A new dromaeosaurid from the Late Cretaceous Khulsan locality of Mongolia

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ABSTRACT

A new dromaeosaurid dinosaur, *Shri devi,* from the Late Cretaceous deposit of the Barun Goyot Formation at Khulsan, Mongolia, is described here. The Barun Goyot Formation (herein referred to as the Barun Goyot) is stratigraphically intermediate between the overlying Nemegt Formation and the underlying Djadokhta Formation, where much of the dromaeosaurid diversity has been reported to date. Sediments of the Barun Goyot are typically considered Upper Campanian in age. Although dromaeosaurid remains have been noted to occur in the Barun Goyot for decades, descriptive and taxonomic work has never been completed for the material. The holotype specimen (IGM 100/980) consists of a partially articulated individual preserving the right hind limb; left tibiotarsus; pelvis; and adjacent cervical, dorsal, and caudal vertebrae. IGM 100/980 is referable to a clade with *Velociraptor* based on the presence of a distinct ambiens tubercle located proximally on the anterior face of the pubis, a well-developed anterior tuberosity proximally located on the ischium, and a rounded longitudinal ischial ridge. It is distinguishable from *V. mongoliensis* based on a weak fourth trochanter (shared with all other dromaeosaurids) and deep anterior pedicular fossae in the cervical vertebrae; epipophyses in the last four cervicals are not raised but are instead represented by rugose circular scars. A suite of axial and appendicular characters are diagnostic for the new species. New discoveries including *Shri devi* allow for an improved understanding of dromaeosaurid anatomy, as well as the temporal and regional variation of the dromaeosaurid fauna of Mongolia and Inner Mongolia (Nei Mongol Autonomous Region, China), during the Late Cretaceous.

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INTRODUCTION

A large diversity of theropod dinosaur remains have been recovered from the Late Cretaceous deposits of Mongolia and Inner Mongolia, China (see refs. In Turner et al., 2012, Cau et al, 2017, Xu et al., 2010), with the joint expeditions of the Mongolian Academy of Sciences and the American Museum of Natural History playing a crucial role in this (Norell and Makovicky, 1997; Norell et al., 1995; Clark et al., 2001; Norell et al., 2006; Turner et al., 2007a; Turner et al., 2009; Turner et al., 2011; Nesbitt et al., 2011; Makovicky et al., 2003; Balanoff and Norell, 2012; Pei et al., 2017).

Although remaining relatively rare, the number of known dromaeosaurid species has increased exponentially in the past decade and a half (Turner et al., 2012). This has led to a concomitant increase in our knowledge of dromaeosaurid diversity, geographic extent, and the distribution of complex featherlike integumentary structures within the clade (Norell and Xu, 2005; Norell et al., 2006; Turner et al., 2007a, 2007b, 2012; Lü and Brusatte, 2015; Cau et al., 2017, Pittman et al., 2020, Ding et al., 2020). Detailed anatomical descriptions have not always followed the rapid pace of discovery; and some species are known from single relatively incomplete specimens. Thus, details of the osteology and anatomical variation present in the postcranial skeleton of dromaeosaurids remain underappreciated.

The oldest Mongolian dromaeosaurid is *Shanag ashile*, a small enigmatic microraptorinelike dromaeosaurid known from the Early Cretaceous Öösh locality of Baykhangor Mongolia (Turner et al., 2007a). Whereas the youngest occurring Mongolian dromaeosaurids, *Adasaurus mongoliensis* Barsbold (1983) and *Achillobator giganticus* Perle et al. (1999), are known from the early Maastrichtian Nemegt Formation and Santonian-Cenomanian Bayanshiree locality, respectively. Four additional dromaeosaurid taxa have been reported from the underlying Djadokhta Formation, including *Velociraptor mongoliensis* Osborn (1924), *Tsaagan mangas* Norell et al. (2006), *Mahakala omnogovae* Turner et al. (2007c), and *Halszkaraptor escuilliei* (Cau et al., 2017). *Velociraptor mongoliensis* is known from Bayn Dzak (Osborn, 1924), Chimney Buttes (Norell and Makovicky, 1999), and Tugrugyin Shireh (Kielan-Jaworowska and Barsbold, 1972), where at the latter locality it cooccurs with the basal dromaeosaurid *Mahakala omnogovae* (Turner et al., 2007c). *Tsaagan mangas* is known from Ukhaa Tolgod where it co-occurs with *Halszkaraptor escuilliei,* the sister taxon of *Mahakala*. A second *Velociraptor* species, *V. osmolskae*, is known from the Djadokhta-equivalent Bayan Mandahu Formation of Inner Mongolia, China (Godefroit et al., 2008; Xu et al., 2010). The latter formation is also home to *Linheraptor exquisitus* (Xu et al., 2010, Xu et al., 2015) the sister taxon of *Tsaagan* (but see comments in Turner et al., 2012). Thus, there are at least five Djadokhta-aged dromaeosaurids with *Velociraptor mongoliensis* the most common and best understood (Barsbold and Osmólska, 1999; Norell and Makovicky, 1997; 1999).

The Barun Goyot Formation occurs beneath the Nemegt and above the Djadokhta Formation, respectively (Dashzeveg et al., 2005). It has prominent outcroppings at Khulsan

and Khermeen Tsav (Gradzinski and Jerzykiewicz, 1974). *Hulsanpes perlei* was described by Osmólska (1982) and referred to Dromaeosauridae. Subsequently this taxon, known only from a partial foot, has been consider a problematic paravian and likely not diagnosable (Makovicky and Norell, 2004; Turner et al., 2012; Agnolín and Novas, 2013). Recently, Cau et al., (2017) recovered *Hulsanpes* in a clade with the basal dromaeosaurids *Mahakala* and *Halszkaraptor*. Although velociraptorine material has been reported from Khulsan (Weishampel et al., 2004) and partially figured by Norell and Makovicky (1999), a detailed examination of this material has not been completed.

Here we describe a new species of dromaeosaurid from Khulsan, which marks the first unequivocal dromaeosaurid taxon from the Late Cretaceous Barun Goyot Formation. This specimen (IGM 100/980) consists of a partial articulated individual preserving the right hind limb, pelvis, and adjacent cervical, dorsal and caudal vertebrae (fig. 1). IGM 100/980 is known from well-preserved partial skeleton that preserves characteristics diagnostic of dromaeosaurids as well as a number of features including the presence of a distinct ambiens tubercle located proximally on the anterior face of the pubis, a well-developed anterior tuberosity proximally located on the ischium, and a rounded longitudinal ischial ridge allows referral of this material to a clade containing *Velociraptor*. Discovery of this new species expands the known range among species of Mongolian dromaeosaurids, provides key new data on the regional and temporal diversity of the Late Cretaceous dromaeosaurid fauna of Mongolia, and the exquisite preservation of IGM 100/980 provides new details on the postcranial skeleton of dromaeosaurids.

The specimen was collected in July 1991 during the first full scale expedition of the joint Mongolian Academy of Sciences American Museum of Natural History expedition to the Gobi Desert. The specimen was found by M.A.N. and excavated over a period of days by M.A.N., James M. Clark, Lowell Dingus, and Altangerel Perle .

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
IGM	Mongolian Institute of Geology, Ulaan Bataar, Mongolia
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, MA
MNU	Mongolian National University, Ulaan Bataar, Mongolia
MPCA	Museo Carlos Ameghino, Cipolletti, Río Negro Province, Argentina
MOR	Museum of the Rockies, Bozeman, Montana
UA	University of Antananarivo, Madagascar
YPM	Peabody Museum of Natural History, Yale University, New Haven, CT

FIGURE 1. Pelvis and right hind limb of IGM 100/980 after initial stage of preparation. Top image is a left lateral view; bottom image is a ventral view of pelvis and medial view of hind limb.

FIGURE 2. Tongka depicting Shri Devi (Palden Lhamo), after which the dromaeosaurid from Khulsan is named.

SYSTEMATIC PALEONTOLOGY
THEROPODA MARSH, 1884
COELUROSAURIA VON HUENE, 1914
MANIRAPTORA GAUTHIER, 1986
DROMAEOSAURIDAE MATTHEW AND BROWN, 1922
Shri devi, new genus, new species

HOLOTYPE: IGM 100/980. Partial articulated skeleton including 23 presacral vertebrae, pelvis, anterior caudal vertebrae and chevrons, right leg including the femur, tibiotarsus, and pes, and the left tibiotarsus.

ETYMOLOGY: "Shri Devi," Sanskrit for a female protector deity in Tibetan/Mongolian Buddhism (fig. 2). Part of the Gelug tradition and particularly venerated in Mongolia, Shri Devi (Palden Lhamo) rides a horse or donkey across an ocean of blood. Her accoutrements include a saddle of a flayed human skin, the book of the law, and the dice of fortune.

FORMATION AND LOCALITY: Bayun Goyot Formation, Khulsan, Ömnögov, Mongolia. No complete section for the Barun Goyot Formation at Khulsan has been constructed. What can be said is that IGM 100/980 is composed of the type of sediments present at other Djadokhta (Ukhaa Tolgod, Udan Sayr, and Bayn Dzak) and Djadokhta-like (Red Beds of Kheerman Tsav, Bayan Mandahu and Khulsan) localities. These are considered to be a mélange of aeolian, debris flow, fluvial, and lacustrine sediments. The environment of these sediments at time of deposition is considered to be an arid to semiarid region, with an equable climate (Dingus et al., 2008, Montanari et al., 2013).

DIAGNOSIS: Referable to a clade including *Velociraptor* based on the presence of a distinct ambiens tubercle located proximally on the anterior face of the pubis, a well-developed anterior tuberosity proximally located on the ischium, and a rounded longitudinal ischial ridge. Distinguishable from *Velociraptor mongoliensis* based on a weak fourth trochanter (shared with all other dromaeosaurids), deep anterior pedicular fossae in the cervical vertebrae, epipophyses in the last four are not raised but instead represented by rugose circular scars. *Shri devi* is furthered diagnosed by the following combination of characters (asterisks denote autapomorphies): epipophysis on the first dorsal vertebra (d1) large and overhanging the posterior margin of the postzygapophysis*; two dorsoventrally aligned pleurocoels on d1 and d2*; posteriorly inclined scar on the lateral surface of the neural arch*; proportionally longer metatarsus (44% femur length compared to 35% femur length in IGM 100/986), and proportionally larger ungual phalanx on pedal digit 2 (1.01% MT II length compared to 90% MT II length in IGM 100/982 and IGM 100/985).

DESCRIPTION

THE AXIAL COLUMN

Twenty-three presacral vertebrae are in preserved in articulation in IGM 100/980. These represent a complete presacral series lacking only the atlas and axis vertebrae. Most of the

FIGURE 3. Cervical vertebrae 3 through 6 of IGM 100/980 in left lateral view.

dromaeosaurid specimens recovered from Djadokhta localities suffer from extensive arthropod scavenging along the intercentral faces (personal obs., but also see Norell et al., 2006). IGM 100/980 is largely unscavenged and therefore provides new information on the cervical vertebrae morphology in dromaeosaurids. The eight post-axial cervicals (figs. 3–11) are present along with 13 dorsals (figs. 12–15). Six sacral vertebrae are present in IGM 100/980 but these are poorly preserved (fig. 16). The proximalmost eight caudal vertebrae are present but variably preserved.

CERVICAL VERTEBRAE: The cervical centra are platycoelous but with the posterior articular surface more concave than the anterior surface (figs. 4-7). Since Ostrom (1969), many workers have noted the pronounced anteroventrally directed anterior intercentral articular surface (Senter et al., 2004; Norell et al., 2006) and overall oblique angling of the centra. In IGM 100/980, and most likely other dromaeosaurids (Norell and Makovicky, 1997; 1999), the anterior articular surface is formed almost entirely from the bases of the neural arch pedicels, with the central body contributing to the articular surface only to a limited degree (figs. 4C, 5C, 6C, 7C). This anterior portion of the centra is weakly concave and slightly rugose. A small rugose tubercle is located on the midline just posterior to the anterior concavity of the centrum body, which may indicate an intercentral ligament attachment point (see Baumel and Witmer, 1993). The postaxial cervical centra are relatively short and wide in ventral view (figs. 4B, 5B, 6B, 7B). In lateral view, the third cervical (c3) to the sixth cervical (c6) centra are wedge shaped or triangular, anteriorly narrow, and broadening posteriorly (fig. 3). By c7 the centra bodies broaden and become more boxlike, with the articular facets no longer so strongly oblique (figs. 8,9). As in other dromaeosaurids, the anterior cervical centra do not extend beyond the posterior limit of the neural arch and are distinctly wider than higher in anterior view (see examples in Turner et al., 2012).
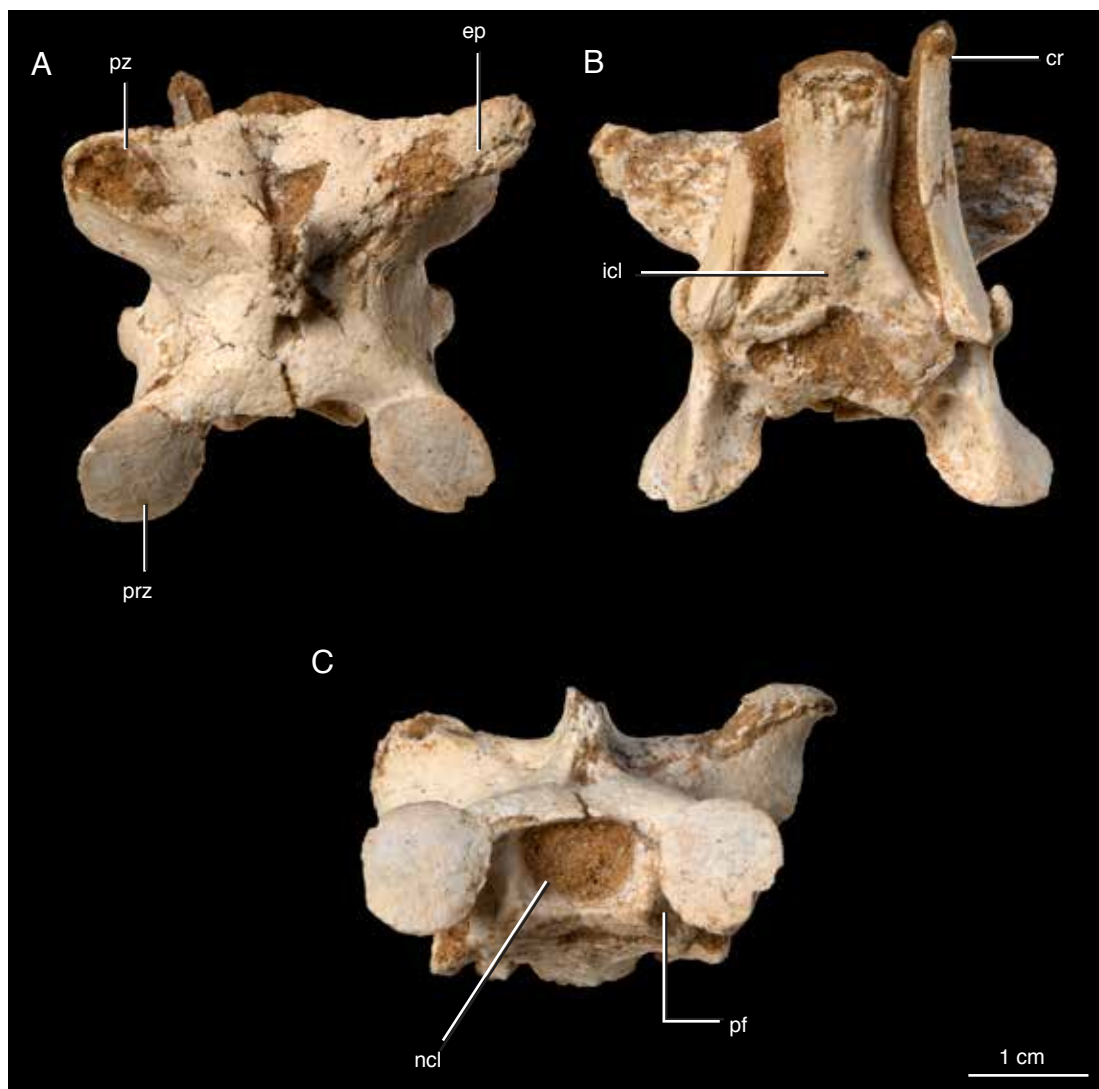
FIGURE 4. Cervical vertebra 3 of IGM 100/980 in **A,** dorsal, **B,** ventral, and **C,** anterior views.

