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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 Djadoktha 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 Huincul, 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.
[a]Estimated 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.

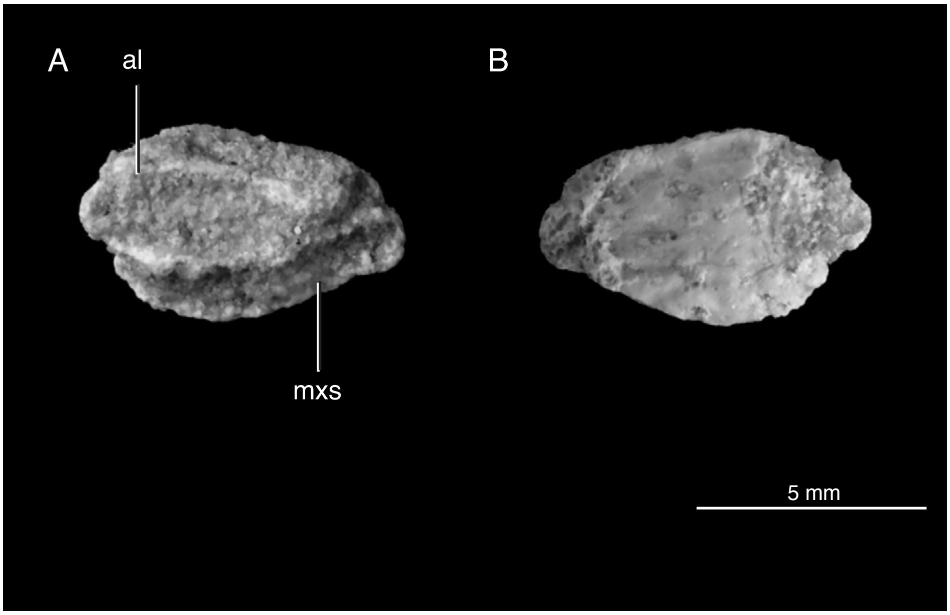

FIGURE 2. Left maxilla of *Mahakala omnogovae* in medial view (**A**) and lateral view (**B**).

