A Review of the Mongolian Cretaceous Dinosaur *Saurornithoides* (Troodontidae: Theropoda)

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ABSTRACT

We review the morphology, taxonomy, and phylogenetic relationships of the upper Cretaceous Mongolian troodontid *Saurornithoides*. *Saurornithoides mongoliensis* is known only by the holotype from Bayan Zag, Djadokhta Formation. This specimen includes a nearly complete, but weathered, skull and mandibles, a series of dorsal, sacral, and caudal vertebrae, and a partial pelvic girdle and hind limb. *Saurornithoides junior*, here referred to *Zanabazar*, also is known only by the holotype from Bugiin Tsav, Nemegt Formation. This specimen consists of a skull and partial mandible, a series of sacral and caudal vertebrae, a partial pelvic girdle, and the distal part of the right hind limb. *Saurornithoides + Zanabazar* is one of the few Mongolian taxa known from both the Djadokhta and Nemegt formations. The monophyly of *Saurornithoides + Zanabazar* has not been seriously questioned historically, yet empirical support for this clade is currently tenuous. A privileged phylogenetic relationship between *Saurornithoides*, *Zanabazar*, and the North American troodontid *Troodon formosus* is supported by numerous characters including the presence of a subotic recess, lateroventrally projecting and hollow basipterygoid processes, a lacrimal whose anterior process is significantly longer than its posterior process, a highly pneumatized parasphenoid rostrum, a constricted neck of the occipital condyle, a symphyseal region of the

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dentary that is slightly recurved medially, and an obturator process located near the middle of the ischiadic shaft. CT data for the skulls of both species facilitated a description of the endocranial anatomy of *Saurornithoides mongoliensis* and *Zanabazar junior*, including a reconstruction of the endocranial space of *Zanabazar junior*. Despite being the largest of the known troodontid species, the endocranial volume of *Zanabazar junior* is considerably smaller than that estimated for *Troodon formosus*, suggesting that the extremely high encephalization quotient of *Troodon formosus* may be autapomorphic among troodontids.

INTRODUCTION

In an important but brief paper published in 1924 (Osborn, 1924), Henry Fairfield Osborn named three small theropod dinosaurs from the upper Cretaceous Djadokhta Formation of Bayan Zag (also known as Bayn Dzak, Shabarakh Usu, or "the Flaming Cliffs"). One of the three was *Saurornithoides mongoliensis*, based upon a single, eroded partial skeleton, comprising a skull and fragmentary postcranial elements. The generic name was chosen to emphasize some of the birdlike features of this dinosaur, especially the shape of the rostrum. The similarity to birds was recognized in the field, as a catalog page from Walter Granger's field book labels the specimen "reptile or toothed bird" (fig. 1). This specimen, collected by "the Chinese assistant, Chih" (Osborn, 1924: 3), remains the only known definitive record of this species, and little more has been added to the published record since Osborn's description.

At the time of Osborn's paper the only known troodontid—*Troodon formosus* (then based solely on teeth)—was confused with the pachycephalosaurid ornithischian *Stegoceras* (Gilmore, 1924), and its theropod affinities were not recognized (see Currie, 1987). Osborn therefore largely limited his comparisons with *Velociraptor mongoliensis*, first described in the same paper. Nevertheless, he presciently suggested that "it may prove to have avian relationships" (Osborn, 1924: 1), a hypothesis now well corroborated. Indeed, recent analyses place troodontids as one of the closest relatives of birds (Xu et al., 2002; Turner et al., 2007a, 2007b), perhaps even the closest (Forster et al., 1998, Hwang et al., 2004).

In 1964, a well-preserved skull and partial skeleton of a troodontid was discovered at the upper Cretaceous locality of Bugiin Tsav by the first joint Mongolian-Soviet Paleontological Expedition (Kurochkin and Barsbold, 2000). It was discovered and collected by R. Barsbold and B. Namsray, the first dinosaur specimen ever collected by a Mongolian professional scientist (Barsbold, personal obs.). This specimen, IGM 100/1, was given the name *Saurornithoides junior* and described by Barsbold (1974). Referral of the new species to *Saurornithoides* was based on similarities with the only other well-known troodontid cranium, the holotype of *Saurornithoides mongoliensis*, and on the cooccurrence of both taxa in the upper Cretaceous of Central Asia. The holotype remains the only known specimen of this species. Although other troodontid material was described from the Nemegt Formation, few new observations of IGM 100/1 have been published since the original description.

Several important Asian and North American troodontid specimens and taxa described in the last 15 years (Currie, 1985, 1987; Currie and Zhao, 1993; Russell and Dong, 1993; Norell et al., 2000; Xu et al., 2002; Xu and Norell, 2004) have greatly improved our knowledge of the group, and currently there are nine named species. Here we further describe and illustrate the holotype specimens of the two species referred to *Saurornithoides*, based in part upon CT scans of both, and compare them with troodontid material collected since Barsbold's (1974) description. These comparisons indicate that while these two species are closely related among troodontids, their sister-taxon relationship, and thus the monophyly of *Saurornithoides* (sensu lato), is questionable and should not be assumed in subsequent analyses.

METHODOLOGY

All specimens were scanned at the University of Texas High-Resolution X-ray Computed Tomography (HRCT) Facility,
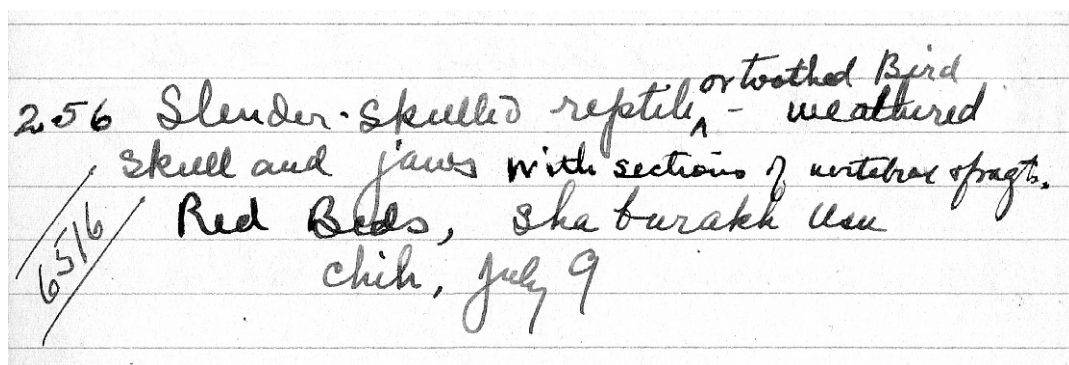
Fig. 1. Entry from the 1923 field book of Walter Granger describing what would become the holotype of *Saurornithoides mongoliensis* (AMNH FR 6516).

and the resulting images are used to aid in the description of internal features of the skull and the cast of the endocranial cavity (endocast). The holotype skull of *Saurornithoides mongoliensis* (AMNH FR 6516) was scanned on 30 April 1998. Scanning was performed on the high-energy system using a brass filter in a garnet-powder wedge, a voltage of 420 kV, and amperage of 4.8 mA. Scans were taken along the coronal axis for a total of 482 slices at an image resolution of 512 × 512 pixels. The garnet wedge was removed from the slices, and the resulting images were used for image processing. The interslice spacing is 0.4 mm and reconstructed field of view is 146 mm. Slices along the horizontal and sagittal axes were reconstructed using VGStudioMax© 1.2.1.

The holotype skull of *Saurornithoides junior* (IGM 100/1), hereafter referred to as *Zanabazar junior*, was scanned on 31 October 2000. Scanning was performed on the high-energy system using a brass filter in an air wedge, a voltage of 420 kV, and amperage of 4.8 mA. Scans were taken along the coronal axis for a total of 625 slices at an image resolution of 512 × 512 pixels. Because of differences in X-ray attenuation, the skull was scanned in sections with different acquisition times and numbers of views resulting in a slight rotational error that is not corrected. The resulting images have an interslice spacing of 0.45 mm and a reconstructed field of view of 117 mm.

The endocranial cast of *Zanabazar junior* was constructed using the original 16-bit imagery in the volumetric rendering program VGStudioMax© 1.2.1. Contrast in the images was increased until the endocranial space (infilled with matrix) and bone were distinguishable from each other. The endocranial cavity was selected using the segmentation tools available in the program, separated into its own volume, and exported as an isosurface volume. Measurements of the braincase and endocast (including volume) were taken in VGStudioMax©. The volume of the endocast was determined by calculating the volume of negative space of the endocranial cavity. To facilitate ease of description, features of the endocranial casts are referred to by the names of the soft tissue structures of the brain that they reflect (e.g., cerebrum rather than cast of cerebrum). The cast of the endocranial space may reflect structures other than the brain, such as meninges and sinuses. This cast, however, is useful in determining relative size and shape of different regions of the brain as well as recognizing the branching points of the cranial nerves (Hopson, 1979). Movies of the HRCT scans and the volumetric rendering of the endocranial casts and skulls are available on the Digital Morphology website (http://www.digimorph.org/specimens/Saurornithoides_mongoliensis; http://www.digmorph.org/specimens/Zanabazar_junior).

Transliteration of Mongolian names follows that suggested by Benton (2000). A list of
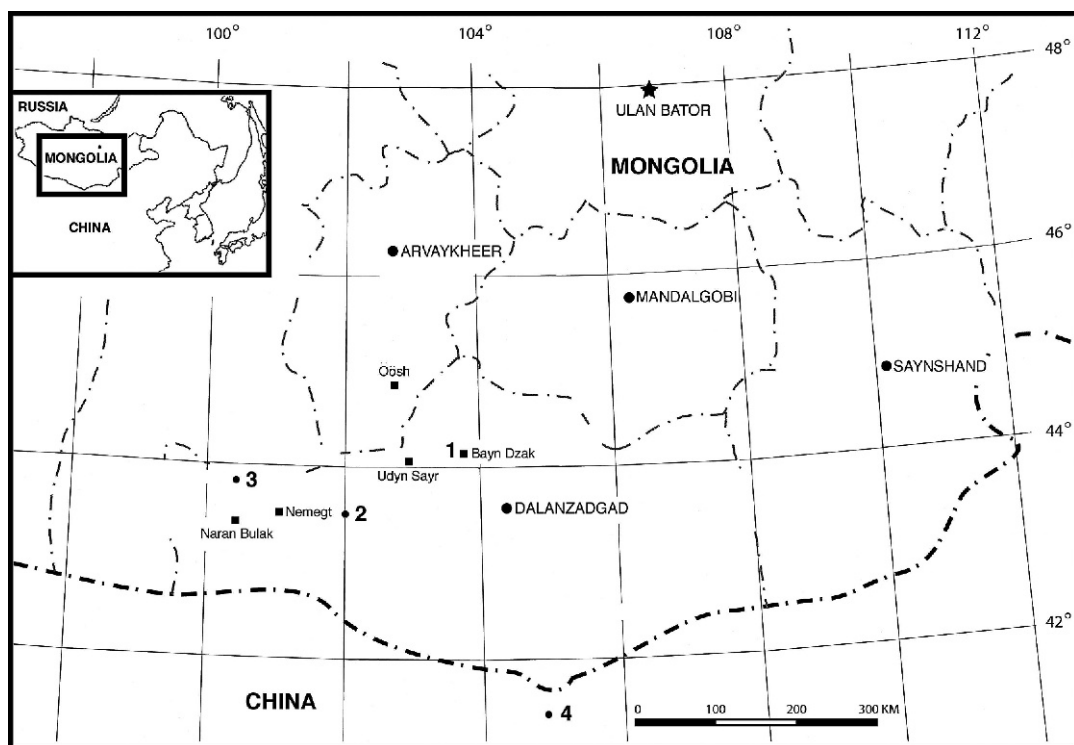
Fig. 2. Map of Mongolia showing the location of Bayan Zag (Bayn Dzak, 1), Ukhaa Tolgod (2), and Bugiin Tsav (3).

institutional and anatomical abbreviations is given in appendix 1.

SYSTEMATIC PALEONTOLOGY

Theropoda Marsh, 1881

Coelurosauria Huene, 1920

Maniraptora Gauthier, 1986

Troodontidae Gilmore, 1924

Saurornithoides Osborn, 1924

TYPE SPECIES: *Saurornithoides mongoliensis* Osborn, 1924, by original designation.

INCLUDED SPECIES: Only the type species is currently referred to *Saurornithoides*.

LOCALITIES AND AGE: *Saurornithoides* is known with certainty only from the location of the holotype of *Saurornithoides mongoliensis*—Djadokhta Formation of Bayan Zag, upper Cretaceous of Mongolia (fig. 2).

DIAGNOSIS: Differs from *Zanabazar junior* in its smaller overall size, lower number of teeth (108 versus 118), the presence of a jugal that is straight beneath the round orbit rather than curved, and the possession of a pneumatic recess on the lateral surface of the prootic dorsal to the trigeminal fenestra (the pneumatic recess is also absent in *Troodon formosus*). The maxillary teeth of *Saurornithoides* exhibit some increase in crown height posteriorly but to a lesser degree than in *Zanabazar junior*. Also in contrast to *Zanabazar junior*, the maxillary teeth of *Saurornithoides* lack replacement gaps. In these latter two characters, *Saurornithoides* agrees with *Mei long*, *Sinovenator changii*, and basal avialans among paravians, whereas *Zanabazar junior* is more similar to *Byronosaurus jaffei* and dromaeosaurs.

