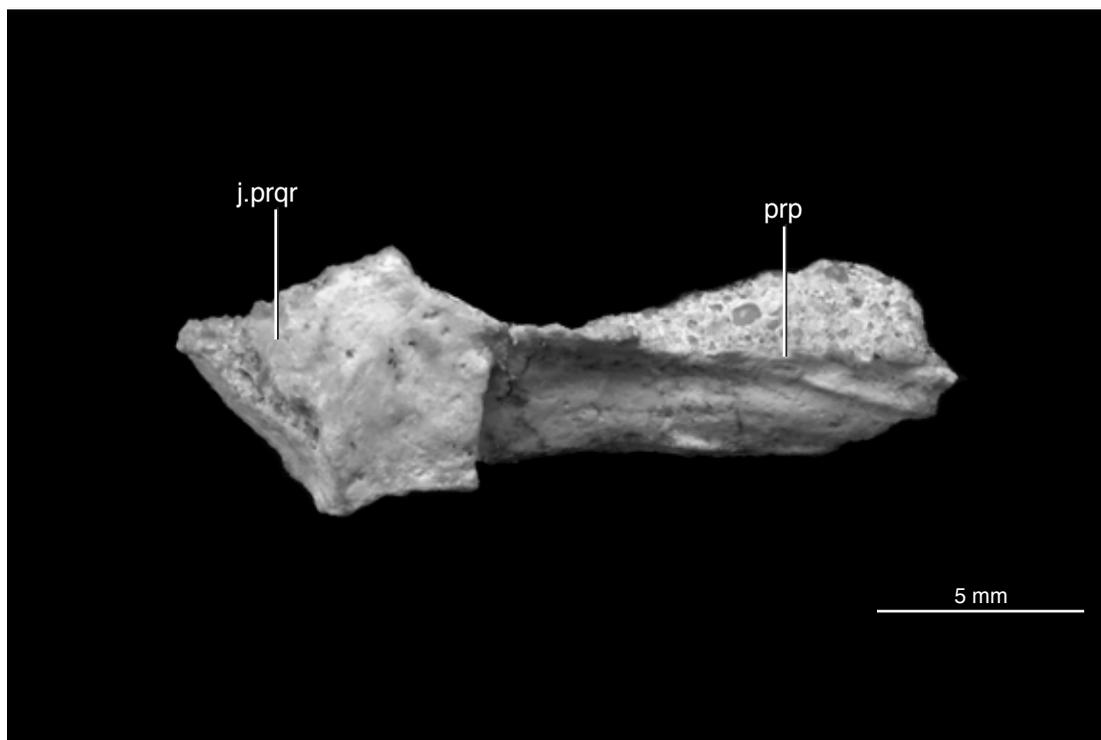


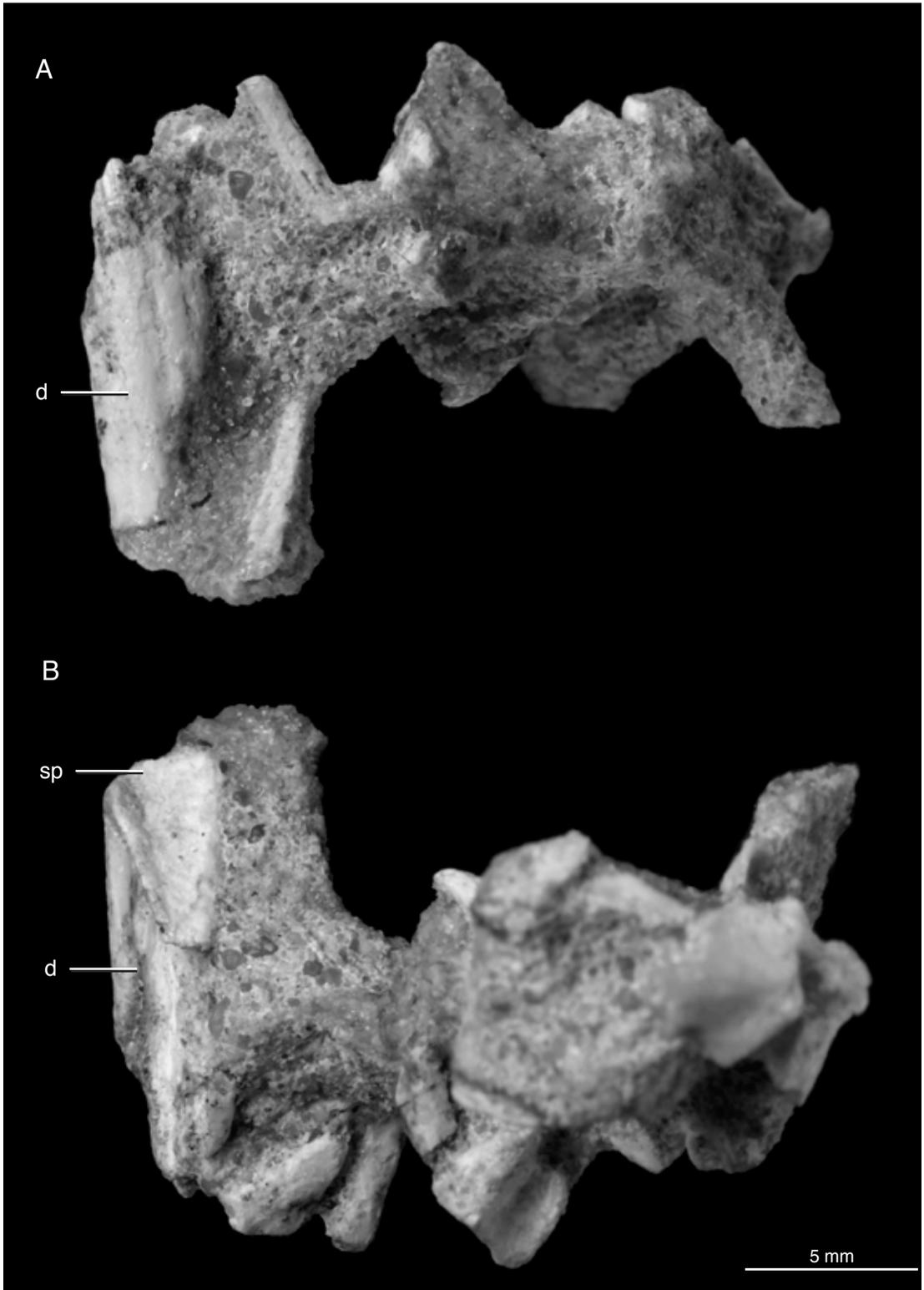
FIGURE 7. Partial right pterygoid of *Mahakala omnogovae* (IGM 100/1033).

pneumatic, or whether it possessed a lateral tab on the quadratojugal process that would have formed the dorsal portion of the enlarged quadrate foramen as in dromaeosaurids (e.g., *Veliciraptor mongoliensis* IGM 100/982, *Dromaeosaurus albertensis* AMNH FARB 5356, *Tsaagan mangas* IGM 100/1015).

ECTOPTERYGOID: The left ectopterygoid is annealed to the same block that has the dentary and splenial (fig. 6). The ectopterygoid is a triradiate element. The jugal ramus is crescent shaped in anterior and lateral views and circular in cross section. The hooked jugal ramus would have contacted the jugal in a weak sutural contact. The pterygoid wing is divided into two processes, one that projects medially to overlay the pterygoid and a second that projects ventrolaterally. This ventrolateral process is not well preserved in IGM 100/1033, but would have formed the “pterygoid flange” or “wing.” There is no recess or pocket on the dorsal surface of the ectopterygoid.

PTERYGOID: A partial right pterygoid was recovered with IGM 100/1033 (fig. 7). The pterygoid is divided into a palatine ramus and the quadrate ramus. Only the palatine ramus and the junction with the quadrate ramus are preserved. The generally broad and fan-shaped quadrate ramus is not recovered.

FIGURE 8. IGM 100/1033, *Mahakala omnogovae*. **A**, Partial right dentary in lateral view. **B**, Partial right dentary and splenial in medial view.



The palatine ramus, as preserved, is broken into two pieces and rotated 90°. The anterior portion of the palatine ramus is weakly striated. The medial margin is slightly inflected ventrally. This inflection is divided from the main body of the pterygoid by a low ridge. This ventrolateral area corresponds to the articulation facet for the palatine.

DENTARY AND SPLENIAL: An 11 mm portion of the right dentary is preserved in a separate block that also contains a small portion of the right splenial and an isolated tooth (fig. 8). The dentary possesses a deep Meckelian groove medially. On the lateral surface a single nerve foramen is present on or near the dorsal edge of the fragment. There are no alveoli preserved. A single tooth was, however, recovered near the dentary/splenial fragment. The tooth is atypical for dromaeosaurids because it is very small and lacks serrations (fig. 9). There is no constriction between the root and the crown. This suite of characteristics



FIGURE 9. Scanning electron micrograph of dentary tooth from *Mahakala omnogovae* (IGM 100/1033) in a dorsally oblique labial view.

is also present in *Buitreraptor gonzalezorum* (Makovicky et al., 2005) and (except for the large sized of the crown) in *Austroraptor cabazai* (Novas et al., 2009).

The splenial is represented by a thin medially concave fragment of bone that is appressed to the medial surface of the right dentary (fig. 8B).

BRAINCASE

OCCIPITAL SURFACE: The occipital surface of the partial braincase is well preserved but divided along the midline by a fracture that separated the braincase into two portions (fig. 10). Besides the fracture, the occipital surface of the braincase is uncrushed and largely intact. Sutural boundaries between the midline supraoccipital and the exoccipital/opisthotics are visible, extending obliquely from the dorsolateral margins of the foramen magnum to the dorsal margin of the paroccipital processes.

The foramen magnum is oval with the long axis oriented transversely. This is unlike the dorsoventrally oriented long axis of the oval foramen magnum seen in all troodontids (Makovicky and Norell, 2004; unknown in *Mei long* IVPP V12733) and the dromaeosaurid *Tsaagan mangas* (IGM 100/1015) or the generally circular foramen magnum in *Velociraptor mongoliensis* (IGM 100/976) or *Deinonychus antirrhopus* (Brinkman et al., 1998). Proportionally, the foramen magnum is large (greater than half the total width of the occiput) and in this respect, similar to the condition in most alvarezsaurids and avialans. Ventral to the foramen magnum,

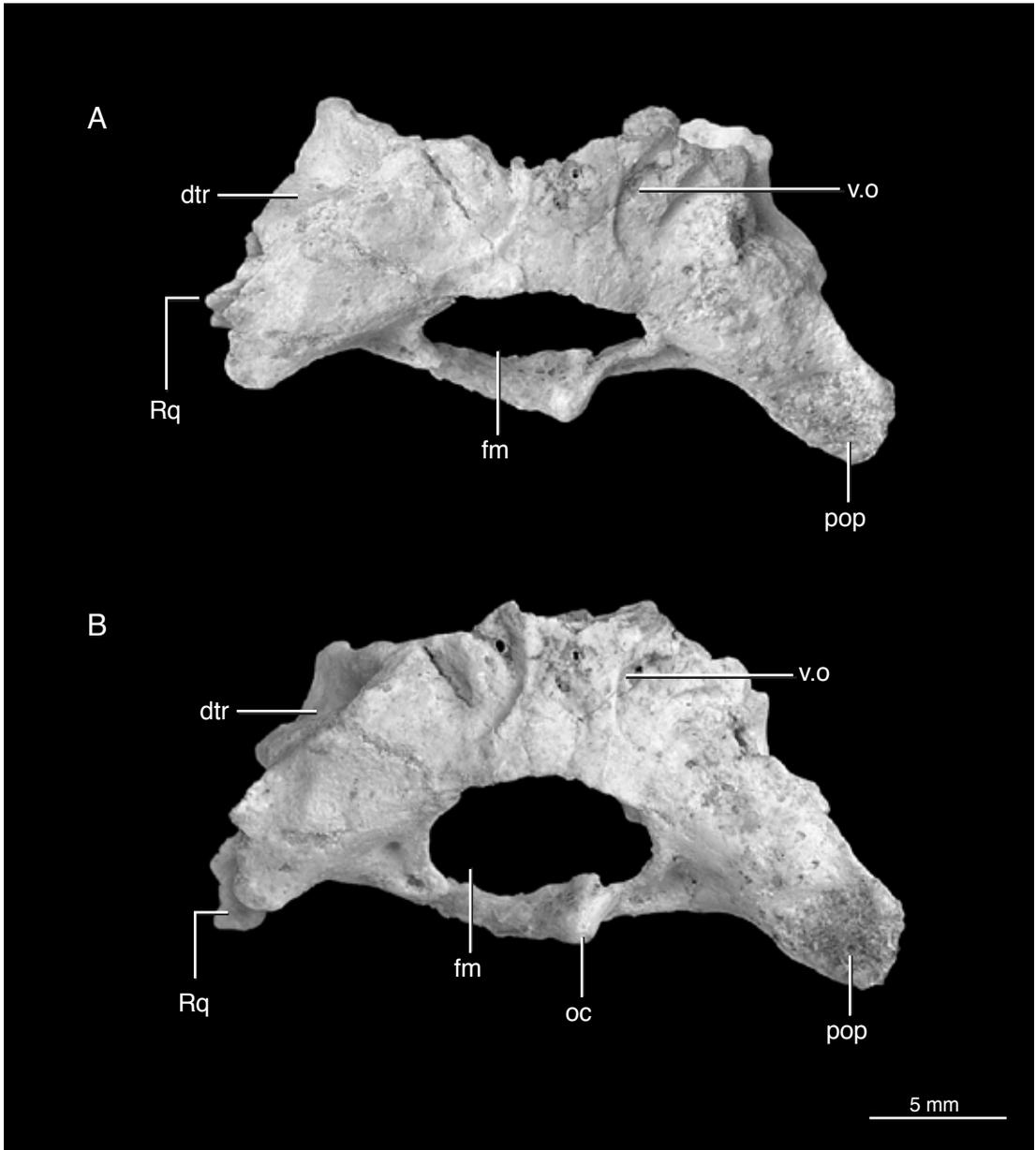


FIGURE 10. Occiput of *Mahakala omnogovae* (IGM 100/1033) in posterodorsal (A) and posterior (B) views.

a thin sliver of basioccipital/exoccipital forms the opening's lower margin. Below this point, the braincase is not preserved and no portion of the occipital condyle is evident. Dorsal to the foramen magnum, the midline surface of the supraoccipital is smooth. Flanking either side of the supraoccipital midline is a crescentic groove, which probably corresponds to the tract of the posterior canal of the middle cerebral vein. Grooves of similar shape and location are present on the occiput of *Mei long* (IVPP V12733). In both *Mei long* and IGM 100/1033, the exit

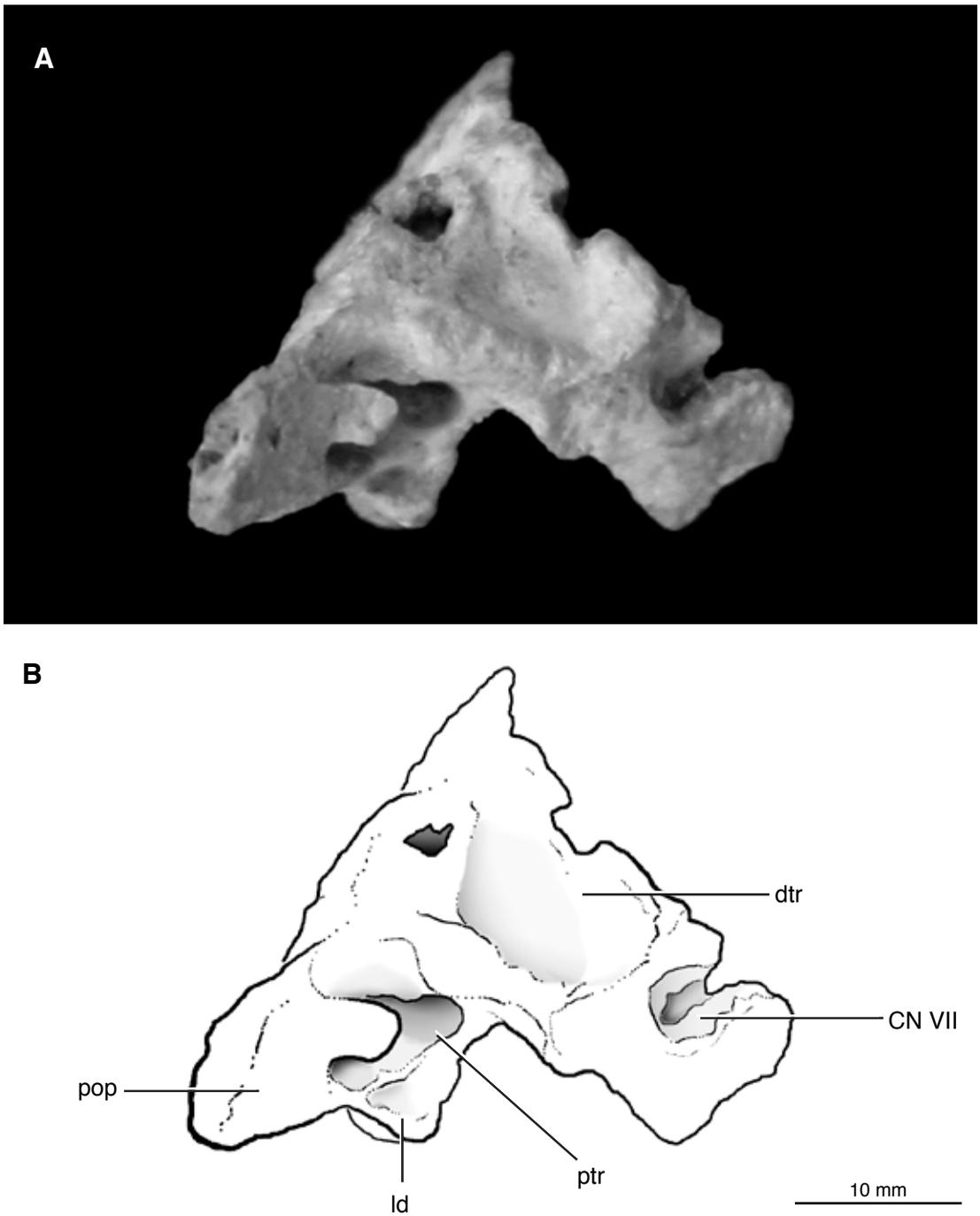


FIGURE 11. Lateral wall of braincase and paroccipital process of *Mahakala omnogovae* (IGM 100/1033) in right lateral view. **A**, Photograph. **B**, Line interpretation.

foramina of the middle cerebral vein are more dorsally located than that of *Deinonychus antirrhopus* (Brinkman et al., 1998) or *Velociraptor mongoliensis* (IGM 100/976). Consequently, the crescentic tract of the vein is more ventrally located in the latter taxa, with a mediolateral orientation versus the dorsoventral orientation of the tract in IGM 100/1033.

As in *Velociraptor mongoliensis* (IGM 100/976), *Deinonychus antirrhopus* (Brinkman et al., 1998), *Tsaagan mangas* (IGM 100/1015), and *Dromaeosaurus albertensis* (AMNH FARB 5356), a posterior-facing depression is present just lateral to the foramen magnum. In *Mahakala omnogovae* the depression is considerably deeper than in *Velociraptor mongoliensis* (IGM 100/976), *Dromaeosaurus albertensis* (AMNH FARB 5356), or *Tsaagan mangas* (IGM 100/1015). Also present in *Mahakala* is the distinct ridge, seen in the formerly mentioned taxa, that divides the dorsal and posterior surfaces of the braincase in occipital view. In *Mahakala* this ridge does not form as sharp an angle as seen in more derived dromaeosaurids but instead a rounded broad ridge. This depression and ridge is lacking in *Bambiraptor feinbergorum* (AMNH FARB 30556), suggesting their presence is not necessarily related to size.

The paroccipital processes are long and slender as in other dromaeosaurids (Norell and Makovicky, 2004). The process is nearly vertical at its base near the foramen magnum. Moving distally along the long axis of the process, the posterior surface twists distally, giving it a slight dorsal aspect as in *Dromaeosaurus albertensis* (AMNH FARB 5356), *Velociraptor mongoliensis* (IGM 100/976), *Tsaagan mangas* (IGM 100/1015), and *Deinonychus* (Brinkman et al., 1998). The paroccipital processes are not perforated along their posterior surfaces as in one specimen of *Velociraptor mongoliensis* (IGM 100/976).

The occipital condyle is not preserved in IGM 100/1033. In *Velociraptor mongoliensis* (IGM 100/976) a ridge divides the posterior surface of the occiput lateral to the foramen magnum from the posteroventral surface of the occiput ventral to the occipital condyle (Norell et al., 2004). There is no indication of such a ridge in *Mahakala omnogovae*. Just lateral to the auditory meatus, the exit foramen for cranial nerve X is present and projects laterally. This nerve foramen is not in a shallow depression unlike *Dromaeosaurus albertensis* (AMNH FARB 5356) or *Velociraptor mongoliensis* (IGM 100/976).

LATERAL WALL: The braincase is well preserved dorsal to the level of cranial nerve VII and the middle ear with the sutural boundaries between the elements in some cases indistinct (fig. 11). The lateral wall of the braincase is divided into two distinct partitions by a large, pronounced ridge separating the more dorsally placed, dorsolaterally oriented surface from the poorly preserved lateral wall. Anteriorly, the lateral braincase wall is missing around the typically large exit foramen for the trigeminal nerve (CN V). Posterior to this, the exit foramen for the facial nerve (CN VII) is preserved on the right side along with the prootic. The dorsal boundary of the otic recess is preserved with the sutural boundaries between the exoccipital, opisthotic, and prootic indistinct. The lateral wall of the braincase is traversed by several cranial nerves and is excavated by three large pneumatic cavities: the anterior tympanic recess, the dorsal tympanic recess, and the posterior tympanic recess (Witmer, 1990). In IGM 100/1033 only the dorsal and posterior tympanic recesses were preserved.

Indications for the exits and paths of the various cranial nerves are few, with only cranial nerve VII definitively preserved.

Just anterior to the paroccipital process above the otic capsule lies a large deep dorsal tympanic recess as in specimens of *Tsaagan mangas* (IGM 100/1015), *Velociraptor mongoliensis* (Norell et al., 2004), *Microraptor* (IVPP uncataloged) and reportedly in *Deinonychus antirrhopus* (Brinkman et al., 1998) and in most other basal coelurosaurs such as ornithomimids (Witmer, 1990; Makovicky and Norell, 1998; Makovicky et al., 2004). Such a recess is present but only shallowly expressed in *Dromaeosaurus albertensis* (AMNH FARB 5356) and *Archaeopteryx lithographica* (BMNH 37001). It is either reduced or absent in various troodontids (Makovicky et al., 2003; Makovicky and Norell, 2004). The dorsal outline of the recess is circular to subtriangular. The floor of the depression is strongly concave. The dorsal tympanic recess does not extend onto the anterior surface of the paroccipital process.

A small posterior tympanic recess lays posterolateral to the opening of the middle ear and deeply invades the anterior base of the paroccipital process. Proportionally, it is similar in size to that in *Velociraptor mongoliensis* (IGM 100/976) and is larger than that of *Tsaagan mangas* (IGM 100/1015) or *Dromaeosaurus albertensis* (AMNH FARB 5356). There is a small tab-shaped projection that extends across the posterolateral corner of the right posterior tympanic recess. No such tab is present on the left side.