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

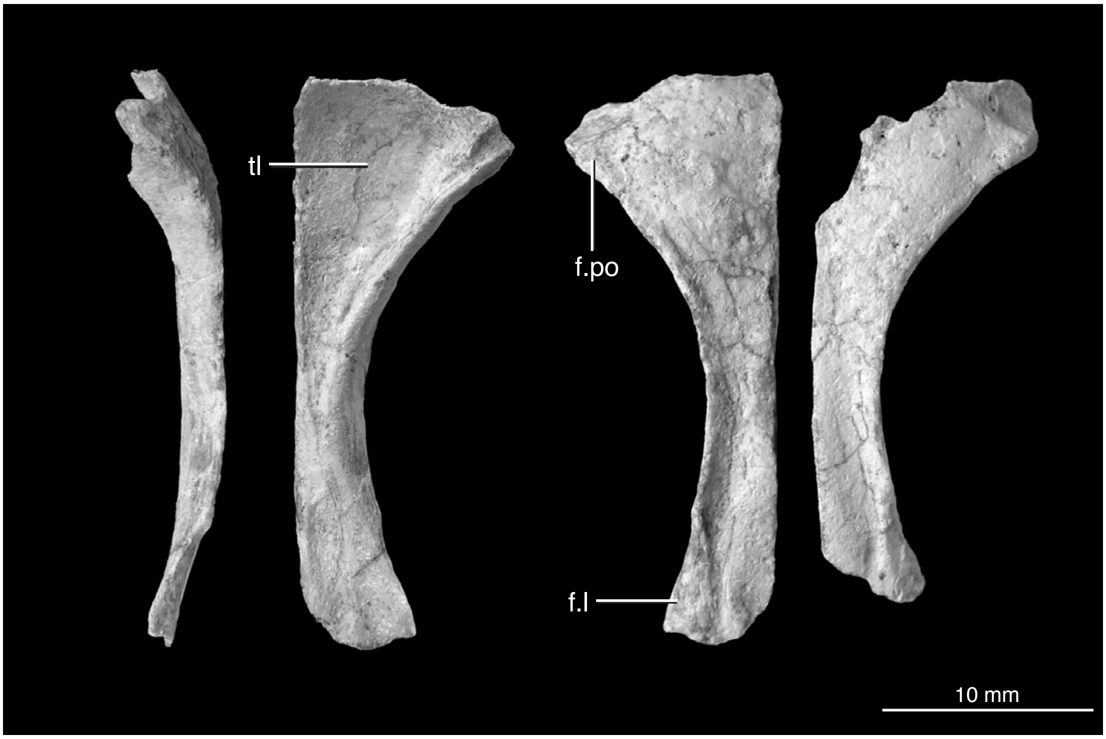

FIGURE 3. Right frontal of *Mahakala omnogovae* in lateral and ventral views (left). Left and right frontals of *Mahakala omnogovae* in dorsal view (right).

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 ending 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 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

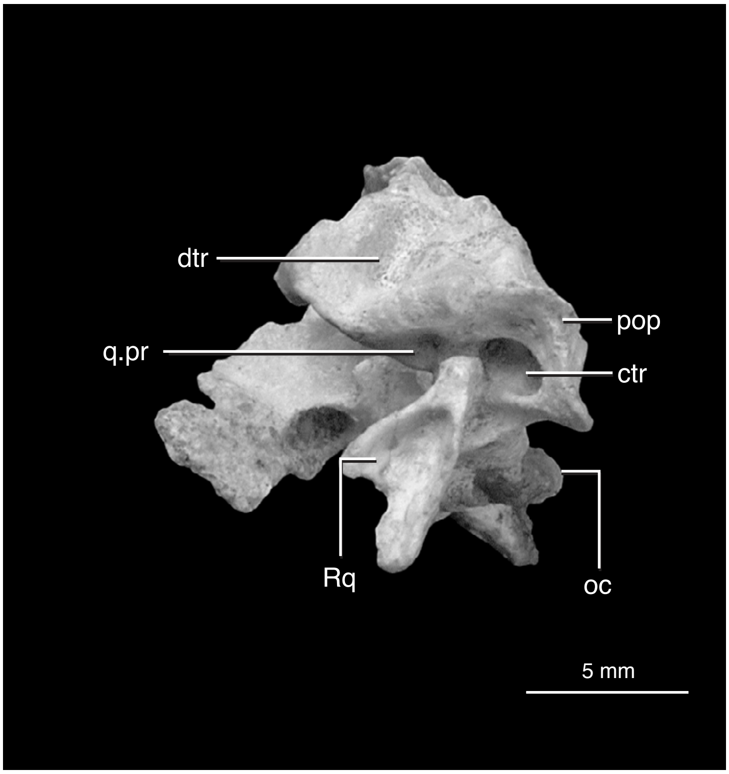

FIGURE 4. Braincase and proximal left quadrate of *Mahakala omnogovae* (IGM100/1033) in left lateral view.

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 midbrain. 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.