All the cervical centra lack hypapophyses although the ventral surface of c10 is keeled as in *Tsaagan mangas* (IGM 100/1015) (fig. 9). The ventral midline regions of c3 to c8 lack any indication of carotid processes or a raised ventral lip (fig. 10). Cervical 9 possesses a raised lip on the anterior margin as in *Velociraptor mongoliensis* (IGM 100/986), cf. *Saurornitholestes langstoni* (MOR 660), and *Tsaagan mangas* (IGM 100/1015).

The parapophyses are oval shaped in lateral view in c3 to c7 and circular in the succeeding cervicals and become larger and more projected as one moves posteriorly through the column (figs. 4A, 5A, 6A, 7A). A single pneumatopore is present just posterior to the parapophysis.

The pedicels meet along the midline anteriorly and appear to come close or meet posteriorly, excluding the centrum from the neural canal. In both anterior and posterior views, the
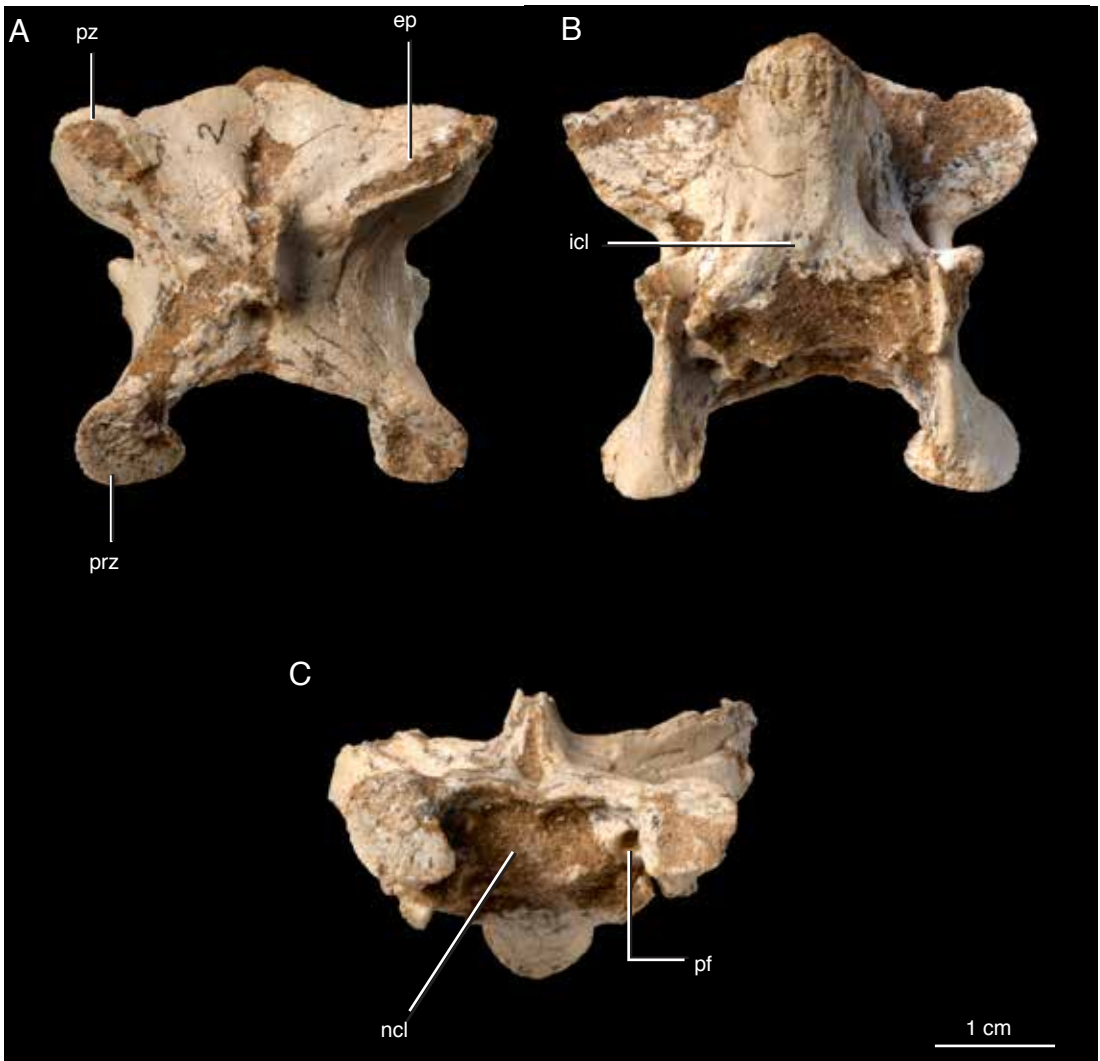
FIGURE 5. Cervical vertebra 4 of IGM 100/980 in **A,** dorsal, **B,** ventral, and **C,** anterior views.

neural canal is quadrangular, slightly wider than high. Deep anterior pedicular fossae are present as in *Deinonychus antirrhopus* (Ostrom, 1969), but unlike *Tsaagan mangas* (IGM 100/1015) or *Velociraptor mongoliensis* (IGM 100/976) (figs. 4B, 5B, 6B, 7B). The pedicular fossae become shallow and broad in c8 and c9, and are all but absent by c10 (fig. 11).

In the anterior cervicals, the flattened diapophyses are short and project ventrally. The diapophyses are closely situated to the lateral wall of the centrum and near their complementary parapophyses, thus forming narrow transverse foramina (*foramen transversarium* of Baumel and Witmer, 1993). By c7 the diapophyses become more robust and dorsolaterally placed. Large ventrally opening pneumatic recesses are present posterior to the diapophyses in c3–c6 (fig. 9). This same recess is laterally opening in c7, dorsolaterally opening in c8 and c9, and dorsally opening in c10. Tracking this recess into the dorsal vertebral series indicates this recess
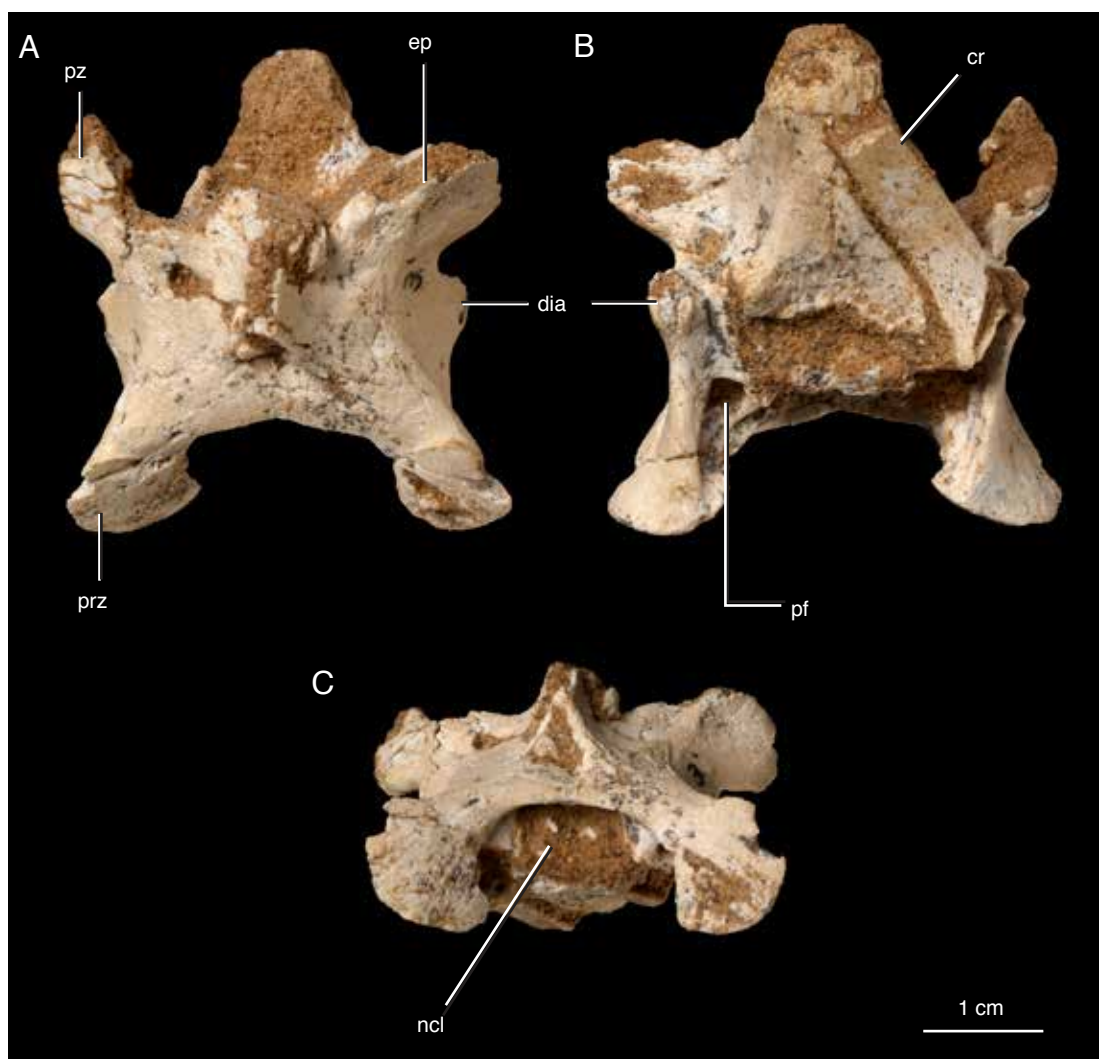
FIGURE 6. Cervical vertebra 5 of IGM 100/980 in **A,** dorsal, **B,** ventral, and **C,** anterior views.

most likely is homologous to the infrapostzygapophseal recesses of the dorsal vertebrae. Given this interpretation, no infradiapophyseal or infraprezygapophyseal recesses are present in the cervical series. This is in contrast to the presence of these recesses in *Tsaagan* (Norell et al., 2006) and *Buitreraptor* (Gianechini et al., 2018).

The anterior cervical prezgyapophyses are oval, located lateral and in line with the neural canal. The prezygapophyseal facets are oriented anteriorly with a slight medial component, as in *Deinonychus antirrhopus* (Ostrom, 1969), *Velociraptor mongoliensis* (IGM 100/976), and *Tsaagan mangas* (IGM 100/1015). In *Tsaagan*, the prezygapophyseal facets are much smaller and narrower relative to centrum size. Moving posteriorly, the prezygapophyses become more widely spaced and circular in outline. By c8 the prezygapophyses face predominately dorsomedially and are no longer inline with the neural canal, being more dorsally located.
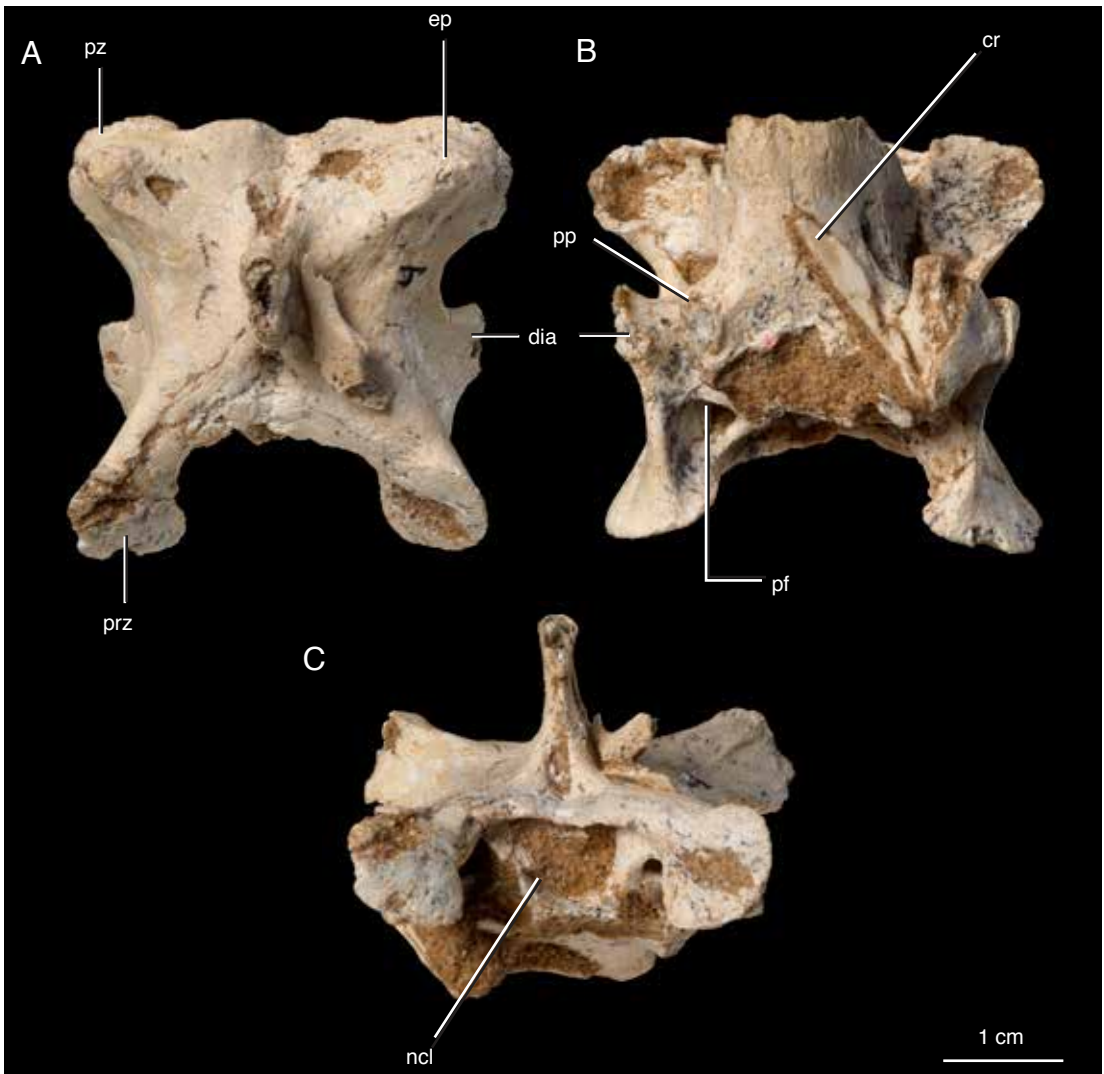
FIGURE 7. Cervical vertebra 6 of IGM 100/980 in **A,** dorsal, **B,** ventral, and **C,** anterior views.