The ear region is inset forming a distinct otic recess as in other coelurosaurs with the exception of some troodontids (Makovicky and Norell, 2004). The interfenestral bar between the fenestra ovalis and the fenestra pseudorotunda is not preserved and neither are other structures associated with the otic recess. Two small depressions surround the otic recess. One of the depressions is located immediately dorsal to the otic recess. This depression is shallow and circular in outline and present on both sides of the braincase. Topographically it is not unreasonable to interpret this as the shallow accessory tympanic recess discussed by Witmer (1990) as a potential extension of the posterior tympanic recess. A small accessory recess is present in *Mononykus olecranus* (Perle et al., 1994), *Shuvuuia deserti* (IGM 100/977), *Archaeopteryx lithographica* (BMNH 37001), *Byronosaurus jaffei* (Makovicky et al., 2003), and *Sinovenator changii* (IVPP V12583). This depression is absent, however, in all dromaeosaurids with known cranial material. As is evident on the left side of the braincase, this depression is closely associated with the articular surface of the quadrate and as such could represent a secondary articulation surface for the mediolaterally expanded quadrate head.

The second depression is located posterolateral to the otic recess. The depression takes the form of a dorsally facing ledge incised into the metotic strut at the confluence of the strut and the paroccipital process. The ledge is quite large and present on both sides of the skull. No such structure is known from other dromaeosaurids or paravian taxa. This ledge could be associated with the tract of the external carotid artery as it enters the middle ear prior to splitting into the stapedia and internal carotid arteries. This placement, however, would be considerably more dorsally placed than is typical for the external carotid artery (Sedlmayr, 2002).

The right side of the braincase preserves the exit foramen of the facial nerve (CN VII), which typically lays posteroventral to the trigeminal foramen (CN V). The facial foramen opens

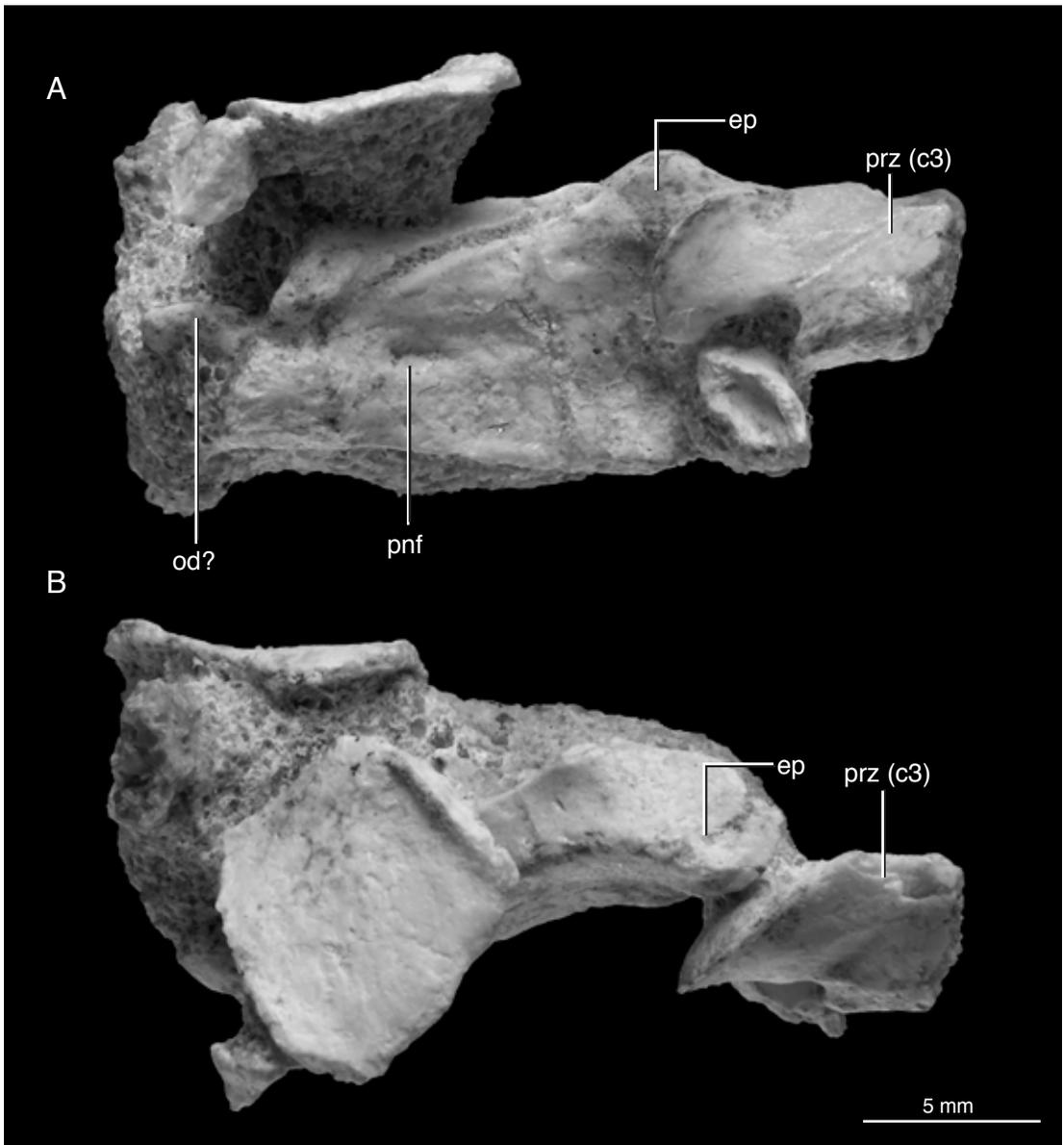


FIGURE 12. Axis of *Mahakala omnogovae* (IGM 100/1033) in left lateral (A) and dorsal (B) views.

posteriorly and leads to a shallow trough that extends posteriorly to the otic recess as in *Tsaagan mangas* (IGM 100/1015), *Dromaeosaurus albertensis* (AMNH FARB 5356), *Velociraptor mongoliensis* (IGM 100/976), *Archaeopteryx lithographica* (BMNH 37001), but unlike *Incisivosaurus gauthieri* (IVPP V13326) and *Byronosaurus jaffei* (Makovicky et al., 2003). The area of the prootic surrounding CN VII is smooth and extensive posteriorly and ventrally. Like other dromaeosaurids, there is no indication of the caudally migrated anterior tympanic recess as is present in most of the maniraptorans (e.g., *Archaeopteryx lithographica* BMNH 37001, *Incisi-*

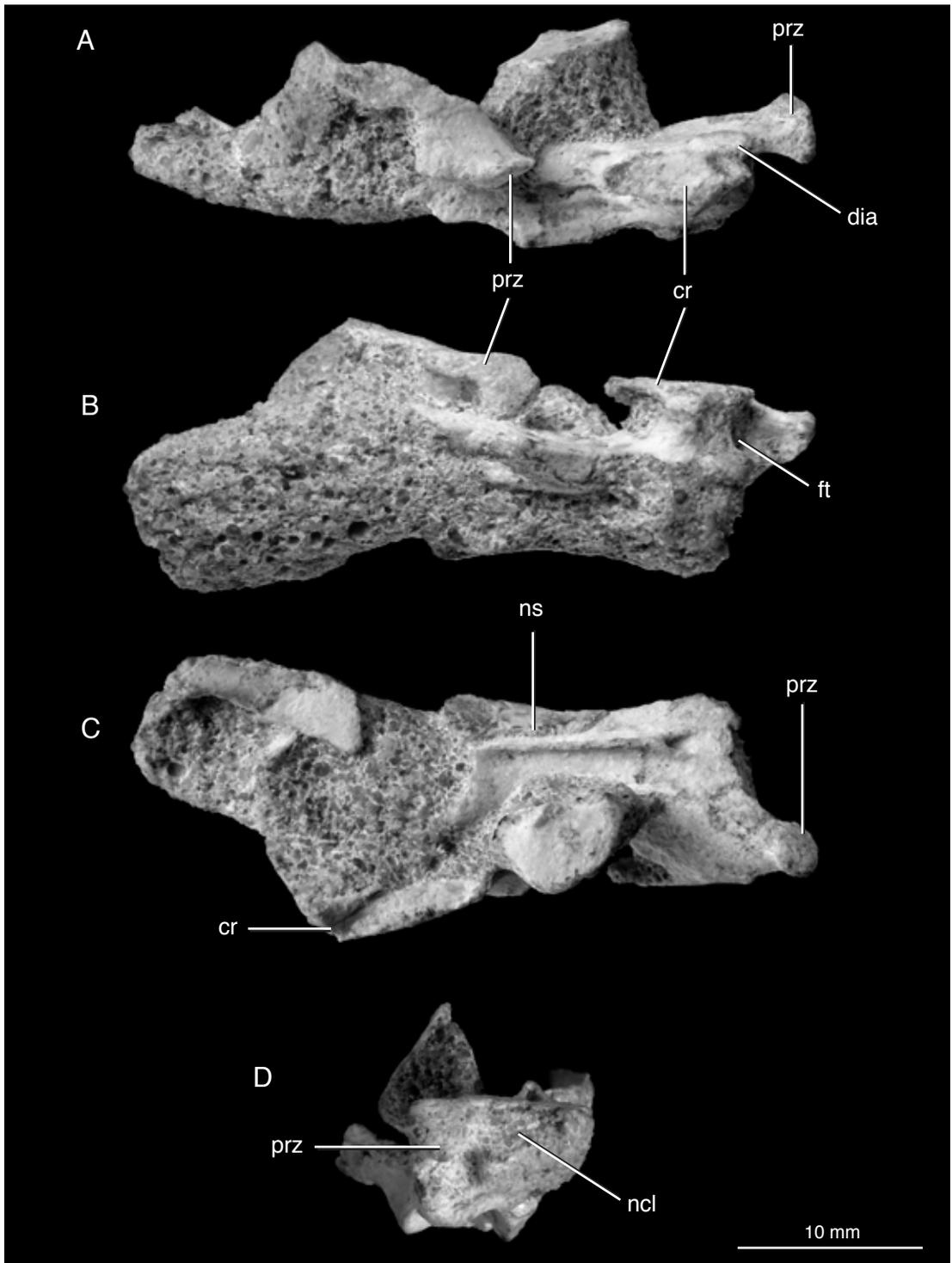


FIGURE 13. Two midcervical vertebrae of *Mahakala omnogovae* (IGM 100/1033) in lateral (A) ventral (B) dorsal (C) and anterior (D) views.

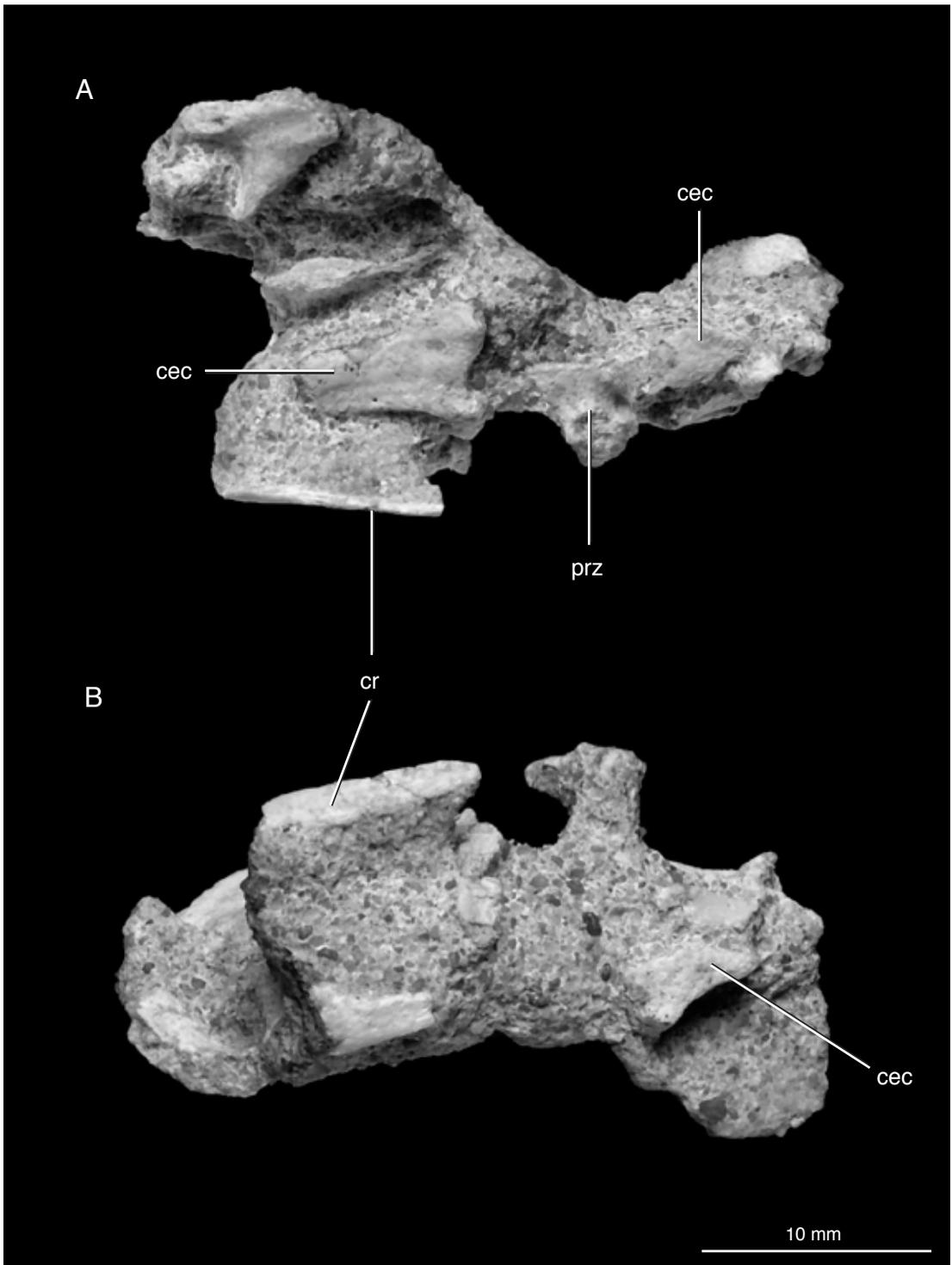


FIGURE 14. Two posterior cervical vertebrae of *Mahakala omnogovae* (IGM 100/1033) in lateral (A) and ventral (B) views.

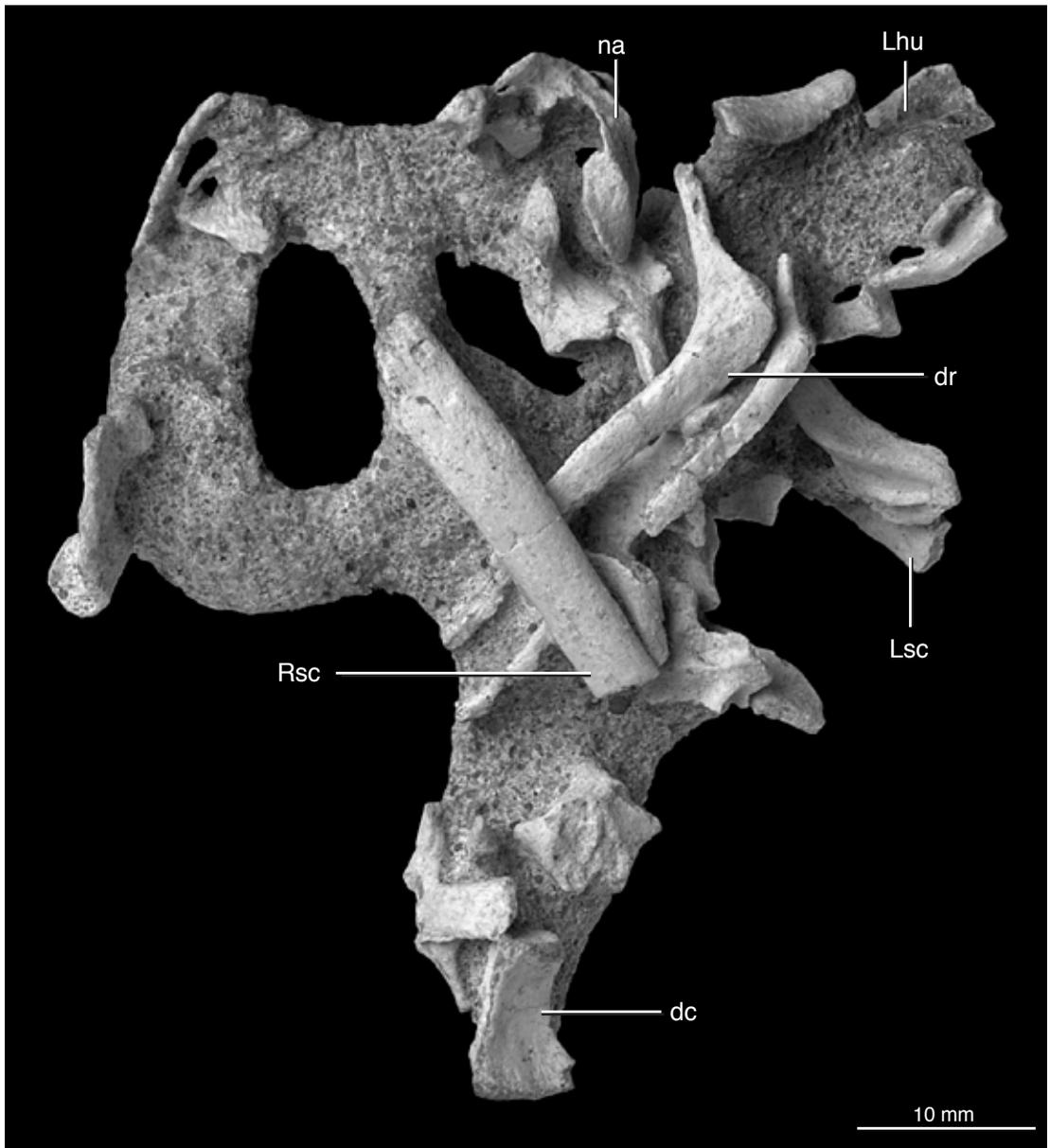


FIGURE 15. Pectoral region of *Mahakala omnogovae* (IGM 100/1033) with elements loosely associated on a single block of matrix.

vosaurus gauthieri IVPP V13326, *Byronosaurus jaffei* IGM 100/983, and *Sinovenator changii* IVPP V12583).

INTERNAL WALL: The left internal wall of the braincase is very poorly preserved, but the right side is well preserved (fig. 5). The most prominent feature of the internal wall of the braincase is the deep floccular recess. The floccular recess is situated within the fused prootic and opisthotic, with the long axis of the recess oblique to the midline. The recess is large as in *Dromaeosaurus albertensis* (AMNH FARB 5356) and *Velociraptor mongoliensis* (IGM 100/982). It is unclear whether the recess extends into the exoccipital as it does in *Velociraptor mongoliensis*. The posterior and anterior crurae of the anterior semicircular canal delimits the medial boundary of the floccular recess as in other dromaeosaurids (e.g. *Tsaagan mangas* IGM 100/1015, *Dromaeosaurus albertensis* AMNH FARB 5356, *Bambiraptor feinbergorum* AMNH FARB 30556, *Velociraptor mongoliensis* IGM 100/982). As in other dromaeosaurids, the lateral semicircular canal floors the floccular recess (Currie, 1995; Norell et al., 2004). Like *Velociraptor mongoliensis* (IGM 100/982) and *Tsaagan mangas* (IGM 100/1015), the anterior and posterior semicircular canals in *Mahakala omnogovae* are rotated further posteriorly than in *Dromaeosaurus albertensis* (AMNH FARB 5356). The medial wall enclosing the ventral portion of the posterior semicircular canal and the endolymphatic duct is missing. Additionally, the medial wall enclosing the confluence of the anterior and posterior semicircular canals is damaged. Nevertheless, it is apparent that the posterior crus of the anterior canal (the vertical vestibular canal in Norell et al. (2004) is inflated as in birds and *Velociraptor mongoliensis* (Norell et al., 2004).

AXIAL SKELETON

CERVICAL VERTEBRAE: The axis vertebra (fig. 12), the left prezygapophysis of c3 and a nearly complete c4 (fig. 13), and portions of two more posterior cervical vertebrae (fig. 14) were recovered in IGM 100/1033. The right side of the axis is not preserved, neither is the neural spine (fig. 12). A small pneumatic foramen is located near the anterior margin of the vertebra near the intercentrum/pleurocentrum suture. This is similar to the condition in *Velociraptor mongoliensis* (IGM 100/976) and *Deinonychus antirrhopus* (YPM 5204) but unlike the apneumatic axis of *Tsaagan mangas* (IGM 100/1015). A small parapophysis is located anterior to the pneumatic opening and above the axis intercentrum. The postzygapophysis is small and bears a weakly developed epipophysis. The epipophysis lies on the anterior margin of the postzygapophysis and does not overhang the postzygapophyseal margin as it does in other paravians. Two small plate-like elements were preserved near the axis vertebra. These elements may correspond to portions of the atlas neurapophyses or the proatlas. The elements are, however, dissimilar to the atlas neurapophysis and proatlas on *Tsaagan mangas* (IGM 100/1015). No indication of a pedicel or epipophysis is present unlike that expected if these were indeed neurapophyses. Furthermore, the elements lack the tripartite arrangement seen in the proatlas of *Tsaagan mangas* (Norell et al., 2006). While this may be due to incomplete preservation of the elements in *Mahakala*, these elements instead may be interpreted as fragments of disarticulated parietals.

A nearly complete cervical as well as part of the succeeding cervical vertebra is preserved from the anterior cervical series (fig. 13). The exact identity of this vertebra is difficult to determine; it can be ruled out to be c3 because the prezygapophyses of c3 are preserved with the axis vertebrae. Therefore, it is likely that it corresponds to anterior cervical c4, c5, or c6. Like other dromaeosaurids, the cervical centrum is platycoelous with a strong anteroventrally projecting anterior intercentral articular surface. In anterior view, the cervical centrum is dorsoventrally compressed, distinctly wider than high. The ventral surface of the centrum is poorly preserved, so it is unclear whether a hypapophysis or carotid processes are present. The centrum appears to be level with the posterior extent of the neural arch.

In dorsal view, the prezygapophyses diverge laterally from the midline and are slanted anterodorsally and slightly medially. Complete postzygapophyses are not preserved, so it is not possible to discern the presence and/or shape of the postaxial epipophyses. The neural arch of the vertebra is much longer than in derived dromaeosaurids like *Velociraptor mongoliensis* (IGM 100/986), *Tsaagan mangas* (IGM 100/1015), *Adasaurus mongoliensis* (IGM 100/20) or even *Microraptor zhaoianus* (Hwang et al., 2002). The long neural arch is more similar to those in the troodontid *Byronosaurus jaffei* (IGM 100/984) and the unenlagiine dromaeosaurid *Buitreraptor gonzalezorum* (MPCA 245). The preserved base of the neural arch is longer than most other dromaeosaurids; however, it is still centered on the neural arch giving the arch a distinct “X” shape in dorsal view.

The diapophysis in *Mahakala omnogovae* is flattened, situated near the anterior margin of the centrum and projects ventrally. A very shallow pneumatic recess is present just posterior to the diapophysis. The parapophysis is short and situated near the diapophysis creating a narrow transverse foramen. Unlike other dromaeosaurids, the cervical rib is strongly fused to the diapophysis and parapophysis with the contact lines nearly obliterated. The rib is triangular proximally and tapers posteriorly with little to no anterior projection (fig. 13).