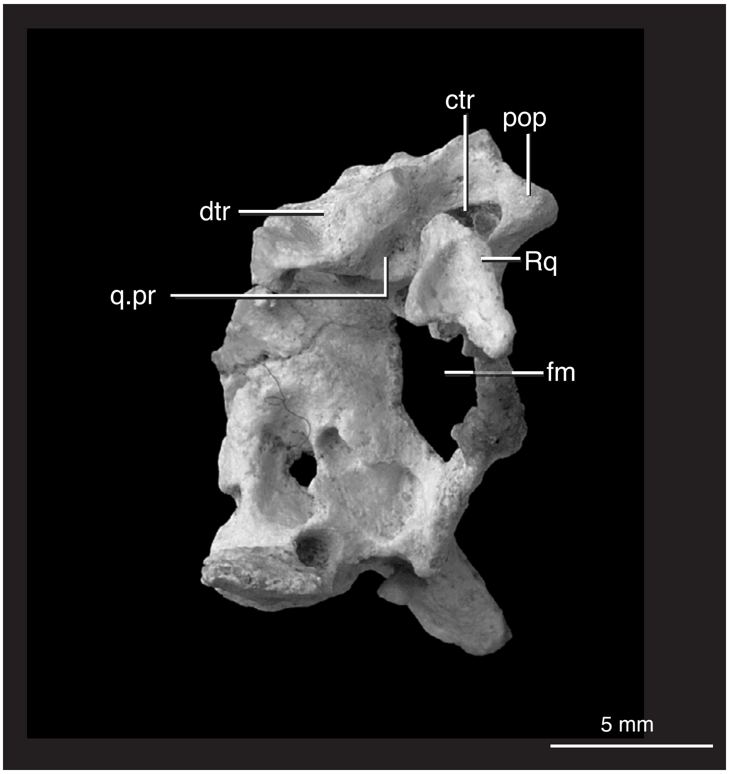

FIGURE 5. Internal surface of braincase and proximal left quadrate of *Mahakala omnogovae* (IGM 100/1033) in left ventrolateral view.