The postzygapophyses are also large and oval to subcircular. Anteriorly, the postzygapophyses have short processes and do not project beyond the posterior margin of the centrum body. By c6 however, the postzygapophyses project farther, exceeding the posterior limit of the centrum. The trend continues to c8, which has the longest and narrowest postzygapophyses. The postzygapophyses in c9 and c10 are considerably shorter than the preceding vertebrae.

In dorsal view, the neural arches are quite broad and square in c3–c7 (figs. 4–7). By c8 the neural arch is more mediolaterally narrow due in large part to the anterior migration of the diapophysis and the lack of the broad lamina linking the prezygapophysis to the postzygapophysis (fig. 11). Prominent epipophyses are situated on the postzygapophyeses of c3–c6. They greatly overhang the posterior margin of the postzygapophysis on c3 and c4, whereas in
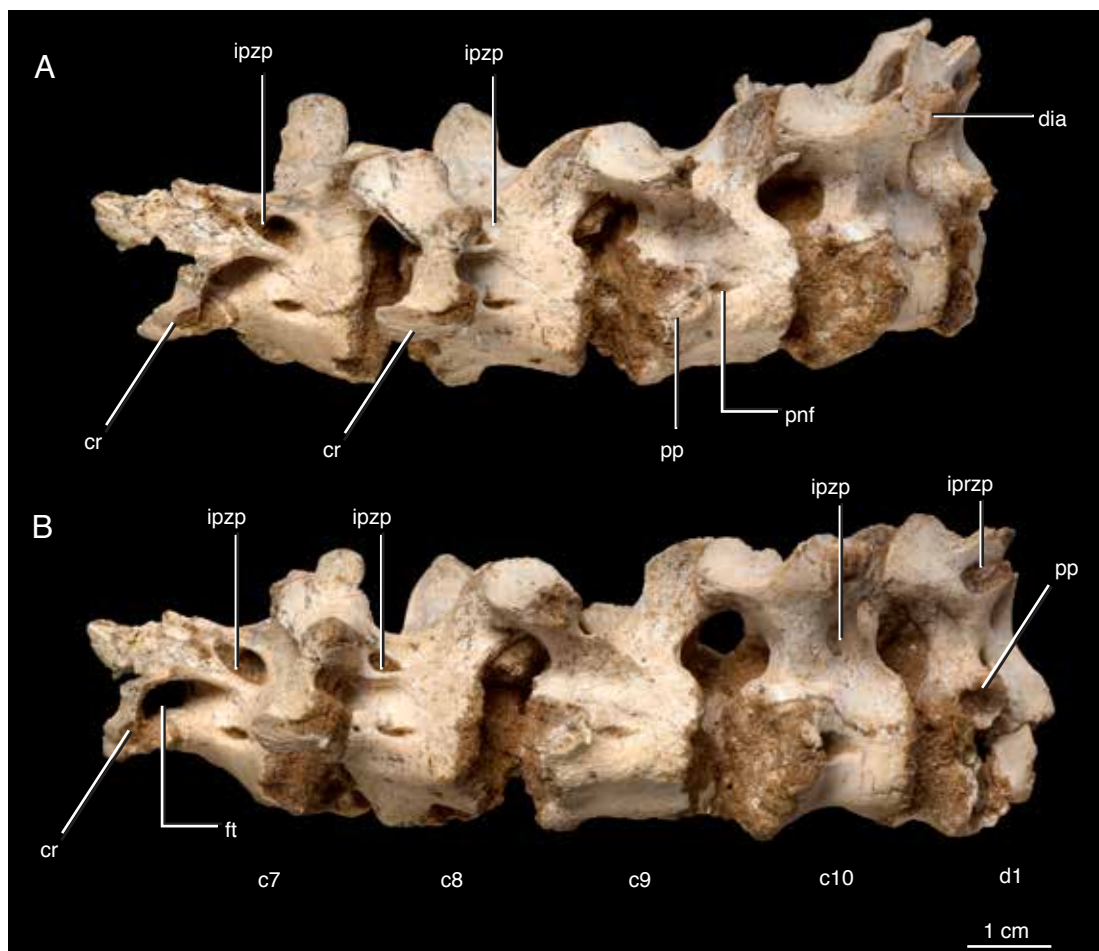
FIGURE 8. Posterior cervical vertebrae (7–10) and first dorsal vertebra of IGM 100/980 in **A,** left lateral and **B,** slight ventrolateral views.

c6 they do not overhang the margin. C5 is not preserved well enough to determine whether the epipophyses overhang the postzygapophyses. In the last four cervicals, the epipophyses are not raised but instead represented by rugose circular scars (fig. 11). This is unlike *Velociraptor mongoliensis* (IGM 100/982) and *Deinonychus antirrhopus* (Ostrom, 1969), which have robust epipophyses throughout the series but similar to *Adasaurus mongoliensis* (IGM 100/20) and *Microraptor zhaoianus* (Hwang et al., 2002). The last two taxa have much smaller epipophyses that do not overhang the postzygapophysis posteriorly. Due to incomplete preparation, it is currently uncertain in IGM 100/980. As in most coelurosaurians, the neural spines are short and centered on the neural arch, giving the arch an X shape in dorsal view (Makovicky and Sues, 1998). A deep midline depression is located posterior to the neural spine. This depression is broad with weakly defined dorsal borders, such as is seen in *Velociraptor mongoliensis* (IGM 100/976) and *Deinonychus antirrhopus* (Ostrom, 1969) but unlike the narrow depression in *Tsaagan mangas* (IGM 100/1015).
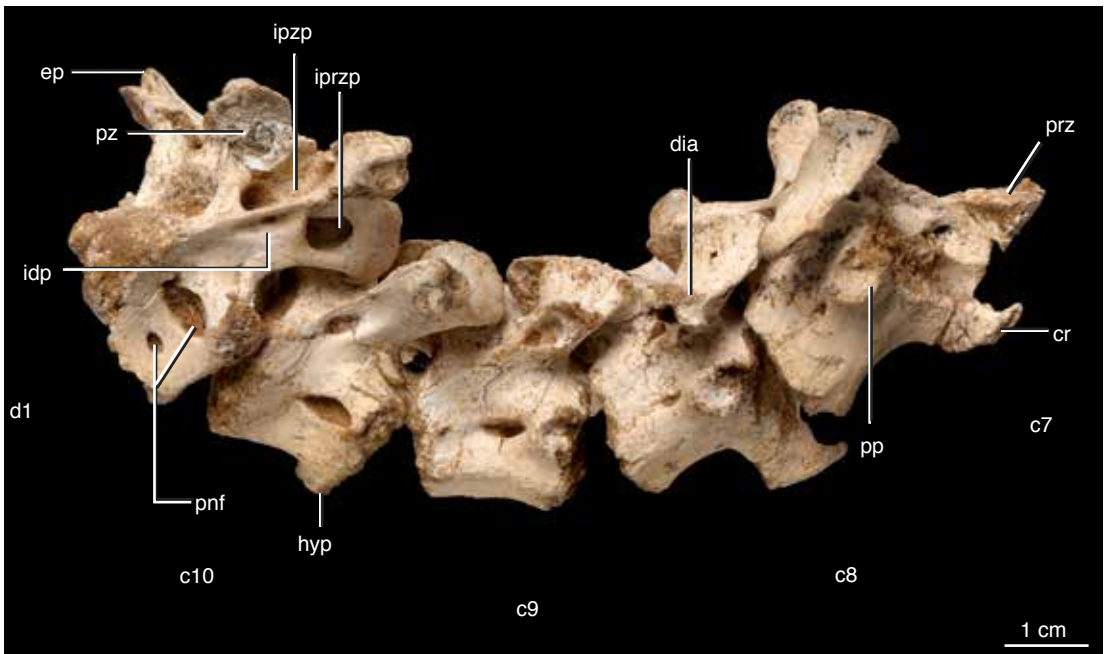
FIGURE 9. Posterior cervical vertebrae (7–10) and first dorsal vertebra of IGM 100/980 in right lateral view.

Only a few cervical ribs are preserved. In c3, the rib is triangular anteriorly with closely placed tubercular and capitular facets (fig. 4). The rib shaft tapers posteriorly and has little to no anterior projection. None of the posterior cervical ribs are completely preserved; however, the left c8 rib shows the presence of a short anterior process.

DORSAL VERTEBRAE: The first nine dorsal vertebrae are well preserved, whereas the last five are poorly preserved particularly around the vertebral centrum (figs. 12–15). The anterior four dorsal vertebrae (d1–d4) are spool shaped, deeply constricted, and have prominent hypapophyses. Beginning at d5 the centra are short and compressed slightly dorsoventrally having a much more boxlike shape. A small ventral keel is present on d5 but absent on all the succeeding vertebrae (fig. 13). All dorsal vertebrae are amphiplatyan, although the intervertebral facets are poorly preserved in the posterior dorsals. Unlike *Velociraptor mongoliensis* (IGM 100/985, IGM 100/986) but similar to *Deinonychus antirrhopus* (Ostrom, 1969), the centra bear large pleurocoels near the suture with the neural arches. A feature unique to *Shri devi* is the presence of a second subsidiary pleurocoel ventral to the main pleurocoel on d1 and d2 (figs. 9, 14).

All prezygapophyses on the dorsal vertebrae are broad and circular (fig. 12). On d1 and d2 the prezygapophyses are anteromedially inclined, posteriorly the prezygapophyses face dorsally and are little differentiated from the dorsal surface of the neural arch. The sizes of the prezygapophyses decrease posteriorly. Small medially directed hypantra are located adjacent to the prezygapophyses.

The articular facets of the postzygapophyses are circular and ventrally directed on all dorsal vertebrae. A prominent epipophysis is located on the dorsal surface of the postzygapophysis on

FIGURE 10. Posterior cervical vertebrae (7–10) of IGM 100/980 in ventral view.

d1 and d2 (fig. 9). The epipophysis is particularly large on d1 and overhang the posterior margin the postzygapophysis, unlike *Velociraptor mongoliensis* (Norell and Makovicky, 1999), *Deinony-chus antirrhopus* (Ostrom, 1969), and *Adasaurus mongoliensis* (IGM 100/20). It is unclear whether this condition is present in *Saurornitholestes* (MOR 660) or *Rahonavis* (UA 8656). The anterior dorsal vertebrae of *Buitreraptor gonzalezorum* (MPCA 245) are not well preserved enough to determine the presence or absence of this feature. Hyposphenes are present medial to the postzyg-apophyses in IGM 100/980. Additionally, both the left and right prezygapophyses and postzyg-apophyses are placed lateral to the neural canal and therefore are separated for their complementary zygapophyses at the midline by a groove for the interspinous ligament.