DORSAL VERTEBRAE: Portions of at least 12 dorsal semiarticulated vertebrae were recovered. The dorsal vertebrae are preserved on two blocks. The vertebrae on both blocks are amphiplatyan, the neurocentral sutures are open, and all lack pneumatic foramina. The first block contains elements of the forelimb and shoulder girdle and is interpreted to have the more anteriorly positioned dorsal vertebrae (fig. 15). This block preserves few vertebral centra. The best preserved is spool shaped, constricted along the midline and possesses a modest hypapophysis. This is similar to other dromaeosaurids (e.g., *Velociraptor mongoliensis* IGM 100/985 and *Deinonychus antirrhopus* [Ostrom, 1969a]). The most anteriorly preserved neural arch consists of the posterior half including the left postzygapophysis. The facets are circular and face ventrally. A small epipophysis is present but does not overhang the postzygapophyseal margin. The postzygapophysis is long and is anteriorly continuous with the large diapophyses, which raises the possibility that this vertebra may correspond to the last cervical as opposed to being the first dorsal vertebra.

The next vertebra in line is also a neural arch fragment. On this vertebra the transverse process is long and well separated from the prezygapophysis. There is no indication of an infraprezygapophyseal fossa or an infradiapophyseal fossa, which is unlike most other drom-

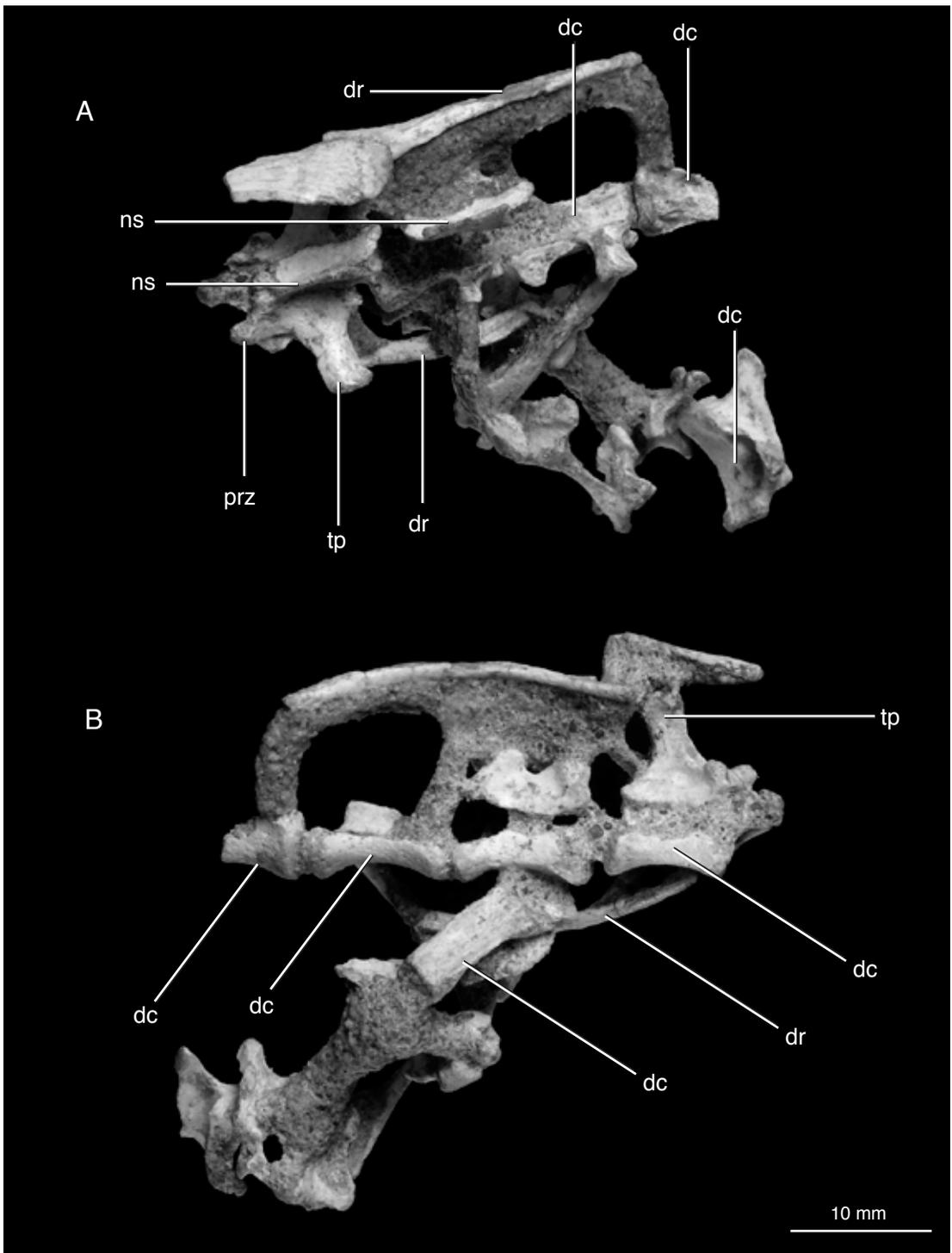


FIGURE 16. Posterior dorsal vertebrae of *Mahakala omnogovae* (IGM 100/1033) in dorsal (A) and ventrolateral (B) views.

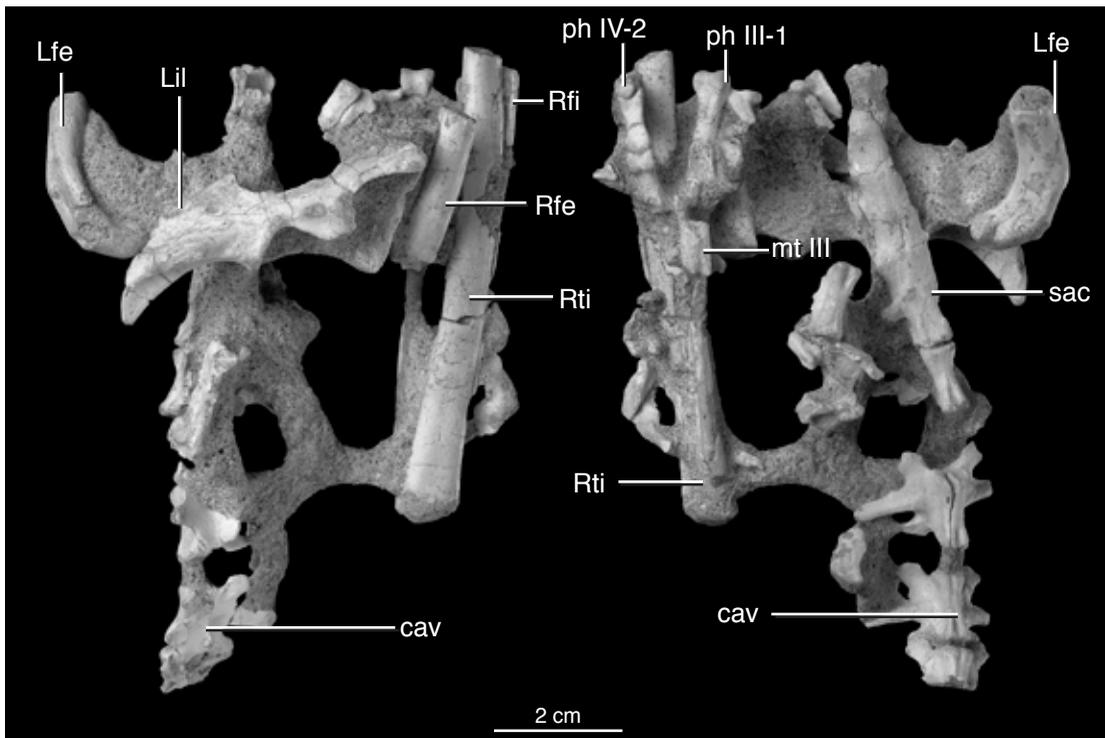


FIGURE 17. Pelvic region of *Mahakala omnogovae* (IGM 100/1033) prior to complete preparation. Dorsal view of pelvic region (left) shows left ilium, dorsal surface of proximal caudal vertebrae, and dorsal surface of right hind limb. Ventral view of pelvic region (right) shows ventral surface of sacrum, proximal caudal vertebrae, and right hind limb.

aeosaurids (e.g., IGM 100/980, *Velociraptor mongoliensis* IGM 100/986, *Deinonychus antirrhopus* [Ostrom, 1969a], *Adasaurus mongoliensis* IGM 100/20) although *Buitreraptor gonzalezorum* (MPCA 245) has very poorly developed vertebral fossa. Dorsally on the postzygapophysis an epiphysis is lacking.

The next vertebra in series (d2 or d3) preserves only the left lateral side. The neural spine is broken and missing. The prezygapophysis is widely placed laterally and the facet is strongly inclined toward the midline. The transverse process is still relatively short and closely positioned to the body of the prezygapophysis. The transverse process of this vertebra and succeeding vertebrae are only slightly inclined. At the confluence of the base of the prezygapophysis and the transverse process a very shallow, roughly circular depression is present. This corresponds to the anterior homolog of the infraprezygapophyseal fossa, as seen in *Deinonychus antirrhopus* (Ostrom, 1969a) and in IGM 100/980. More posteriorly, a caudally facing depression is located posterior to the transverse process near the body of the centrum, but above a very minute posterior centrodiaepophyseal lamina. This depression corresponds to the infra-postzygapophyseal fossa.

The second block contains at least six more posterior dorsal vertebrae (fig. 16). Of these, the anteriormost is best preserved. This vertebra is very similar to the posterior dorsals of other

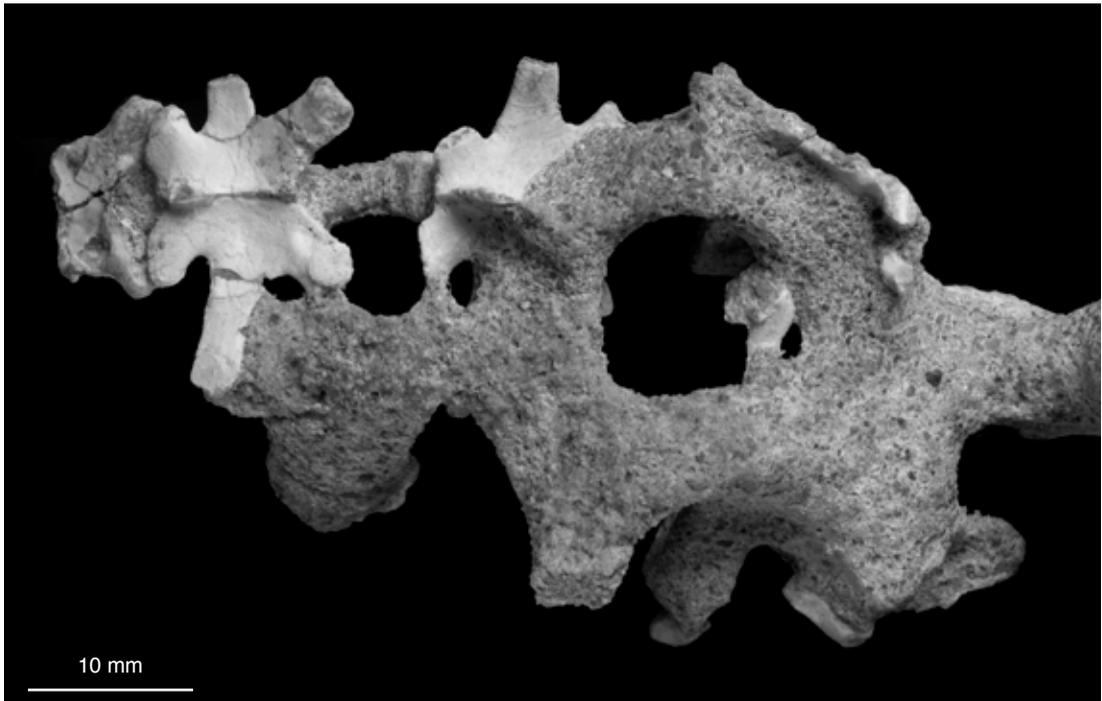


FIGURE 18. Caudal vertebrae 2 through 4 of *Mahakala omnogovae* (IGM 100/1033) in dorsal view. Caudal 4 is only the posterior half of vertebra.

dromaeosaurids (Norell and Makovicky, 1999) and troodontids (Makovicky and Norell, 2004). The centrum is longer than it is wide and the lateral surface lacks any indication of pneumatization. The prezygapophyses are short. The facets are small and very slightly inclined to the midline. This is in contrast to taxa like *Velociraptor mongoliensis* (IGM 100/986), which have very broad flat prezygapophyseal facets, whereas it is similar to the condition in *Buitreraptor gonzalezorum* (MPCA 245). The postzygapophyses are like the prezygapophyses in that they are short and very small. The transverse process is short, wide, and only slightly inclined. The neural spines are rectangular and have no indication of possessing an expanded spine table, unlike other dromaeosaurids (e.g., IGM 100/980).

Like other dromaeosaurids (Norell and Makovicky, 1999), the dorsal vertebrae of *Mahakala omnogovae* have parapophyses that are raised on a short pedicel, but remain ventral to the transverse process. Dorsal to the parapophysis and adjacent to the prezygapophysis is a very shallow and narrow infraprezygapophyseal fossa. By the look of these more posterior dorsal vertebrae, a true infradiapophyseal fossa is present, but this fossa is shallow compared to most other dromaeosaurids like *Velociraptor mongoliensis* (IGM 100/985) or *Rahonavis ostromi* (UA 8656) but is similar to the condition in *Buitreraptor gonzalezorum* (MPCA 245). A triangular infrapostzygapophyseal fossa is present.

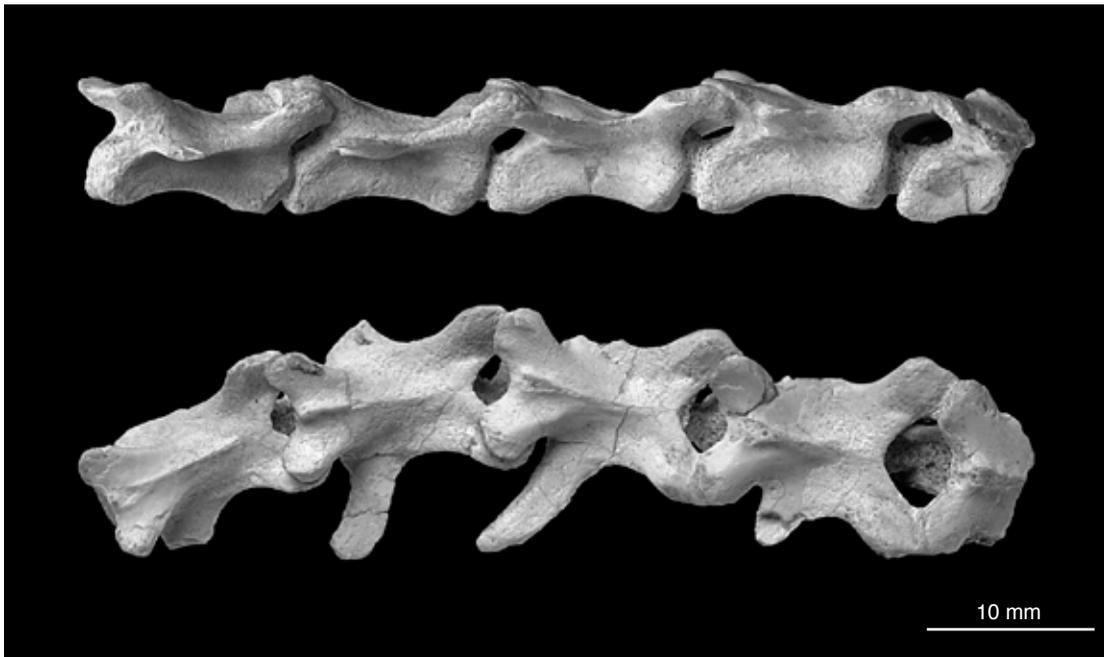


FIGURE 19. Caudal vertebrae 4 through 8 of *Mahakala omnogovae* (IGM 100/1033) in lateral (top) and dorsal (bottom) views.

SACRAL VERTEBRAE: Six coossified centra form the sacrum, as in *Rahonavis ostromi* (UA 8656) and mature specimens of *Velociraptor mongoliensis* (IGM 100/986; Norell and Makovicky, 1999), one more than in IGM 100/985 and *Deinonychus antirrhopus* (Ostrom, 1969a). The length of the sacral series is shorter than the ilium length (fig. 17). The first and second sacral vertebrae have remnants of their neural arches, which are fused. The areas of contact between these neural arches and their respective centra were not preserved, thus preventing determination of neurocentral suture closure in this specimen. A bony lamina is displaced and lies over the first caudal vertebrae. This is interpreted to be the fused neural arches from the more posterior sacral vertebrae.

The sacral centra are short and broad, except for the first and sixth, which are narrower and longer, similar in proportions to the posterior dorsals and anterior caudals, respectively. As in *Velociraptor mongoliensis* (IGM 100/985 and IGM 100/986) there are no pneumatic foramina present in the anterior sacral elements (in contrast to the condition of *Saurornitholestes langstoni* TMP 67.20.36). The degree or absence of pneumaticity is unknown for other sacral vertebrae. As in other maniraptorans, there is a poorly defined sulcus on the ventral surface of sacral centra running from the posterior half of the second vertebra to the posterior end of the fourth vertebra.

CAUDAL VERTEBRAE: There are 20 preserved caudal vertebrae beginning with the proximalmost and continuing uninterrupted posteriorly. The most posterior preserved vertebra is nonetheless fairly large and retains distinct prezygapophyses and postzygapophyses. There are

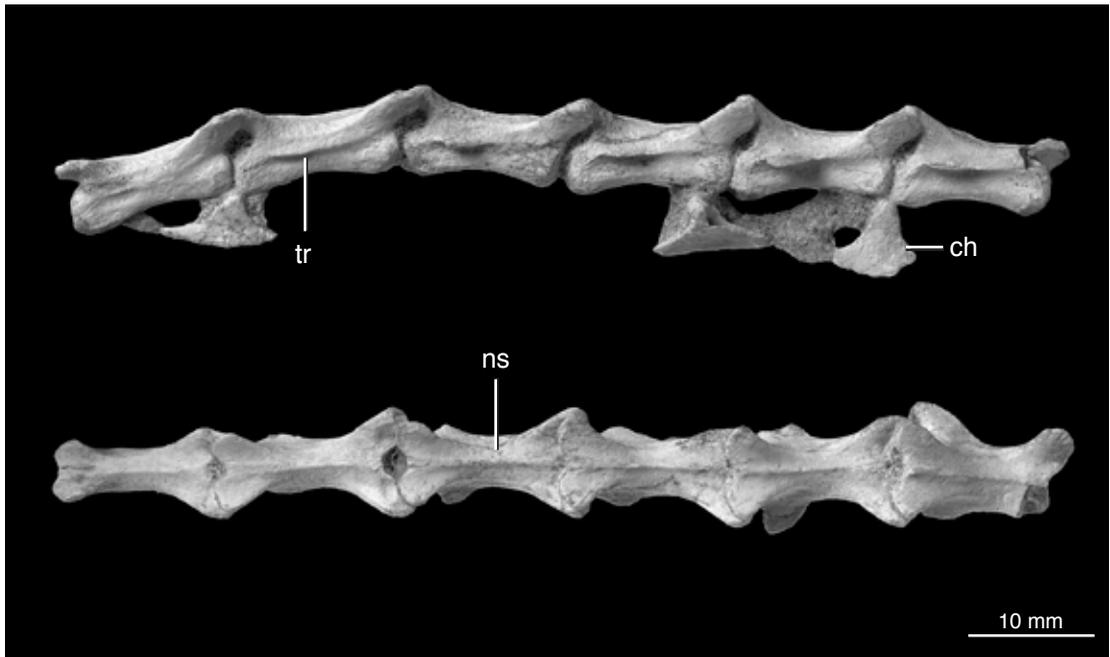


FIGURE 20. Caudal vertebrae 9 through 14 of *Mahakala omnogovae* (IGM 100/1033) in lateral (top) and dorsal (bottom) views. Anterior is to the right.

eight proximal caudals associated with the sacral elements (figs. 18, 19). These proximal caudals are identified as caudals 1 through 8, although a proximal caudal vertebrae may be missing in this specimen since the first caudal (articulated with the sacrum) is not articulated to the other seven elements. A second set of six articulated caudals represents the subsequent elements (caudals 9–14) since the morphology of its most anterior element closely resembles the last vertebrae of the preceding block (fig. 20). There are three articulated distal caudals that are consistent in size to caudals 15–17 (fig. 21). Finally, three isolated distal caudals are preserved and, based on their size, are likely caudals 18–20.

The transition point in caudal vertebrae occurs at the midpoint of the second set of vertebrae, identified here between caudal 11 to caudal 12. Therefore, even if the identification of these caudal vertebrae is wrong, the transition point is more posteriorly located on this specimen than in *Rahonavis ostromi* (at caudal 9) and perhaps *Velociraptor mongoliensis* (at caudal 10).

The anterior caudal centra are proportionately longer than in *Velociraptor mongoliensis* (IGM 100/985) and *Rahonavis ostromi* (UA 8656). Their centra are subquadrangular in cross section and have a pronounced sulcus on their ventral surface. The articular facets for the hemal arches are not well developed.

The zygapophyses of anterior caudals have subhorizontal articular facets, in contrast to *Velociraptor mongoliensis* (IGM 100/985), *Rahonavis ostromi* (UA 8656), *Ornitholestes hermanni* (AMNH FARB 619), *Tyrannosaurus rex* (Brochu, 2003), and all other coelurosaurs. In these



FIGURE 21. Caudal vertebrae 15 through 17 of *Mahakala omnogovae* (IGM 100/1033) in lateral (top) and dorsal (bottom) views. Anterior is to the left.

taxa the articular facets are more vertically oriented and do not extend laterally to the degree seen in *Mahakala omnogovae*. The prezygapophyses of the anterior caudals in IGM 100/1033 are anterolaterally oriented and their articular ends are notably expanded. Posteriorly, between caudal 7 and caudal 16, the prezygapophyses of IGM 100/1033 gradually decrease in their lateral expansion, but their anterior development is not significantly modified. Similar large prezygapophyses are also present in *Rahonavis ostromi* (UA 8656), but only on the first four caudal vertebrae, and they are not as laterally extended as in *Mahakala omnogovae*.