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-

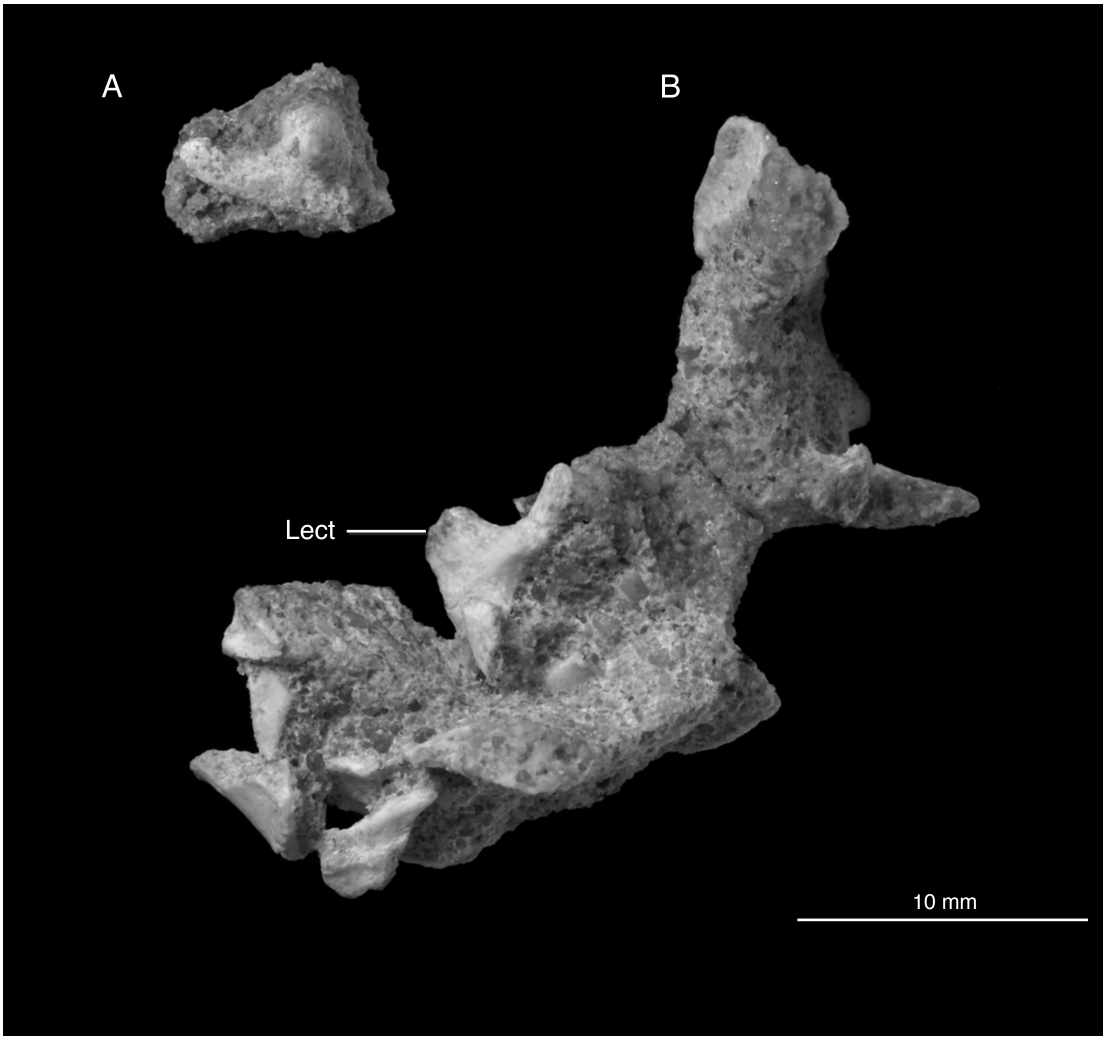

FIGURE 6. IGM 100/1033, *Mahakala omnogovae*. **A**, Possible right ectopterygoid in dorsal view. **B**, Left ectopterygoid in dorsal view.

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

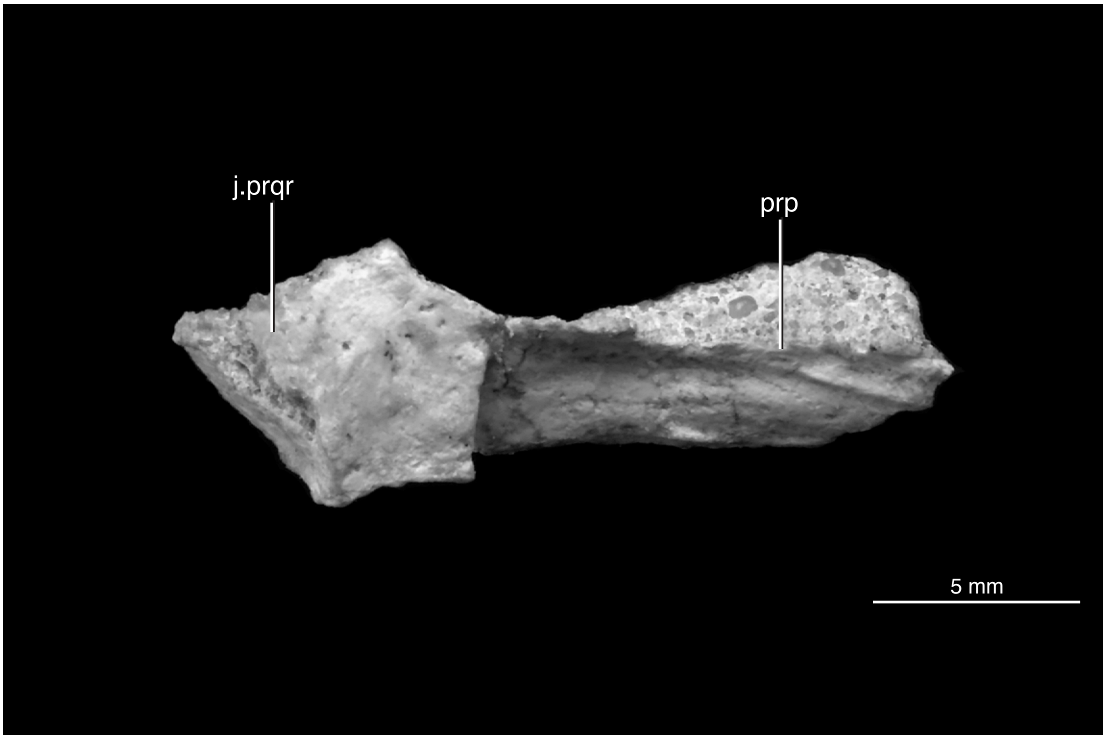

FIGURE 7. Partial right pterygoid of *Mahakala omnogovae* (IGM 100/1033).

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., *Velociraptor 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.