The transverse processes of the anterior dorsal vertebrae are long and thin, as in other dromaeosaurids (Norell and Makovicky, 1999; Turner et al., 2012), while the last two dorsals possess short transverse processes, which have deep recesses at their base. Like other drom-aeosaurids (Norell and Makovicky, 1999; Turner et al., 2012), the dorsal vertebrae of IGM 100/980 indicate that the parapophyses are raised on a short process or pedicel, but remain
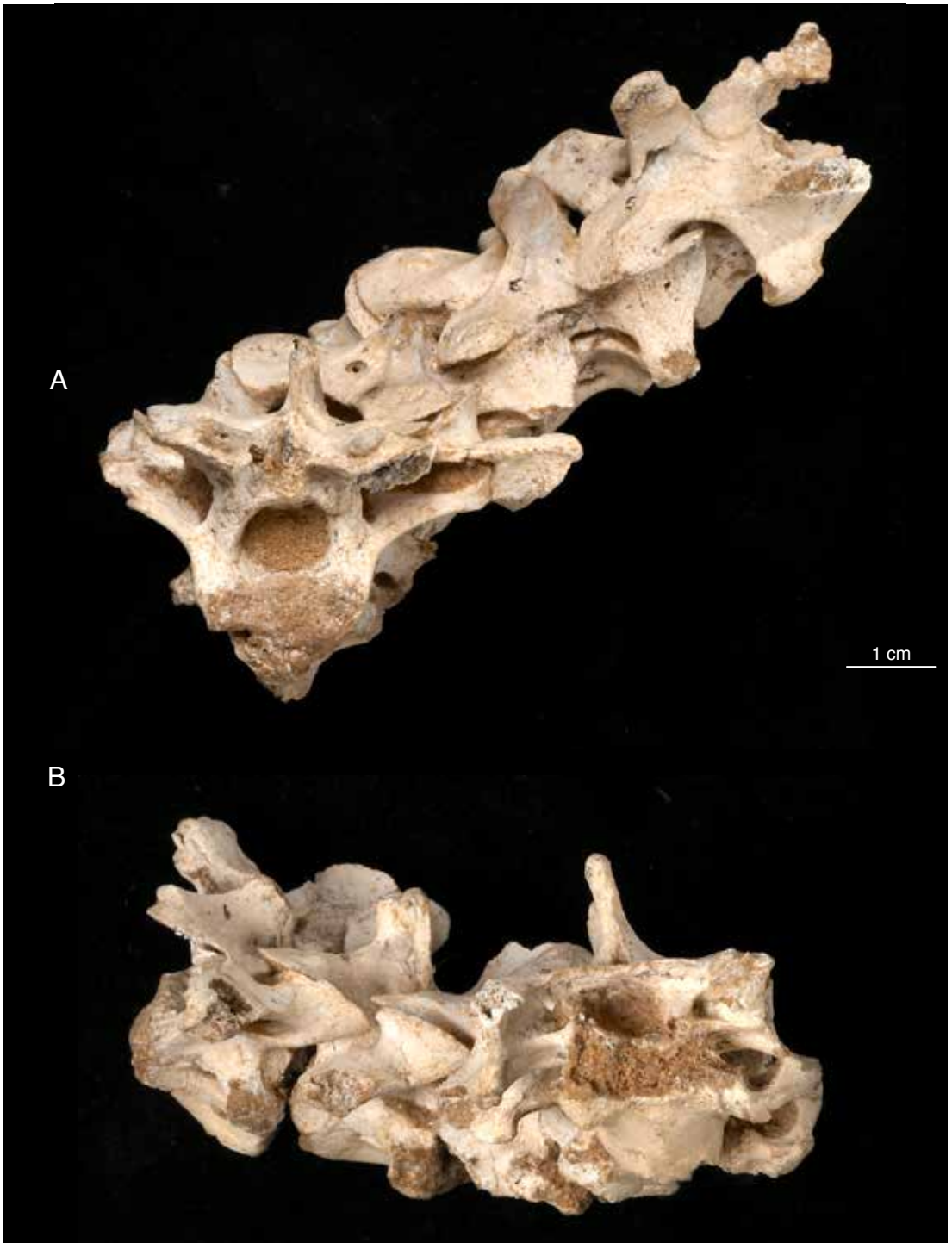
FIGURE 11. Posterior cervical vertebrae (7–10) and first dorsal vertebra of IGM 100/980 in **A,** posterior view with preceding vertebrae arch anterolaterally and **B,** anterior view with successive vertebra arch posterolaterally.
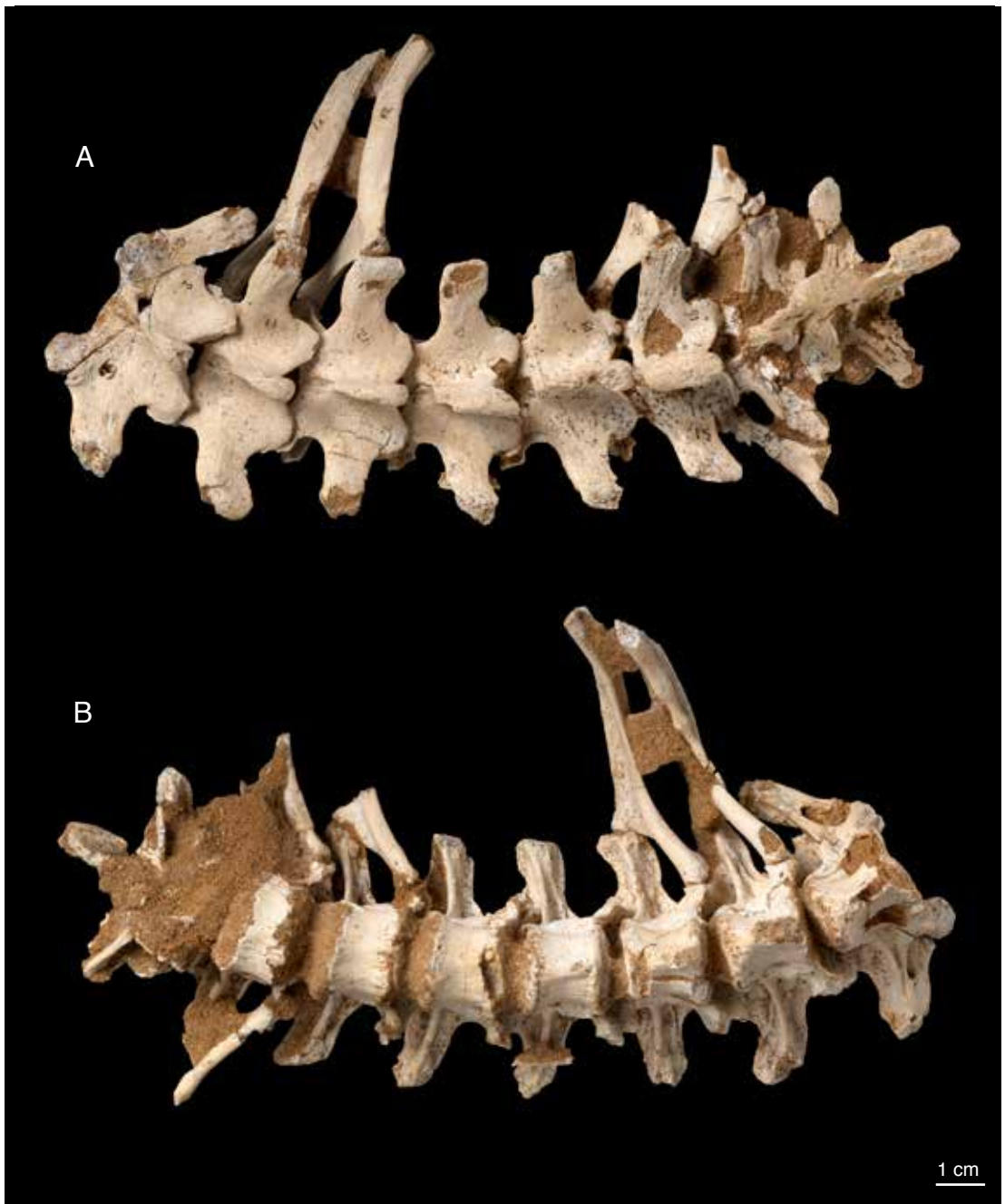
FIGURE 12. Dorsal vertebrae (2–9) of IGM 100/980 in **A,** dorsal and **B,** ventral views.
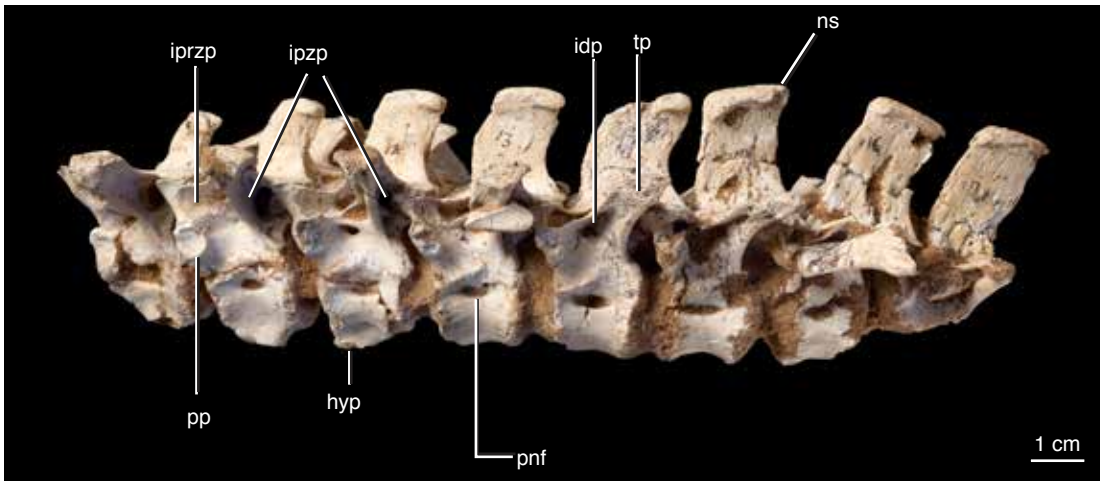
FIGURE 13. Dorsal vertebrae (2–9) of IGM 100/980 in left lateral view.

ventral to the large transverse process. This too is like *Deinonychus antirrhopus* (Ostrom, 1969) but unlike *Velociraptor mongoliensis* (IGM 100/986). In the later taxon, the parapophyses on the posterior dorsals are located nearly on level with the transverse processes (Norell and Makovicky, 1999). Another feature unique to *Shri devi* is prominence of the neurocentral sutures on the dorsal vertebrae in which the suture is marked by a raise rugose scar (fig. 13).

The neural spines are tall and anteroposteriorly expanded. Posteriorly, the neural spines are distinctly rectangular in lateral profile. The spines expand distally to form a "spine table" as in many coelurosaurians (e.g., *Balaur*). Unlike ornithomimosaurians and tyrannosaurids but similar to other dromaeosaurids, the scars for the interspinous ligaments terminate below the apex of the neural spine.

A large, laterally exposed pneumatic opening is located at the confluence of the base of the prezygapophysis and the transverse process. The homologous structure in *Deinonychus antirrhopus* was termed the hapidocoel by Ostrom (1969). Tracing this structure posteriorly, it is evident that this excavation is homologous with the infraprezygapophyseal fossa of the posterior dorsals. Already by d2 it is evident that the posterior border of the infraprezygapophyseal fossa is formed from a thin paradiapophyseal lamina (sensu Wilson, 1999). The infraprezygapophyseal fossa is triangular in all dorsals and decreases in size posteriorly. A large excavation just dorsal to the neurocentral suture on d1 corresponds the infradiapophyseal fossa of the more posterior dorsal vertebrae. In the first four dorsal vertebrae, the infradiapophyseal fossa is variable in depth, but it is typically more ventral than posterior to the infraprezygapophyseal fossa. By d5, the infradiapophyseal fossa is consistent in depth and located more posteriorly than ventrally compared to the infraprezygapophyseal fossa. The posterior border of the infradiapophyseal fossa is formed by a robust posterior centrodiapophyseal lamina (sensu Wilson, 1999). The infrapostzygapophyseal fossa is deep in all dorsal vertebrae. It is divided into separate dorsal and ventral components by a thin transverse lamina in d2–d5.

TABLE 1. Measurements of vertebrae in *Shri devi* (in millimeters)

	IGM 100/980	
	max. length of centrum	max width across transverse process
Cervical vertebrae		
3	28	27
4	28.3	27
5	30.6	30
6	24.2	34.3
7	19.55	38
8	18.5	46.4
9	19.6	42
10	19.1	57.2
Dorsal vertebrae		
1	21.5	n/a
2	19.5	60
3	17.5	56.9
4	16.3	n/a
5	17.25	52.6
6	17.5	51.8
7	17	50
8	16.9	46
9	n/a	46
0	n/a	n/a
11	n/a	n/a
12	n/a	n/a
13	n/a	n/a
14	n/a	n/a
Caudal vertebrae		
1	18.8	n/a
2	18.8	46.7
3	20	61
4	21.05	59
5	23.4	65
6	21[a]	n/a
7	n/a	n/a
8	n/a	n/a
Sacral vertebrae		
1	n/a	n/a
2	n/a	n/a
3	n/a	37.04
4	n/a	57.5
5	n/a	75.3

[a] Estimated values.

FIGURE 14. Dorsal vertebrae (2–9) of IGM 100/980 in right lateral view.

Various fragmented dorsal ribs are preserved along the vertebral column. Dorsal rib 3 and 4 (dr3 and dr4) are the best preserved (fig. 15). The capitular process is rounded with a sharp dorsal edge that is continuous with the ventral margin of the circular tubercular facet. The rib shafts are subrounded, with a ventrally placed sulcus running the length of the preserved shaft. Posteriorly the rib shafts are concave. The ventral surface of dr3 has a series of regular swellings on it that may reflect some minor bone pathology.

Sacral Vertebrae: Five sacral vertebrae are present but are poorly preserved and little can be said regarding their morphology (fig. 16). The ribs associated with these vertebrae are also poorly preserved and their contact with the ilium is visible for the third and fifth sacral. The neural spines are damaged in such a fashion that it is not evident whether they are fused as in *Velociraptor mongoliensis* (IGM 100/985). The presence or absence of a zygapophyseal ridge is also unknown.

Caudal Vertebrae: Portions of eight caudal vertebrae comprise the known tail of IGM 100/980 (fig. 17). The first two caudals are poorly preserved. The transverse process of the anteriormost caudal is expanded and contacts the medial surface of the postacetabular wing of the ilium. In *Velociraptor mongoliensis* (IGM 100/985), the anteriormost caudal was also integrated functionally into the sacrum (Norell and Makovicky, 1997). In IGM 100/985 bone-to-bone contact is absent, but a ligamentous bond has been suggested based on the presence of scarring along the medial ilium surface. It is unclear whether this difference between *Velociraptor mongoliensis* (IGM 100/985) and *Shri devi* (IGM 100/980) reflects an ontogenetic or phylogenetic variation. Anteriorly, the caudal centra are short and boxlike but become longer posteriorly. The transverse processes are swept back as in other dromaeosaurids (Norell and Makovicky, 2004) but unlike other dromaeosaurids they do not flare distally. Ventrally, the caudal centra (at least those posterior to caudals I and II) possess midline grooves. In the preserved caudal vertebrae, the prezygapophyses are short and have medially facing articular facets, which correspond to the laterally inclined postzygapophyseal surfaces. Caudals 3, 4 and 5

FIGURE 15. Dorsal vertebra 2 in anterior view with successive dorsal vertebrae (3–9) of IGM 100/980 curving laterally.

possess neural spines that progressively elongate axially and angle more toward the posterior. The first three chevrons are elongated as in *Velociraptor mongoliensis* (Norell and Makovicky, 1997). The distal ends of the more posterior chevrons are not preserved, but in other dromaeosaurids (Norell and Makovicky, 2004) the processes expand anteroposteriorly.

The Pelvic Girdle

The pelvis is represented by both ilia, both ischia, the left pubis, as well as the distal half of the right pubis (figs. 1, 16, 18). The elements are generally well preserved. The anterodorsal surface of the left ilium is damaged, as is the usually small anteroventral "hook," or point process, of the anterior blade. Posteriorly, a large wedge-shaped crack passes through the iliac blade immediately posterior to the ischiadic peduncle. The right ilium is better preserved—only the extremity of the anterior blade is partially damaged and a small crack is present near the ischiadic peduncle. The right pubis is largely damaged (fig. 1). A portion of the proximal contact is preserved along with the midshaft where it forms part of the pubic apron. The left pubis is nearly complete, with it lacking only the distalmost extreme. Both ischia are essentially complete.

The ilium of IGM 100/980 is dolichoiliac as in other dromaeosaurids (Norell and Makovicky, 2004). The dorsal and ventral margins are parallel along most of the length of the ilium, although the anteroventral and posteroventral margins bend ventrally very slightly. The dorsal rim of the ilium appears to display a sinuous outline like that present in *Velociraptor mongoliensis* (IGM 100/985, IGM 100/986). Also, like *Velociraptor mongoliensis*, the anterior margin of the ilium is convex. This contrasts the more squared-off margin in *Deinonychus antirrhopus* (Ostrom, 1976) and *Achillobator giganticus* (MNUFR 15). The anteroventral rim bends posteroventrally to form a small pointed process very similar that described by Norell and Makov-

FIGURE 16. Pelvis and sacrum of IGM 100/980: **A,** dorsal view revealing posterior sacral vertebrae; **B,** ventral view.

icky (1997, 1999) for *Velociraptor mongoliensis* (IGM 100/985). An antiiliac shelf is essentially absent in IGM 100/980. Like *Velociraptor mongoliensis* (IGM 100/985), only the lateral flexion of the ventral border of the ilium near the pubic peduncle forms a surface that would correspond to the cuppedicus fossa. Measured from the midpoint of the acetabulum, the anterior blade is considerably longer than the posterior blade. If measured from the extremities of the blades back to the pubic and ischiadic peduncles respectively, the anterior blade is shorter than the posterior blade. This is due in part to the very broad pubic peduncle, a trait common among other dromaeosaurids. The lateral surface of the pubic peduncle is concave and directed anterolaterally. The posterior surface of the peduncle forms the majority of the anterior edge of the acetabulum. The contact facet for the pubis faces posteroventrally.