The postzygapophyses of IGM 100/1033 are not as large as the prezygapophyses. They are only slightly elevated from the rest of the neural arch, unlike other paravians and nearly all other coelurosaurs. Furthermore, the postzygapophyses do not exceed the posterior vertebral centrum margin in any of the preserved caudal vertebrae and the facets face ventrally, not laterally as in other coelurosaurs. In contrast to *Mahakala*, the postzygapophyses of caudal vertebrae 5–11 of *Rahonavis* (UA 8656) are extremely elongate, greatly exceeding posteriorly the vertebral centra. The postzygapophyses exceed the posterior vertebral margin in most other coelurosaurs (e.g., *Velociraptor mongoliensis* IGM 100/986, *Tyrannosaurus rex* [Brochu, 2003], *Ornitholestes hermanni* AMNH FARB 619). In *Velociraptor mongoliensis* and other dromaeosaurids, the postzygapophyses are positioned on the posterior margin of the neural spine. Moving posteriorly, the neural spines get progressively shorter but extend posteriorly to a greater extent, bringing the postzygapophyseal facets with them and thereby beyond the posterior margin of

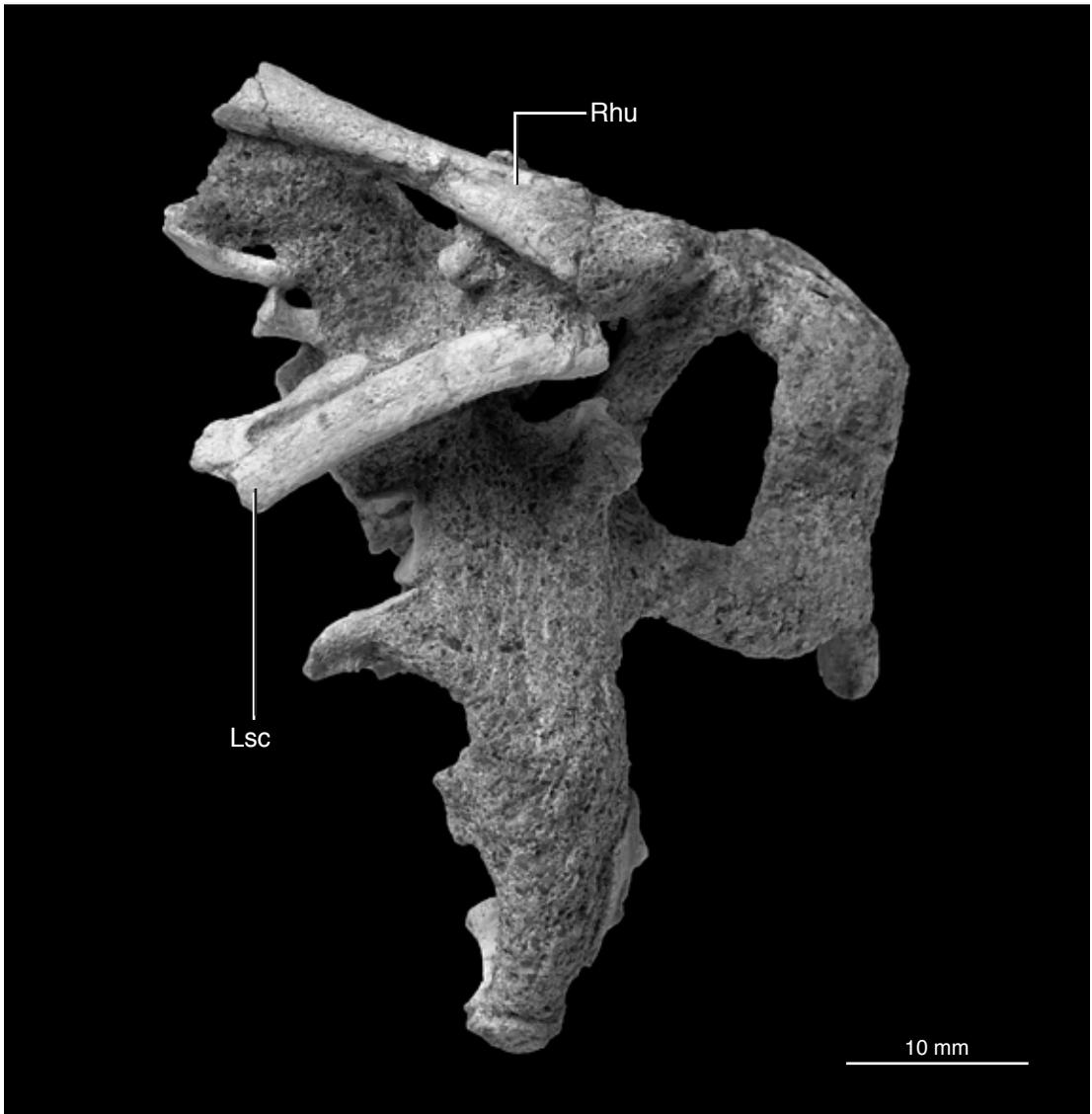


FIGURE 22. Left scapula and right humerus of *Mahakala omnogovae* (IGM 100/1033). Scapula in dorsal view and humerus in ventral (anterior) view.

the vertebral centrum. In *Mahakala omnogovae* the postzygapophyses are completely separate from the neural spines.

The neural arch of the first caudal vertebrae was not preserved. The neural spine of the vertebra is anteroposteriorly short occupying the posterior region of the neural arch. As in *Rahonavis ostromi* (UA 8656), the neural spine is tall and directed dorsally, in contrast to the posteriorly directed neural spine of *Velociraptor mongoliensis* (IGM 100/985). The next two caudal vertebra

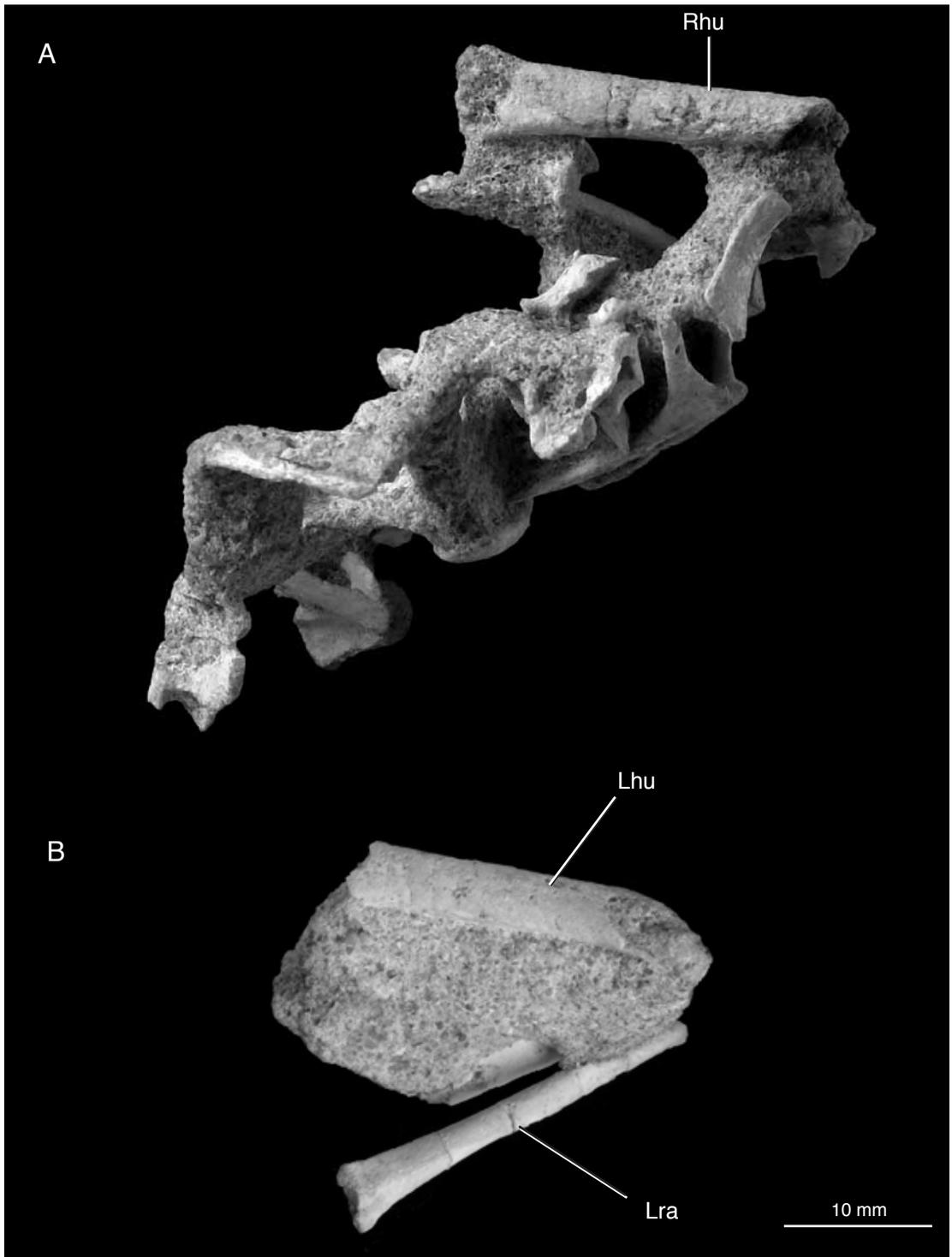


FIGURE 23. Humerii of *Mahakala omnogovae* (IGM 100/1033). A, Right humerus in dorsal (posterior) view. B, Distal half of left humerus in anterior (dorsal) views.

of IGM 100/1033 (identified here as caudals 3–4), have an extremely reduced neural spine, although the dorsal tips are missing. This reduction in the neural spine development occurs much more posteriorly in *Rahonavis ostromi* (caudal 6), *Velociraptor mongoliensis* (IGM 100/986), and other dromaeosaurids or coelurosaurs in general. In caudal 6 and subsequent vertebrae, the neural spine is just a low and elongated ridge, whereas in *Rahonavis ostromi* (UA 8656), *Buitreraptor gonzalezorum* (MPCA 245), and *Velociraptor mongoliensis* (IGM 100/986) reduced neural spines are found more posteriorly (caudal 8 and caudal 14, respectively).

The transverse processes of caudal vertebrae develop progressively posteriorly. In anterior caudals (2–3), these are directed laterally and not posterolaterally as in *Velociraptor mongoliensis* (IGM 100/985), *Rahonavis ostromi* (UA 8656), and all other coelurosaurs. By caudal 6, the transverse processes extend posterolaterally as a slender thin lamina. Between caudals 10–14, the lateral extent of these processes becomes progressively reduced to a thin and elongated ridge. This is similar to the thin ridge seen on the lateral surface of the caudal centra in *Buitreraptor gonzalezorum* (Makovicky et al., 2005), *Rahonavis ostromi* (UA 8656), and *Microraptor zhaoianus* (Hwang et al., 2002).

The chevrons are poorly preserved in IGM 100/1033. One isolated anterior chevron resembles the morphology of the anterior chevrons of *Rahonavis ostromi* and *Velociraptor mongoliensis* (fourth and third, respectively). Posteriorly, there are several chevrons preserved in articulation to caudals 10, 11, 12, 14, and 15. As in *Rahonavis ostromi* and *Archaeopteryx* these are anteroposteriorly elongated and triangular in lateral view. The chevrons of *Mahakala omnogovae*, however, lack the lateromedially broad ventral surface that characterizes these chevrons in *Rahonavis ostromi* (UA 8656), *Microraptor zhaoianus* (Hwang et al., 2002), *Velociraptor mongoliensis* (IGM 100/986), or *Deinonychus antirrhopus* (Ostrom, 1969a). In *Velociraptor mongoliensis* (IGM 100/986) the 11th chevron is the first that has a well-developed anterior process. No such processes are present in the chevrons of *Mahakala omnogovae*.

FORELIMB

SCAPULA: The left and right scapulae are represented by the middle three-quarters of each element, which are preserved in association with the anterior dorsal vertebrae and appear to be roughly in life position (fig. 22). Missing is the anteriormost end of each scapulae as well as the distal ends. The scapulae are narrow, straplike, and have a strongly compressed ovoid cross section. The scapula of *Mahakala omnogovae* is slightly curved mediolaterally and appears to taper distally as in *Rahonavis ostromi* (UA 8656) and *Unenlagia comahuensis* (MCF PVPH-78).

HUMERUS: The humeri are only partially preserved in IGM 100/1033 (figs. 22, 23). The right humerus has the distal region of the deltopectoral crest and most of its shaft, whereas the left humerus is known from a poorly preserved portion of the shaft lacking the distalmost articular surfaces but preserving most of the proximal humeral end. Both humeri are preserved in close proximity to the scapulae. The preserved length of the left humerus (estimated to be about 95% complete) is approximately 45% of the femoral length and an estimated humeral length would still be only about 50% of the femoral length. Despite the fragmentary nature of



FIGURE 24. Right ulna of *Mahakala omnogovae* (IGM 100/1033) in lateral (A), anterior (B), medial (C), and posterior (D) views.

this element, the shaft between the distal end of the deltoid crest and the beginning of the distal expansion of the humerus appears to be reduced, suggesting that the entire humeral length may not have been much longer than 40 mm. This humerus-to-femur proportion (~45% to 50%) is in contrast to the condition of most maniraptorans, which have proportionally longer humeri, e.g., *Velociraptor mongoliensis* (IGM 100/985; humerus/femur >60%), *Anchiornis huxleyi* (Xu et al., 2009; humerus/femur ~95%), and *Archaeopteryx lithographica* (London specimen; humerus/femur ~120%).

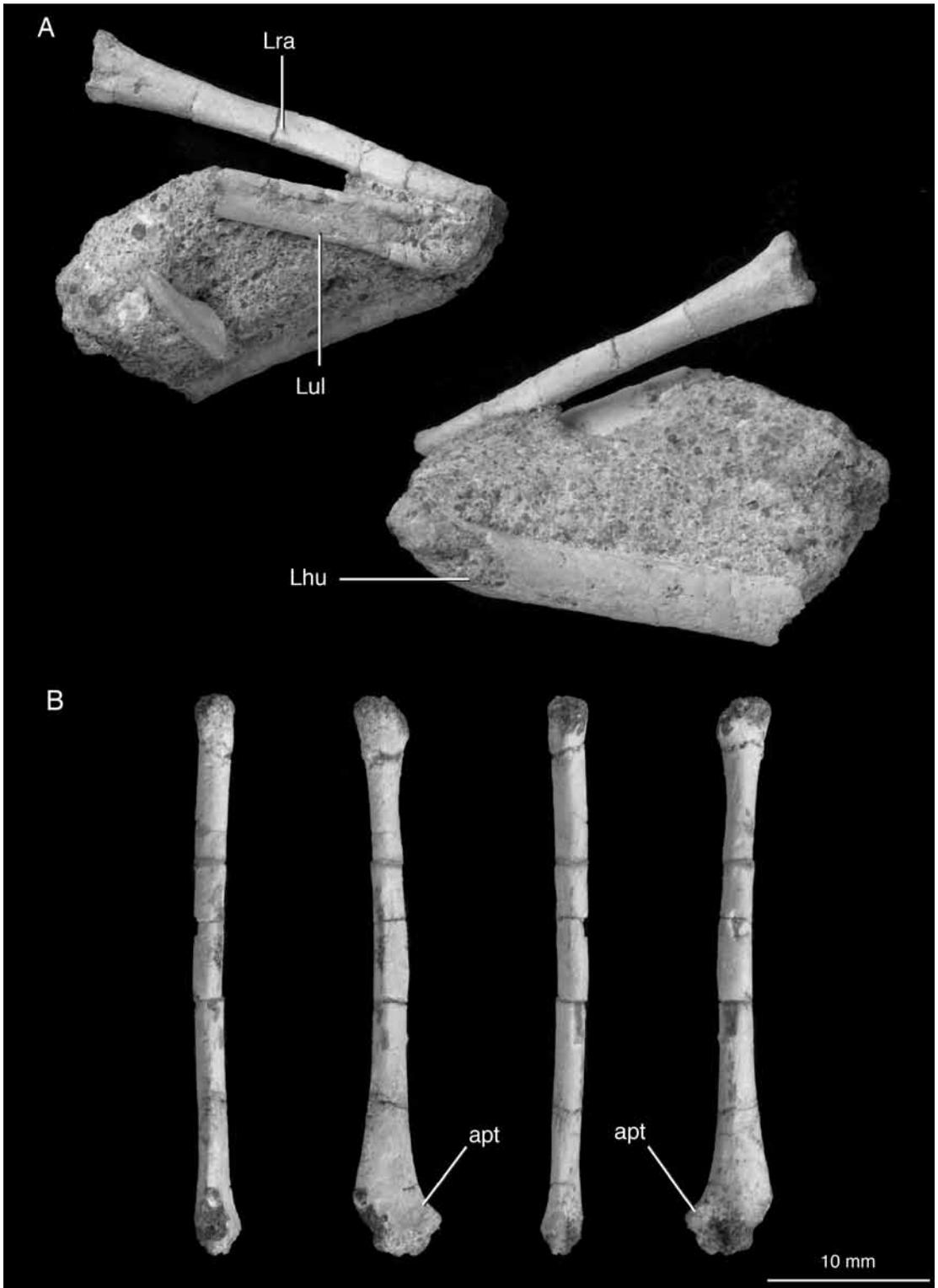
The preserved distal end of the deltopectoral crest indicates it may have been similar to *Velociraptor mongoliensis* (IGM 100/985). The humerus shaft in IGM 100/1033 is subcircular in cross section. No muscle scars are evident on either humerus. It is clear that the humerus is not shorter than the ulna as in derived avialans, but is at least equal in length or slightly longer.

The proximalmost portion of the left humerus is poorly preserved and appears to have been damaged by burrowing arthropods as is common in Djadokhta fossils (fig. 23). As a result the bicipital crest cannot be described, but it is apparent that the humeral head is straplike with a flat articular surface. The proximal end of the humerus is apneumatic. The deltopectoral crest projects dorsally (in line with the long axis of the humeral head), is not perforated like in basal avialans, such as *Sapeornis chaoyangensis* (IVPP V13396) and *Confuciusornis sanctus* (IVPP V11370), and is narrower than the humeral shaft width. The dorsal surface (posterior surface in avians) of the deltopectoral crest is flat.

ULNA: Portions of both ulnae are preserved (figs. 24, 25). The right is missing the olecranon and most of the proximal articular surface as well as its distal end. A distal portion of the left is preserved lacking its epiphysis. Although the proximal and distal tips are missing, it is apparent that the ulna, and the entire forelimb, would have been extremely short in comparison with the hind limb. This condition is unusual for paravians. Given the dimensions and morphology of the preserved portions of the humerus, the ulna may have been slightly shorter than the humerus.

The ulna is distinctly bowed as in most maniraptorans (Gauthier, 1986). Its shaft is strongly compressed and anteroposteriorly broad with its posterior margin tapering to a narrow edge. The shaft is subtriangular in cross section at its midpoint, narrowing toward the posterior edge. Just distal to the proximal articular surfaces the shaft is even more compressed, becoming almost straplike. This strongly compressed ovoid cross section contrasts with the subcircular or triangular cross section common to most other maniraptorans. A small biceps tubercle is present on the ulna. There is a pronounced muscular impression developed as triangular depression with distinct edges on the anterior surface of the distal half. This depression has distinct edges and broadens distally. There is no evidence of quill knobs as has been reported in *Velociraptor mongoliensis* (Turner et al., 2007b).

RADIUS: The right radius is the only forelimb element that is complete. It is 36 mm long (fig. 25). In outline, the radius of *Mahakala omnogovae* is relatively simple, elliptical in cross section at middiaphysis, and expanded at both ends. The proximal end of the radius is only slightly expanded and this region of the shaft is subcircular in cross section where it forms the humeral cotyla. This portion of the radius is slightly abraded. No bicipital radii tubercle is visible. The shaft of the radius is only slightly bowed. The distal region of the shaft is expanded



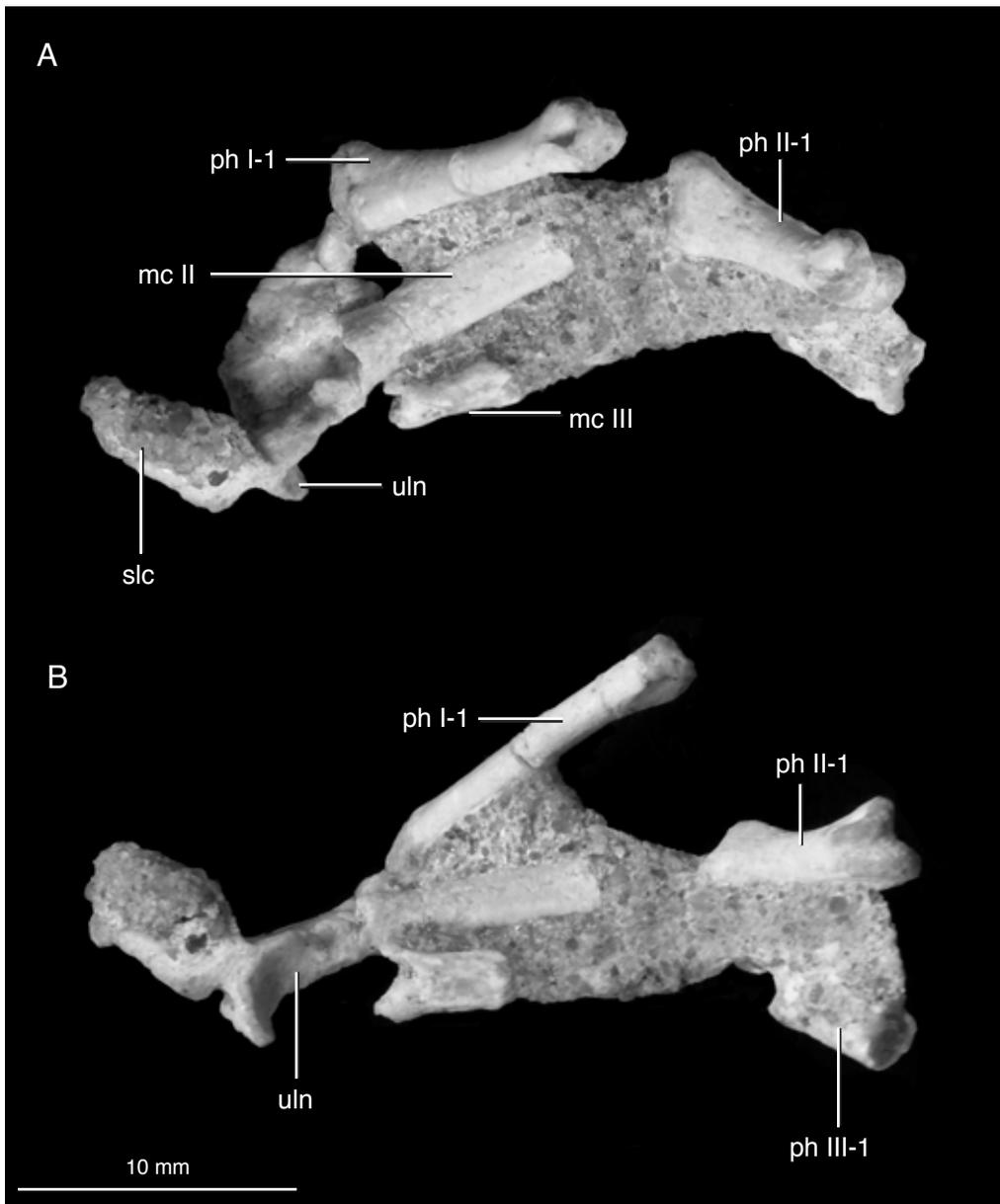


FIGURE 26. Right manus of *Mahakala omnogovae* (IGM 100/1033) in dorsal (A) and ventral (B) views.



FIGURE 25. Radii of *Mahakala omnogovae* (IGM 100/1033). A, Left radius in posterior (left) and anterior (right) views. B, Right radius (from left to right) in lateral, posterior, medial, and anterior views.