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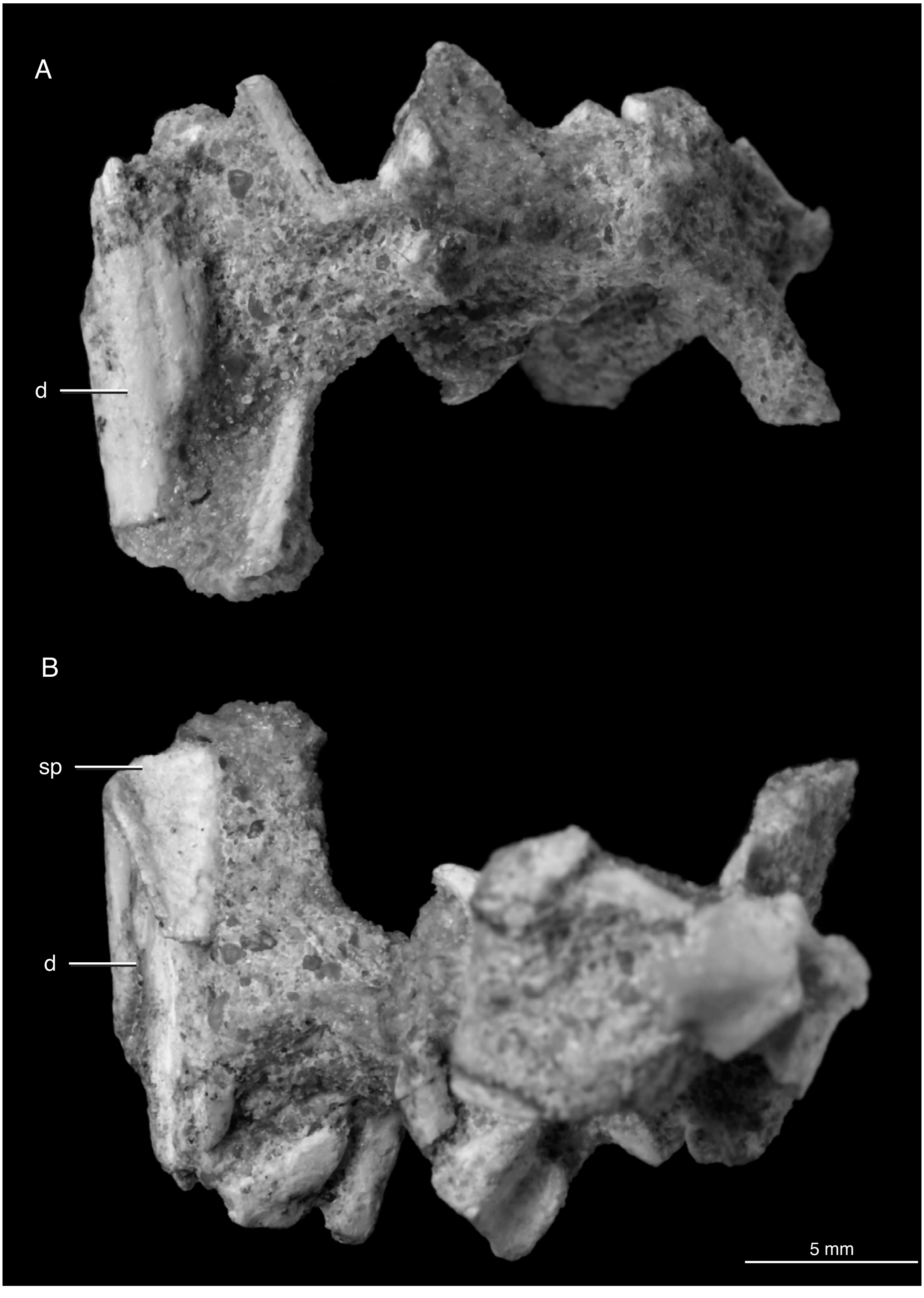
FIGURE 8. IGM 100/1033, *Mahakala omnogovae*. **A**, Partial right dentary in lateral view. **B**, Partial right dentary and splenial in medial view.


A
d
B
sp
d
5 mm

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 Meckalian 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 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).