COMMENT: The monophyly of *Saurornithoides* as historically recognized—including *Saurornithoides mongoliensis* and *Saurornithoides junior*—has not previously been questioned. A sister-taxon relationship between these two taxa, however, is difficult to support empirically. This may be due in part to the

overall poor preservation of the holotype of *Saurornithoides mongoliensis*. Morphological disparity does exist between the known specimens of these two taxa and, although this list of differences is less than we might normally expect when taxonomically separating specimens at the generic level, the retention of *junior* in *Saurornithoides* implies a privileged relationship with *mongoliensis* that cannot currently be supported. The one polarized character previously considered to support the monophyly of *mongoliensis* + *junior* was the position of the facial foramen (CN VII) within the lateral depression of the braincase (Turner et al., 2007b). It now appears likely that this feature also is present in *Troodon formosus* and therefore is derived at a slightly more inclusive position on the troodontid tree (see below).

Saurornithoides mongoliensis Osborn, 1924

HOLOTYPE: AMNH FR 6516, a weathered skull with articulated mandible and associated partial postcranial skeleton. The outer surfaces of the skull and skeleton are highly weathered, and the postcranial skeleton is fragmentary. The skull is missing the dorsal and lateral walls of the braincase and the occiput dorsal to the foramen magnum, and most of the frontals were eroded away (fig. 3). The lower temporal and posttemporal bars are missing on both sides except for a suborbital section of the jugal on the right. The head of the right quadrate is preserved but not the left, and the upper temporal bars are missing on both sides. The illustration of the right side of the skull by Osborn (1924; fig. 4) combines some aspects of the left: the interfenestral bar is preserved only on the left side, but is illustrated on the right side. Both dentaries are preserved but are eroded ventrally. Only the anterior parts of the postdentary bones are preserved on both sides. The preserved postcranial elements include four dorsal vertebrae, six sacral vertebrae, the first four caudal vertebrae, a partial left ilium, parts of both pubes, parts of both ischia, the proximal part of the left femur, the impression of the left tibia, and the distal end of the left pes. Most of these bones were preserved in a concretion, with which a few isolated bones were associated. Many of the elements were removed from the concretion after Osborn's description. A cast of the pelvic region in the concretion was made before the specimens were removed and is figured here (fig. 5). An isolated series of three caudals originally was referred to the holotype (fig. 6). These caudals are short, have rounded centra, and bear tall, rodlike neural spines. We reinterpret these caudal elements as being midcaudal vertebrae of a protoceratopsian, which probably were surface collected as a nodule near the *Saurornithoides mongoliensis* holotype and mistakenly referred to it. These vertebrae are now catalogued as AMNH FR 30613.

TYPE LOCALITY: Djadokhta Formation at Bayan Zag, Omnogov Aimag, Mongolia (figs. 2, 7). Unfortunately, the precise locality at the Flaming Cliffs where the specimen was collected was not recorded. The page from Walter Granger's field book cataloguing the specimen is reproduced in figure 1.

AGE: The Djadokhta Formation is considered to be Late Campanian based primarily upon the vertebrate fauna (Loope et al., 1998; Dingus et al., 2008).

DIAGNOSIS: Same as for *Saurornithoides*.

REFERRED SPECIMENS: Two incomplete troodontid specimens from the Djadokhta Formation have been referred to *Saurornithoides mongoliensis*. Currie and Peng (1993) referred a specimen, IVPP V10597, from Bayan Mandahu, China, to *Saurornithoides mongoliensis*. The specimen comprises a left hind limb including the femur, a partial tibia and fibula, tarsals, and an articulated foot. However, the hind limbs of the *Saurornithoides mongoliensis* and *Zanabazar junior* holotypes lack features diagnostic at the species or genus level, so we consider IVPP V10597 to be referable only to Troodontidae. Norell and Hwang (2004) provisionally referred a fragmentary specimen from Ukhaa Tolgod (IGM 100/1083) to *Saurornithoides mongoliensis*, but it, too, lacks features diagnostic of this species. The specimen includes a maxillary fragment, quadrate, six vertebrae, and a few bones from the feet. The pattern of tooth placement in the maxilla is similar to that of *Saurornithoides mongoliensis* rather than *Byronosaurus jaffei* (Makovicky et al., 2003), the only other
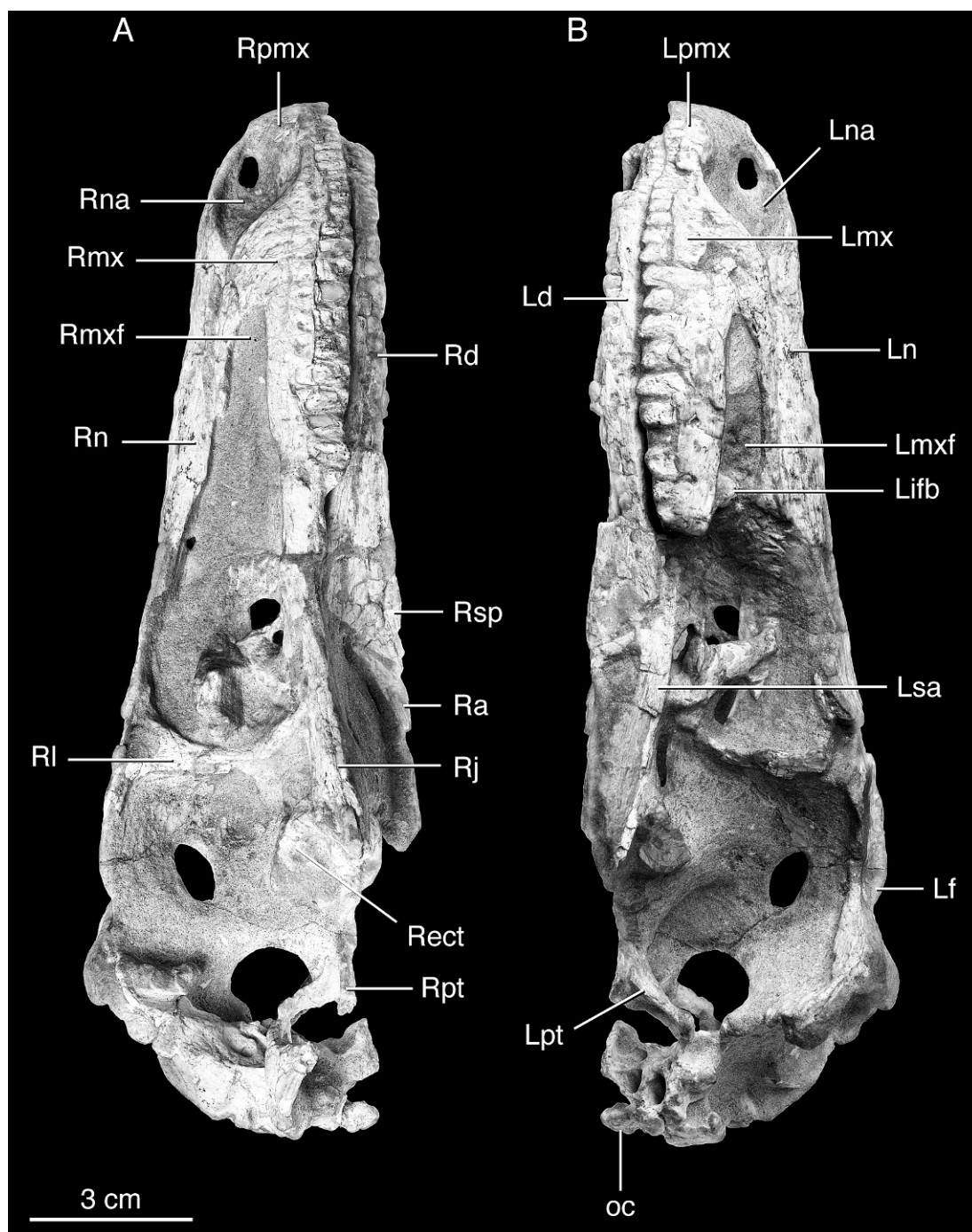
Fig. 3.   The holotype skull of *Saurornithoides mongoliensis* (AMNH FR 6516) in right lateral (**A**) left lateral (**B**), ventral (**C**), and dorsal (**D**) views.
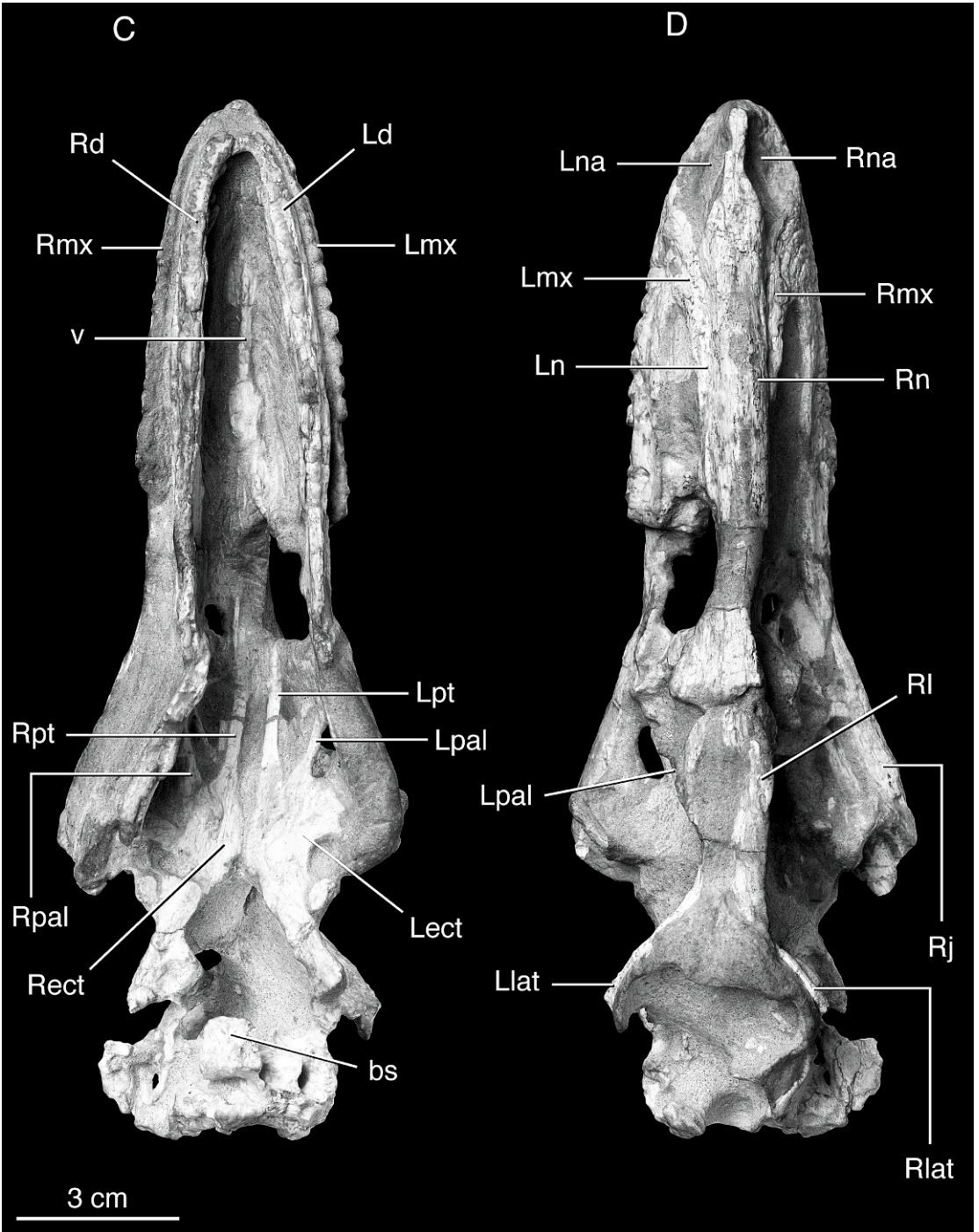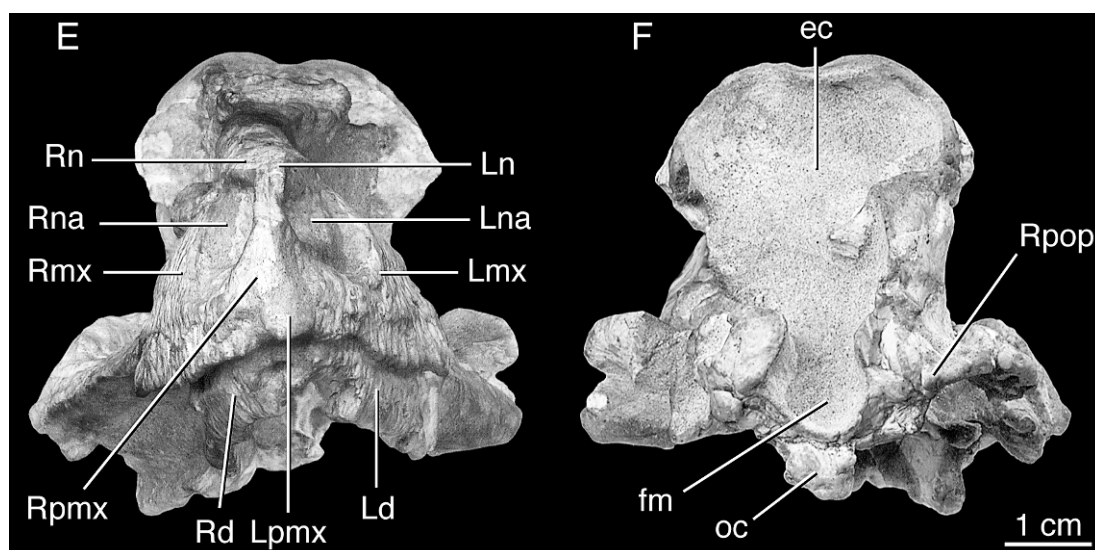
Fig. 3. *Continued.*

Fig. 3. *Continued*. The holotype skull of *Saurornithoides mongoliensis* (AMNH FR 6516) in anterior (**E**) and posterior (**F**) views.

troodontid described from this formation. It is likely that this specimen and the Chinese specimen are *Saurornithoides mongoliensis* based on their stratigraphic occurrences, but the lack of definitive morphological evidence negates a generic level taxonomic assignment.