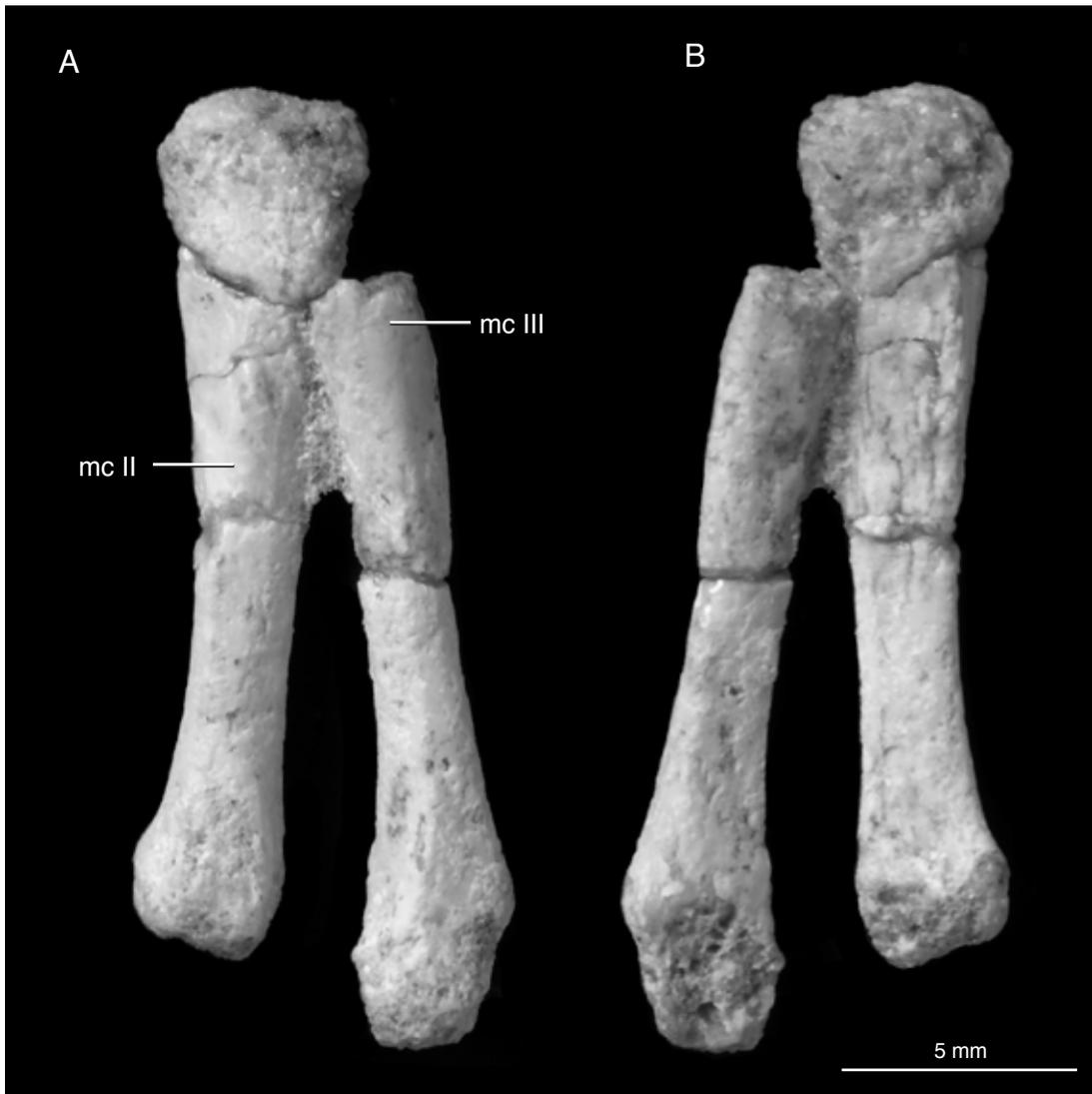


FIGURE 27. Left metacarpals II and III of *Mahakala omnogovae* (IGM 100/1033) in dorsal (A) and ventral (B) views.

and flattened as in *Velociraptor mongoliensis* (Norell and Makovicky, 1999), *Deinonychus antirrhopus* (Ostrom, 1969a), and avialans. Distally, the anterior face of the radius is divided by a midline mound. Medial (ventral in Aves) to this mound is a shallow depression corresponding to a tendon in avians (Baumel and Witmer, 1993). This portion of the radius terminates in a slightly hooked ventral aponeurosis tubercle. The lateral edge of the distal radius is damaged. A flat area of muscular origin is visible on most of the posterior surface of the shaft and is further demarcated by two small projected edges near the radial midpoint. The left radius is not as well preserved as the right element, but its morphology is consistent with that seen in the right radius, except that a distinct intermuscular line runs along the shaft of the radius.

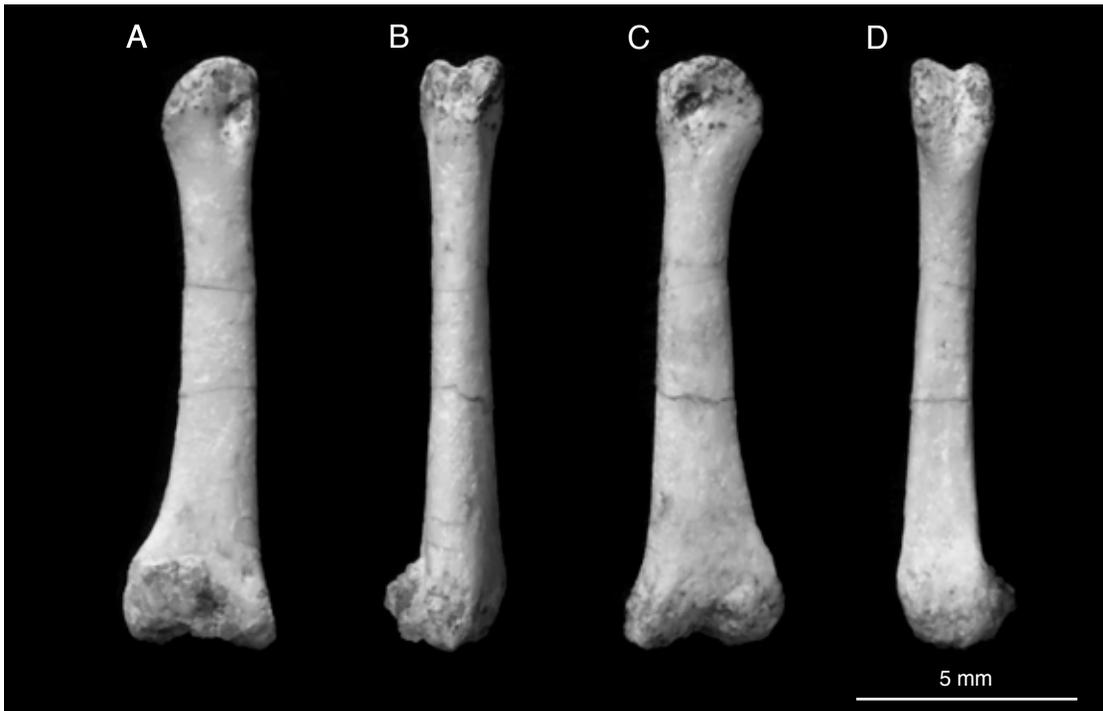


FIGURE 28. Right manual phalanx II-2 of *Mahakala omnogovae* (IGM 100/1033) in medial (A), dorsal (B), lateral (C), and ventral (D) views.

CARPUS: Two elements preserved proximally on the right autopodium are here interpreted to be the semilunate carpal and the ulnare (fig. 26). The semilunate is poorly preserved, so little of its morphology can be characterized. It is apparent that it covered the proximal surfaces of metacarpals I and II, as in most theropods with semilunate carpals. The ulnare is roughly pyramidal, contacting the posterior proximal surface of metacarpal II and bearing a concave facet for metacarpal III.

MANUS: Elements of the right and left manus were preserved in partial articulation (figs. 26–29). The bone surfaces of the right hand are extremely poorly preserved. Individual elements are hard to unambiguously discern. Right metacarpal I, phalanx I-1, metacarpal II, and phalanx II-1 appear to be preserved, with fragments of metacarpal III and phalanx III-1 adjacent to metacarpal II (fig. 26). Right phalanx II-2 is disarticulated (fig. 28). If identified correctly, phalanx II-2 is significantly longer than II-1. Phalanx I-1 approximates II-2 closely in length. The element tentatively identified as a portion of right metacarpal I is expanded and flat with a flared distal articular surface. Right metacarpal I is closely appressed to the adjacent metacarpal II.

Left metacarpals II and III are preserved with metacarpal III distally displaced slightly, so that it appears artificially longer than metacarpal II (fig. 27). Metacarpal II is only slightly longer than metacarpal III. A tubercle is present on the proximodorsal surface of metacarpal II. A similar tubercle is present in dromaeosaurids *Velociraptor mongoliensis* (IGM 100/982) and *Deinonychus antirrhopus* (Ostrom, 1969a), as well as in the oviraptorosaurs *Khaan mcken-*

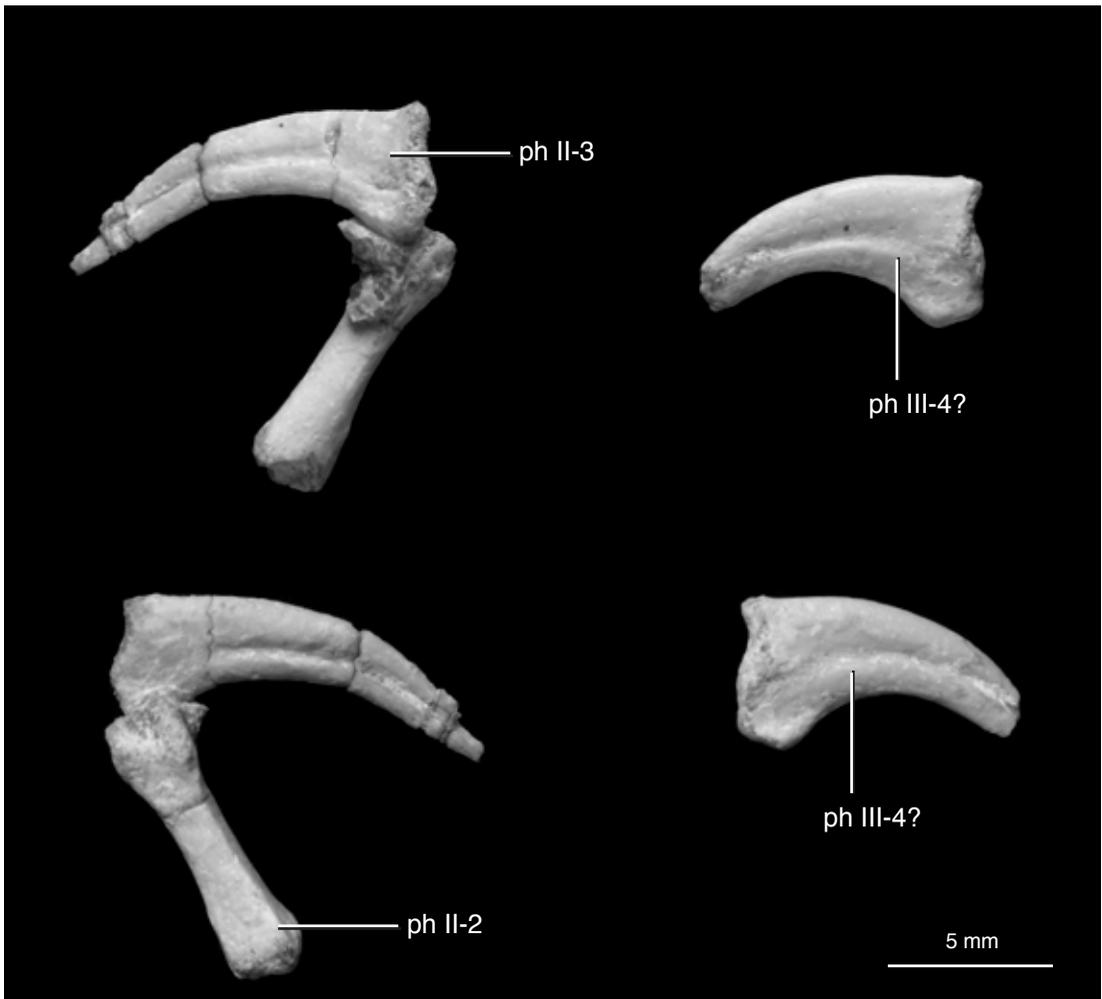


FIGURE 29. Manual phalanges of *Mahakala omnogovae* (IGM 100/1033).

nai (IGM 100/1127) and *Citipati osmolskae* (IGM 100/978). The tubercle corresponds topographically with a tubercle (the *processus intermetacarpalis* of Baumel and Witmer, 1993) on the proximal posterodorsal surface of the carpometacarpus in many avialans, including *Archaeopteryx lithographica*. When present in avians, this tubercle serves as the insertion for *M. extensor metacarpi ulnaris*. A facet for metacarpal I is developed on the proximal anterior surface of metacarpal II. The ventral edge of this facet is developed into a prominent flange. Distally a flexor pit is present, as in *Velociraptor mongoliensis* (IGM 100/982), but which has not been described for Avialae.

Metacarpal III is expanded at both ends and triangular in cross section. The shaft of metacarpal III is not significantly thinner than metacarpal II. This contrasts with the condition of *Velociraptor mongoliensis* (IGM 100/982) and *Deinonychus antirrhopus* (Ostrom, 1969a). Addi-

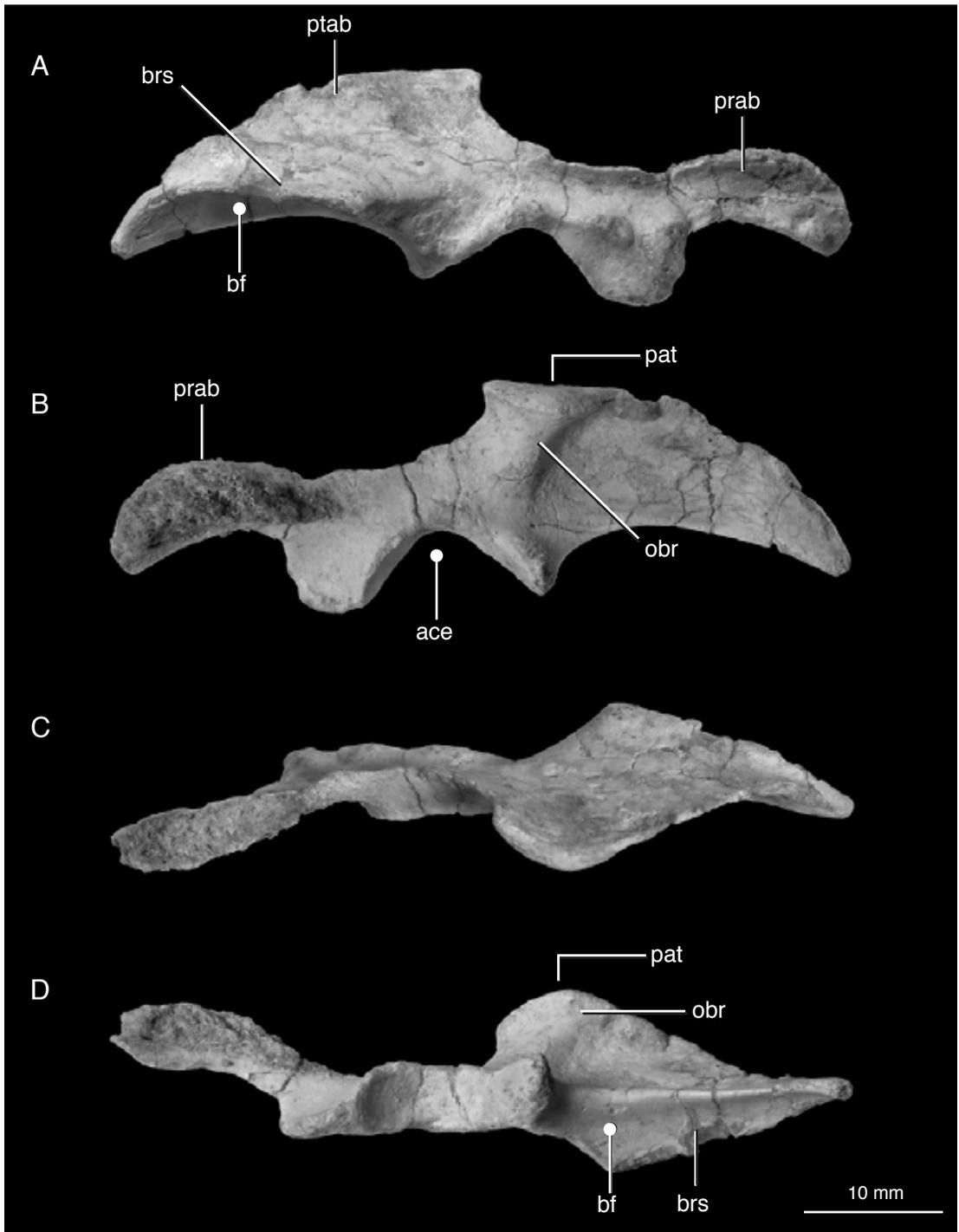


FIGURE 30. Left ilium of *Mahakala omnogovae* (IGM 100/1033) in medial (A), lateral (B), dorsal (C), and ventral (D) views.

tionally, the shaft of metacarpal III in *Mahakala omnogovae* is not curved like that seen in *Deinonychus antirrhopus*.

Three manual unguals are preserved. The lateral grooves do not closely approach the articular surface (fig. 29). Their development, in shallowing and becoming inconspicuous near the articular surface closely approximates the condition in *Velociraptor mongoliensis* (IGM 100/982) and *Archaeopteryx lithographica* (Wellnhofer, 1993). This trait, however, appears to be variable in *Velociraptor mongoliensis* where the groove extends close to the articular surface on the caudal surface of some of the ungual phalanges.

PELVIS

ILIUM: A nearly complete left ilium is preserved in IGM 100/1033 (fig. 30). The ilium is dolichoiliac, low in lateral view, and anteroposteriorly longer than the sacrum. As in most nonavian dinosaurs, the postacetabular region of the ilium is longer than the preacetabular portion, but only slightly so. The dorsal margin of the preacetabular process of the ilium was not preserved anterior to the supratrochanteric process. The ventral margin is downturned and the anteroventral end of the preacetabular blade is rounded and seems to lack the anteroventral hook or "pointed process" present in most coelurosaurs. In contrast to the condition of other dromaeosaurids and basal avialans, the preacetabular blade lacks the ridge (the antiliac shelf) that overhangs the pubic peduncle to form the lateral border of the cuppedicus fossa. Thus, the area of attachment of the *M. cuppedicus* is undivided from the lateral surface of the preacetabular blade. The lateral surface of the pubic peduncle, however, is wide and anterolaterally concave as in dromaeosaurids (e.g., *Velociraptor mongoliensis* IGM 100/985; *Deinonychus antirrhopus* MCZ 4371).

The pubic peduncle is wedge shaped, with its main axis oriented anterolaterally. It is anteroposteriorly longer than the ischiadic peduncle, as in dromaeosaurids and basal avialans (Ostrom, 1969a; Norell and Makovicky, 1997, 1999). Its medial surface is slightly concave and is bordered dorsally by three swollen and rugose areas for the attachment of the transverse processes of the second, third, and fourth sacra. These bulges are dorsoventrally aligned; the anteriormost is located near the anterior edge of the pubic peduncle, the middle one above the posterior margin of the pubic peduncle, and the posteriormost at the midpoint of the acetabulum. The posterior face of the pubic peduncle forms the anterior wall of the acetabulum. The acetabular wall has a constant width along its anterior, dorsal, and posterior walls, in contrast to the constriction present in *Velociraptor mongoliensis* (IGM 100/985) between the pubic and ischiadic peduncles. The lateral surface of the ilium above the acetabulum is laterally concave with no ridge dividing the ilium into anterior and posterior concavities, as in many other theropods including some specimens of *Velociraptor mongoliensis*.

The ischiadic peduncle is triangular and twisted laterally as in *Velociraptor mongoliensis* (Norell and Makovicky, 1997). Despite these similarities, the ischiadic peduncle of IGM 100/1033 has almost the same ventral extension than the pubic peduncle, whereas the ischiadic peduncle is markedly reduced in dromaeosaurids and basal avialans.

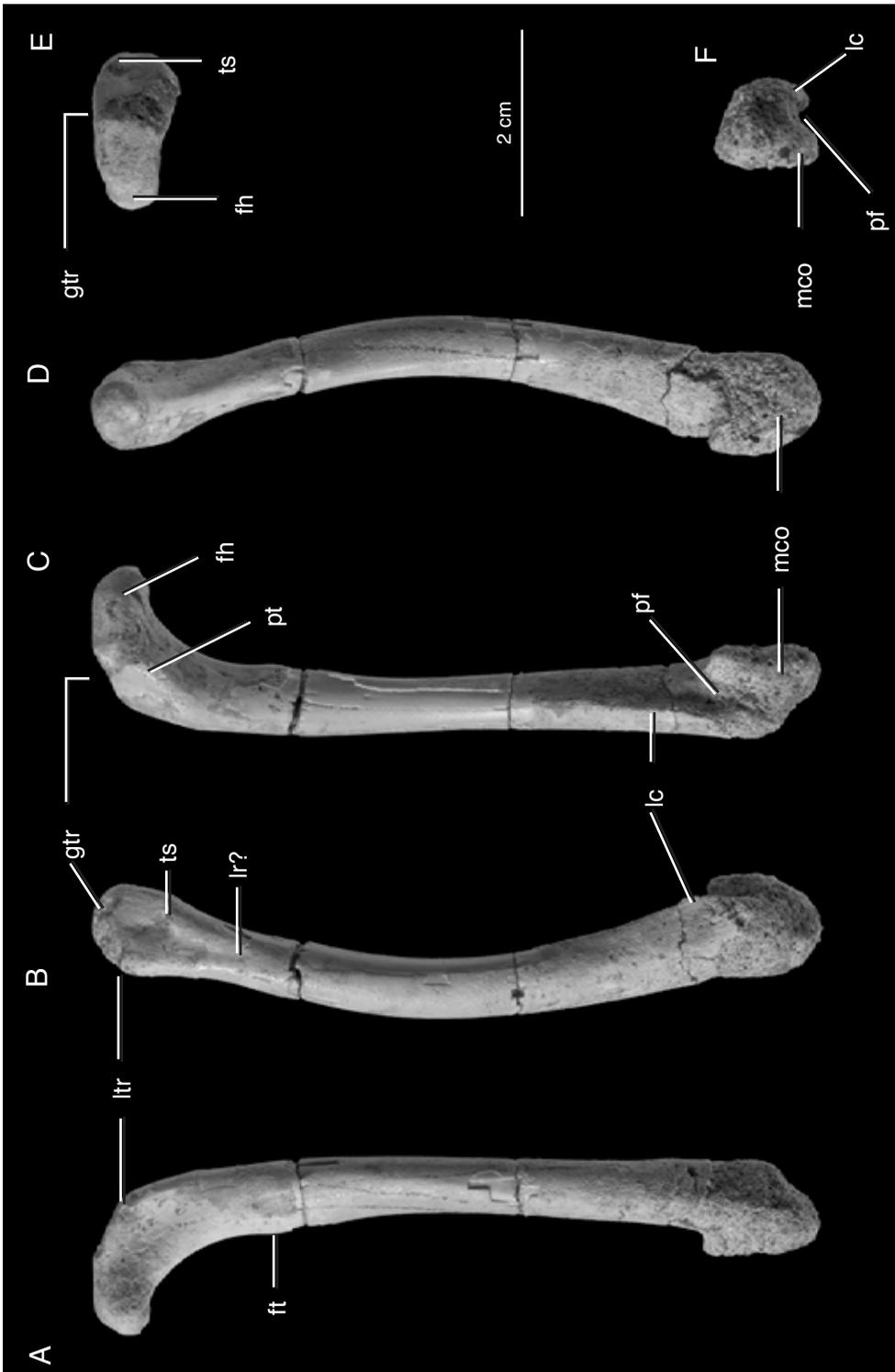


FIGURE 31. Left femur of *Mahakala omnogovae* (IGM 100/1033) in anterior (A), lateral (B), posterior (C), medial (D), proximal (E), and distal (F) views.