The region surrounding the antitrochanter and ischiadic peduncle is damaged on both ilia. It is clear, nevertheless, that the ischiadic peduncle would have been reduced like in other dromaeosaurids. Posterior to the acetabulum, the dorsal rim of the ilium tapers slightly toward the ventral margin. Similar to the condition in various specimens of *Velociraptor mongoliensis*
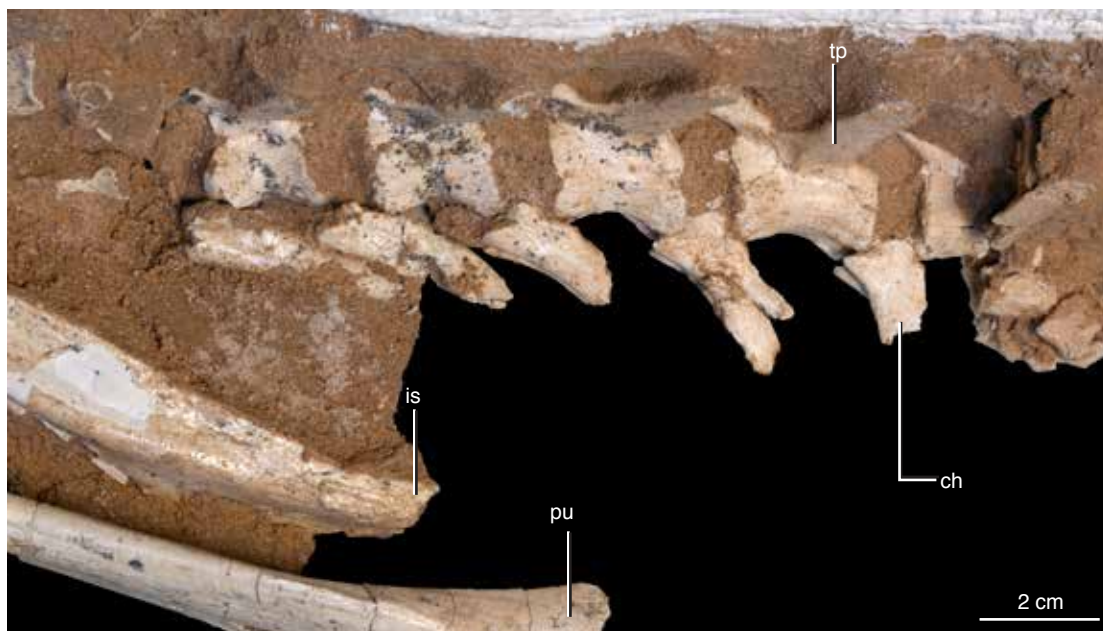
FIGURE 17. Anterior caudal vertebra of IGM 100/980 in lateral view.

(e.g. IGM 100/982, IGM 100/985, IGM 100/986), the ventral surface of the postacetabular blade forms a broad, flat brevis shelf.

One of the most striking features of IGM 100/980 is the extreme length and opisthopubic condition of the pubis. Norell and Makovicky (1999) noted these features for this taxon in their discussion of the similar morphology present in *Velociraptor mongoliensis*. The degree of retroversion is marked by an angle of between 155° and 160° between the long axis of the pubis and the intersecting line described by the body of the ilium. The distal ends of both pubes are not preserved; however, based on the portion preserved it can be estimated that the pubis would have been nearly twice the length of the ischium. The proximal end is preserved only in the left pubis. The proximal articulation is subtriangular in cross section, with the lateral and posteromedial surfaces slightly concave. From the contact with the ilium, the pubis curves laterally creating the large pubic canal common among maniraptorans (Norell and Makovicky, 1997) before it curves back to the midline expanding mediolaterally and compressing dorsoventrally. Here the two pubes contact one another fusing to form the pubic apron. The pubic apron off IGM 100/980 probably only extends for about half the length of the pubis similar to *Velociraptor mongoliensis* (IGM 100/985) and other dromaeosaurids, except *Achillobator giganticus*, which has a more extensive pubic apron (Norell and Makovicky, 2004). Proximally at the angle formed by the vertical anterior surface of the pubis and the posteriorly directed shaft, there is a small tubercle that was interpreted in *Velociraptor mongoliensis* by Norell and Makovicky (1997) as the attachment site for ambiens muscle. The shaft of the pubis in *Microraptor zhaoianus* (Hwang et al., 2002) and *Sinornithosaurus millenii* (Xu et al., 1999) bears a small tubercle slightly proximal to the pubic apron on the lateral surface of the pubis. No such tubercle is present in IGM 100/980.

TABLE 2. Measurements of Pelvic Girdle in *Shri devi* (in millimeters)

	IGM 100/980	
	left	right
Ilium		
Length	183.8	161.7[b]
Length anterior to acetabulum	90.5	74.9[b]
Length posterior to acetabulum	60[a]	53[a]
Height above acetabulum	30.4	32.3
Pubis		
Length (proximodistal)	192.2[b]	245[a]
Width of apron at symphysis	51.2	
Ischium		
Length (proximodistal)	116.8[b]	118[a,b]
Width across peduncles	30.6[b]	35.8
Width across obturator process	65[a]	69.2
Obtruator process apex to iliac peduncle	>85	>85

[a] Estimated values.

[b] Incomplete element.

Both ischia are present and well preserved in IGM 100/980. In overall shape, the ischia of the new taxon are similar to those of *Velociraptor mongoliensis* (IGM 100/985), *Deinonychus antirrhopus* (Ostrom, 1969), and *Achillobator giganticus* (Perle et al., 1999). The iliac peduncle of the ischium is poorly preserved. The adjacent pubic process of the ischium is preserved; however, it projects from the body of the ischium to contact the posterior surface of the proximal pubis. In *Velociraptor mongoliensis* (IGM 100/985) just below the pubic process a tubercle is preserved. IGM 100/980 also preserves a tubercle on the anteroventral surface of the ischium, but it is located near the start of the obturator process, which is more distally located than its location in IGM 100/985. The obturator processes are large and triangular. They comprise more than two-thirds the length of the ischia. The posterior edge of the ischium is nearly straight, contrasting the more concave edge in IGM 100/985. Although in contact with one another, the ischia have not fused.

The Hind Limb

The right femur and tibia, along with the left tibia of IGM 100/980 are present. Proximally, the femur is poorly preserved with the femoral head weathered to reveal cortical bone whereas the broad anterior face medial to the lesser trochanter is crushed inward. Just distal of middiaphysis the shaft is damaged and distally the condyles are heavily weathered. The femur is bowed anteriorly as in other dromaeosaurids (e.g., *Velociraptor mongoliensis* IGM 100/986, *Neuquenraptor argentinus* (Novas and Pol, 2005), *Deinonychus*
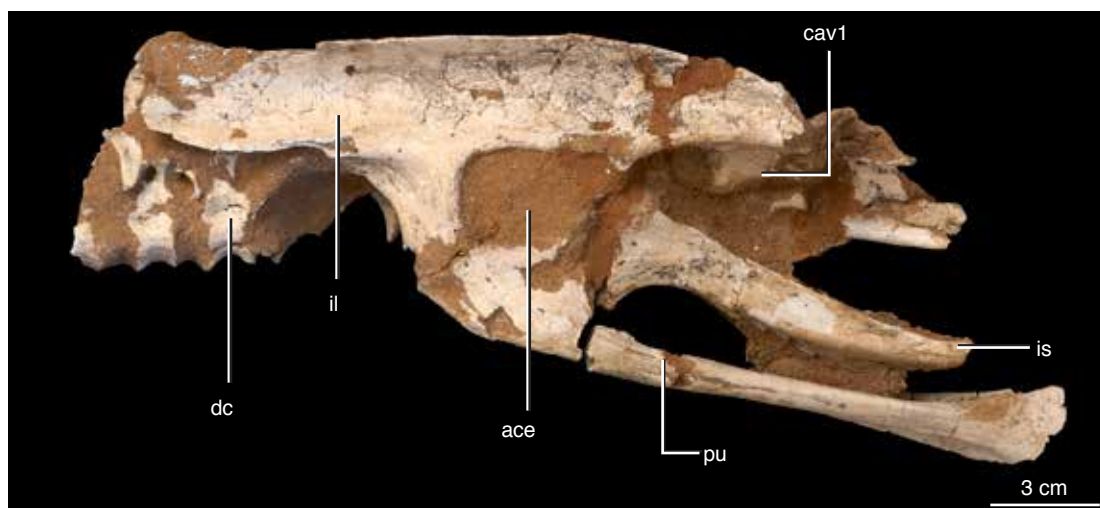
FIGURE 18. Pelvis in left lateral view of IGM 100/980 after final preparation from jacket.

antirrhopus (Ostrom, 1976)) and basal avialans (e.g., *Archaeopteryx lithographica*). The femoral head is incomplete, though posteriorly a deep groove is evident as in *Velociraptor mongoliensis* (IGM 100/986). Ventrally the neck of the femoral head is short, whereas dorsally, the femur is too weathered to comment on the shape and position of the greater trochanter. In anterior view, the ventral margin of the lesser trochanter is preserved. A poorly developed fourth trochanter is present on the posteromedial angle of the femur as in other dromaeosaurids (Norell and Makovicky, 2004), but unlike the well-developed fourth trochanter of *Velociraptor mongoliensis* (IGM 100/986, IGM 100/982). In IGM 100/980, the fourth trochanter is short (~22 mm) and expressed as a shallow depression with slightly rugose, raised sides. It is unclear whether a large vascular foramen is present posterior to the fourth trochanter, as it is in many other theropods, due to cracks in that region of the femur (Perle et al., 1994). The lateral ridge is expressed as a weakly developed rugose line present on the lateral surface of the proximal end of the femur. This feature is not as prominent as in *Velociraptor mongoliensis* (IGM 100/986). The lateral ridge is bounded dorsally by a shallow depression, and grades ventrally into a well-defined ridge along the long axis of the femur toward the lateral condyle. In the posterior midshaft region, this well-defined ridge is joined at a 45° angle by a smooth, raised ridge that is bounded ventrally by the junction of the medial and lateral supracondylar ridges.

Two large condyles comprise the distal end of the femur. Supracondylar ridges extend proximally forming a deep popliteal fossa. As in *Velociraptor mongoliensis* (IGM 100/986), this fossa is not enclosed distally by midline expansions of the two condyles. The lateral condyle is slightly larger than the medial one; however, the distalmost portion of the lateral condyle is heavily eroded up to the level of the ectocondylar tuber. The tuber is large and deflected laterally.

The tibia is longer than the femur (115% femur length) as in all other dromaeosaurids, except *Achillobator giganticus* (Norell and Makovicky, 2004). Proximally, the tibia forms a triangular articular surface for the femur. Posteriorly, the medial side of the articular surface is
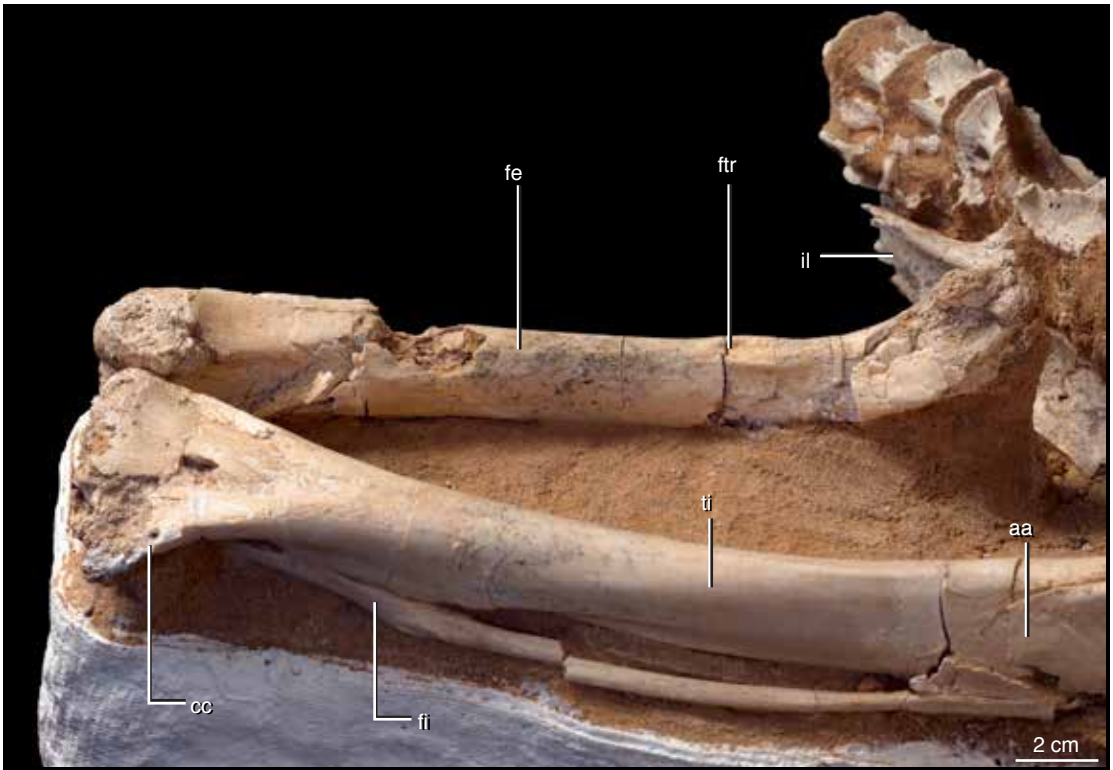
FIGURE 19. Right hind limb of IGM 100/980 prior to final preparation from jacket. Femur is in posteromedial view, tibia and fibula are in anterior view.

expanded to overhang the shaft as it does in *Velociraptor mongoliensis* (IGM 100/986). A large cnemial crest is present, but the anterior edge does not hook laterally as in most theropods. The cnemial crest of *Velociraptor mongoliensis* (IGM 100/986) and *Rahonavis ostromi* (UA 8656) also lack a lateral hook; however, a large boss is present on the lateral margin of the crests in these taxa. Interestingly, IGM 100/980 lacks such a rugose boss. Although slightly shorter than the tibiae of large *Velociraptor* individuals (e.g., IGM 100/986) the cnemial crest in *Shri devi* is about two times larger and extends further distally down the tibial shaft. Distal to its articulation with the femur, the tibia is generally round in cross section and bears a prominent fibular crest. Distal to the fibular crest (about mid shaft) the tibia is anteroposteriorly flattened, assuming an oval to subtriangular cross section.

The distal end of the tibia is widely flared in anterior view and rectangular in shape in distal view. Precise details of the tibiotarsus are limited because of poor preservation of much of the distal portion of the tibia and astragalus/calcaneum. The extent to which the astragalus wrapped onto the posterior face of the tibia is unclear, but it appears to be no more than in *Velociraptor mongoliensis* (IGM 100/986 and IGM 100/982), *Deinonychus antirrhopus* (YPM 5226), *Neuquenraptor argentinus* (Novas and Pol, 2005), *Microraptor zhaoianus* (Hwang et al., 2002), or *Rahonavis ostromi* (UA 8656). The contribution of the calcaneum to the tibiotarsus and its degree of fusion cannot be discerned due to poor preservation. The ascending process of the astragalus is well developed and separated from the body of the

TABLE 3. Measurements of Hind Limb in *Shri devi* (in millimeters)

	IGM 100/980	
	left	right
Femur		
Length		205
Distal transverse width		36
Distal length		33
Proximal transverse width		43[a]
Proximal anteroposterior length		34.3
Tibiotarsus		
Length		246
Greatest distal transverse width		31
Greatest distal depth	18.4	21.5
Greatest proximal transverse width		54.7
Greatest proximal depth		21.5
Ascending process of astragalus length	41	44
Fibula		
Width at narrowest point		3.1
Width at narrowest point on proximal end		8.9
Proximal length		22.5

[a] Estimated values

[b] Incomplete element

astragalus by a deep groove that shallows slightly toward the lateral and medial extremities. The ascending process is taller laterally than medially and forms an extensive contact with the fibula.