DESCRIPTION

SKULL

PREMAXILLA: The anterior end of the rostrum is rounded in dorsal view (fig. 3D). The premaxillary-maxillary suture is indistinct but can be traced on the left side. It is similar in position to that of *Zanabazar junior*, so the premaxilla forms only the anterior third of the ventral edge of the naris in lateral view. The slender ascending processes of the premaxillae join to form nearly the entire internarial bar. The internarial bar is wide and dorsally flattened as in other troodontids, *Shuvuuia deserti*, and some ornithomimids. It overlies the nasals above the posterior end of the nares, and ends opposite the posterior narial border. The distal end of the ascending process appears to separate the nasals anteriorly as in *Byronosaurus jaffei*, *Zanabazar junior*, and *Velociraptor mongoliensis* (AMNH 6515). The premaxilla attenuates posteriorly, and an apparent lateral expansion

on the right side is actually formed by the maxilla. Within the narial chamber, the premaxilla forms the anterior part of the dorsally convex floor. The contact with the maxilla in this floor, however, is unclear.

NASAL: The nasals are elongate and transversely vaulted, as in *Byronosaurus jaffei* and *Zanabazar junior*. Anteriorly, they form the posterodorsal border of the nares and for a short distance separate the maxillary from the premaxillary internarial bar. Laterally, the nasal meets the maxilla along a straight suture just dorsal to the maxillary fenestra. A nasal-maxillary suture is present in all troodontids with the exception of *Sinovenator changii* (Xu and Norell, 2004). The lateral surfaces of both nasals are not preserved posterior to the interfenestral bars.

LACRIMAL: The right and left lacrimal are present with the right being the more complete of the two. The lacrimal is T-shaped, with anterior and posterior processes contributing to the dorsal margin of the external antorbital fenestra and orbit, respectively. The antorbital process is distinctly longer than the orbital process. The vertical shaft of the lacrimal is slightly concave anteriorly, which results in a slightly convex anterior margin of the orbit.

MAXILLA: The maxilla forms most of the anterolateral surface of the rostrum. Ante-
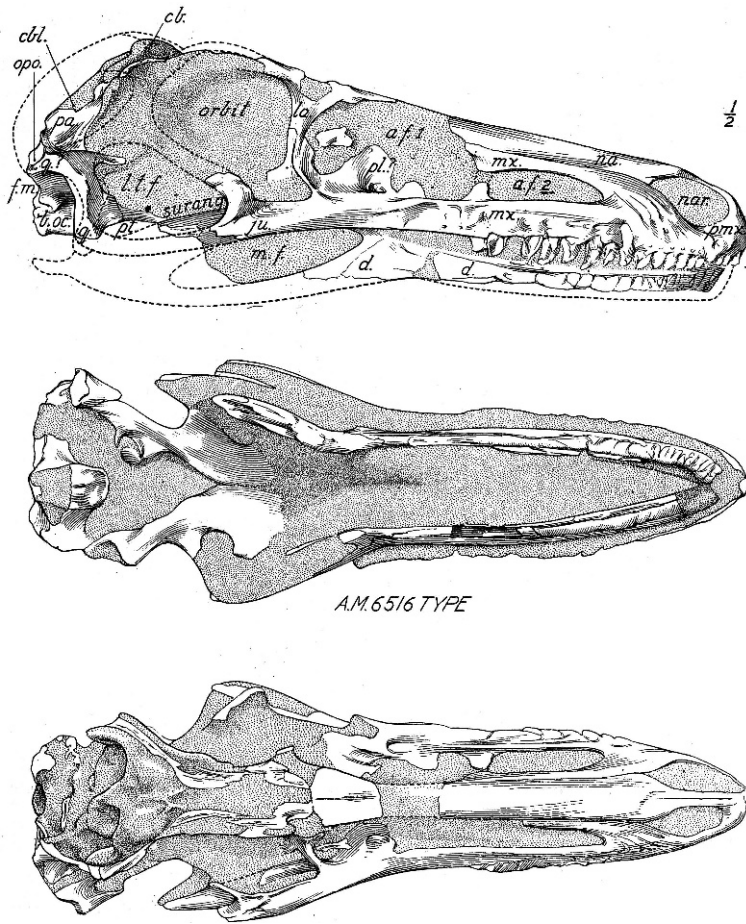
Fig. 4.   Illustrations of the holotype skull of *Saurornithoides mongoliensis* in right lateral (top), ventral (middle), and dorsal (bottom) views (after Osborn, 1924). The original illustrations show some inaccuracies (e.g., the interfenestral bar is illustrated on the right side but preserved only on the left side). The abbreviations used by Osborn do not necessarily correspond to those in appendix 1. Those that differ include: **af1**, antorbital fenestra; **af2**, maxillary fenestra; **boc**, basioccipital; **cb**, cerebrum; **cbl**, cerebellum; **ju**, jugal; **la**, lacrimal; **mf**, mandibular fenestra; **na**, nasal; **nar**, external naris; **pa**, parietal; **q**, quadrate.

riorly, the maxilla contacts the premaxilla, posterior to which it forms most of the posterior border of the naris before contacting the nasal dorsally. The contact with the nasal is recessed, so the posterior corner of the naris is acute. The lateral floor of the naris has a rough texture, which does not appear to be due to erosion. Dorsal to the tooth row, a line of supralabial foramina lie in a shallow supralabial groove. A large pit is present on the floor of the right naris close to the presumed contact with the premaxilla. In the CT sections, it does not appear to communicate internally with the supraalveolar canal or any other structure and appears to be an artifact. A similar pit, however, is present on the floor of the nasal chamber in a neonate specimen of *Byronosaurus* (Bever and Norell, 2009).

As in other troodontids, a deep antorbital fossa is not developed around the antorbital and maxillary fenestrae. A dorsal, or nasal, process of the maxilla forms the dorsal border of the subelliptical maxillary fenestra, excluding the nasal from this opening. The dorsal process thins posteriorly and it is not preserved posterior to the interfenestral bar. An incomplete interfenestral bar is preserved on
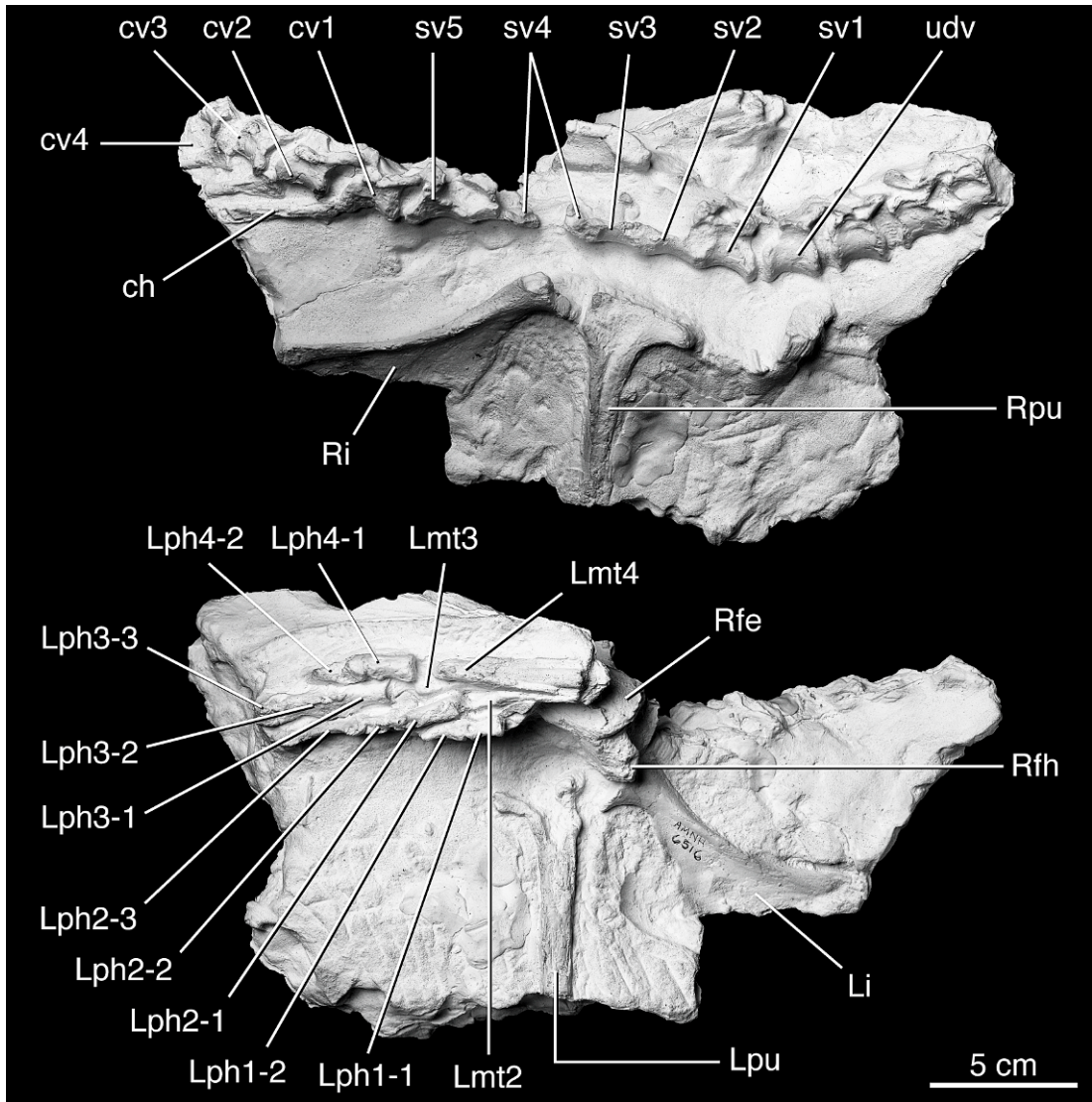
Fig. 5. Photograph of a cast made from the original block containing the preserved postcranium of *Saurornithoides mongoliensis*. Individual elements were removed and prepared in isolation after the block was cast.

the left side and it separates the anterior maxillary fenestra from the antorbital fenestra. The bar is constricted at midheight and is slightly inset from the lateral surface of the skull dorsally. An inset interfenestral bar is present in all known troodontids with the exception of *Byronosaurus jaffei* (Makovicky et al., 2003). Ventrally, a shallow groove separates the interfenestral bar from the labial ramus of the maxilla. A small cavity can be observed on the posterior surface of the interfenestral bar that corresponds to the lower interfenestral foramen (interfenestral canal) seen in *Byronosaurus* (Norell et al., 2000; Makovicky et al., 2003; Bever and Norell, 2009). In *Byronosaurus*, this cavity communicates between the maxillary fenestra and antorbital fenestra. CT scans reveal that this was also the case in *Saurornithoides mongoliensis*. The caudal margin of the max-
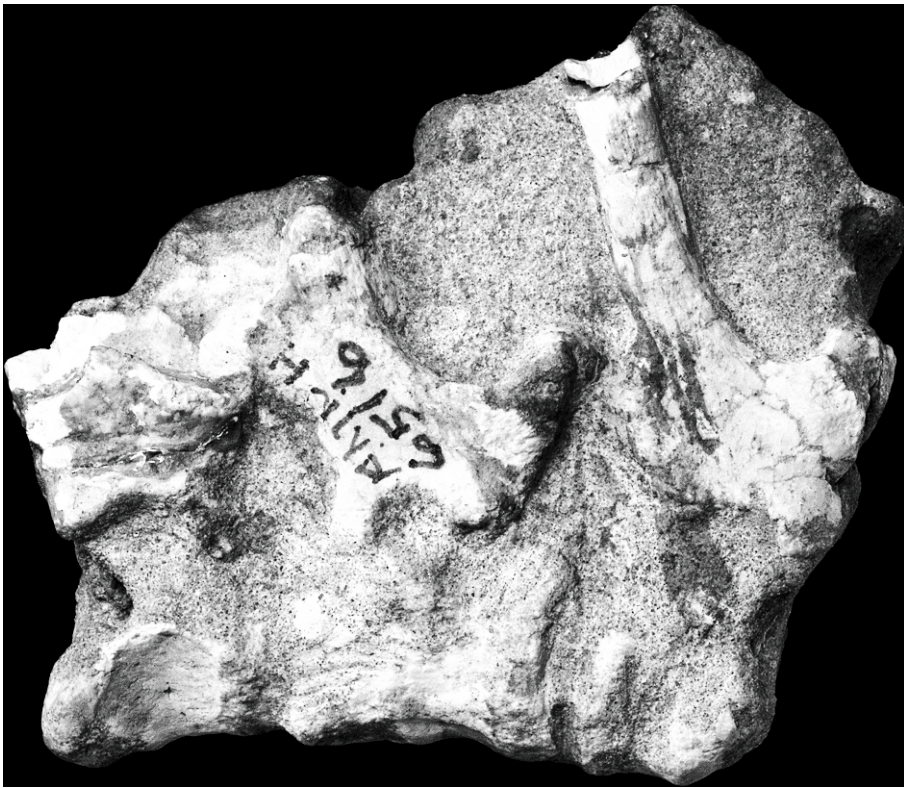
Fig. 6.   Three caudal vertebrae originally described as belonging to the holotype of *Saurornithoides mongoliensis* but which are now identified as protoceratopsian (AMNH FR 30613; AMNH 6516, visible on the specimen, is its original specimen number before it was recognized as protoceratopsian and recatalogued).

illary fenestra lies completely anterior to the rostral margin of the antorbital fossa.