The postacetabular region is similar in shape to the condition described for dromaeosaurids (Barsbold, 1983; Norell and Makovicky, 1997, 1999), in which the postacetabular blade is downturned and has a convex dorsal margin in lateral view. The supratrochanteric process is more developed and the posterior end of the postacetabular process is more laterally directed than in *Velociraptor mongoliensis* (e.g., IGM 100/985, IGM 100/986). This well-developed supratrochanteric process is similar to that seen in *Unenlagia comahuensis* (MCF PVPH-78) and *Rahonavis ostromi* (UA 8656). Also like these taxa, a distinct ridge extends dorsally from the acetabulum to the supratrochanteric process.

The medial side of the postacetabular blade has a continuous longitudinal thin ridge for the attachment of transverse processes of the posterior sacral vertebrae. This ridge appears posteriorly to the posterior margin of the ischiadic peduncle and reaches the posterior end of the postacetabular blade. The surface of the ilium does not have the rugosities noted for dromaeosaurids in this region (Norell and Makovicky, 1997). Lateral to this ridge the brevis fossa extends down to the ventral edge of the postacetabular ilium. This fossa is narrower than in *Velociraptor mongoliensis* (IGM 100/985).

Although disassociated from the sacrum, if the ilium were placed in articulation the postacetabular blade likely would diverge from the sacrum as in *Velociraptor mongoliensis* (Norell and Makovicky, 1997). Also like *Velociraptor*, the postacetabular blade of the ilium in dorsal aspect forms a sigmoid curve with the anterior portion laterally concave becoming convex posteriorly.

HIND LIMB

FEMUR: The left femur is well preserved except for its distal end (fig. 31). It is typically anteriorly bowed and the femoral head is medially offset, bearing a notch on its posterior edge that is less developed than in *Velociraptor mongoliensis* (IGM 100/986) and *Deinonychus antirrhopus* (MCZ 4371).

On its dorsal surface the femoral head is separated from the greater trochanter by a slightly marked anteroposterior depression, the fossa articularis antitrochanterica (Baumel and Witmer, 1993). The tubercle or groove present in avialans for the insertion of the tendon of the M. obturatoris medialis (Hutchinson, 2001) is absent in IGM 100/1033, as in dromaeosaurids and other nonavian dinosaurs.

The lesser trochanter is present and its anterior edge is continuous with the robust greater trochanter. It is unclear, however, whether this would have formed a true trochanteric crest as seen in alvarezsaurids (Perle et al., 1994), *Rahonavis ostromi* (UA 8656), or oviraptorosaurs. No accessory trochanteric crest is present on the lesser trochanter. The fourth trochanter is present as a smooth and poorly developed ridge. The vascular foramen is located proximally to the fourth trochanter, in contrast to the condition usually found in theropods (Perle et al., 1994; Norell and Makovicky, 1999).

The morphology of the posterolateral surface of the proximal femur resembles that of *Deinonychus antirrhopus* (MCZ 4371), *Velociraptor mongoliensis* (IGM 100/986), and *Microraptor zhaoianus* (Hwang et al., 2002). There are three structures in this region of the proximal

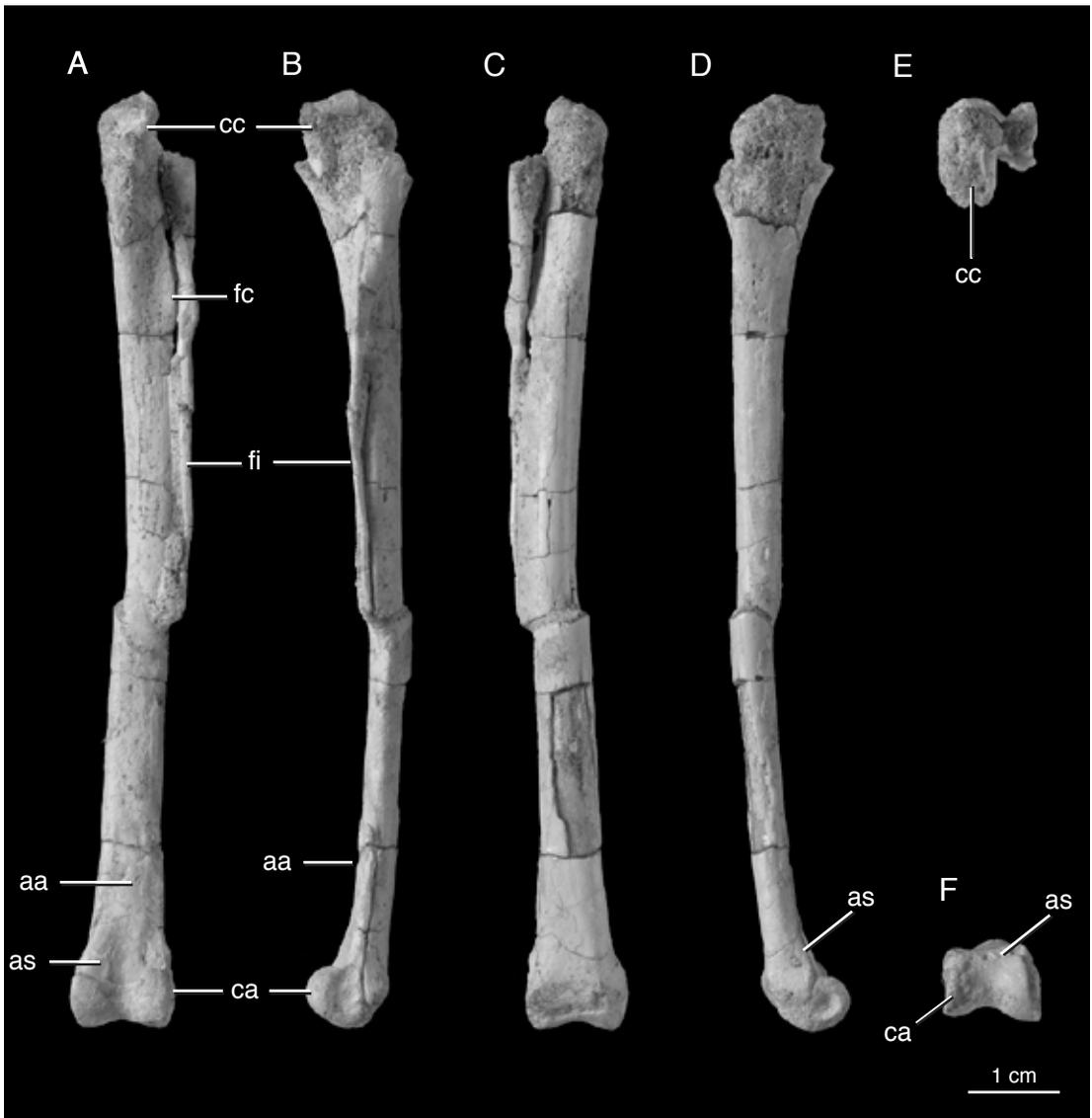


FIGURE 32. Left tibiotarsus and fibula of *Mahakala omnogovae* (IGM 100/1033) in anterior (A), lateral (B), posterior (C), medial (D), proximal (E), and distal (F) views.

femur of maniraptorans: the posterior trochanter, the trochanteric shelf (the lateral ridge, in part, of Norell and Makovicky, 1999), and the linea intermuscularis lateralis (Hutchinson, 2001). The trochanteric shelf, site of insertion of *M. iliofemoralis externus*, is usually placed distal and lateral to the lesser trochanter and is separated from the lesser trochanter by a shallow groove or depressed area. The trochanteric shelf is also commonly associated with a proximally located depression, and is connected distally to the linea intermuscularis lateralis (Novas, 1996; Norell and Makovicky, 1999; Hutchinson, 2001). The posterior trochanter, site of insertion of the *M. ischiotrochantericus* (Ostrom, 1976a; Hutchinson, 2001), is equivalent to the

posterior portion of the trochanteric shelf. The femur of IGM 100/1033 seems to lack a linea intermuscularis lateralis, although the trochanteric shelf is proximodistally elongated. In contrast to the condition of *Velociraptor mongoliensis* (IGM 100/986), the lateral ridge is not developed and the moundlike trochanteric shelf is closely connected to the posterior trochanter. This is similar to the moundlike trochanteric shelf in *Buitreraptor gonzalezorum* (MPCA 245), *Microraptor zhaoianus* (Hwang et al., 2002), and *Rahonavis ostromi* (UA 8656). In the latter taxon however, the trochanteric shelf is located very proximally and is nearly adjacent to the trochanteric crest. Anterior to the trochanteric shelf near the angle between the lateral and anterior face of the femur, there is another very small and weakly defined tuberosity that corresponds to the attachment site of *M. puboischiofemoralis internus 1* (Hutchinson, 2001).

The distal end of IGM 100/1033 is partially eroded and several details of the condyle morphology were not preserved. However, the proximal end of the medial condyle is abruptly finished forming a step seen in medial view, similar to the condition of *Deinonychus antirrhopus* (MCZ 4371). This feature is absent or only weakly expressed in *Velociraptor mongoliensis* (IGM 100/986) and *Unenlagia comahuensis* (MCF PVPH-78) and it is absent in *Adasaurus mongoliensis* (IGM 100/20). In these three dromaeosaurid taxa, the medial condyle projects as a slightly marked ridge that curves gradually into the profile of the medial condyle. The lateral condyle is completely eroded, but, in contrast to *Deinonychus antirrhopus* and *Velociraptor mongoliensis*, a markedly high ridge or crest extends from the distal third of the shaft down to the ectocondylar tuber area. This crest extends close to $\frac{1}{3}$ the total femur length and may have been continuous distally with the ectocondylar tubercle, although the tubercle itself is not preserved in the IGM 100/1033. The development of this crest is unlike the condition in present in alvarezsaurids, troodontids, and dromaeosaurids in which the lateral margin of the posterodistal femur is unprojected (or only weakly projected—e.g., *Velociraptor mongoliensis* IGM 100/986) proximal to the ectocondylar tubercle. An elongate crest continuous with the lateral distal condyle and in the approximate position of that in *Mahakala omnogovae* is present in *Vorona berivotrensis* (FMNH PA 717) and in some enantiornithines (e.g., *Neuquenornis volans*; Chiappe and Calvo, 1994). In *Mahakala* this ridge appears to be an extension of the small supracondylar ridge present in most other deinonychosaurs and is therefore not necessarily the same structure as that seen in *Vorona* and enantiornithines. The structure in those taxa instead forms from a proximal migration of the ectocondylar tubercle up the shaft of the femur. The anterior face of the distal femur is smooth with no indication of a longitudinal ridge proximal to the medial condyle.

FIBULA: The proximal end of the left fibula was incompletely preserved, however, this region is anteroposteriorly expanded with respect to the shaft of the fibula (fig. 32). Distal to this expansion, the fibula extends anteriorly and bears a laterally projected iliofibularis tubercle, located at the level of the distal end of the fibular crest of the tibia. In *Rahonavis ostromi* and *Ornithurae*, this tubercle is located posteriorly (Forster et al., 1998). Distal to this tubercle, the fibular shaft becomes splintlike and is closely appressed against the lateral edge of the tibia. The distal end of the left fibula is missing below the midpoint of the tibial shaft. Despite this, the fibula does not seem to articulate with the calcaneum because the calcaneum lacks a notch for

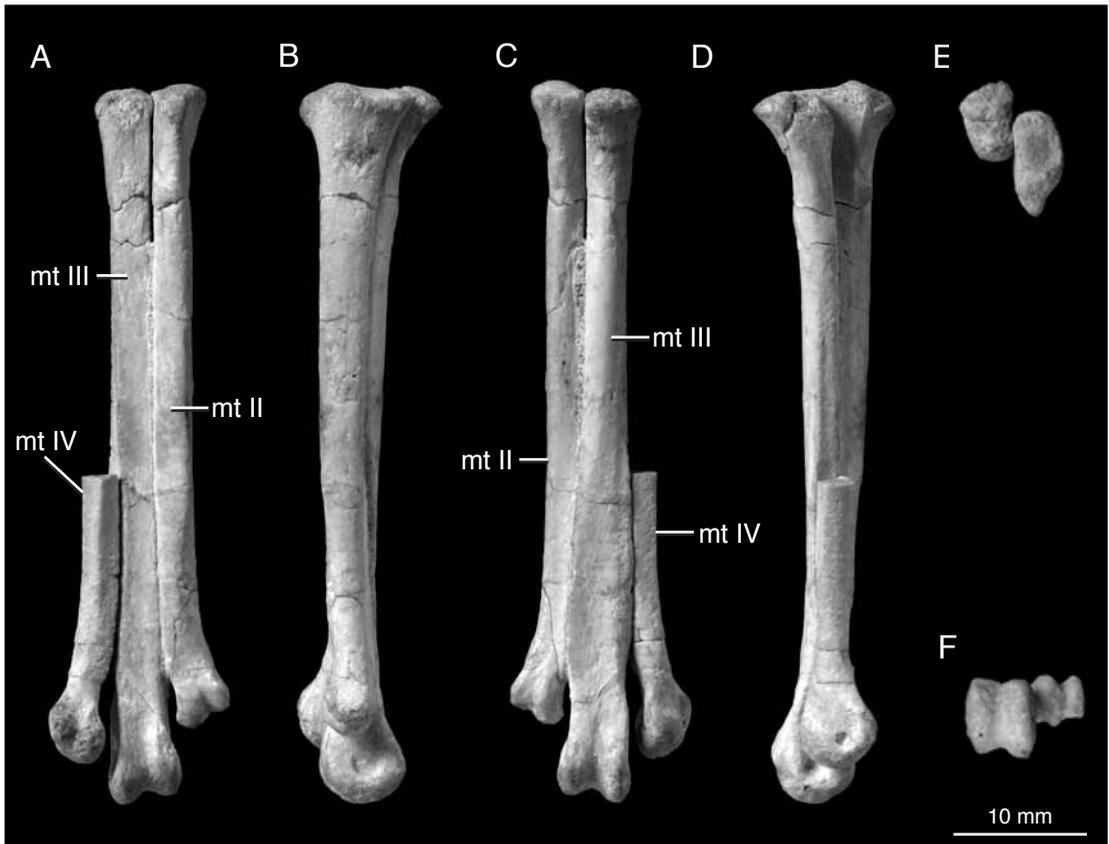


FIGURE 33. Left metatarsus of *Mahakala omnogovae* (IGM 100/1033) in posterior (A), medial (B), anterior (C), lateral (D), proximal (E), and distal (F) views.

the fibular reception as present in dromaeosaurids and other nonavian theropods.

TIBIOTARSUS: The right tibiotarsus only partially preserves the middiaphysis of the shaft (fig. 32). The left tibiotarsus is preserved entirely except for most of its proximal end (fig. 32). The general shape of the proximal end is, however, present as an internal mold.

The left tibia is longer than the left femur. The distal part of the cnemial crest is the only preserved bone of the proximal end. At this point the tibia is lateromedially compressed. As in *Rahonavis ostromi* (UA 8656), *Velociraptor mongoliensis* (IGM 100/986), and *Deinonychus antirrhopus* (MCZ 4371), a short fibular crest is present on the lateral surface of the proximal section of the shaft. However, this crest is less developed in IGM 100/1033 than in the above-mentioned taxa. Distal to the fibular crest the shaft has an ovoid cross section. Distal to the cnemial crest, the anteromedial face of the tibia possesses a sharp angle between the anterior and medial faces. This sharp angle diminishes after the midpoint of the tibia. A small distally facing foramen is present on the medial face of the tibia near the midpoint.

The distal end of the tibia expands mediolaterally and is slightly wider than the shaft width. The anterior surface is completely covered by the astragalus and calcaneum. The astragalus is hourglass shaped with a wide and tall ascending process. The ascending process is slightly less

than the total length of the tibia and covers the anterior surface of the tibia distally. The ascending process is not notched as in alvarezsaurids (e.g., *Mononykus olecranus* IGM 100/7), but does have a mediolaterally slanted proximal terminus as in most other coelurosaurs. The ascending process is separated from the condylar portion of the astragalus by a transverse fossa, as in most coelurosaurs.

The astragalus is fused to the calcaneum and has a wide medial condyle separate from the lateral condyle, which is narrower and more proximodistally developed than the medial one. The medial condyle projects further anteriorly than the lateral condyle, as in all coelurosaurs except derived avialans. Both condyles taper medially, forming an intercondylar groove that is about $\frac{1}{3}$ the width of the anterior face of the tarsus. There is a restricted extension of the articular surface for the distal tarsals onto the posterior surface of the tibia. This surface is marked by rough bone texture and the short extension of extensor ridges onto the posterior surface of the tibia.

On its anterior surface, the calcaneum is not as prominent as in *Deinonychus antirrhopus* (Ostrom, 1969a), being more continuous with the anterior surface of the astragalus as in *Velociraptor mongoliensis* (IGM 100/986). The lateral surface of the calcaneum is distinctly concave and does not have the notch for articulation with the distal fibula present in dromaeosaurids and other nonavian theropods. These conditions are shared by IGM 100/1033, *Rahonavis ostromi*, and basal avialans (Forster et al., 1998).

METATARSALS: The complete second and third metatarsals are preserved in articulation in the left pes of IGM 100/1033 (fig. 34). Additionally, the distal third of the fourth metatarsal was preserved on the left pes. The metatarsus of IGM 100/1033 is more slender than that of *Velociraptor mongoliensis* (IGM 100/985), *Saurornitholestes langstoni* (TMP 67.20.36), and *Deinonychus antirrhopus* (MCZ 4371). Unlike subarctometatarsalian taxa like *Microraptor zhaoianus* (Hwang et al., 2002), *Neuquenraptor argentinus* (MCF PVPH 77), and *Sinornithosaurus millenii* (Xu et al., 1999), *Mahakala omnogovae* has an unconstricted metatarsal III and is most similar in shape and proportions to the pes of *Rahonavis ostromi* (UA 8656).

A complete right metatarsal I is preserved in disarticulation on the lateral side of the right pes. The left metatarsal I is incompletely preserved, lacking its most proximal section, and is associated in a block along with some phalanges of digit II (fig. 33). Metatarsal I is extremely short in comparison with other elements of the metatarsus. This extreme shortening of metatarsal I is also present in *Rahonavis ostromi* (UA 8656), and is more pronounced than in other dromaeosaurids. On the lateral surface of its proximal end an extensive and concave surface for the attachment to metatarsal II is present. This articular surface is drop shaped, with a pointed proximal region and a widely expanded distal end. The distal expansion of this facet is sharply delimited and more extensive than the articular surface found in *Velociraptor mongoliensis* (IGM 100/985 and 100/986) and *Deinonychus antirrhopus* (YPM 5240). The distal end of this articular facet is located just above the proximal end of the distal articular head. The posterior face of metatarsal I is triangular and slightly concave as in *Velociraptor mongoliensis* (Norell and Makovicky, 1997), *Adasaurus mongoliensis* (IGM 100/21), and *Deinonychus antirrhopus* (YPM 5217). The distal articular head of metatarsal I of IGM 100/1033 is medially offset

from the rest of the metatarsal, as in *Rahonavis ostromi* (UA 8656; Forster et al., 1998). In *Velociraptor mongoliensis* this condition is present (Norell and Makovicky, 1997), although the distal articulation is not as divergent from the metatarsus.

As in *Rahonavis ostromi* (UA 8656) and other dromaeosaurids the medial surface of the distal articulation lacks a ligament pit. The lateral surface, in contrast, has a deep ligament pit. This pit is also found in *Deinonychus antirrhopus* (Ostrom, 1969a), *Adasaurus mongoliensis* (IGM 100/21), and *Velociraptor mongoliensis* (IGM 100/985 and 100/986). In *Velociraptor mongoliensis*, this pit was previously described as dorsally located, based on its position in the right pes of IGM 100/985 (Norell and Makovicky, 1997); however, the right metatarsal of this *Velociraptor* specimen is slightly twisted medially. The left pes of IGM 100/985 has the metatarsal I correctly articulated showing the lateral orientation of the pit of *Velociraptor*. The distal articular surface of metatarsal I of IGM 100/1033 is incipiently ginglymoid. Dorsally, it is undivided and elevated with respect to the shaft of the metatarsal, whereas ventrally two divergent ridges are separated by a wide groove. This resembles the condition of the distal articular surface of *Velociraptor mongoliensis* (Norell and Makovicky, 1997), *Adasaurus mongoliensis* (IGM 100/21), *Neuquenraptor argentinus* (MCF PVPH 77), and *Deinonychus antirrhopus* (Ostrom, 1969a).

Metatarsal II is slender. Its proximal end is lateromedially compressed and has an anteroposteriorly elongated articular surface. A well-developed tubercle is present on the posterior face of the proximal end. This structure is present but less developed in *Velociraptor mongoliensis* (IGM 100/986) and is posteriorly covered by the proximal end of metatarsal III and the medial distal tarsal. A slightly elevated crest extends distally from this bulge and disappears at the distal end of the metatarsal shaft. A similar structure, although not so proximally extended, was noted in *Velociraptor mongoliensis* and other dromaeosaurids (Norell and Makovicky, 1997) as topologically congruent with the medial plantar crest of Aves (Baumel and Witmer, 1993).

The anterior surface of metatarsal II is convex on its proximal end and becomes flat along the shaft. There is no tubercle on the anterolateral corner of the shaft of metatarsal II, in contrast to the condition seen in *Velociraptor mongoliensis* and enantiornithine birds (Chiappe, 1991; Chiappe and Walker, 2002; Norell and Makovicky, 1997, 1999), in which this structure was interpreted as the probable area of insertion of *M. tibialis cranialis*. Additionally, the tubercle located on the anterior surface just above the ginglymoid trochlea in some specimens of *Velociraptor mongoliensis* (Norell and Makovicky, 1997) is also absent in IGM 100/1033. Its medial surface is flat and contacts the metatarsal III from its proximal articular end down to the beginning of the distal articular end. The lateral surface, instead, is slightly convex in cross section and thins distally as the medial plantar crest disappears.