The proximal end of the fibula has a concave medial face. The fibula is fractured in two places—one distal to the iliofibularis tubercle and the other just proximal to the apex of the ascending process of the astragalus. The fibula is fairly robust proximally along its contact with the fibular crest of the tibia. The iliofibularis tubercle is large and rugose. Distal to the tubercle the fibula attenuates becoming thin, rodlike and slightly oval in cross section. The distalmost end of the fibula is not preserved. No distal tarsals are preserved in IGM 100/980.

PES

Digit I is complete, well preserved, and lies in articulation with metatarsal II (figs. 23–25). The first metatarsal is subtriangular distally with the anteromedial face weakly concave, becoming slightly convex proximally. Its lateral edge is marked by a sharp angle. The distal articulation is slightly offset from the shaft and development of the anterior lip of the articulation surface with the first phalanx less than that of *Velociraptor mongoliensis* (e.g., IGM 100/985, IGM 100/986, IGM

FIGURE 20. Right femur of IGM 100/980 after final preparation in **A,** anterior, **B,** posterior, **C,** medial, and **D,** lateral views.

100/982) or *Deinonychus antirrhopus* (YPM 5217). The lateral surface distal to the articulation with metatarsal II bears a shallow fossa that elongates proximodistally and is bordered on each side by slightly raised rugosities. The equivalent fossa in *Velociraptor mongoliensis* (AMNH FARB 6518, IGM 100/985, IGM 100/986), *Deinonychus antirrhopus* (YPM 5217), and *Bambiraptor feinbergorum* (AMNH FR 30554) occupies nearly the entire lateral surface. It is pitlike and significantly deeper than that of IGM 100/980. The distal articular surface is divided by a slight depression. The first phalanx and ungual are extremely similar to those of other dromaeosaurids (Norell and Makovicky,

FIGURE 21. Right tibia, fibula, and astragalocalcaneum of IGM 100/980 after final preparation in **A,** lateral, **B,** medial, **C,** anterior, and **D,** posterior views.

1997). The first phalanx is broad proximally and distally, and constricted in the medial. The proximal articulation is nonginglymoid, while the distal articulation is weakly ginglymoid. Well-developed medial and lateral ligament scars are present distally. The ungual is triangular in cross section and not strongly curved. The medial and lateral surfaces bear a midline groove for the claw sheath.

The proximal articulation surface of metatarsal II is not preserved (fig. 24). Proximally, the anterior face of the metatarsal is flat with a sharp angle delimiting the anterior from the medial surface. More distally, the anterior face becomes slightly convex and gently curves into the convex medial surface. The proximal portion of the metatarsal is not as strongly appressed to metatarsal III as other dromaeosaurids (Norell and Makovicky, 1997). As a result, metatarsal

FIGURE 22. Left tibia and partial astragalus of IGM 100/980 in **A,** anterior, **B,** posterior, **C,** lateral and **D,** medial views.

II is broader proximally than in taxa such as *Velociraptor mongoliensis* (IGM 100/985; IGM 100/986), *Bambiraptor feinbergorum* (AMNH FARB 30554), or *Rahonavis ostromi* (UA 8656) and distinct posterior surface is present along the entire preserved metatarsal. This is similar to the condition in *Deinonychus antirrhopus* (YPM 5205) and contrasts the condition in the former taxa, in which a posteromedially oriented surface is present proximally (Norell and Makovicky, 1997). Two prominent tubercles are present on the shaft of the metatarsal. One is midway down the length of the shaft at the angle formed by the medial and posterior faces. Norell and Makovicky (1997) tentatively homologized this with the avian medial plantar crest. The other tubercle, corresponding to the M. tibialis cranialis insertion, is present on the antero-lateral corner along the contact with metatarsal III. In *Velociraptor mongoliensis* (IGM 100/985, IGM 100/986) metatarsal II narrows slightly while it overlaps part of metatarsal III just proxi-
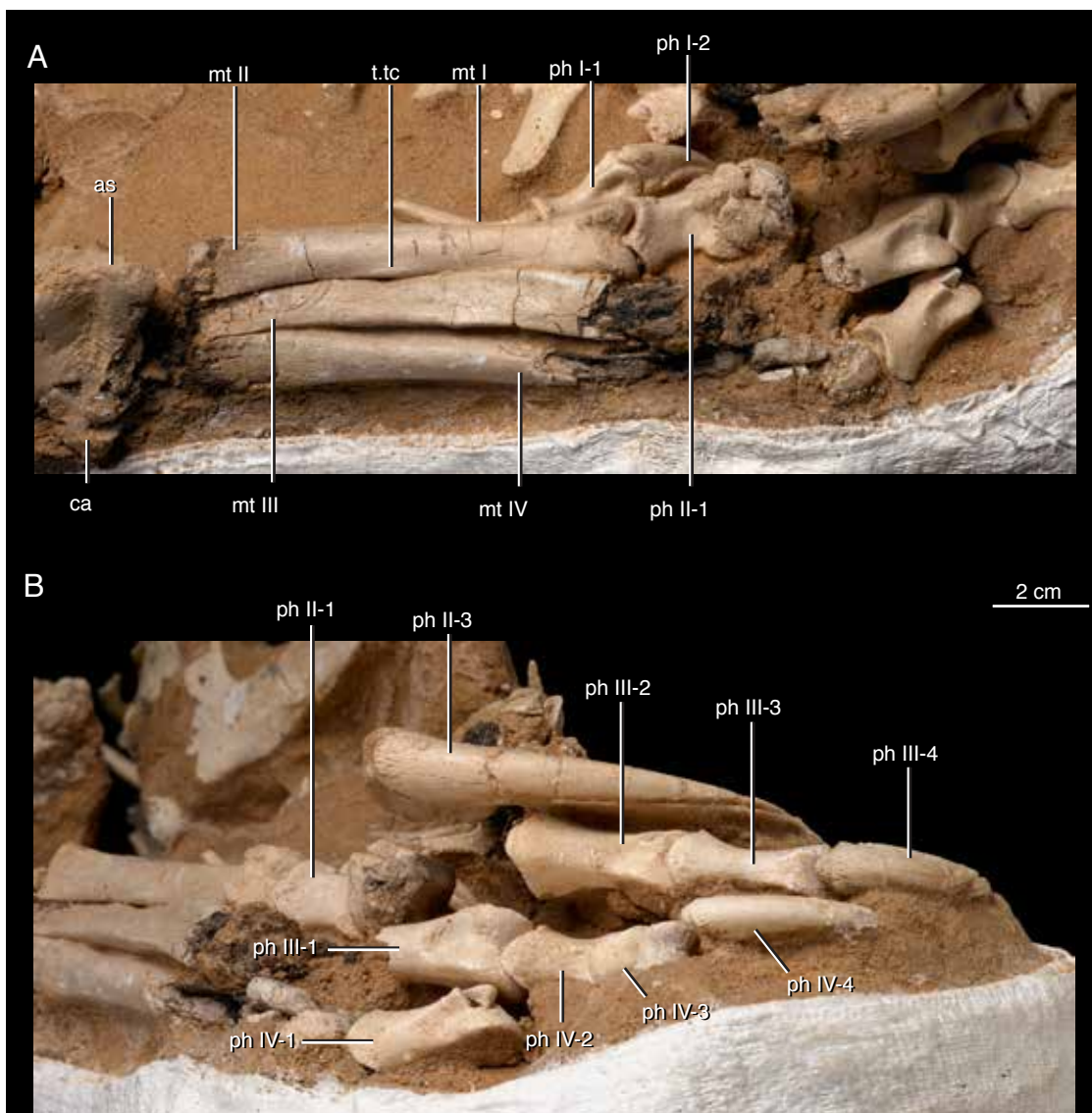
FIGURE 23. Foot of IGM 100/980 prior to final preparation: **A,** right metatarsus in anterior view; **B,** pedal phalanges of right pes in dorsal view.

mal to the distal articulation. Metatarsal II of IGM 100/980 lacks this constriction remaining as wide distally as it is proximally. As in all other dromaeosaurids, the distal articulation consists of a deeply incised ginglymus (Norell and Makovicky, 2004). In *Velociraptor mongoliensis* (IGM 100/985, IGM 100/986, IGM 100/982) and to a lesser extant in *Deinonychus antirrhopus* (YPM 5205), there is a small tubercle located on the proximal part of the lateral articular ridge. This tubercle is absent in IGM 100/980, though a slight rugosity is present. Phalanx II-1 and the ungual are well preserved, but a localized shear in the surrounding matrix displaced the distal phalanges from the proximal one (fig. 26). This movement has all but obliterated phalanx
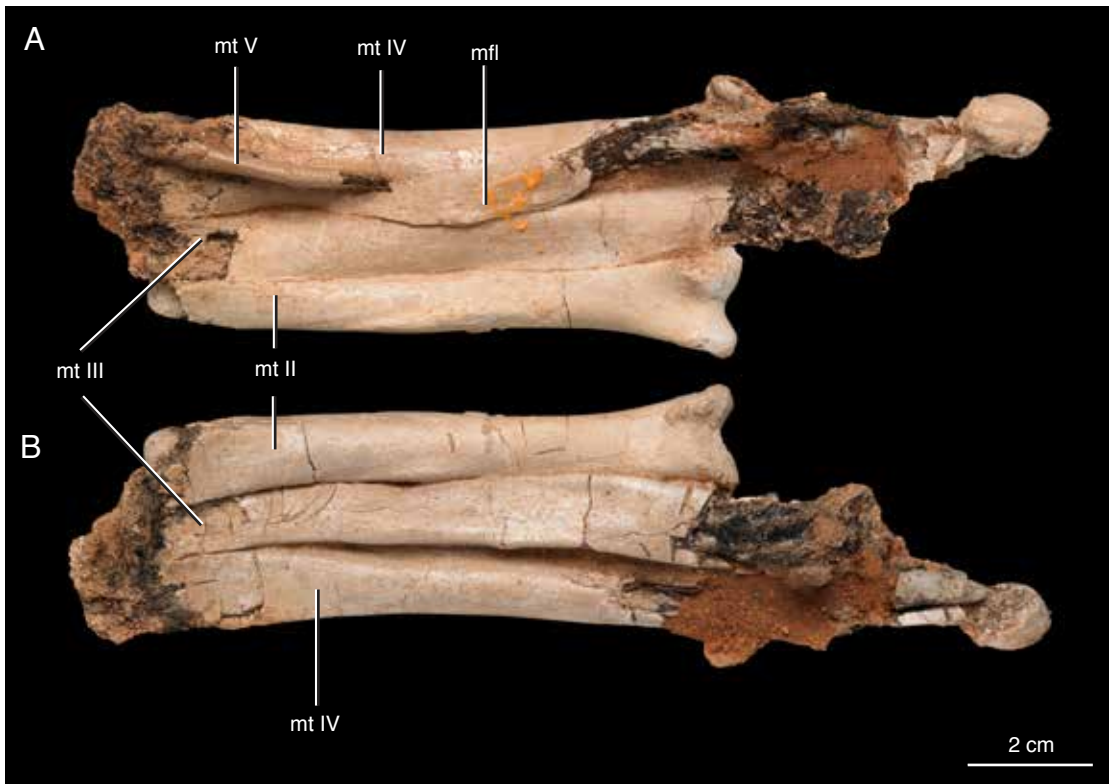
FIGURE 24. Right metatarsus of IGM 100/980 after final preparation in **A,** posterior and **B,** anterior views.

II-2, III-1, and IV-1, and has offset the distal phalanges with their corresponding digit. Phalanx II-1 is wide and flat like that of other dromaeosaurids. A weakly developed ridge defines the border between the plantar and medial surfaces of the phalanx. Unlike *Velociraptor mongoliensis* (Norell and Makovicky, 1997), the ridge in IGM 100/980 does not extend to the medial condyle of the distal trochlea and in this respect is similar to *Deinonychus antirrhopus* (YPM 5205), which appears to lack the ridge completely. The proximal ginglymus and distal trochlea are large and dorsoventrally expanded in relation to the markedly constricted shaft of the phalanx. The medial and lateral surfaces of the trochlea have shallow ligament pits. The ligament pits are placed slightly dorsal to the center of the lateral outline of the trochleae. The two contact facets on the proximal ginglymus are unequal, with the medial one slightly narrower than the lateral. The dorsal surface is generally flat with a shallow depression just proximal to the expanded trochlea. Phalanx II-2 is nearly completely unpreserved; however, it is clear from what is preserved that it possessed the expanded heel and tall, narrow trochlea characteristic of Dromaeosauridae (Norell and Makovicky, 2004). The digit II ungual is hypertrophied as in most other dromaeosaurids (Norell and Makovicky, 2004). This hypertrophy is greater than in *Velociraptor mongoliensis* (e.g., IGM 100/985). In the Khulsan dromaeosaurid the length along the outer curvature of the ungual is approximately the same length as metatarsal II, while in *Velociraptor mongoliensis* this ratio is closer to 90%. A large flexor tubercle is present on the

TABLE 4. Measurements of Pes in *Shri devi* (in millimeters)

	IGM 100/980
	right
METATARSALS	
Metatarsal I	
Length	30.9
Distal transverse width	12.3
Distal length	14.0
Metatarsal II	
Length	90[a]
Distal transverse width	15.5
Distal depth	16.5
Proximal transverse width	12.72
Proximal depth	13
Metatarsal III	
Length	117[a]
Distal transverse width	16.7[a]
Distal depth	13.4[a,b]
Proximal transverse width	10.3
Proximal depth	n/a
Metatarsal IV	
Length	124[a]
Distal transverse width	n/a
Distal depth	n/a
Proximal transverse width	17.7
Proximal depth	12.1
Metatarsal IV	
Diameter	3.4
PHALANGES	
I1	
Length	22.5
Distal transverse width	8.5
Proximal transverse width	12.0
Proximal height	11.8
Distal Height	9.3
I2	
Proximal transverse width	8.0
Proximal height	15.1
Facet height	10[a]

TABLE 4 *continued*

	IGM 100/980
	right
II1	
Length	25.8
Distal transverse width	15.2
Proximal transverse width	16
Proximal height	14.3
Distal height	14.6
II2 (too fragmentary)	
II3	
Length along outer curvature	91.3
Proximal transverse width	11.3
Proximal height	28.5
Facet height	18.6
III1	
Length	47[a,b]
Proximal transverse width	n/a
Proximal height	n/a
Distal transverse width	14.4
Distal height	15.9
III2	
Length	30
Distal transverse width	13.5
Proximal transverse width	15.2
Proximal height	15.8
Distal height	15.7[a]
III3	
Length	28.4
Distal transverse width	11.25
Proximal transverse width	13.2[a]
Proximal height	14.0
Distal height	12.6
III4	
Length along outer curvature	49.4
Proximal transverse width	11.0
Proximal height	18.3
Facet height	14.8
IV1	
Length	41.5[a]

TABLE 4 *continued*

	IGM 100/980
	right
Distal height	15.4[a,b]
IV2	
Length	27.1
Distal transverse width	11.8
Proximal transverse width	14.1
Proximal height	14.7
Distal height	12.4
IV3	
Length	23.4
Distal transverse width	12.5
Proximal transverse width	12.6
Proximal height	12.5
Distal height	11.7
IV4	
Length	22.4
Distal transverse width	10.1
Proximal transverse width	12
Proximal height	12.9
Distal height	10.3
IV5	
Length along outer curvature	36.5
Proximal transverse width	9.6
Proximal height	15.6
Facet height	13.1

[a] Estimated values.