Posterolaterally, the maxilla is poorly preserved on the right side and incomplete on the left. The maxilla appears to be overlapped by the jugal for several centimeters anterior to the jugal-lacrimal contact on the right side of the skull, but the contact is obscured by several breaks filled with red glue. The tooth row, although incomplete, is short (73 mm) compared to the preserved skull length (191 mm). It ends slightly posterior to the base of the interfenestral bar as in *Byronosaurus jaffei* and *Zanabazar junior*.

Sections of the palatal portion of the maxilla are poorly exposed on the ventral surface of the skull. Nevertheless, there is evidence that *Saurornithoides mongoliensis* possessed a secondary palate as in other troodontids (Makovicky and Norell, 2004; Bever and Norell, 2009). Small plates of bone adhere to the anterolateral edges of the vomer (just posterior to the premaxilla), and an almost complete section of the shelf extends from the base of the interfenestral bar toward the midline. The CT data (fig. 8) clearly show that maxillary shelves extend to the midline to meet the vomer, as in *Byronosaurus jaffei* (Norell et al., 2000) and dromaeosaurids such as *Velociraptor mongoliensis* (Norell and Makovicky, 1999; Barsbold and Osmólska, 1999). The palatal shelves are formed of extremely thin bone and extend posteriorly to the level of the interfenestral bar, a position corresponding to the anterior rim of the choana in other maniraptorans.

VOMER: The vomers are paired posteriorly, approximately at the level of the last maxillary tooth (the left vomer is slightly better preserved posteriorly). Anteriorly, the vomers are preserved as highly appressed rods that form a single midline structure. This

Fig. 7. Photograph of the Flaming Cliffs—Djadokhta Formation at Bayan Zag, Omnogov Aimag, Mongolia. The exact location from which the holotype of *Sauronithoides mongoliensis* was collected is unknown.

structure thins distinctly at a point approximately in line with the anterior margin of the external maxillary fenestra. This rostral projection forms a contact with the premaxilla (fig. 3C).

JUGAL: Only the right jugal is preserved, and it is missing the subtemporal ramus and the ascending process and is highly weathered laterally. The suborbital ramus of the jugal is oriented obliquely, extending posterolaterally from the anterior end of the round orbit (evident on the left side also, from the position of the ectopterygoid). The suborbital ramus is straight, lacking the curvature beneath the orbit present in *Zanabazar junior*. The bone does not appear to be expanded laterally beneath the orbit as in *Zanabazar junior*, in which a large cavity penetrates the bone, but it is too poorly preserved to be sure. The position of the postorbital bar, as suggested by the position of the ectopterygoid, indicates the orbit narrowed ventrally and

broadened posteriorly as it rose vertically. The contact with the maxilla appears to be well anterior to the posterior end of the antorbital fossa, as in other troodontids, but this region is broken and gaps are filled with red glue.

PALATINES: Both palatines are exposed in ventral view (fig. 3C). In dorsal view (fig. 3D), the left palatine is visible but eroded, whereas the right palatine is incompletely exposed. They are tetraradiate in shape and vaulted, extending obliquely toward the midline to overlie the pterygoids. The ventromedial surface of each palatine is gently concave. On the right side, the palatine apparently becomes horizontal laterally and contacts the jugal and/or maxilla. A slender process extends posteriorly and slightly medial from the body of the bone to contact the body of the pterygoid. The palatine overlies the pterygoid on the right side, but the suture is not apparent on the left side.
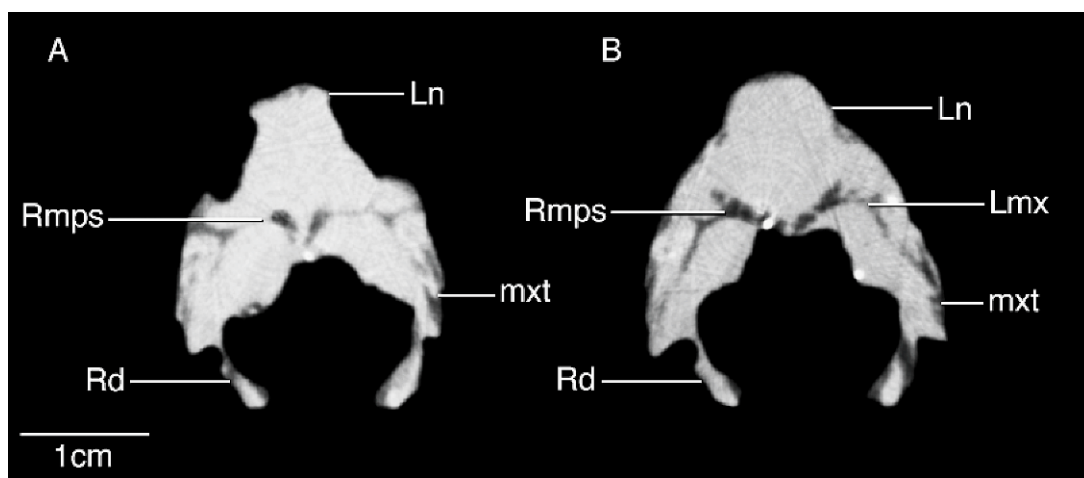
Fig. 8.   Transverse CT slices (59, **A**; 76, **B**) through the rostrum of *Saurornithoides mongoliensis* (AMNH FR 6516) showing the extensive palatal shelves of the maxilla.

PTERYGOIDS: The pterygoids are broad bones that are well preserved on both sides. The dorsoventrally flattened quadrate ramus diverges posterolaterally very strongly from the midline, suggesting the presence of a parasphenoid bulla posterior to it (although none is preserved). The body of each pterygoid is flat but extends dorsomedially, so that the two bones form a vaulted surface. The pterygoids rise anteriorly, and a slender process extends anteriorly from each bone near the midline. The body of the pterygoid meets its opposite along the midline, but the anterior processes are slightly separated, forming a narrow interpterygoid vacuity with parallel edges. The anterior (interchoanal) process extends anteriorly to at least the level of the palatines, medial to the posterior part of the antorbital fenestra.

An unusual dorsal process extends from the posterior end of the pterygoid to the region of the quadrate's contact with the prootic. On the right side this process is delicate and curves dorsolaterally, thinning dorsally. On the left side, which appears to be better preserved, this process is broad, extends dorsally without curving, and is deeply excavated along the posterior surface.

ECTOPTERYGOIDS: The ectopterygoids generally are poorly preserved and exposed (they were not differentiated from the pterygoid or jugal by Osborn, 1924: fig. 4 top and middle), but the posteroventral surface of the medial part is well preserved on the left side. The medial portion of the bone is flat and a posterolateral "hook" is apparent, similar to that of other theropods. The ectopterygoid contacts the palatine anteriorly along the medial edge of the pterygoid, although the contact is obscure on the left side and not exposed on the right. The lateral part of the bone is not exposed and is not discernable in the CT scans, so a ventral pocket cannot be identified.

QUADRATE: A small portion of the right quadrate is preserved in articulation with the quadrate ramus of the pterygoid. It is horizontally oriented, and concave ventrally.

FRONTALS: Only very small fragments of the ventral part of the frontals are preserved. Small fragments of the descending cristae calvarii frontalis define an hourglass-shaped fossa between the orbits.

PARIETALS: The only preserved part of the parietals is on the anterolateral side of the braincase, but the overall shape of the anterior part is evident from the partial endocast. The endocast indicates that the forebrain area was greatly expanded, to approximately the same extent as in *Troodon formosus* (Hopson, 1979), *Zanabazar junior*, and *Sinovenator changii* (Xu et al., 2002).

SCLERAL OSSICLES: Fragments of three scleral ossicles adhere to the front of the braincase on the right side of the skull (fig. 9). Two are nearly complete but incompletely exposed, the third and outermost piece is
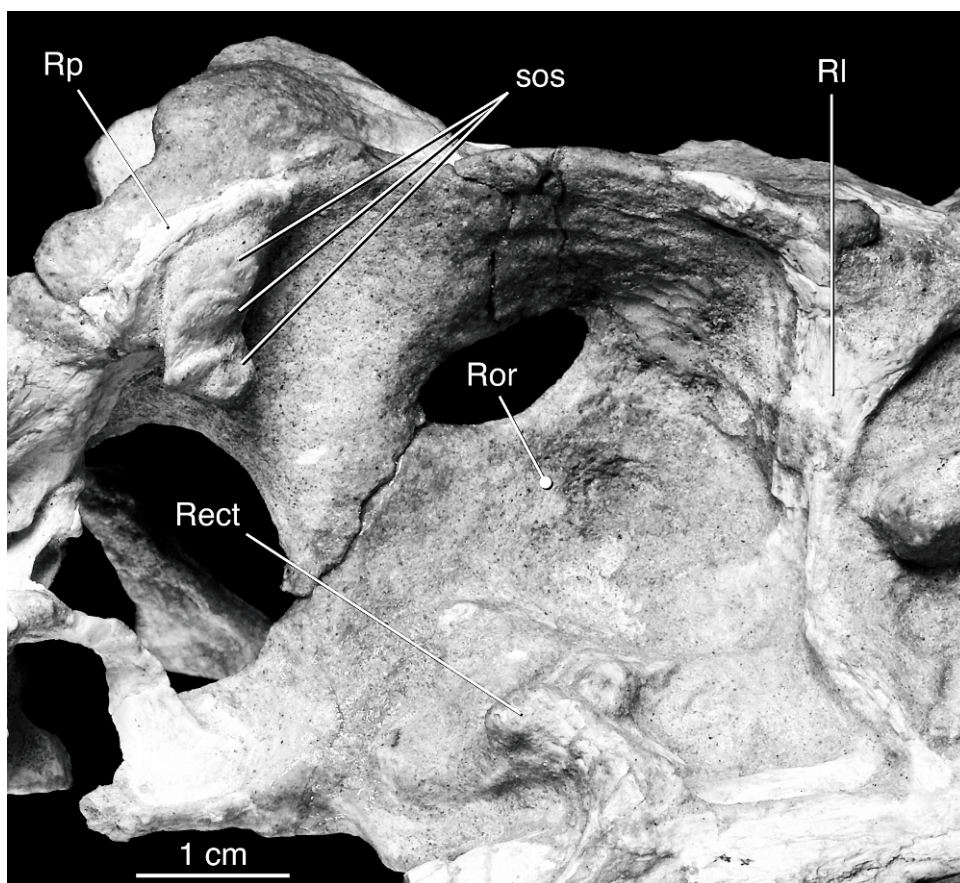
Fig. 9. Photograph of the right orbit of *Saurornithoides mongoliensis* (AMNH FR 6516) showing a small remnant of the scleral ring (three scleral ossicles).

mostly incomplete. The internal surface of the middle ossicle is well exposed, and unless the edges of the bone have been eroded its overall shape was rectangular with its long axis parallel to the circle of ossicles. The ossicles are only slightly concave internally, and there is no evidence for an "L" shape as in birds with tubular eyes (Martin, 1985).

EXOCCIPITAL/OPISTHOTIC: The presumably fused exoccipital and opisthotic are heavily eroded, and most of the paroccipital processes are missing. The more complete right paroccipital process appears short as in other troodontids (fig. 3C). CT scans show that the base of the paroccipital process antero-dorsal to the middle ear, comprising the opisthotic, is invaded by several pneumatic diverticula (fig. 10)—as in *Bryonosaurus jaffei* (Makovicky et al., 2003; Bever and Norell,

2009). The medial surface of the exoccipital is not exposed within the endocranial cavity, but the bone around the foramen magnum is eroded and the openings for the hypoglossal nerves are gone. The lateral opening into the middle ear region is preserved on the left side, but the crista interfenestralis is broken, making the fenestrae ovalis and pseudorotun-da appear fully confluent. The surface of the opisthotic dorsal to the otic region lacks an obvious caudal tympanic fossa, as found in dromaeosaurids and some other theropods. An endocast of the right vertical semicircular canal is exposed where the bone has fractured.