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

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,

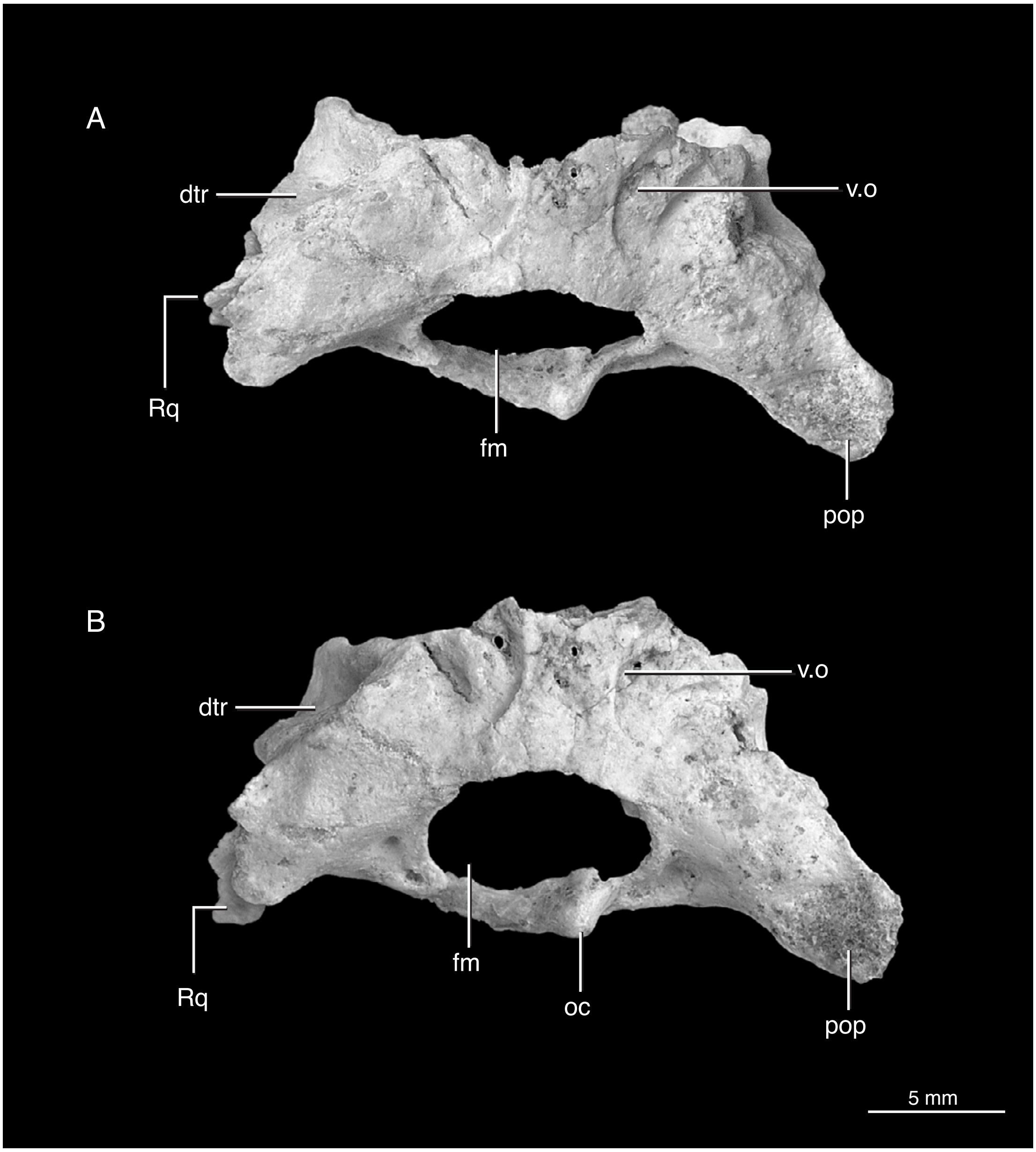


FIGURE 10. Occiput of *Mahakala omnogovae* (IGM 100/1033) in posterodorsal (**A**) and posterior (**B**) views.