The distal end of the metatarsal II of *Mahakala omnogovae* deflects medially, a condition absent in *Velociraptor mongoliensis* (IGM 100/985) and *Deinonychus antirrhopus* (MCZ 4371). The distal end of the metatarsal II is perhaps also slightly medially deflected in *Saurornitholestes langstoni* (TMP 67.20.36); however, it cannot be definitively determined due to preservation. The distal end of metatarsal II is composed of an asymmetrical ginglymoid articular surface, as in dromaeosaurids (Ostrom, 1969a; Currie and Peng, 1993), including *Rahonavis ostromi* (UA 8656; Forster et al., 1998) and other unenlagiines. There are no ligament pits present on

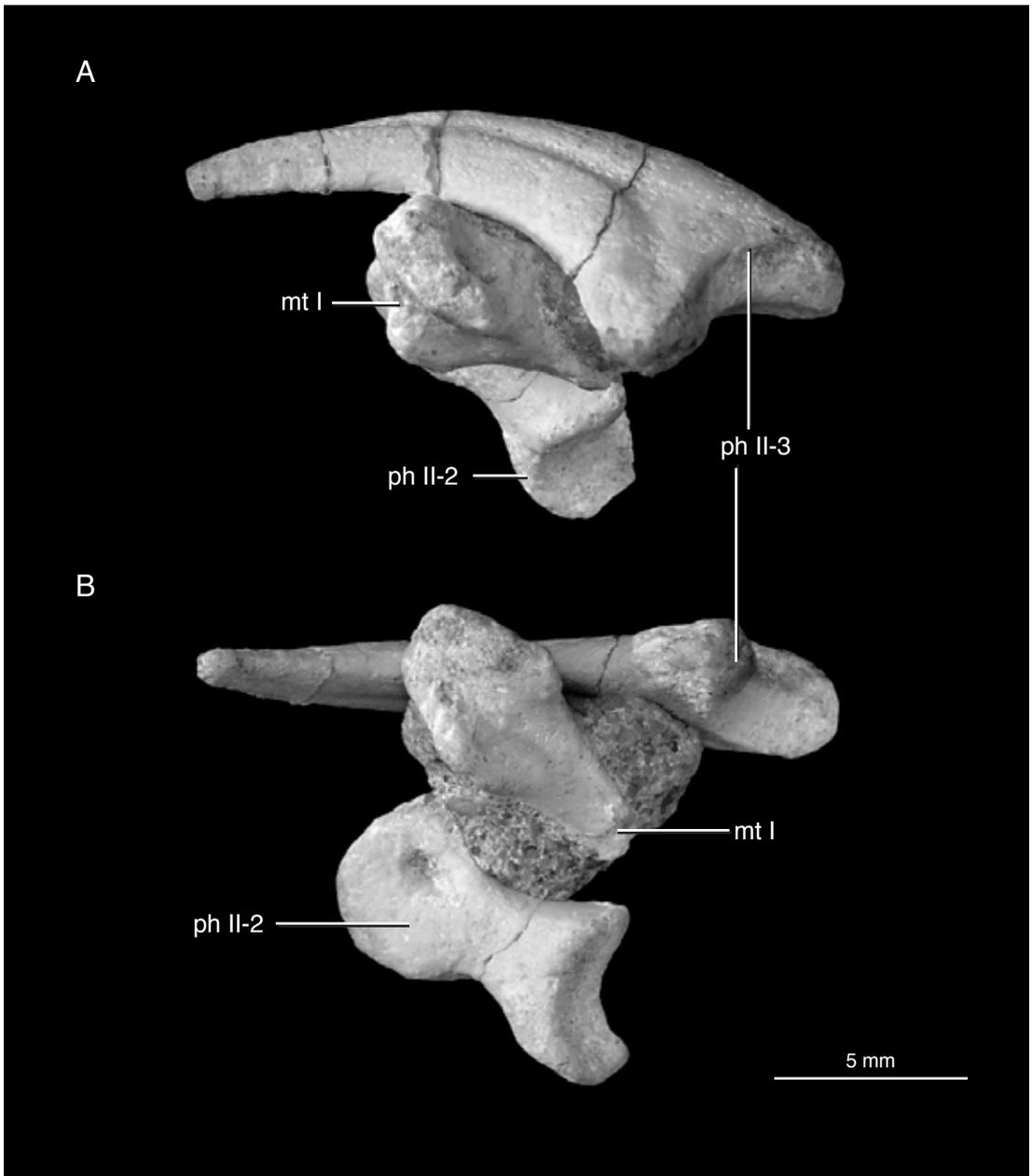


FIGURE 34. Left pedal phalanges of *Mahakala omnogovae* (IGM 100/1033). **A**, Pedal ungual of digit 2 in lateral view. **B**, Penultimate pedal phalanx of digit 2 in lateral view.

the medial and lateral surfaces of the distal end of metatarsal II. This character is also found in *Rahonavis ostromi* (UA 8656; Forster et al., 1998), but contrasts with the condition in *Buitreraptor gonzalezorum* (MPCA 245), *Neuquenraptor argentinus* (MCF PVPH 77), *Velociraptor mongoliensis* (IGM 100/985 and IGM 100/986), and *Deinonychus antirrhopus* (Ostrom, 1969a).

The third metatarsal is the longest element of the metatarsus. Its proximal articular surface is anteroposteriorly elongate. The posterior edge of the proximal end of the left element is damaged. On the anterior surface of metatarsal III a small bulge lies near its proximal end. Distal to this structure the anterior surface is convex. This condition contrasts with the marked longitudinal mound present in dromaeosaurids such as *Velociraptor mongoliensis* and *Deinonychus antirrhopus* (Norell and Makovicky, 1997). Despite this difference, at the midpoint of the shaft, the anterior surface of metatarsal III of IGM 100/1033 becomes flat and wide as in *Velociraptor mongoliensis* (IGM 100/985 and IGM 100/986).

The posterior surface differs in two characters from the condition described in *Velociraptor mongoliensis* (Norell and Makovicky, 1997). First, the proximal half of metatarsal III faces posterolaterally in *Velociraptor mongoliensis* (IGM 100/985, IGM 100/986), whereas in *Mahakala omnogovae* it faces posteriorly along the entire length of metatarsal III. Second, at the distal end of the shaft, just above the distal ginglymoid trochlea, a distinctly concave surface is present in *Velociraptor mongoliensis* but not in IGM 100/1033.

The lateral surface of metatarsal III has an almost continuous flat surface for its contact with metatarsal IV. This surface occupies the entire anteroposterior length of the proximal end of metatarsal III. The contact surface narrows distally down to the beginning of the shaft, where it becomes anteroposteriorly longer. Near the distal end of the shaft, this surface becomes narrow again and disappears above the origin of the ginglymoid trochlea. This last point of contact with metatarsal IV lies more distally than in *Velociraptor mongoliensis* (IGM 100/985, IGM 100/986).

The distal ginglymoid trochlea has its lateral condyle slightly more developed than the medial one. As in *Velociraptor mongoliensis* (Norell and Makovicky, 1997), the medial ligament pit is larger and shallower than the lateral pit.

The distal third of the left metatarsal IV is disarticulated from metatarsals II and III. Fragments of the right metatarsal IV are preserved in articulation with the poorly preserved right pes. The lateral edge is concave, but its surface is anteroposteriorly convex. A triangular flat surface is present on its medial face. This is the distal end of the articulation facet with metatarsal III and matches with that of metatarsal III. According to this contact, the metatarsal IV is shorter than metatarsal III, as in *Microraptor zhaoianus* (Hwang et al., 2002), *Buitreraptor gonzalezorum* (MPCA 245), *Neuquenraptor argentinus* (MCF PVPH 77), *Saurornitholestes langstoni* (TMP 67.20.36), *Velociraptor mongoliensis* (IGM 100/985), and *Deinonychus antirrhopus* (MCZ 4371).

The distal end of metatarsal IV bears a single articular head. Its anterior surface is convex, undivided, and projects proximally as a thin ridge. Lateral to this ridge, a shallow extensor pit is present in IGM 100/1033. Its posterior surface is divided into lateral and medial ridges by a shallow sulcus. These two ridges are located lateral to the medial edge of the shaft, resulting in a laterally offset distal head of metatarsal IV. The lateral ridge is more developed posteriorly



FIGURE 35. Left digit III pedal phalanges of *Mahakala omnogovae* (IGM 100/1033), prior to full preparation of the left tibia and metatarsus.

than the medial ridge, opposite to the condition of *Velociraptor mongoliensis* (Norell and Makovicky, 1997). Consequently, the lateral ligament pit is more proximodistally elongate, deep, and posteriorly located than the medial pit.

PHALANGES: Only the unguual phalanx of digit I was preserved on the medial side of the poorly preserved right pes of IGM 100/1033. The unguual of IGM 100/1033 is well developed and similar in length to the unguual on the fourth digit. A condition similar to this is found in *Deinonychus antirrhopus* (Ostrom, 1969a) but not in *Velociraptor mongoliensis* (IGM 100/985) in which the digit I unguual is shorter than that of the unguual of the fourth digit. However, the first pedal unguual of IGM 100/1033 resembles the condition of *Velociraptor mongoliensis* in its weakly marked curvature, differing from the first unguual of *Deinonychus antirrhopus* (Ostrom, 1969a) and *Rahonavis ostromi* (UA 8656). The proximal articular surface of the unguual phalanx of IGM 100/1033 is lateromedially narrow and bears a slightly marked dorsoventral ridge that separates two articular concavities. A well-developed flexor tubercle is present on its proximoventral surface. The lateral face of this unguual is not as expanded as in *Velociraptor mongoliensis* (Norell and Makovicky, 1997). Thus, IGM 100/1033 possesses a suboval cross section of its first

pedal ungual. An isolated partial phalanx consisting of the distal half is present near the right side of the sacrum. This element is approximately the correct size to be referable to phalanx I-1; however, this identification is tentative at best.

The two distal phalanges of the second left digit were preserved in disarticulation with metatarsal II (fig. 34). Phalanx II-2 has a well-developed proximal heel and a hypertrophied ginglymoid trochlea separated by a constricted shaft, a suite of characters only present in dromaeosaurids (Norell and Makovicky, 2004) including *Rahonavis ostromi* (Forster et al., 1998; Makovicky et al., 2005; Turner et al., 2007a, 2007c) and not seen in *Archaeopteryx* (contra Mayr et al., 2005). Unlike *Buitreraptor gonzalezorum*, *Sinovenator changii*, *Microraptor zhaoianus*, *Rahonavis ostromi* (UA 8656), and *Neuquenraptor argentinus* (MCF PVPH-77), which have a small asymmetric flexor heel; *Mahakala omnogovae* has a symmetrically developed flexor heel more like that seen in more derived troodontids and dromaeosaurids. The proximal articular facet of phalanx II-2 is asymmetric and ginglymoidal. A dorsoventral ridge separates the two concave articular surfaces, of which the medial one is the widest and deepest. The ventral heel is projected proximally and has on its ventral surface a lateral and a medial ridge separated by a shallow groove. The medial ridge on the ventral surface of the heel is more developed and projects more ventrally than the lateral one. This condition is also present in *Velociraptor mongoliensis* (IGM 100/986) and *Deinonychus antirrhopus* (Ostrom, 1969a). The shaft of phalanx II-2 is dorsoventrally constricted with respect to the proximal and distal ends, but it is lateromedially constricted only with respect to the proximal end. As in dromaeosaurids including *Rahonavis ostromi* (Forster et al., 1998), the distal trochlea is narrow, asymmetrical, deeply grooved, and its articulation arc spans for approximately 180°. The proximal extension of the articular surface is twice the length onto the ventral surface than onto the dorsal surface. The lateral ligament pits of phalanx II-2 are located dorsal to the center of the articular arc. The medial pit is slightly deeper than the proximal one.

As in dromaeosaurids and basal avialans, the ungual phalanx of digit II is long and strongly curved. Its cross section is tall and narrow, and its dorsal edge is broader than its ventral edge. Both the lateral and medial surfaces of the claw are grooved; the lateral groove is more dorsally positioned than the medial as in other dromaeosaurids (Kirkland et al., 1993; Rauhut and Werner, 1995; Norell and Makovicky, 1997). In dorsal view, the lateral edge is slightly convex, while the medial is slightly concave. Thus, the claw of digit II is slightly curved medially along its proximodistal length as in *Velociraptor mongoliensis* (IGM 100/985).

The phalanges of digit III are the longest elements of the pes. The left digit III is entirely preserved in articulation with metatarsal III (fig. 35). Only the right phalanx III-1 is in articulation with remains of metatarsal III, whereas a right phalanx III-3 is preserved but disarticulated (fig. 16).

Phalanx III-1 is the longest phalanx; it is slender and slightly constricted along the shaft. On the dorsal surface of the proximal end a proximally projecting lip extends over the distal ginglymoid trochlea of metatarsal III. The ventral surface of the proximal end bears two longitudinal ridges on its medial and lateral edge. In contrast to the condition in some specimens of *Velociraptor mongoliensis* (IGM 100/985), there is no concave surface between the ridges in

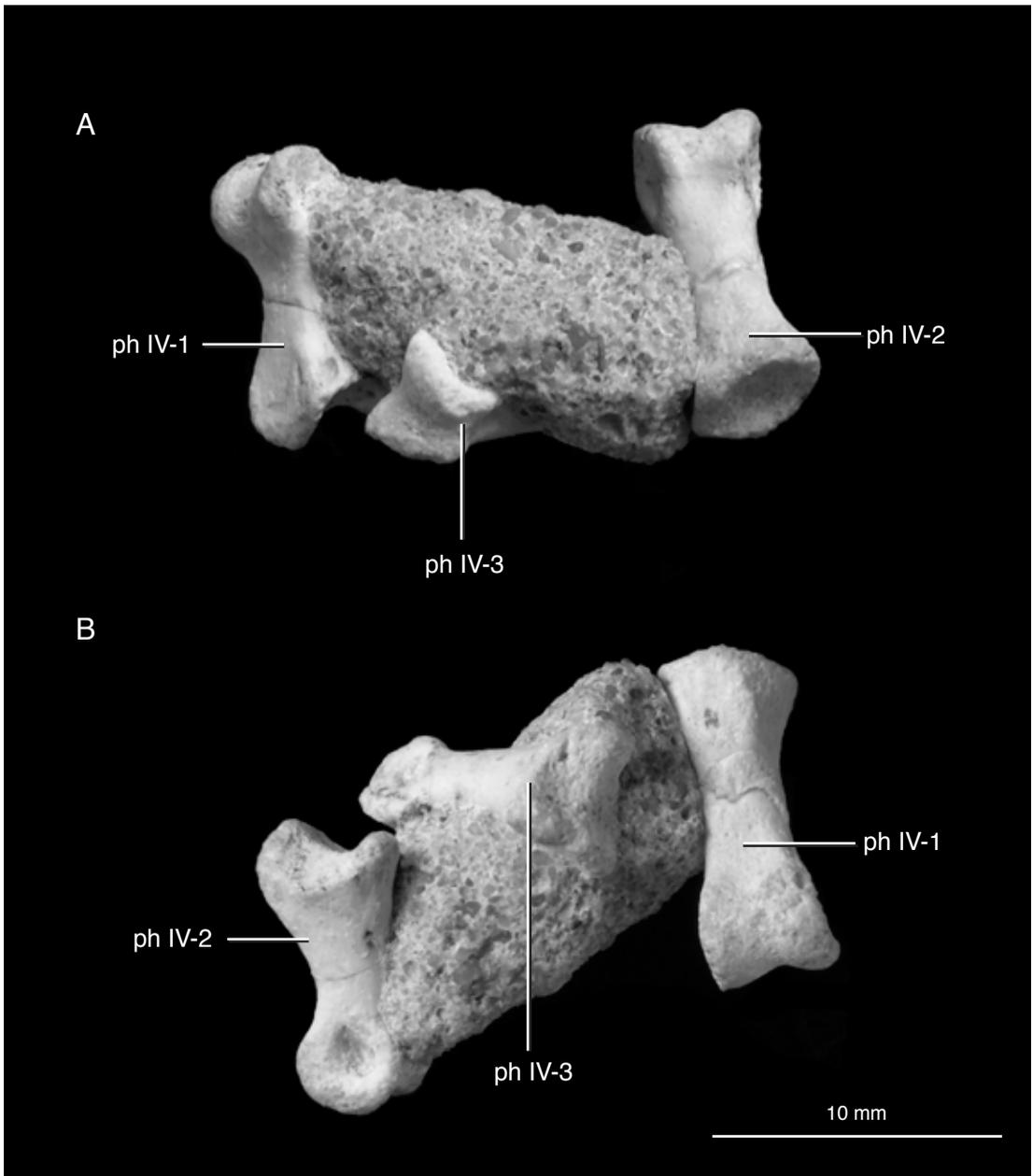


FIGURE 36. Left digit 4 pedal phalanges of *Mahakala omnogovae* (IGM 100/1033).

IGM 100/1033. The shaft is almost quadrangular in cross section. The distal end has a deep extensor pit on its dorsal surface. The lateral and medial surfaces have well-developed ligament pits, the lateral deeper than the medial. In *Velociraptor mongoliensis* (IGM 100/985 and IGM 100/986) these pits are present but are more expanded and not as well delimited as in IGM 100/1033. The trochlea is ginglymoid and is slightly twisted medially, a condition shared with *Velociraptor mongoliensis* (Norell and Makovicky, 1997).

Phalanx III-2 is shorter than the preceding phalanx; however, as in *Rahonavis ostromi* (Forster et al., 1998), this element still is slender and elongate. This differs from the condition in *Velociraptor mongoliensis* (Norell and Makovicky, 1997), whose phalanx III-2 is short and stout. Additionally, in IGM 100/1033 and *Rahonavis ostromi* (Forster et al., 1998), the proximal end is not as dorsoventrally expanded with respect to the distal dorsoventral expansion as in *Velociraptor mongoliensis* (IGM 100/985 and 100/986). The proximal end bears a dorsal lip similar to that of the previous phalanx. Ventrally, the two longitudinal ridges are present, but here these are separated by a shallow concavity. As noted above, the shaft of IGM 100/1033, *Microraptor zhaoianus* (Hwang et al., 2002) and *Rahonavis ostromi* (UA 8656) is more elongate and slender than in *Velociraptor mongoliensis* (IGM 100/985 and IGM 100/986). The distal end has a marked extensor pit on its dorsal surface as in *Velociraptor mongoliensis* (Norell and Makovicky, 1997) and other dromaeosaurids. However, in IGM 100/1033 the extensor pit is distinctly separated from the groove of the ginglymoid articular surface by a marked step (similar to the condition in *Neuquenraptor argentinus*) whereas in *Velociraptor mongoliensis* (IGM 100/985 and IGM 100/986) the pit and the ginglymoid groove are nearly continuous. The lateral ligament pits of the distal end are well developed as in the previous phalanx and they also differ from *Velociraptor mongoliensis* in extension and delimitation. The distal ginglymoid articular surface is also twisted medially in this phalanx, as in *Velociraptor mongoliensis* (Norell and Makovicky, 1997).

Phalanx III-3 is similar to the preceding phalanx, but it has a shorter proximodistal development. Other differences are the absence of an extensor pit on the dorsal surface of the distal end and the dorsal displacement of the lateral ligament pits in phalanx III-3.

The ungual of digit III is similar to those described in dromaeosaurids (Ostrom, 1969a; Norell and Makovicky, 1997). It is a slightly curved claw with a wide and flat ventral surface, and a triangular cross section. Its lateral and medial sides are grooved, the lateral groove located more dorsally than the medial one. Proximally, a massive flexor tubercle lies on the ventral surface of the claw.

The right phalanges IV-1, IV-2, and the proximal end of IV-3 were preserved in articulation with the right pes. Additionally, the distal end of phalanx IV-3 articulated with phalanx IV-4 and an isolated complete ungual was found in disarticulation from the right pes (fig. 36). A set of three left phalanges and an isolated proximal fragment of the ungual were also preserved and they closely match in shape and size with those of the right pes.

Phalanx IV-1 is short and narrow as in *Velociraptor mongoliensis* and *Microraptor zhaoianus* (Hwang et al., 2002), in contrast to the condition of *Rahonavis ostromi* (Forster et al., 1998) where this element is elongated. Additionally, phalanx IV-1 is medially bowed, a condition present in *Velociraptor mongoliensis* (Norell and Makovicky, 1997) but not in *Rahonavis ostromi*

(UA 8656). In lateral view, the shaft of IGM 100/1033 has a dorsoventral constriction with respect to both proximal and distal ends. In *Velociraptor mongoliensis* (IGM 100/986), this constriction is notably marked due to the dorsoventral expansion of the proximal end. In *Rahonavis ostromi* (Forster et al., 1998), this condition is also reduced, even more than in *Mahakala omnogovae* (IGM 100/1033). Phalanx IV-1 has a distinctive concave and undivided proximal articular surface. The edges of the proximal articular surface form a circumference, except for its dorsomedial part, which is slightly expanded. The ventral surface of the proximal end is flat, in contrast with the marked ridges present in *Velociraptor mongoliensis* (IGM 100/986). The shaft is subquadrangular in cross section. A slightly marked extensor pit is present on the dorsal surface of the distal end. This depression is separated from the ginglymoidal groove by a distinct step that is absent in some specimens of *Velociraptor mongoliensis* (IGM 100/986). The lateral and medial ligament pits are well developed, although the lateral is deeper than the medial one. In *Rahonavis ostromi* (Forster et al., 1998) and *Velociraptor mongoliensis* (IGM 100/985 and IGM 100/986) these pits are not as well delimited. The distal articular surface is ginglymoid and its lateral and medial ridges are subparallel. The medial ridge is proximally more developed than the lateral ridge.

Phalanx IV-2 has a dorsoventrally expanded proximal end due to the presence of a well-developed proximodorsal lip, a condition also found in dromaeosaurids including *Rahonavis ostromi* (UA 8656). The ventral side of the proximal end is flat and lacks well-developed ridges. A longitudinal ridge divides the proximal articular surface. The medial articular concavity is wider than the lateral surface. On the distal end, the lateral ligament pits are deep and well delimited. In *Velociraptor mongoliensis* these are not as deep, and in some cases (IGM 100/985), they are only poorly delimited. The distal articular surface is ginglymoid and differs from the previous phalanx because the lateral and medial ridges diverge ventrally. However, as in the previous phalanx, the medial ridge is more expanded ventrally than the lateral ridge.

Phalanx IV-3 is slightly shorter than the previous phalanx; however, this length reduction is not as marked as in *Velociraptor mongoliensis* (Norell and Makovicky, 1997), *Rahonavis ostromi* (UA 8656), or *Deinonychus antirrhopus* (although in this taxon it varies considerably among individuals). Some characters show the same condition present in phalanx IV-2 and the same set of similarities and differences with *Velociraptor*. First, a longitudinal ridge divides the proximal articular surface. Second, the medial articular concavity is wider than the medial surface. Third, the proximal articular surface projects proximodorsally as a well-developed lip. Fourth, the ventral side of proximal end is flat. Fifth, there are deep and well-delimited lateral and medial ligament pits. Sixth, on the distal ginglymoid articular surface, the ridges diverge ventrally.

Phalanx IV-4 is similar in size and shape to the previous phalanx, although it is slightly reduced in its proximodistal dimension. Its proximal end has a well-developed proximodorsal lip that articulates with the preceding ginglymoid trochlea. The ventral surface of the proximal end is flat. On the lateral and medial surfaces of the distal end, the ligament pits are displaced dorsally, as is characteristic in all nonungual phalanges. The distal ginglymoid trochlea is not as dorsoventrally developed as in other phalanges of digit IV. Additionally, the medial and lateral ridges of the distal articular surface diverge ventrally less markedly than in the preceding

phalanges. The trochlea is twisted medially with respect to the proximal end, a condition also found in some specimens of *Velociraptor mongoliensis* (IGM 100/985) although the degree of torsion is much smaller.

The ungual phalanx of the fourth digit is similar to that of dromaeosaurids (Ostrom, 1969a; Norell and Makovicky, 1997). Its ventral surface is flat and wide, and it has a triangular cross section along its entire length. The lateral and medial surfaces bears marked grooves, the lateral located slightly dorsal to the medial groove. This element is similar in shape and size to the ungual of digit III; however, the proximal flexor tuber is more acute and ventrally developed in the ungual of digit IV. Other differences of ungual IV include a smaller dorsoventral expansion at, and a narrower ventral surface on, the proximal end.