PROOTIC: The right and left prootic are relatively well preserved, although the dorsal extent of the left prootic is missing (fig. 11). The lateral surface of this element is charac-terized by a distinct lateral depression that is
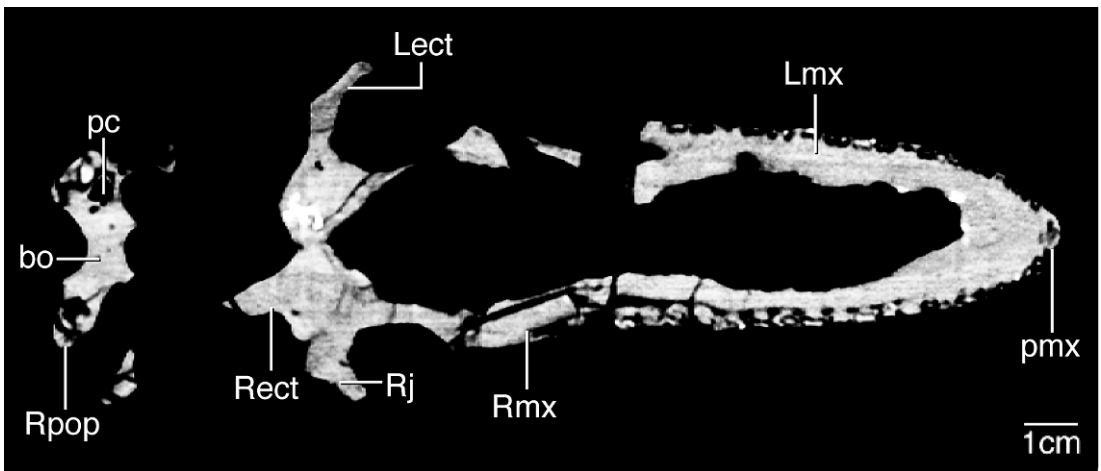
Fig. 10.   Horizontal CT slice (302) through the skull of *Saurornithoides mongoliensis* (AMNH FR 6516) showing the presence of a vacuity in the base of the paroccipital process. The space is inferred to reflect pneumatization of the process by diverticula of the caudal tympanic sinus.

delineated anterodorsally by a prominently developed otosphenoidal crest. This crest lies adjacent to, and forms the ventral margin of, the external opening of the trigeminal nerve (CN V), which is completed in bone by the laterosphenoid (preserved only on the right side). The external foramen of the facial nerve (CN VII), passes through a vertical strut that lies distinctly ventral to the otosphenoidal crest and therefore within the lateral depression (as in *Zanabazar junior*). A slight ridge extending obliquely across the trough between the facial and trigeminal foramina in *Byronosaurus jaffei* (Makovicky et al., 2003) may correspond to the expanded dorsal extension of the lateral depression in *Saurornithoides mongoliensis* and *Zanabazar junior*.

A small depression, possibly pneumatic in origin, lies just dorsal to the trigeminal foramen (preserved on the right side only; fig. 11B). The depression is absent in both *Zanabazar junior* and *Troodon formosus*. A similar, but much smaller, depression is present in *Byronosaurus jaffei*. The depression in *Byronosaurus jaffei* is separated from a concavity in the opisthotic interpreted as the dorsal tympanic recess by a low ridge (Norell et al., 2000; Makovicky et al., 2003). The anatomical origin of this depression in *Saurornithoides mongoliensis* remains obscure

but may reflect a rostral extension of the dorsal tympanic recess.

LATEROSPHENOID: The right laterosphenoid is well preserved but missing the capitate process, and the left is missing most of its dorsal portion (fig. 11B). The trigeminal opening is relatively small but similar in size to that of other troodontids. No other openings are apparent.

BASISPHENOID: The basisphenoid is only partially preserved, although it apparently was not exposed to weathering. A square portion of the ventral surface is preserved along the midline articulated to the basioccipital (fig. 3C). Its lateral wall is missing, exposing a well-developed pneumatic recesses beneath the endocranial cavity. A small piece of what appears to be the basipterygoid process is preserved on the right side adhering to the pterygoid; if so, the basisphenoid was about twice as long as the preserved portion. The parasphenoid rostrum and parasphenoid process are absent. However, the widely divergent posterior ends of the pterygoids suggest that an expanded bulla was present, as in other troodontids with the exception of *Sinovenator changii*.

BASIOCCIPITAL: The basioccipital is extremely eroded and fragmentary, but a few important features can be determined. The basioccipital contribution to the occipital
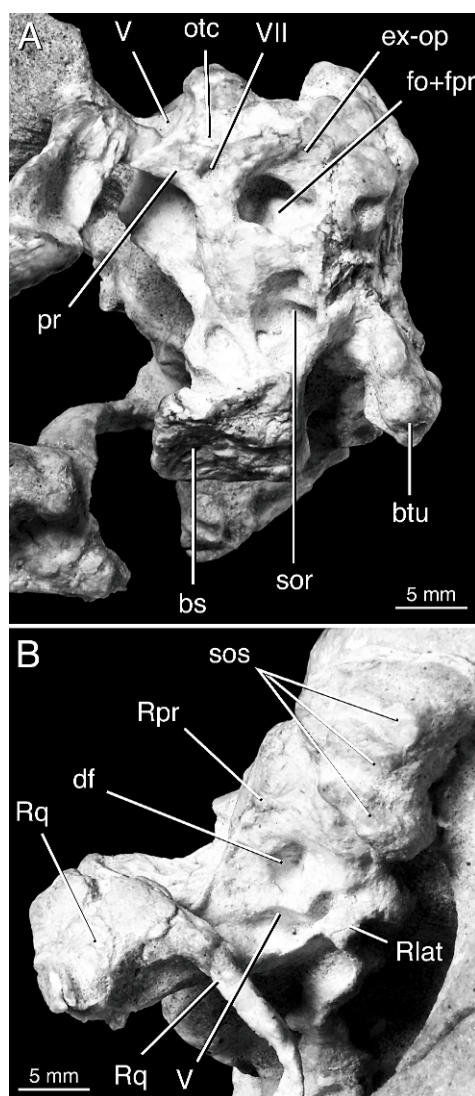
Fig. 11. The braincase of *Saurornithoides mongoliensis* (AMNH FR 6516) in left lateral (**A**) and right anterolateral (**B**) views.

condyle is extremely worn, and ventral to the base of the condylar neck is a depressed area as in *Zanabazar junior* and *Troodon formosus* (Currie and Zhao, 1993) but absent in *Byronosaurus jaffei*. Below the condyle, the basal tubera are eroded except for the apex of their V-shaped terminus—a derived feature common to troodontids (Makovicky et al., 2003). The ventral surface is extremely eroded, but a small foramen of unclear identity lies between the basioccipital tubera in the same

area as a similar foramen in *Troodon formosus* (Currie and Zhao, 1993). The basioccipital makes up the posterior part of the lateral depression. The basioccipital is solid where it meets the basisphenoid and there is no indication of a basisphenoidal recess at their contact (the loss of a basisphenoidal recess is a derived feature of troodontids).

MANDIBLE

DENTARY: Although the dentaries are extremely abraded ventrally, a few features are evident. In ventral view, the dentaries are slightly recurved medially giving the lower jaw a U-shaped appearance (fig. 3C), which corresponds with the shape of the rostrum. In lateral view, the dentaries appear to be subtriangular with anteriorly converging margins, assuming the ventral edge of the bone is typical of troodontids. The lateral surface of the jaw displays the characteristic troodontid feature of a line of pits that lie in a groove ventral to the tooth row. This feature is especially apparent on the posterior one-third of the left dentary's lateral surface. Posteriorly, the dentary meets the splenial along a straight anteroventral-posterodorsal oriented suture. Exact contacts with the remaining postdentary bones cannot be determined.

SPLENIAL: The splenial, best preserved on the right side (fig. 3A), is exposed laterally in a small triangular area between the dentary and the angular as in other deinonychosaurs. The medial part of the bone is more extensive and covers almost the whole preserved medial surface of the dentary. In medial view, the bone is triangular, mirroring the shape of the dentary. Although its anterior extent is not clear, it at least approaches the symphyseal region.

SURANGULAR: Both surangulars are partially preserved. Their length posterior to the level opposite the ectopterygoids is missing. The surangulars are deflected posterolaterally from their contact with the dentary, but this has been unnaturally accentuated on the right side where the surangular is preserved farther laterally than is the angular below it.

A lateral mandibular fenestra is apparent on both sides. The smooth edge of the angular's dorsal surface suggests this is a natural feature
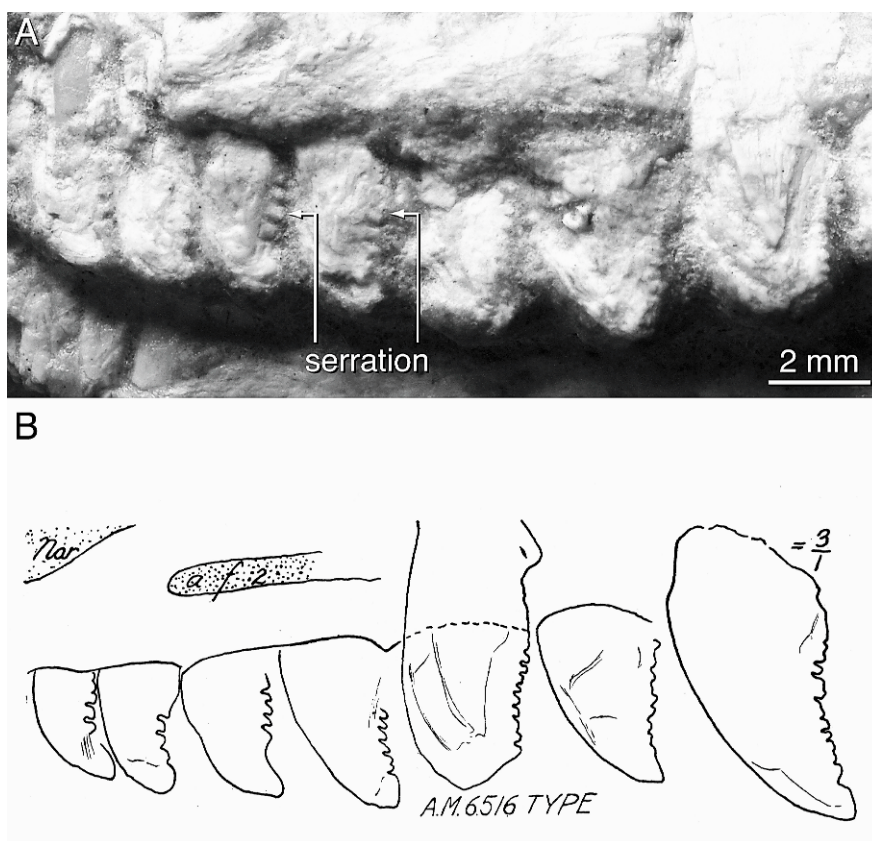
Fig. 12. Photograph of the closely appressed upper dentition of *Saurornithoides mongoliensis* (AMNH FR 6516) showing the distinct posterior serration (**A**), and Osborn's original illustration of the same region (**B**).

rather than a product of breakage. The precise length of the fenestra is indeterminate, but the preserved and exposed portions of the angulars and surangulars suggest the opening was anteroposteriorly oval and moderately long.

ANGULAR: The only preserved part of the angular is a section of the anterior end of both sides. It curves dorsally along the posterior edge of the triangular lateral part of the splenial.

PREARTICULAR: What may be the anterior end of the prearticular is preserved on the right side. It is a flat bone that curves dorsally and has a concave anteroventral edge.

TEETH

The teeth of AMNH FR 6516 generally are poorly preserved, especially the upper tooth row. The maxillary and premaxillary teeth are visible on the lateral surface of the skull, but these are predominately the tooth roots, as the labial margin of the maxilla has been eroded. The teeth are closely packed, as in other troodontids, and there is a marked increase in the size of the teeth posteriorly on the tooth row. Adjacent teeth, however, exhibit less than 30% difference in crown height (Currie and Varricchio, 2004; Turner et al., 2007b). On the left maxilla, some teeth preserve the distal end and serrated posterior edge (fig. 12). These teeth are typical of most troodontids in being blade-shaped with posteriorly pointing apices. Where preserved, the posterior margin of each tooth is lined with large denticles (Barsbold, 1974).

Some of the premaxillary teeth are missing in each premaxilla, but there is no evidence for
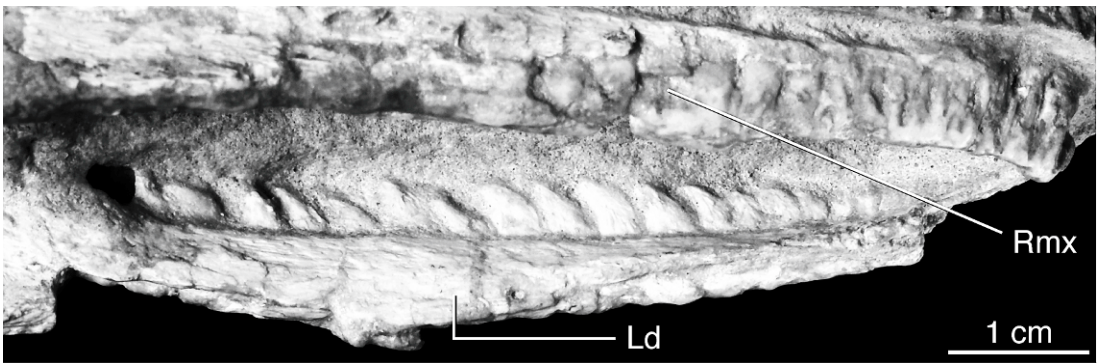
Fig. 13.   Medial view of the left dentary tooth row of *Saurornithoides mongoliensis* (AMNH FR 6516). The jaw is preserved in occlusion so that the mandibular teeth are visible only in medial view.

a number other than four as in other troodontids. The small anteriormost tooth is preserved, exposed in cross section, only on the right side, and the second is not preserved on either side. The third and fourth teeth are separated on both sides by the interceding bone and septum, which gives the superficial impression of a fifth tooth. The third and fourth teeth are subequal in size and appear to be mediolaterally compressed, but they are very poorly preserved.