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 crescentric 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

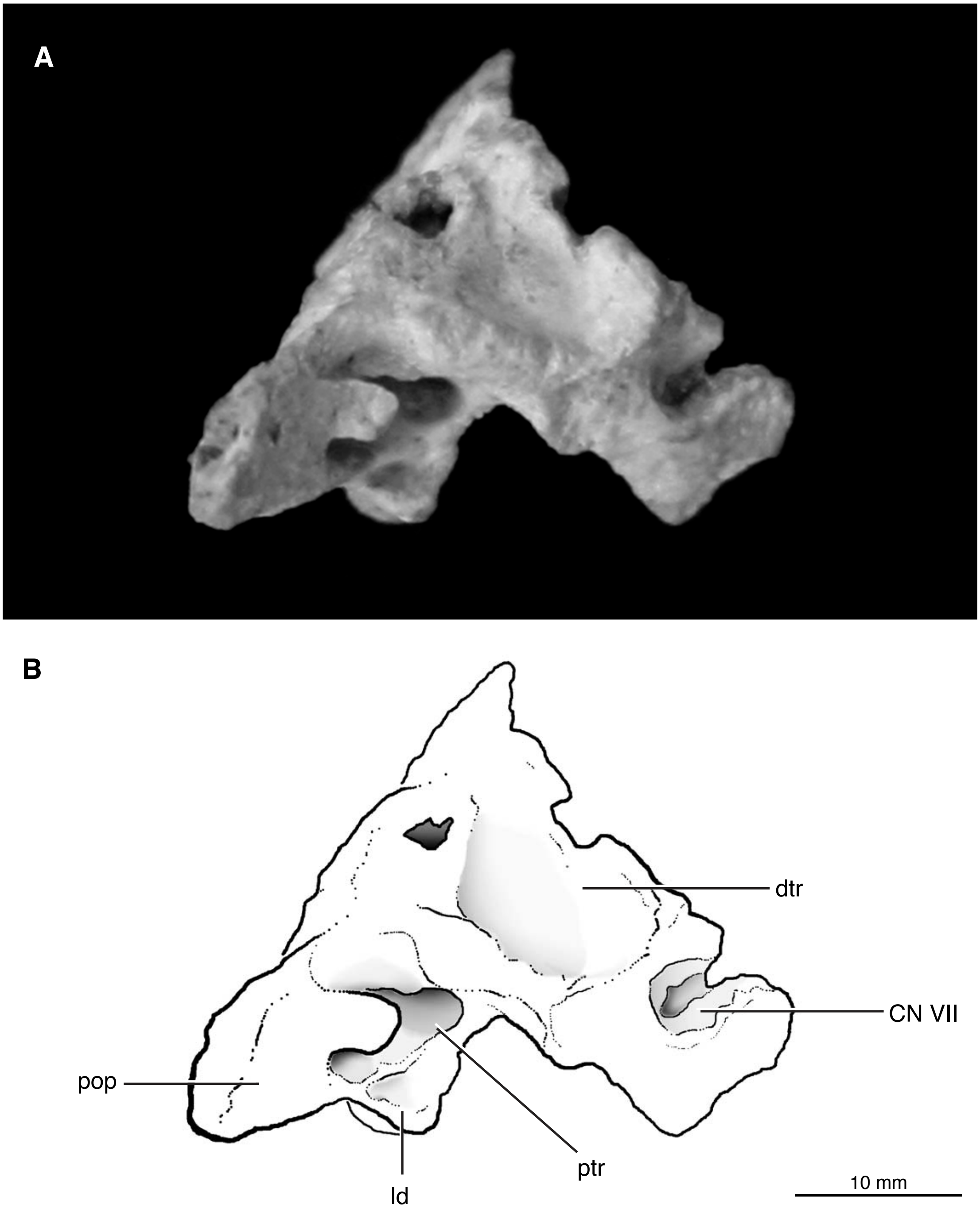


FIGURE 11. Lateral wall of braincase and paroccipital process of *Mahakala omnogovae* (IGM 100/1033) in right lateral view. **A**, Photograph. **B**, Line interpretation.

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 stapedial 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