[b] Incomplete element.

ventral border of the ungual near the articulation facet. The same location on the dorsal surface lacks a tubercle, but is deeply sculpted with interconnecting grooves. Prominent claw sheath grooves are present on the lateral and medial surfaces. The medial groove is positioned near the midline of the ungual, while the lateral groove proximally is positioned near the midline but then curves dorsally ending on the dorsal surface of the phalanx.

As in other dromaeosaurids, metatarsal III is compressed slightly between MT II and MT IV but not to the extent seen in the arctometatarsalian condition (Norell and Makovicky, 2004; Holtz, 1995) of many paravians like *Almas* (Pei et al., 2017) and *Microraptor* (Xu et al., 2000, Hwang et al., 2002). A large longitudinal mound or protuberance is located distal to the proximal articulation on the anterior face of the metatarsal along the lateral border with MT IV (fig. 24). As noted by Norell and Makovicky (1997), this protuberance is also present
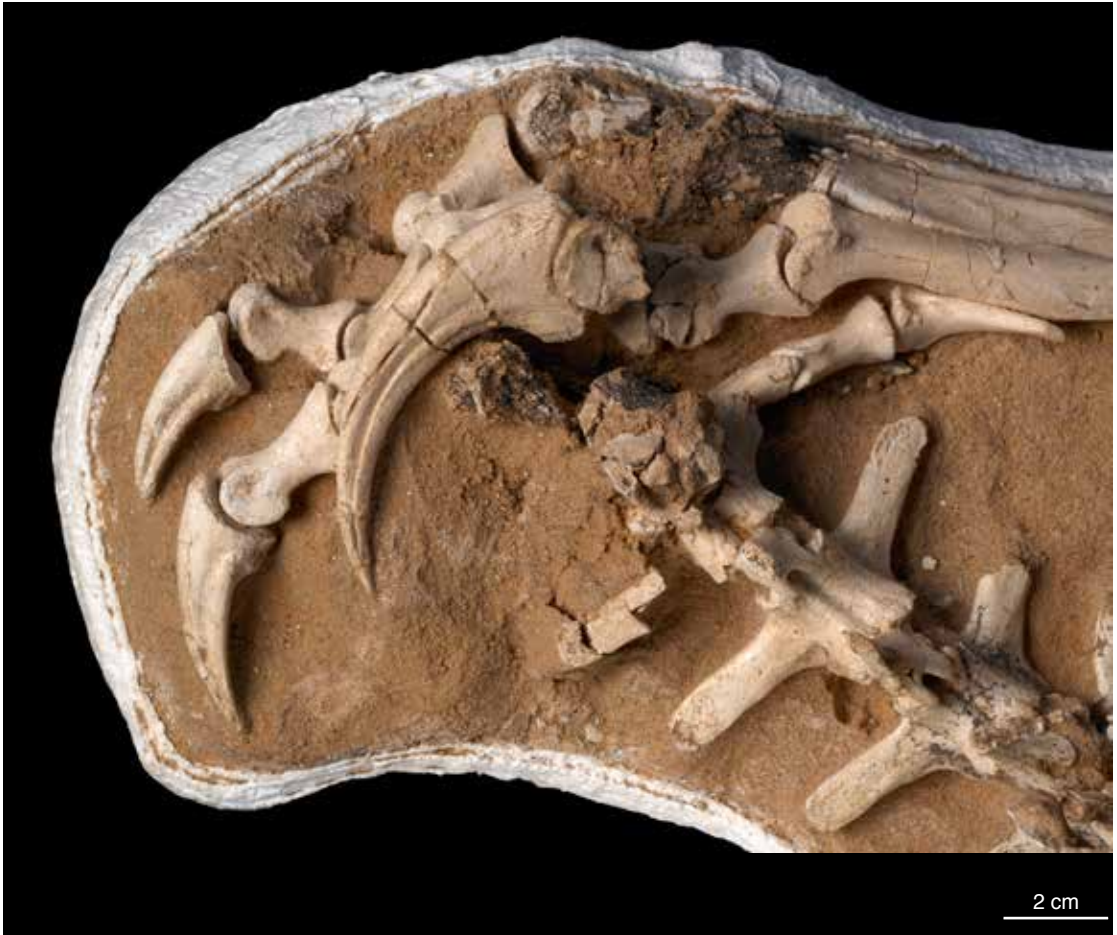
FIGURE 25. Foot of IGM 100/980 prior to final preparation detailing the enlarged trenchant ungual phalanx.

in *Velociraptor mongoliensis* (AMNH FARB 6518, IGM 100/986), *Deinonychus antirrhopus* (AMNH FARB 2136), and a currently undescribed dromaeosaurid from Khulsan (IGM 100/981). In IGM 100/980, the lateral placement of the protuberance differs from the mediolaterally centered protuberance in *Velociraptor mongoliensis* (IGM 100/986). The protuberance gives the middle of the metatarsal a medial aspect. Below the mound the medial aspect diminishes, as the anterior surface of the bone appears to twist laterally while the surface expands mediolaterally and the mound ends. The articulation with MT IV on the posterior face of MT III is planar as compared with the recessed articulation on the anterior face. The distalmost 2.5 to 3 cm of the metatarsal is not preserved, but invading plant material preserves the distal extent of the element.

Phalanx III-1 is not preserved proximally. The space left open between the distal portion of the phalanx and the distal extreme of metatarsal III, however, indicates that the phalanx would have been relatively long as in other dromaeosaurids (e.g., *Velociraptor mongoliensis*
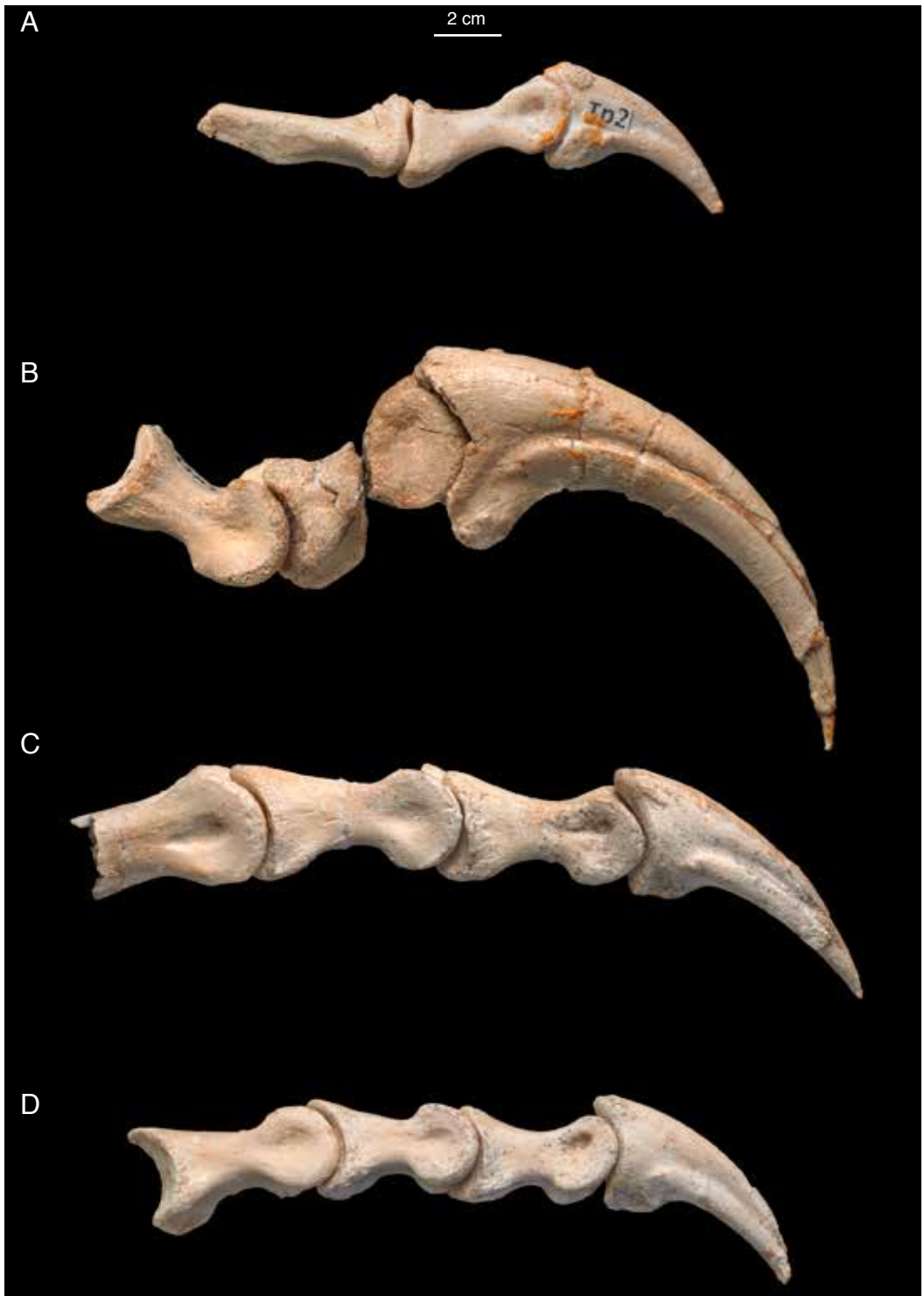
FIGURE 26. Pedal unguals of right pes after final preparation: **A,** digit I; **B,** digit II; **C,** digit III; **D,** digit IV.

IGM 100/986, *Deinonychus antirrhopus* YPM 5205, *Neuquenraptor argentinus* (Novas and Pol, 2005), *Microraptor zhaoianus* (Hwang et al., 2002)). The distal articulation is ginglymoid. A deep circular extensor pit marks the dorsal surface of the distal phalanx and ligament pits are centered on the lateral and medial surfaces. Phalanx III-2 is shorter and stouter as in other dromaeosaurids (Norell and Makovicky, 1997). The proximal articulation is not appreciably skewed medially, while the distal articulation facet has a wider lateral trochlear ridge than medial. An extensor pit is present on the dorsal surface just proximal to the distal trochlea, but it is shallower than the same pit on phalanx III-1. Phalanx III-3 is similar to III-2 although the shaft of the bone is narrower than III-2, unlike in *Deinonychus antirrhopus* (YPM 5205), where the phalanges are more similar in cross-sectional area. The proximal lateral articulation facet of III-3 is wider than the medial in order to accommodate the wider lateral trochlear ridge of phalanx III-2. Also unlike *Deinonychus antirrhopus* (YPM 5205), the ligament pits on phalanx III-3 in IGM 100/980 are shallow and indistinct. There is no dorsal extensor fossa. The ungual is weakly curved and bears a small flexor tubercle.

Metatarsal IV is anteroposteriorly wide proximally. It begins to narrow mediolaterally distally (fig. 24). It does not, however, flatten dorsoventrally as much as *Velociraptor mongoliensis* (IGM 100/986) does. It appears to retain a general rectangular cross section (like in *Deinonychus antirrhopus* YPM 5205) as opposed to the posteromedially slanted ovular cross section of *Velociraptor mongoliensis* (IGM 100/985, IGM 100/986). The metatarsal is not, however, as robust as that of *Achillobator giganticus* (MNUFR 15). The posterior face of MT IV is flat until a raised rugosity about halfway down the plantar surface. The distal end of this rugosity is weathered. The medial edge of MT IV creates a convex shelf that overhangs and creates a planar articulation with MT III. The extension of the medial boundary in IGM 100/980 is more exaggerated than in *Velociraptor mongoliensis* (IGM 100/985). The distal end of the metatarsal is damaged like MT III. In dromaeosaurids MT IV ends in a simple rounded articular surface (Norell and Makovicky, 1997). There is no reason to suspect that IGM 100/980 would have differed from this.

Phalanx IV-1 is almost entirely eroded, only the lateral distal trochlear ridge preserves (fig. 23). Phalanx IV-2 is shorter than phalanx 2 of digit II. It has a dorsoventrally deep articular surface. The shaft of the phalanx does not appear to bend medial to any appreciable degree. The medial ridge of the distal trochlea is damaged. The lateral and medial ligament fossae are shallow. The proximal lateral articulation facet is wider than the medial facet. There is a shallow extensor fossa on the dorsal surface just proximal to the trochlea. Phalanges IV-3 and IV-4 are both short and stouter than IV-2. The ligament fossae on the penultimate phalanx are dorsally displaced (like seen in digit III) and is the common condition in most theropods. The ungual of digit IV is the shortest of the pedal unguals. It is only weakly curved and bears a poorly developed flexor tubercle ventrally. There are symmetrical claw-sheath grooves on each side of the ungual. The phalanges in digit III and IV have a proximally directed tongue at the dorsal margin of the proximal facet that overhangs the articulation, like in *Velociraptor mongoliensis* (IGM 100/985).

Metatarsal V is preserved, but is lacking the distal end and has weathering damage to the proximal end. It is slender and is curved slightly medially. MT V articulates with the posterior face of MT IV; proximally, the articulation with the distal tarsals is weathered.

PHYLOGENETIC PLACEMENT

To test the phylogenetic placement of IGM 100/980 we have integrated the new taxon into a current version of the Theropod Working Group matrix. A total of 157 coelurosaurian taxa and 853 characters (140 ordered) were used in the analysis, with *Allosaurus fragilis* and *Sinraptor dongi* rooting the most parsimonious trees. The dataset was treated with equally weighted parsimony analysis implemented in TNT v. 1.5 (Goloboff et al., 2003; Goloboff and Catalano, 2016) (see discussion by Goloboff et al., 2019). A heuristic tree search strategy was conducted using multiple replications of new technology searches until it produced 20 hits to the shortest length (xmult = hits 20). The best trees obtained at the end of the xmult search were subjected to a final round of TBR branch swapping. Zero-length branches were collapsed if they lacked support under any of the most parsimonious reconstructions (i.e., rule 1 of Coddington and Scharff, 1994). Dataset and supplementary files are available on MorphoBank (http://morphobank.org/permalink/?P3733).

This analysis resulted in 100,000 most parsimonious trees (memory overflowed) of 3381 steps (CI = 0.321, RI = 0.781). A reduced strict consensus, excluding the conflicting positions of a number of fragmentary dromaeosaurid taxa (see tnt file on Morphobank), reveals *Shri devi* to be the sister taxon to *Velociraptor mongoliensis* (fig. 27). A differing combination of three ambiguous synapomorphies support sister taxon status of *Shri devi* with *V. mongoliensis*. In some of the most parsimonious trees character 151.0 (ilium, preacetabular process, anteroventral corner, form: subtriangular, ventral margin of preacetabular process is shallowly concave) unites the two taxa. In another set of trees, character 232.1/2 (metatarsal II, tuber along extensor surface: present) unites the two taxa. In some trees both of these characters (151.0 and 232.1/2) support the monophyly of *Shri devi* and *V. mongoliensis*. Lastly, in the final set of best trees, character 232.1/2 and character 433.1 (metatarsal II, distal extent of MT II relative to MT IV: mt II shorter than mt IV, but reaching distally farther than base of mt IV trochlea) unites the two taxa.