Nineteen tooth positions are apparent on the maxilla (not 15 as indicated by Osborn, 1924, or the 17–18 by Barsbold, 1974), ending posteriorly beneath the interfenestral bar well short of the orbit. The anterior teeth are small and expand to nearly double in size at the eighth position and remain large to the end of the tooth row. All the teeth are damaged in some way, but those on the left generally are better preserved, except the first five. The sixth left tooth has straight edges nearly to the tip, where it curves sharply posteriorly, and most posterior teeth apparently had the same shape. No teeth preserve denticles on the anterior edge, and those denticles preserved on the posterior edge are relatively large, as in other derived troodontids, in comparison with, for example, dromaeosaurids. Osborn illustrated seven teeth (Osborn, 1924: fig. 4), interpreted here as the 6th–13th. In this same figure, Osborn mistakenly indicates that the maxillary, or secondary antorbital fenestra as implied by his label of ''a.f.2,'' was a slit low on the facial surface of the maxilla; there is no such feature on the specimen in the area

indicated by the figure. The fenestra is correctly labeled in his figure 3.

Teeth on the lower jaws are much better preserved and can be seen in lingual view on the inside of the skull where the jaws still lie in articulation with the rostrum. These teeth are small anteriorly, increasing in size posteriorly mirroring the size change in the upper dentition (fig. 13). The small anterior teeth are only slightly curved posterodistally, whereas curvature is more pronounced on the larger posterior teeth. Seventeen teeth are exposed lingually on the left side and 15 on the right, but on the left side eight are exposed anteriorly where the left dentary is broken and three teeth are exposed at the posterior end in lateral view. More are certainly present but unexposed on the right side anteriorly and posteriorly, and on the left there are two unfilled spaces between teeth. Thus, the left dentary indicates at least 31 tooth positions (contra Barsbold, 1974), and possibly one or two more were present anteriorly. Denticles are poorly exposed on the lower teeth.

VERTEBRAE

DORSAL VERTEBRAE: Four dorsal vertebrae were preserved on the main block (fig. 5). They correspond to the first four presacral vertebrae and were found in articulation with the sacrum (fig. 14). Although these vertebrae are adjacent to one another and all are from the posterodorsal region of the vertebral column, they differ from one another in centrum shape. The vertebral centrum of the
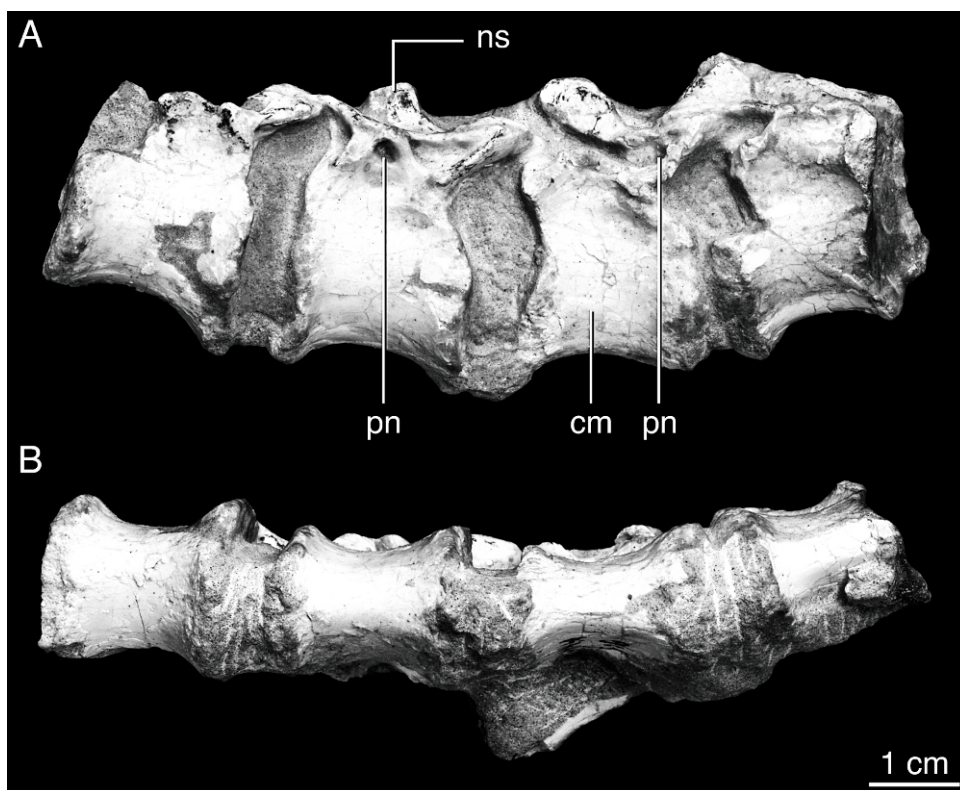
Fig. 14. Lateral (**A**) and ventral (**B**) views of the preserved dorsal vertebrae of *Saurornithoides mongoliensis* (AMNH FR 6516). Anterior is to the left.

posterior vertebrae is much more round ("spool shaped") in cross section than in the more anterior vertebrae, which are laterally compressed and have oval-shaped centra. The vertebral centra are platycoelous, and no suture between the neural arch and the centrum is apparent. No obvious pneumatic foramina are present on the sides of the centra. The neural spines and transverse processes are broken just distal to their bases. The neural arches are pneumatic and have three small pneumatic fossae, which lie in a row just ventral to the base of the transverse process. The parapophyses are high on the centrum and are not raised or stalklike as in dromaeosaurids (Makovicky, 1995; Norell and Makovicky, 1999). Pre- and postzygapophyses lie on the same level and the intervertebral articulations are inclined slightly medially. The presence of pneumatic signatures on the dorsal vertebrae is of interest as troodon-

tids generally are considered to contain pneumatic cervical vertebrae but apneumatic dorsals (Turner et al., 2007b).

SACRAL VERTEBRAE: The sacrum is poorly preserved on two blocks removed from the original concretion (fig. 15). As in other troodontids (Varricchio, 1997), there were six sacral vertebrae. The four anterior vertebrae are preserved in articulation with the last dorsal. The centra are subrectangular in ventral view with the ventral surface transversely broad and nearly flat. Flatness is especially marked in the third sacral. In the first four sacrals, the neural arch is preserved only on the first sacral, where it is incomplete and fused to the centrum. A single large pneumatic fossa lies at the base of the neural spine on the lateral surface of the first sacral. The midline sulcus, usually found on the ventral surface of the midsacral centra of maniraptorans (typically between sacral ver-
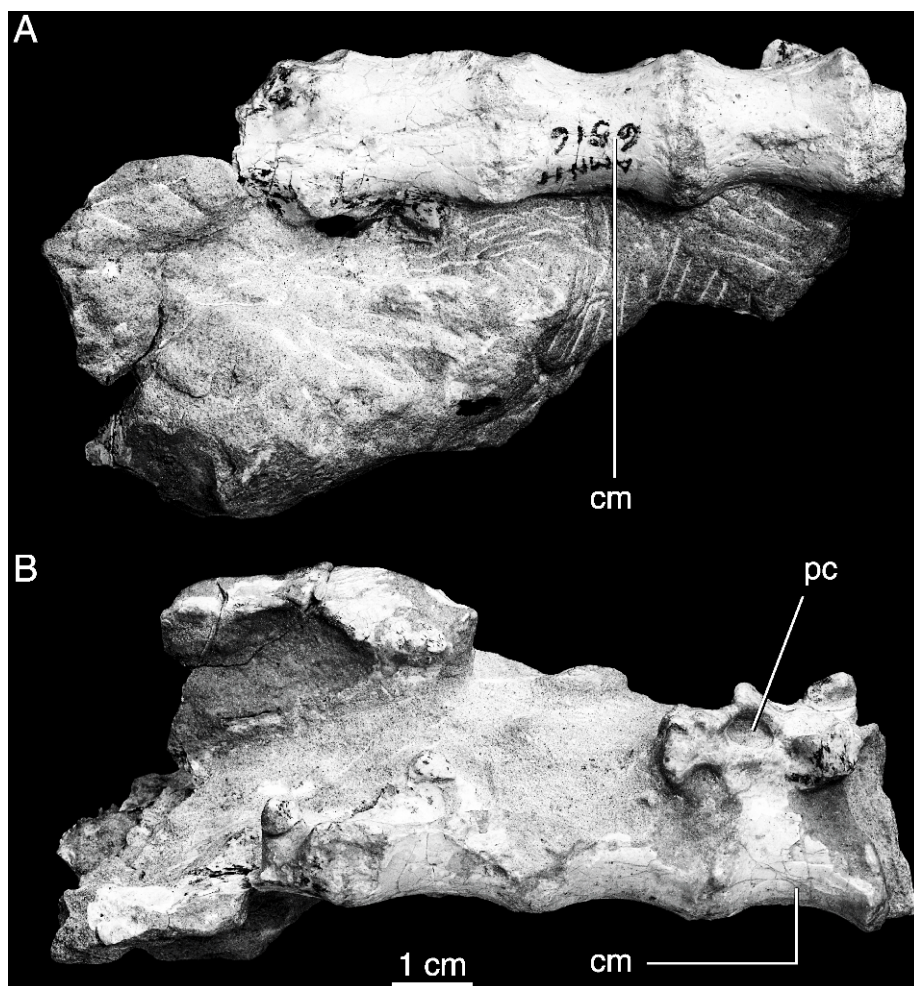
Fig. 15.   Ventral (**A**) and left lateral (**B**) views of the four preserved sacral vertebrae of *Saurornithoides mongoliensis* (AMNH FR 6516). Anterior is to the left.

tebrae 4 and 5), cannot be observed in AMNH FR 6516, because this region of the sacrum is not preserved (fig. 5).

The second block contains the posterior part of sacral 5 and 6. These centra are much rounder in cross section than the anterior sacrals and they are constricted medially. The bases of the neural processes are preserved but appear to be incomplete. The last sacral preserves the left transverse process. It is rectangular in dorsal view and does not appear to expand distally, but it is poorly preserved. It curves dorsolaterally.

CAUDAL VERTEBRAE: Four caudal verte-brae were found articulated to the last sacral (fig. 16). Like the posterosacrals, the centra have a subrectangular, boxy appearance. The neural spines are broken at their bases. No pneumatic features are apparent. Long, rod-shaped caudal chevrons occur between the caudal vertebrae beginning after the first caudal. The pronounced ventral sulcus seen in dromaeosaurid caudals is lacking. The zygapophyseal articulations are inclined me-dially.

ASSOCIATED MATERIAL: Associated with AMNH FR 6516 is a block containing three articulated caudal vertebrae (fig. 6) and a second block that contains a partial sacrum and parts of two ilia. These blocks were
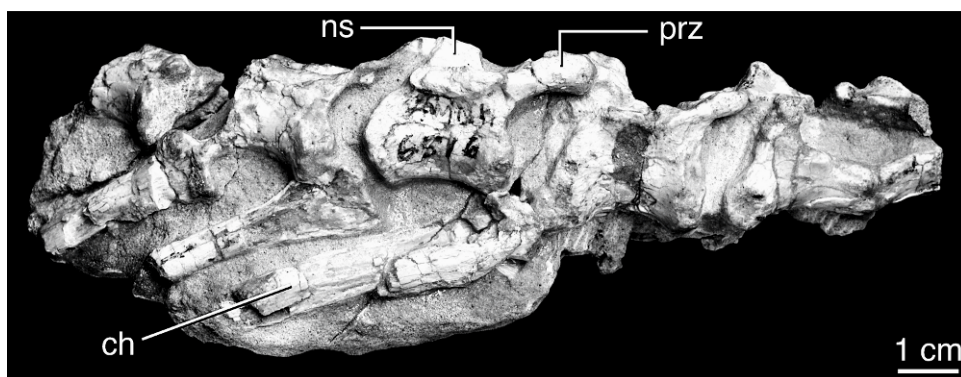
Fig. 16. Right lateral view of the four preserved caudal vertebrae of *Saurornithoides mongoliensis* (AMNH FR 6516).

catalogued as part of the type specimen. The sacrals appear to have narrow, tall centra and the ilia are parallel and lack either a cuppedicus shelf or a pronounced brevis fossa. The caudals have tall, erect neural spines and heavy barrel-shaped centra. These elements are unlike the vertebrae of *Saurornithoides mongoliensis* found articulated to the main AMNH FR 6516 block and described above. Instead these are almost certainly tail and hip sections of a protoceratopsian that were found as associated float near the *Saurornithoides mongoliensis* type specimen. These vertebrae now are catalogued as AMNH FR 30613.