DISCUSSION

Mahakala omnogovae is the third (or perhaps fourth) dromaeosaurid theropod from the Djadokhta Formation of Central Asia. It is one of the roughly 26 valid dromaeosaurid species known from a complete or nearly complete skeleton. Although discovered in comparatively younger Cretaceous deposits, the basal position of *Mahakala* has several implications relevant to understanding the early history of dromaeosaurids and deinonychosaurs. This taxon possesses a bizarre and interesting combination of characters not seen in other dromaeosaurids. For example, at the confluence of the metotic strut and posterior tympanic recess there is a unique ledge-like depression that is unknown in other dromaeosaurids. Because it enters the middle ear, we have interpreted this ledge as associated with the tract of the external carotid artery.

Typically maniraptorans are characterized by a trend toward forelimb and manus elongation. *Mahakala omnogovae* is aberrant in that it has a very shortened forelimb and strongly autapomorphic ulna. The shortened humerus is less than 50% of the femur length. The ulna is strongly compressed and anteroposteriorly broad. It has a triangular cross section because the bone tapers posteriorly to a narrow edge. Other recently discovered dromaeosaurid taxa illustrate that independent shortening of the forelimb occurred in the history of Dromaeosauridae. The Late Cretaceous *Austroraptor cabazai* from the Allen Formation of Argentina (Novas et al., 2009) is a member of the unenlagiine clade of dromaeosaurids and, though it is three orders of magnitude larger than *Mahakala*, possesses a humerus that is approximately 50% shorter than the femur. Similarly, *Tianyuraptor ostromi*, likely a bizarre microraptorine (see the analysis presented here and in Turner et al., in press), possesses a humerus 65% shorter than the femur (Zheng et al., 2010). Given the basal position of *Mahakala* within Dromaeosauridae and the deeply nested positions of both *Tianyuraptor* and *Austroraptor* it is suboptimal to infer a short-armed condition at the base of Dromaeosauridae. It is interesting to consider, however, that most (with the exception of *Anchiornis* and *Jingfengopteryx*) troodontids have proportionally short forelimbs. This, combined with the basalmost position of *Mahakala* within the Dromaeosauridae, raises the possibility that short arms were the ancestral Deinonychosaurian condition with elongate forelimbs evolving convergently in avialans and dromaeosaurids more derived than *Mahakala*. In this scenario only the short forelimbs of *Tianyuraptor* and *Aus-*

troraptor would be interpreted as reversals. Needless to say, further study is needed taking into consideration phylogenetic patterns of body size and allometry before differing patterns of limb elongation and/or reduction can be fully understood.

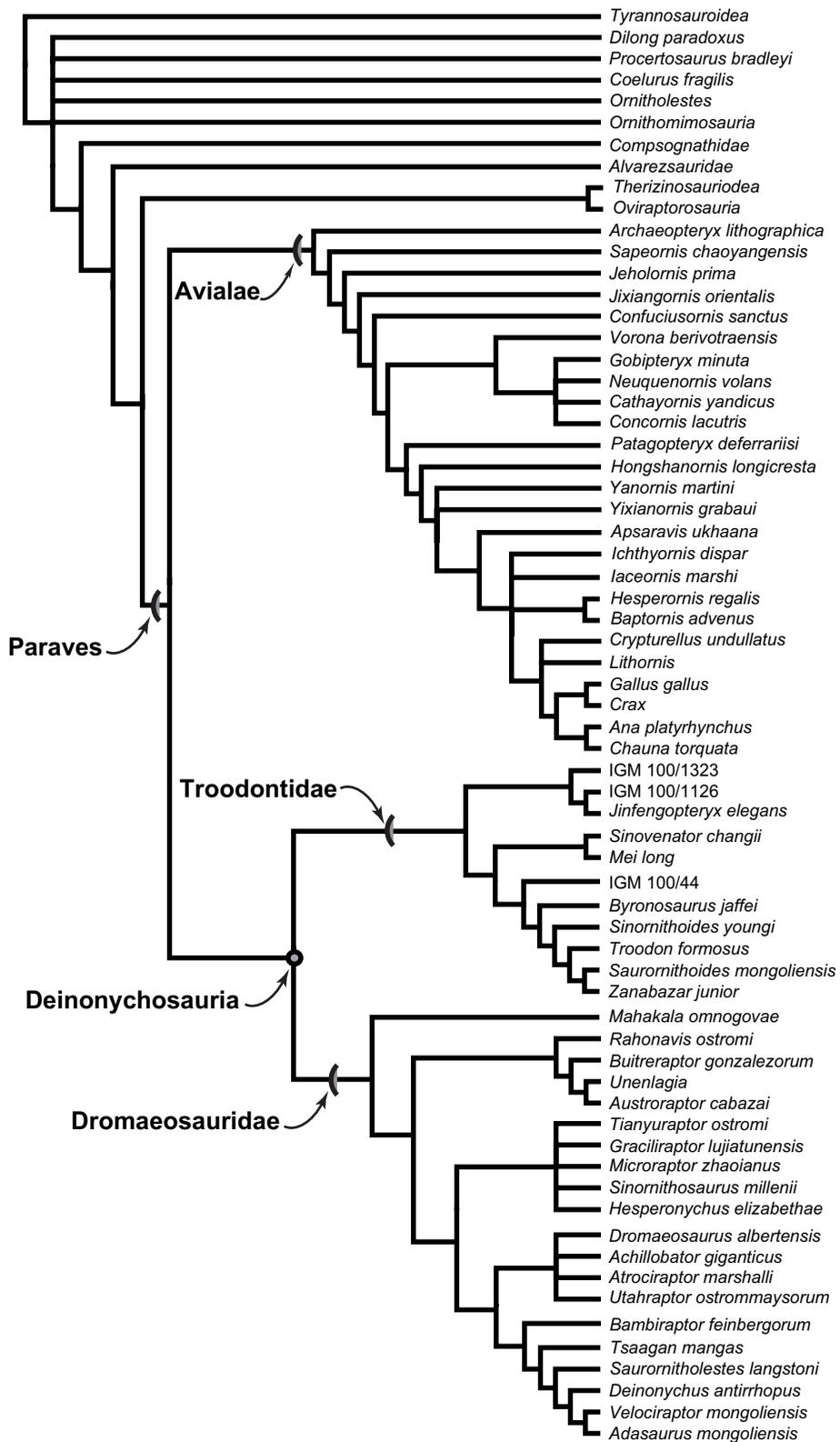
An elongate lateral crest continuous with the lateral distal condyle of the femur is present in *Vorona berivotrensis* (FMNH PA 717) and in some enantiornithines (e.g., *Neuquenornis volans*). A similar crest is present in *Mahakala omnogovae*. In the latter taxon the crest extends close to $\frac{1}{3}$ total femur length and may have been continuous distally with the ectocondylar tubercle. The analogous structure in *Vorona* and enantiornithines is formed from a proximal migration of the ectocondylar tubercle up the shaft of the femur. We have interpreted this structure *Mahakala* to be nonhomologous with the ridge in the former taxa and instead to be an extension of the small supracondylar ridge present in most other deinonychosaurs.

In the vertebral column two features are unique to *Mahakala omnogovae*. The first is that the cervical ribs fuse to the apophyses in anterior cervical vertebrae. The second is the complex architecture of the anterior caudal vertebrae. These vertebrae in *Mahakala omnogovae* are unusual in their morphology. In all coelurosaurs we examined the anterior caudal vertebrae exhibit a transitional morphology from the sacral series to the more elongate mid- and distal caudals. This involves a transversely narrow neural arch (narrower than the centrum) and narrow and posteriorly backswept transverse processes. The prezygapophyses are typically short, close to the midline, with articular facets nearly vertically oriented. In *Mahakala* the anterior caudal centra are proportionately longer than in other dromaeosaurids or more basal coelurosaurs. Furthermore, the centra are subquadrangular in cross section and have a pronounced sulcus on their ventral surface. The articular facets for the hemal arches are not well developed. Perhaps most notably the neural arches are broad, forming a prominent connection between the subhorizontal, laterally directed prezygapophyses and the perpendicularly oriented transverse processes. The prezygapophyses of the anterior caudals are anterolaterally oriented and their articular ends are notably expanded.

Mahakala omnogovae provides important data on estimating the ancestral dromaeosaurid and deinonychosaur body size. Although small taxa have been found previous to *Mahakala* (e.g., *Sinovenator*, *Mei*, *Sinornithosaurus*, *Buitreraptor*), most of these taxa are twice as long as *Mahakala* and nearly an order of magnitude more in estimated mass. Consequently, inclusion of *Mahakala* is of critical importance for the reconstruction of the basal dromaeosaurid, troodontid, deinonychosaur, and paravian conditions (Turner et al., 2007c). In the preliminary description of *Mahakala* and subsequent analysis (Turner et al., 2007d; Turner, 2008), it was shown that the exclusion of *Mahakala* during the optimization of the paravian body mass markedly changes the reconstructed basal conditions for paravians clades. Thus, *Mahakala* is decisive for inferring extreme miniaturization at the base of Paraves and Deinonychosauria.

Ghost lineage duration and phylogenetic placement for all basal paravians reveals that the small paravian taxa, regardless of their temporal occurrence, are recovered basally in their respective clades. Given their generally fragile skeletons, small taxa are typically preserved only

FIGURE 37. Phylogenetic relationship of *Mahakala omnogovae*. Strict consensus of 40,000 most parsimonious reconstructions of coelurosaurian interrelationships found in our phylogenetic analysis of 472 characters and 102 taxa. Non-paravian clades have been collapsed for display of the cladogram.



in exceptional circumstances, often requiring Lagerstätten conditions (e.g., Jehol deposits, Solnhofen, Ukhaa Tolgod, etc.). The duration of the ghost lineages for these small taxa, it would seem, are best viewed as indicators of the temporal distribution of paravian-preserving Lagerstätten. It is expected that the first dromaeosaurids and troodontids discovered were the large-bodied members of currently recognized clades. The early discovery and shorter ghost lineages of these large-bodied taxa are likely reflections of their higher preservation potential. If large-bodied taxa were present along the ghost lineages of the small-bodied paravians, then representatives would likely have been sampled. Nevertheless, it is true that part of the early radiation of paravians is documented from Early Cretaceous deposits in Asia that show a bias toward preserving small-bodied taxa. Notable exceptions, however, are the finds of *Shenzhousaurus* and *Beipaiosaurus*, and the Early Cretaceous Öösh deposits from Mongolia, which do not show such a taphonomic bias. The converse is true for Early Cretaceous deposits from North America, which tend to preferentially preserve larger-bodied taxa. With improved sampling from other taphonomic settings in North America and Asia, it remains a possibility that hypotheses of body size evolution could be altered.

PHYLOGENY

In our initial description of *Mahakala omnogovae*, we tested its phylogenetic placement with a dataset of 69 coelurosaurian taxa and 251 characters. *Allosaurus fragilis* and *Sinraptor dongi* were used to root the most parsimonious trees. Equally weighted parsimony analysis recovered *Mahakala omnogovae* as the basalmost member of the Dromaeosauridae in all the most parsimonious reconstructions. Here we discuss the phylogenetic position of *Mahakala* based on a revised and expanded dataset developed by Turner et al. (in press). This dataset consists of 102 taxa and 472 characters. This character matrix is referred to as TWIG 2011.1. The character list, data matrix, and supplemental analysis data are available at <http://www.anat.stonybrook.edu/people/facultypage/turner> and at <http://research.amnh.org/paleontology/staff/mark-norell>.

The dataset was analyzed with equally weighted parsimony using TNT v. 1.0 (Goloboff et al., 2008a, 2008b). A heuristic tree search strategy was conducted performing 1000 replicates of Wagner trees (using random addition sequences, RAS) followed by TBR branch swapping (holding 10 trees per replicate). The shortest trees obtained at the end of the replicates were subjected to a final round of TBR branch swapping. Zero-length branches were collapsed if they lack support under any of the most parsimonious reconstructions (i.e., rule 1 of Coddington and Scharff, 1994).

This search strategy resulted in 5620 most parsimonious trees of 1863 steps (CI = 0.34, RI = 0.74), found in 1000 replications of RAS + TBR. Additional TBR branch swapping of these 5620 trees found 34,380 additional optimal topologies resulting in a total of 40,000 most parsimonious topologies. The large number of trees represents the maximum allowable number of trees stored in memory for TNT given the available RAM. As a result it is unlikely that this number represents the complete set of most parsimonious topologies. Nevertheless, a stable consensus reconstruction was obtained well before the completion of the initial 1000 replica-

tions of RAS + TBR, so although the complete set of MPTs is not available, it is unlikely that agreement on the relationships present in the consensus topology would change with additional sampled topologies. As in the previous analysis, *Mahakala omnogovae* was found to be the basalmost member of a monophyletic Dromaeosauridae (fig. 37). The monophyly of the clade is well supported (jackknife GC value of 34 and Bremer of 2), and the seven unambiguous synapomorphies are discussed below, as are the character-state changes within the clade that resulted from the inclusion of the *Mahakala*.

Accessory tympanic recess absent: A small recess is located dorsal to the crista interfenestralis in *Mononykus olecranus*, *Shuvuuia deserti*, *Archaeopteryx lithographica*, *Byronosaurus jaffei*, and *Sinovenator changii*. This structure was considered by Witmer (1990) to be an extension from the posterior tympanic recess. An accessory recess is known to be absent in large basal taxa such as *Allosaurus fragilis*, *Sinraptor dongi*, and *Tyrannosaurus rex*. The ornithomimids *Struthiomimus altus*, *Gallimimus bullatus*, and *Ornithomimus edmonticus* and the troodontid *Troodon formosus* also lack an accessory recess. Although unknown for many dromaeosaurids due to lack of completeness, its unambiguous absence in *Dromaeosaurus albertensis*, *Velociraptor mongoliensis*, *Tsaagan mangas*, and (importantly) *Mahakala omnogovae* results in this character state optimizing as a synapomorphy for Dromaeosauridae.

Paroccipital process elongate and slender, with dorsal and ventral edges nearly parallel: All maniraptorans (except *Erlikosaurus andrewsi* [Clark et al., 1994], *Citipati osmolskae* [IGM 100/978], and *Chirolestes pergracilis* [Currie and Russell, 1988]) have short paroccipital process with a convex distal end. Dromaeosaurids share a derived morphology (known to be present in *Mahakala omnogovae*, *Sinornithosaurus millenii*, *Dromaeosaurus albertensis*, *Tsaagan mangas*, *Adasaurus mongoliensis*, *Velociraptor mongoliensis*, and *Deinonychus antirrhopus*) of the paroccipital process being elongate and slender, with dorsal and ventral edges nearly parallel.

Paroccipital process with a dorsal edge twisted rostrally at the distal end: Currie (1995) identified this particular morphology as well as recognizing it as a character that was diagnostic of Dromaeosauridae. Even with the greatly expanded morphological and taxonomic diversity within dromaeosaurids, this twisted morphology of the paroccipital process remains an unambiguous synapomorphy for the clade as well as nearly nonhomoplastic (only paralleled in *Ornitholestes hermanni*).

MTII with ginglymoid distal articulation: The presence on the distal end of metatarsal II of a distinct deeply grooved and strongly asymmetrical ginglymus was one of the hallmark features in *Deinonychus antirrhopus* noted by Ostrom (1969). Given the “extraordinary” nature of this morphology Ostrom (1969) used this feature to unite *Dromaeosaurus albertensis*, *Deinonychus*, and *Velociraptor* together, distinctive of other deinonychosaurs (“dromaeosaurids” at Ostrom’s writing). Together with a suite of modifications to phalanx II-1, phalanx II-2, and the ungual phalanx, the ginglymoid articulation of the metatarsal II accounts for the extreme hyperextensible “raptorial” claw. Currently, this feature is shared convergently with some avialans like *Vorona berivotrensis* UA 8651 and *Ichthyornis dispar* (Marsh, 1872, 1880; Clarke, 2004). Among dromaeosaurids it is unknown in *Tsaagan mangas*, *Buitreraptor gonzalezorum*, *Neuquenraptor argentinus*, *Shanag ashile*, and *Achillobator giganticus*.

Anterior cervical centrum shape: In nearly all maniraptoriforms except dromaeosaurids the anterior cervical centrum extends beyond the posterior limit of the neural arch. In Dromaeosauridae, the anterior cervical centrum is level with or shorter than the posterior extent of each neural arch, which ultimately is a reversal to the plesiomorphic tetanuran morphology. For example, in more basal theropods (e.g., *Coelophysis*, *Dilophosaurus* UCMP 37302, *Allosaurus fragilis* [Madsen, 1976], *Tyrannosaurus rex* FMNH PR 2081), the anterior cervical centra do not extend beyond the posterior limit of the neural arch. The reversal to the plesiomorphic anterior cervical centrum morphology that is synapomorphic for dromaeosauridae is known in *Microraptor zhaoianus* (Hwang et al., 2002), *Tsaagan mangas* (IGM 100/1015), *Saurornitholestes langstoni* (TMP 67.20.36), *Velociraptor mongoliensis* (IGM 100/976), *Deinonychus antirrhopus* (AMNH FARB 3015), and *Mahakala omnogovae* (IGM 100/1033).

Stalklike parapophyses on dorsal vertebrae: In their detailed analysis of dromaeosaurids and in particular *Velociraptor mongoliensis* morphology Norell and Makovicky (1999) showed that parapophyses on the posterior trunk vertebrae were distinctly projected on pedicels. This feature remains a consistent dromaeosaurid synapomorphy even seen in primitive forms like *Microraptor*.

Location of anterior tympanic recess: Turner et al. (in press) identified a new synapomorphic character for dromaeosaurids pertaining to the reduced pneumaticity of the dromaeosaurid braincase relative to most derived maniraptorans. In extant avians (Witmer, 1990), *Archaeopteryx lithographica* (BMNH 37001), *Incisivosaurus gauthieri* (IVPP V13326), and basal troodontids (IGM 100/1126 and IGM 100/1323) the anterior tympanic recess migrated caudally to be located below the exit of cranial nerves VII and V. In dromaeosaurids, the lateral braincase wall has typically been considered less pneumatic (see Currie, 1995; Norell et al., 2006). The so-called basiptyergoid recess identified by Norell et al. (2006) is in fact a very anteriorly located anterior tympanic recess. Therefore, an anteriorly placed anterior tympanic recess with little or no development posterior to the basiptyergoid processes optimizes as a dromaeosaurid synapomorphy. This trait is evident in *Velociraptor mongoliensis* (IGM 100/982), *Adasaurus mongoliensis* (IGM 100/20), *Dromaeosaurus albertensis* (AMNH FARB 5356), *Microraptor* (IVPP uncataloged), and *Mahakala omnogovae* (IGM 100/1033).

CONCLUSIONS

Although known from only a single specimen, *Mahakala omnogovae* nevertheless represents a centrally important paravian taxon. Because it is fragmentary, it displays only a subset of classical “dromaeosaur” characteristics. *Mahakala* is nonetheless important for understanding patterns of character change within Dromaeosauridae as well as the evolution of such character systems such as the highly modified tail with extensive zygapophyses and hemal processes that span several vertebrae seen in more derived forms. Moreover, the small body size of *Mahakala* and its basal position within dromaeosaurids (a phylogenetic position further supported in the expanded analysis of this study) proves critical for reconstructing the ancestral size of Dromaeosauridae as well as the more inclusive paravian clade (Turner et al., 2007a).

The bizarrely short forelimbs of *Mahakala* have been placed in a broader context with the recent discoveries of the similarly short-limbed dromaeosaurids *Tianyuraptor ostromi* and *Austroraptor cabazai*. This indicates that a pattern of forelimb evolution much more complex than previously thought existed within this increasingly interesting clade.

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APPENDIX 1 ABBREVIATION LIST

Upper case L and R as a prefix signifies left and right.

aa	ascending process of astragalus	d	dentary
ace	acetabulum	dc	dorsal centrum
al	alveolus	dia	diapophysis
apt	aponeurosis tubercle on ulna	dr	dorsal rib
as	astragalus	dtr	dorsal tympanic recess
bct	biceps tubercle	ect	ectopterygoid
bf	brevis fossa	ep	epipophysis
brs	brevis shelf	f.l	lacimal facet
ca	calcaneum	f.po	postorbital facet
cav	caudal vertebra	fc	fibular crest
cc	cnemial crest or crista cranii	fe	femur
cec	cervical centrum	fh	femoral head
ch	chevron	fi	fibula
CN VII	facial foramen	fm	foramen magnum
CN X	vagus foramen	ft	foramen transversarium, or fourth trochanter of femur
cr	cervical rib		
ctr	caudal tympanic recess	gtr	greater trochanter

hu	humerus	pnf	pneumatic foramen
il	ilium	pop	paroccipital process
j.prqr	junction of palatine and quadrate ramus of pterygoid	prab	preacetabular blade of ilium
lc	lateral crest	prp	palatine ramus of pterygoid
ld	ledge below posterior tympanic recess	prz	prezygapophysis
lr	lateral ridge	pt	pterygoid, or posterior trochanter
ltr	lateral trochanter	ptab	postacetabular blade of ilium
mc	metacarpal	ptr	posterior tympanic recess
mco	medial condyle	q	quadrate
mt	metatarsus	q.pr	contact surface on prootic for quadrate
mxs	maxillary shelf	ra	radius
na	neural arch	sac	sacrum
ncl	neural canal	sc	scapula
ns	neural spine	slc	semilunate carpal
obr	oblique ridge	sp	splenic
oc	occipital condyle	ti	tibia
od	odontoid	tl	tectal lobe
ofd	olfactory depression	tp	transverse process
pap	parapophysis	tr	transverse process ridge
pat	posterior antitrochanter	ts	trochanteric shelf
pf	pneumatic foramen, or popliteal fossa	ul	ulna
ph	phalanx	uln	ulnare
		v.o	occipital vein track

APPENDIX 2

PHYLOGENETIC ANALYSIS DETAILS

The character list and data matrix employed in this study is based on Turner et al. (in press) and represents an expansion of the Theropod Working Group (TwiG) matrix. A total of 100 coelurosaurian taxa and 472 characters (51 ordered) were used in the analysis, with *Allosaurus fragilis* and *Sinraptor dongi* used to root the most parsimonious trees. The dataset is available by request from the first author or online (<http://www.anat.stonybrook.edu/people/facultypage/turner>).

Characters 16, 17, 18, 27, 40, 68, 76, 110, 113, 125, 132, 157, 169, 174, 198, 200, 244, 241, 315, 316, 320, 323, 338, 346, 369, 377, 383, 386, 391, 393, 420, 428, 433, 449, 455, 458, 465, 469, 475, 487, 492, 497, 499, 502, 509, 510, 511, 513, 519, 529, and 531 were ordered because they either represent potentially nested statements of primary homology or include presence/absence states. The dataset was treated with equally-weighted parsimony analysis implemented in TNT v. 1.0 (Goloboff et al., 2008a, 2008b). A heuristic tree search strategy was conducted performing 1000 replicates of Wagner trees (using ran-

dom addition sequences) followed by TBR branch swapping (holding 10 trees per replicate). The best trees obtained at the end of the replicates were subjected to a final round of TBR branch swapping. Zero length branches were collapsed if they lack support under any of the most parsimonious reconstructions (i.e., rule 1 of Coddington and Scharff, 1994). This analysis resulted in 40,000 most parsimonious trees of 1863 steps (CI = 0.34, RI = 0.74). For the purpose of the phylogenetic analysis, we followed Makovicky et al., (2005), and tentatively considered *Neuquenraptor argentinus* a junior synonym of *Unenlagia comahuensis*. *Unenlagia comahuensis* and *U. paynemili* were treated as a single terminal taxon.

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