DISCUSSION

The new taxon described here further increases the known dromaeosaurid diversity from the Late Cretaceous of Mongolia—up from only three a decade ago to at least 10 species spanning nearly the complete body size range for the clade. The geological and stratigraphic work by Dashzeveg et al. (2005) and Dingus et al. (2008) greatly improved the understanding of the interrelationships of Late Cretaceous fossil-bearing localities in Mongolia. By combining this work with the expanded faunal diversity of dromaeosaurids we can begin to examine the regional variation and potential nonoverlap in the dromaeosaurid fauna in the Late Cretaceous of Mongolia to better assess its biogeographical and/or temporal significance. With the presence of *Adasaurus mongoliensis* (see Barsbold, 1983) from Bayankhongor, it has been appreciated for more than 30 years that the dromaeosaurid fauna of the much younger Nemegt Formation differed from the classic Upper Cretaceous strata of the Djadokhta Formation. Similarly, considering a geographic scale there is a growing understanding of faunal differences between the dinosaur and other vertebrate components of the Djadokhta Formation exposures
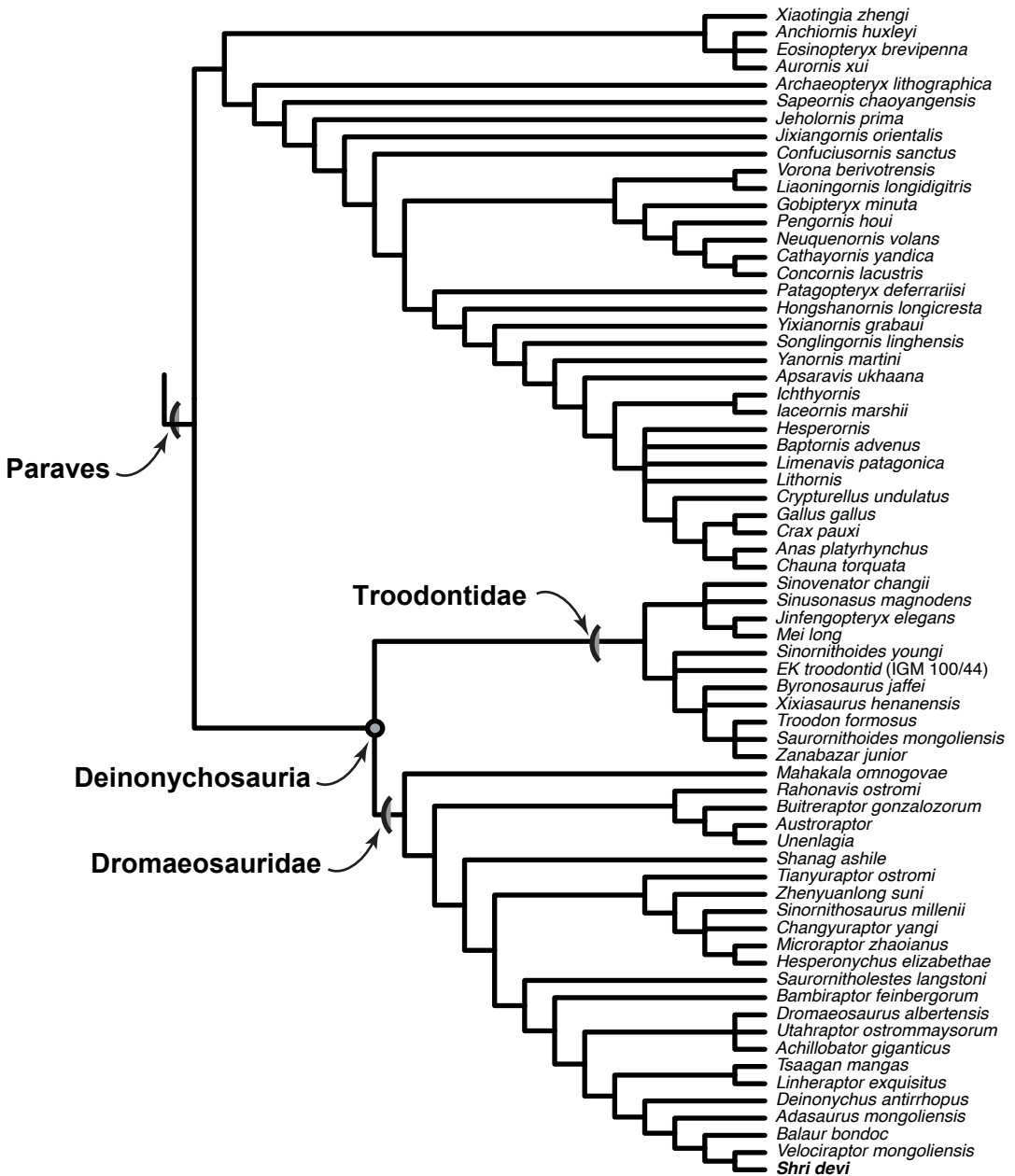
FIGURE 27. Phylogenetic relationship of *Shri devi*. Reduced strict consensus of 100,000 most parsimonious trees (3381 steps, CI = 0.321, RI = 0.781), excluding the conflicting positions of a number of fragmentary dromaeosaurid taxa. Nonparavian clades have been excluded for the display of the cladogram.

at Bayn Dzak, Tugrugyin Shireh, and Ukhaa Tolgod with the likely correlative Bayan Mandahu and Wulansuhai Formations outcropping at Bayan Mandahu, Inner Mongolia, China (Jerzykie-wicz et al., 1993; Eberth, 1993; Gao and Hou, 1996; Gao and Norell, 2000; Wible and Rougier, 2000; Smith et al., 2001; Lambert et al., 2001; Longrich et al., 2010). This faunal distinction includes dromaeosaurids with the presence in Bayan Mandahu of a distinct species of *Veloci-raptor—V. osmolskae*, as well as *Linheraptor exquisitus*, a dromaeosaurid extraordinarily similar to *Tsaagan mangas* from Ukhaa Tolgod (see Turner et al., 2012 and Xu et al., 2015).

Specific differences in the dromaeosaurid fauna among Djadokhta Formation localities and between Djadokhta and Barun Goyot formations has not be emphasized and at least until recently generally assumed to be minimal (e.g., Godefroit et al., 2008). This assumption con-formed with a similar pattern in the squamates from these formations, which were considered to show little substantial difference (Gao and Norell, 2000). Indeed 82 years elapsed from Osborn's (1924) description of *Velociraptor mongoliensis* before a second dromaeosaurid taxon was reported from the Djadokhta Formation (i.e., *Tsaagan mangas* from Ukhaa Tolgod [Norell et al., 2006]).

Dashzeveg et al. (2005) identified two members with the Djadokhta Formation: a lower Bayn Dzak Member and an upper Tugrugyin Member. Dingus et al. (2008) examined the geol-ogy of Ukhaa Tolgod and referred the strata at Ukhaa Tolgod to the Bayn Dzak Member of the Djadokhta Formation. Thus, based on superpositional relationships, there is basic temporal ordering of some of the dromaeosaurid-bearing localities: Ukhaa Tolgod is slighter older than Tugrugyin Shireh, which is slighter older than Barun Goyot outcropping at Khulsan. Although it is likely that Bayn Dzak is at least penecontemporaneous with Ukhaa Tolgod the exact order-ing is currently uncertain.

More than a decade ago Norell et al. (2006) noted that the limited diversity of Mongolian dromaeosaurids was probably an underestimation, and further suggested that regional differ-ences likely existed among Djadokhta localities at least with respect to the dromaeosaurid fauna. Key dromaeosaurid discoveries have fleshed out dromaeosaurid faunal diversity—*Tsaa-gan mangas* (Norell et al., 2006), *Mahakala omnogovae* (Turner et al., 2007c), *Velociraptor osmolskae* (Godefroit et al., 2008), *Linheraptor exquisitus* (Xu et al., 2010), *Halszkaraptor escuil-liei* (Cau et al., 2017), and *Shri devi* (this paper). Moreover, there is renewed phylogenetic evidence that the enigmatic *Hulsanpes* is a dromaeosaurid (as originally proposed by Osmólska [1982]). *Mahakala*, *Halszkaraptor*, and *Hulsanpes* are all small-bodied taxa lacking many of the apomorphies of velociraptorines like *Tsaagan* and species of *Velociraptor* (Turner et al., 2011, 2012) and appear to form a basal diverging clade (Halszkaraptorinae) among dromaeosaurids (Turner et al., 2012; Cau et al., 2017). With these data, a pattern now emerges among the locali-ties of Ukhaa Tolgod, Tugrugyin Shireh, and Khulsan; each locality's dromaeosaurid fauna consists of a halszkaraptorine and a velociraptorine distinct from those in the other two locali-ties (Ukhaa Tolgod—*Halszkaraptor* and *Tsaagan*; Tugrugyin Shireh—*Mahakala* and *Velocirap-tor mongoliensis*; Khulsan—*Hulsanpes* and *Shri devi*). It appears that Tugrugyin Shireh and Bayn Dzak share the same velociraptorine (*V. mongoliensis*) with no halszkaraptorine yet known from Bayn Dzak. The geographically much more distant Bayan Mandahu localities have
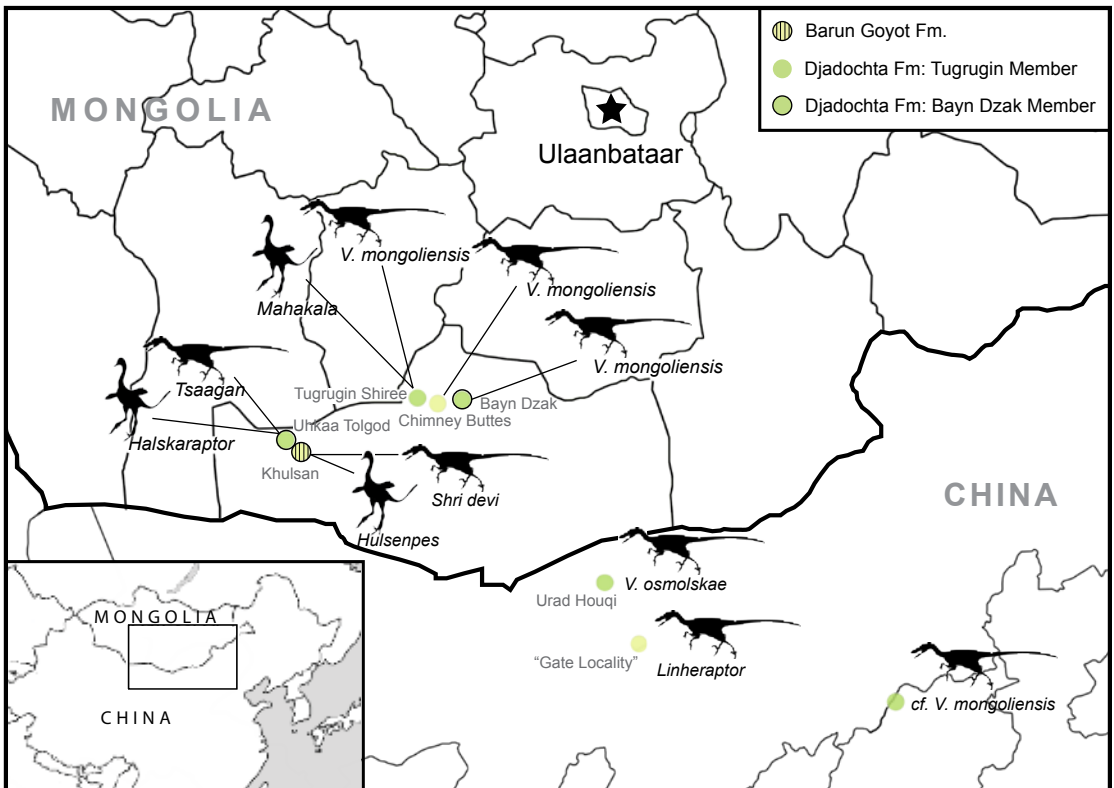
FIGURE 28. Map depicting the geographic and temporal distribution of the Late Cretaceous dromaeosaurid fauna of Mongolia and Inner Mongolia (Nei Mongol Autonomous Region, China).

their distinct velociraptorines as well (*V. osmolskae* from Bayan Mandahu Formation; *Linheraptor* from Wulansuhai Formation) but no recovered halszkaraptorine so far (fig. 28).

SUMMARY

Dromaeosaurid remains are known to occur in the Barun Goyot Formation at Khulsan, Mongolia (Norell and Makovicky, 1999; Weishampel et al., 2004). Material collected in 1991 by the joint expedition between the American Museum of Natural History and the Mongolian Academy of Sciences is revealed to be a distinct new species of dromaeosaurid. This specimen is important both because it provides new details and expands the known variation present among velociraptorine dromaeosaurids, but also because it helps complete a picture of the regional and temporal diversity present among Mongolian dromaeosaurids at the end of the Cretaceous. By combining the improved geological and stratigraphic context for dromaeosaurid-bearing localities with our present understanding of dromaeosaurid species diversity, we are able to demonstrate a previously unappreciated pattern of species occurrence within the dromaeosaurid fauna. We find it likely that both geographic isolation caused by structurally controlled topography (basin-and-range style extensional topography; see Graham et al., 2012) and differences in age

have shaped the Late Cretaceous Mongolian dromaeosaurid fauna. It remains to be determined how paleoenvironmental differences may have influenced this pattern. Furthermore, it is important to consider that these are very rare animals typically known from only a couple of occurrences at most in each locality. But these confounding effects may gain some clarity as local palaeoenvironmental insights are increasingly considered within a regional context

ACKNOWLEDGMENTS

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APPENDIX

Anatomical Abbreviations

aa   ascending process of astragalus

ace   acetabulum

as   astragalus

c   cervical vertebra (may be accompanied by number designating position)

ca   calcaneum

cav   caudal vertebra

cc   cnemial crest

ch   chevron

cr   cervical rib

d1   first dorsal vertebra

dc   dorsal vertebra

dia   diapophysis

ect   ectocondylar tuber

ep   epipophysis

fe   femur

fi   fibula

ft   foramen transversarium

ftr   fourth trochanter of femur

hyp   hypapophysis

icl   intercentral ligament attachment point

idp   infradiapophyseal fossa

if   iliofibularis tubercle

il   ilium

ipzp   infraprezygapophyseal fossa

iprzp   infrapostsygapophyseal fossa

is   ischium

lco   lateral condyle

lr   lateral ridge

ltr   lesser trochanter

mco   medial condyle

mfl   medial flange

mt   metatarsal

ncl   neural canal

ns   neural spine

pf   pneumatic foramen

ph   phalanx

pnf   pneumatopore

pp   parapophyses

prz   prezygapophyses

pu   pubis

pz   postzygapophysis

t.tc   M. tibialis cranialis tubercle

ti   tibia

tp   transverse process