PELVIS

ILIUM: Only a small fragment of the left ilium, a small flat plate of bone, is preserved adjacent to the sacrum (fig. 5). No morphological features are preserved and this element is identified only by its position relative to the articulated skeleton (the matrix of Turner et al. [2007b] scores the ilium of *Saurornithoides mongoliensis* as having a straight posterior edge (character 165); however, it should be scored as unknown).

PUBIS: Both proximal pubes were preserved in semiarticulation on the original block (fig. 5). They have subsequently been removed (fig. 17). In addition to these elements, a more distal fragment representing a section through the pubic apron is preserved on an associated block. It is apparent from their original orientation that the pubes lay in a propubic orientation in life. The proximal

end of the pubis is expanded anteroposteriorly. The lateral surfaces are concave, however, this may be enhanced by postmortem preservational factors. The thin iliac articulation is expanded to form a large anterior hook in lateral view. Unlike *Velociraptor mongoliensis* (where the pubis is retroverted; Norell and Makovicky, 1997), the iliac articulation, the acetabular rim, and the ischiac articulation lie along the same horizontal line. Posteriorly, the ischiac process is poorly preserved. Distally, the pubic shaft is thin, straight, and teardrop shaped in cross section (thicker laterally). A straight distal end of the pubic shaft also is present in *Troodon formosus* and *Sinornithoides youngi*, whereas the shaft curves posteriorly in *Sinovenator changii* and most other paravians.

A more distal section of pubis is preserved separately (see Norell and Makovicky, 1999: fig. 26). This corresponds to the anterior face of the proximal pubic apron and the shafts just proximal to it. Although poorly preserved, the shafts are flattened anteroposteriorly, convex anteriorly and concave posteriorly. The distal ends of the pubes are not preserved.

ISCHIA: Nearly complete right and left ischia are preserved in articulation. These elements were found in near articulation with the pelvis (fig. 5), but they have been disarticulated during preparation (fig. 18). The iliac articulation is short, less than half the length of the proximal end of the bone. Anterior to this, the dorsal border of the ischium contributes to the acetabulum, and this surface is
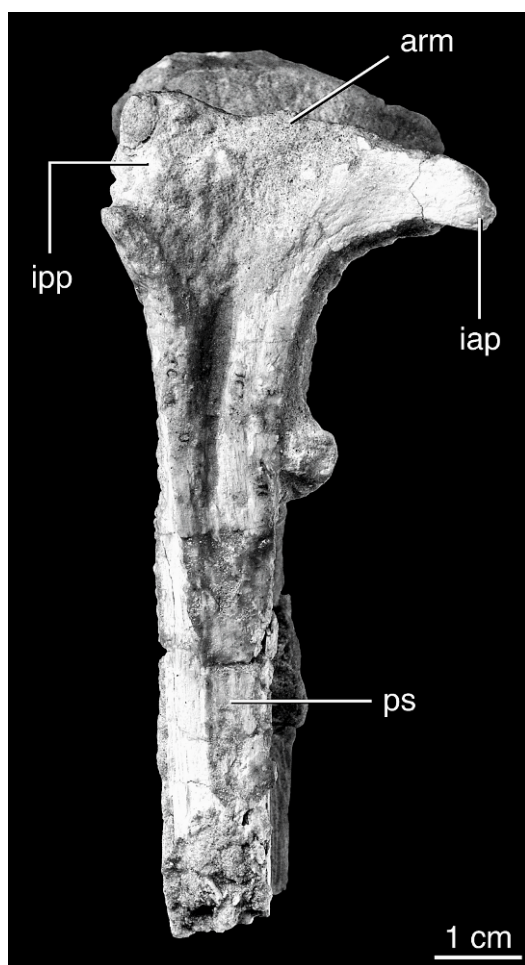
Fig. 17. Lateral view of the left pubis of *Saurornithoides mongoliensis* (AMNH FR 6516).

nearly flat. The pubic process is very short, but its tip is broken. Unlike the condition in other troodontids and most dromaeosaurids, the ischia are fused distally into a symphysis as in many oviraptorosaurs. The lateral surface is anterodorsally convex proximally, whereas the medial border is flat. A shallow groove parallels the posterodorsal margin of the ischium on the medial surface about one-third of the way below it. In lateral view, the ischium is constricted distal to the acetabular process before markedly expanding posteriorly. This posterior expansion of the ischium is combined with the development of a thick ridge along the posterodorsal edge of the bone. This ridge weakens distally, grading into

a large, elevated region. The anterior edge of the ischium in lateral view is concave proximally and nearly vertical distally until midshaft. Posteriorly, beneath the symphysis, the ventral edge of the bone is nearly horizontal. This gives the entire ischium its triangular profile. The apex of this triangular region is the obturator process, which lies approximately at the midpoint of the length of the ischium (as in *Troodon formosus* but in contrast to the more distal position of this process in *Sinornithoides youngi*, *Mei long*, and *Sinovenator changii*). The triangular obturator process contains a short rostral projection along the ischial shaft as in *Zanabazar junior* and *Sinornithoides youngi*. The projection is shorter than that of *Sinovenator changii* (Xu et al., 2002). The lateral face of the ischiadic blade is concave—in contrast to the flat blade of *Mei long* and *Sinovenator changii* (Makovicky et al., 2005).

HIND LIMB

FEMUR: Only the proximal half of the left femur is preserved (fig. 19). It was found associated with the main block between the left foot and the vertebral column (fig. 5). The femur is poorly preserved and severely eroded. The femoral head is distorted, and although ventrally it gradually curves anteromedially, dorsally it apparently projected perpendicular to the femoral shaft. It is not separated from the femoral shaft by a constricted neck, but this may be an artifact of preservation. A large trochanteric crest is obvious in lateral view. A small notch separates the greater from the lesser trochanters. In lateral view, the outline of the trochanteric crest is slightly convex dorsally and nearly flat. It is separated medially from the femoral head by a shallow trough. The femoral head projects dorsal to the maximum height of the trochanteric crest. The greater and lesser trochanters lie along a continuous arc in dorsal view with the lesser trochanter deflected slightly medially. On the posterior surface of the femur, distal to the trochanteric crest, lies a large rugose knob—the posterior trochanter. Slightly more proximally on the lateral surface of the femur lies a small bump bordered dorsally by a small depression. Ventrally, this bump grades into
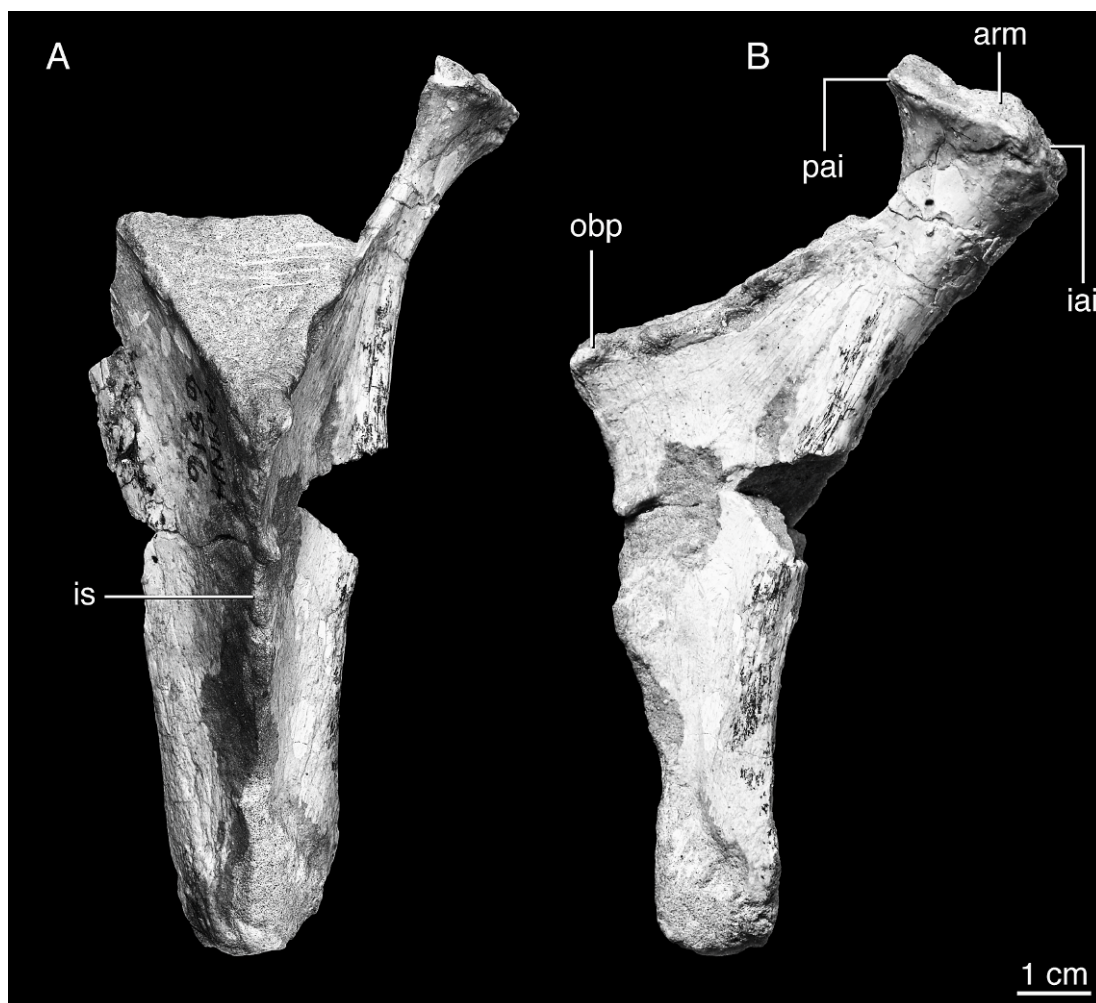
Fig. 18.   Anterior (**A**) and right lateral (**B**) views of the fused ischia of *Saurornithoides mongoliensis* (AMNH FR 6516).

the lateral ridge (Norell and Makovicky, 1999), which separates the lateral surface of the femur longitudinally into anterolateral and posterolateral faces.

TIBIA: The left tibia is preserved only as a natural mold on the original articulated block of AMNH FR 6516. No morphological features are preserved, and all that can be determined is that it was a long, slender bone lying in articulation with the femur and pes.

PES: Only the distal end of the left foot of AMNH FR 6516 is preserved (fig. 20). It is extremely fragmentary and was damaged since being described by Osborn (1924). Although

the three primary metatarsals are badly damaged, it is apparent they correspond to the general troodontid condition of a long central MT III attenuating proximally, a shorter but more robust MT IV, and a thin MT II similar in length to MT IV. Only fragments of MT I are preserved, adhering to the lateral surface of MT II. These fragments indicate that it articulated on the medial surface of the foot, rather than on the posterior or plantar surface. MT V is not preserved.

Phalanx I-1 is subtriangular in cross section with a concave depression on its plantar
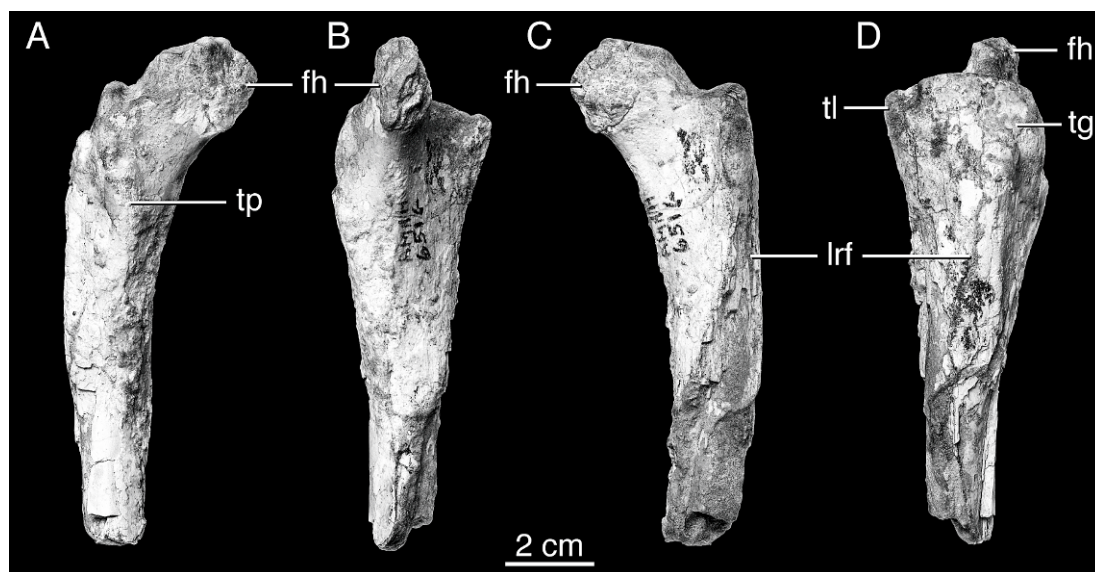
Fig. 19.   Proximal end of the left femur of *Saurornithoides mongoliensis* (AMNH FR 6516) in posterior (**A**), medial (**B**), anterior (**C**), and lateral (**D**) views.

surface. As preserved, its plantar surface faces laterally, almost in an intermediate position between the normal and the reversed hallux position. However, positions of this element, in death, even when articulated can be deceiving and do not necessarily represent a reversed or subreversed condition (Middleton, 2001). The distal articular surface of Phalanx I-1 is typical of other maniraptorans. A deep ligament fossa lies on the lateral surface of the distal articular surface, while the corresponding feature on the medial surface is small and shallow. Phalanx I-2, the ungual, is poorly preserved and the distal tip is missing. Proximally, it was only slightly concave ventrally and lacked a large flexor tubercle, as is typical of maniraptoran hallux claws. Shallow grooves lie on the lateral and medial surface of the claw.

Metatarsal II is extremely crushed and lacks both ends. The digits are preserved in a position proximal to the end of MT III similar to that of other troodontids, suggesting that MT II ended in the typical troodontid position. Digit II preserves its entire complement of phalanges. Phalanx II-1 is preserved poorly yet retains some of the modifications seen in other maniraptorans. The proximal surface is not exposed and may not be preserved. The ventral

edge of the proximal end is eroded, and there is no evidence for a slight heel as illustrated by Currie and Peng (1993: fig. 2g). The shaft is thin in plantar view and not constricted at midshaft, where it is subrectangular in cross section. The distal articular surface is extensive, narrow, and displaced dorsally, so that it projects superior to the shaft of the phalanx in lateral view. This allowed extensive dorsoventral mobility of Digit II. A deep ligament fossa lies on the lateral surface of the articular end, whereas the corresponding pit on the medial surface is shallower. Phalanx II-2, like in other theropods is short, and like in other troodontids, dromaeosaurids, and some avialans, is highly modified with a heel or posterior lappet that forms the posteroventral articulation surface. However, it is damaged and its posterior extent is unknown. The plantar surface of Phalanx II-2 is slightly concave. The distal articulation with Phalanx II-3 is ginglymoid and does not extend above the dorsal edge of the shaft. A large lateral ligament fossa and slightly smaller medial ligament fossa are preserved near the distal articular surface. Phalanx II-3, the ungual, is moderately large and curved. Although its anterior tip is damaged, a significant amount of this phalanx is present (more than is
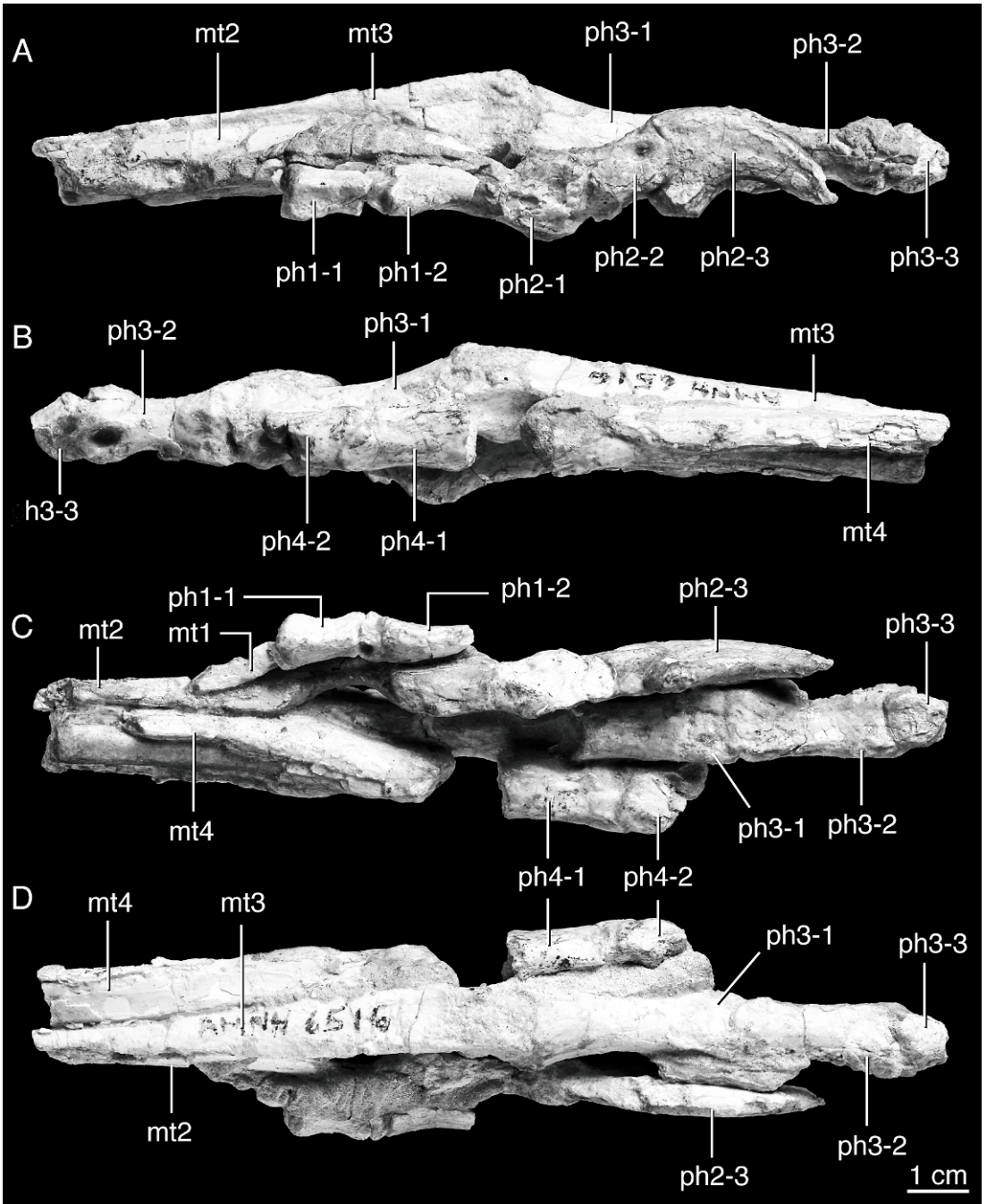
Fig. 20. Partial left pes of *Saurornithoides mongoliensis* (AMNH FR 6516) in right lateral (**A**), left lateral (**B**), ventral (**C**), and dorsal (**D**) views.

illustrated by Currie and Peng, 1993: fig. 2g). In ventral view, this phalanx is asymmetric, as the lateral side slightly bulges and the medial side is nearly flat. The posterior articular surface is curved and defined by a small ridge on the lateral surface, but a dorsal "lip" is absent. A large flexor tubercle with a rugose inferior surface lies ventrally. Both the lateral and the medial surfaces show shallow but well-defined grooves.

Metatarsal III is extremely eroded. Proximally, MT III is a tiny triangular splint of bone lying on the anterior surface of the junction between MT II and IV. Distally, its triangular form broadens and becomes co-equal in size with MT IV. The distal articular surface of MT III is not ginglymoid and not expanded laterally or dorsally. The articular surface does expand posteriorly forming a ball-shaped articulation surface visible in plantar view. On the lateral and medial surface of the element just posterior to the distal articular surface are very shallow ligament fossae. The proximal articular surface of Phalanx III-1 is not preserved, except along its dorsal edge. This phalanx is long and is the stoutest of the preserved phalanges. The distal articulation is expanded slightly both dorsally and ventrally in medial and lateral views but not nearly to the extent of Phalanx II-1. A shallow extensor pit lies on the dorsal surface just posterior to the articular surface. This pit is delineated medially and laterally by a pair of ridges that extend onto the body of the phalanx from the posterior margin of the articular surface. The articular surface itself is deeply grooved resulting in a distinct medial and lateral condyle. The medial articular surface is excavated by a deep ligament fossa. The lateral surface is obscured by matrix.

Phalanx III-2 is smaller than III-1. Posteriorly, a small ridge on the dorsal surface of Phalanx III-2 forms an articulation with III-1. This articulation overrides the articular surface of the posterior phalanx. Ventrally, the surface of Phalanx III-2 is flat and expanded posteriorly toward the articular surface. The anterior articular surface is slightly expanded ventrally and divided into lateral and medial condyles, although not as markedly as in Phalanx III-1. The dorsal anterior articular surface is extremely eroded, however, a slight, shallow extensor pit is visible. The lateral surface displays a very large and deep ligament fossa. The corresponding region on the medial surface is not preserved. Only the posteriormost portion of Phalanx III-3 is preserved and it is extremely eroded, obscuring any features of interest.

Metatarsal IV is poorly preserved and the distal end is absent. It is thick and heavy as in other troodontids (Currie and Peng, 1993). The shaft is round in cross section as in most theropods including *Sinornithoides youngi* but in contrast to the anteroposteriorly compressed shaft of *Mei long*, *Sinovenator changii*, and some dromaeosaurids (e.g., *Velociraptor mongoliensis*). In plantar view, MT IV curves laterodistally allowing for posterior exposure of MT III. The dorsal surface is flat. Most of the lateral part of the bone is missing, exposing a sandstone endocast of the marrow cavity. Phalanx IV-1 is preserved only slightly proximal to the level of Phalanx III-1, suggesting that MT IV reached nearly as far as MT III. The exposed proximal surface of Phalanx IV-1 is a single deep depression indicating that this articulation was not ginglymoid. The ventral surface of Phalanx IV-1 is more rounded than corresponding areas on the third digit where these surfaces are flat, especially just anterior to the posterior articular surface. The distal articular area is only slightly expanded and large ligament fossae on the lateral and medial surfaces appear to be lacking. Only the proximal end of Phalanx IV-2 is preserved.

SYSTEMATIC PALEONTOLOGY

Zanabazar, new genus

TYPE SPECIES: *Zanabazar junior* (Barsbold, 1974).

DERIVATION OF NAME: In honor of Zanabazar (1635–1723), the first Bogd Gegen of Mongolia.

INCLUDED SPECIES: Type species only.

LOCALITY AND AGE: Nemegt Formation at Bugiin Tsav, Omnogov Aimag, Mongolia (figs. 2, 21). The Nemegt Formation overlies the Djadokhta Formation and is considered to be Maestrichtian based primarily upon the
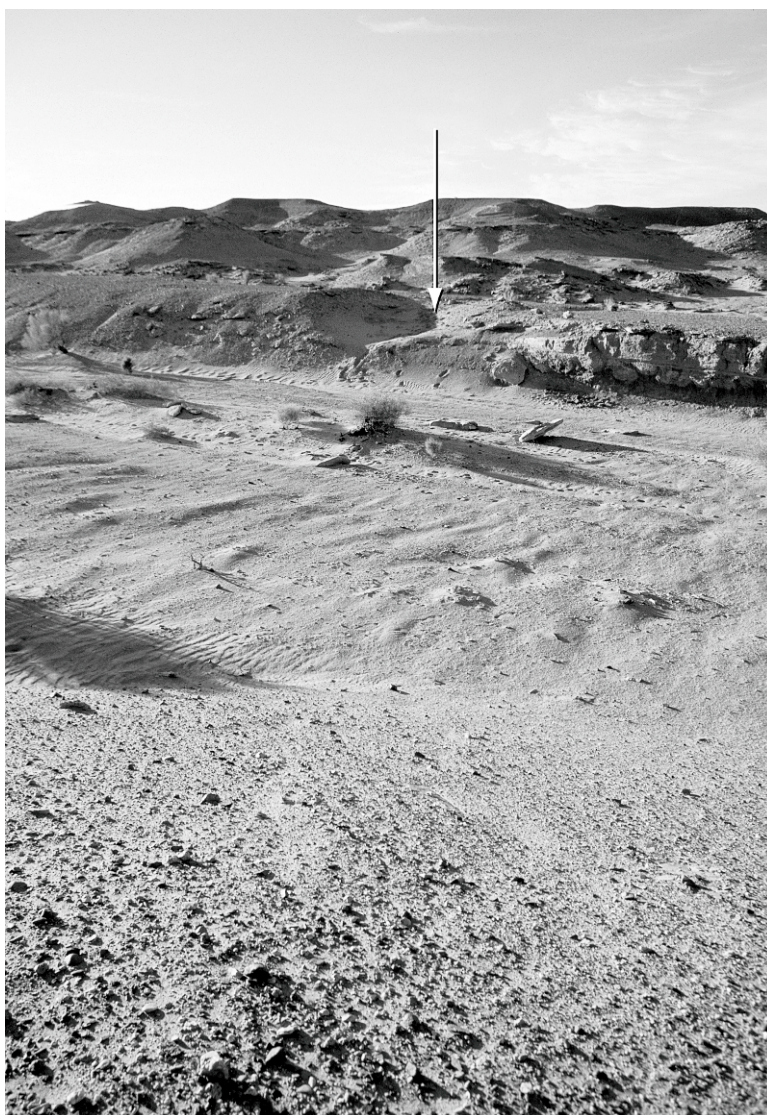
Fig. 21.   Photograph of the Nemegt Formation at Bugiin Tsav, Omnogov Aimag, Mongolia showing the location (arrow) where the holotype of *Zanabazar junior* (IGM 100/1) was collected.

vertebrate fauna (Jerzykiewicz and Russell, 1991).

DIAGNOSIS: Differs from *Saurornithoides mongoliensis* and most other troodontids (save *Troodon formosus*) in lacking a small depression on the lateral wall of the braincase just dorsal to the trigeminal foramen. The holotype of *Zanabazar junior* is the largest published troodontid specimen (midline length of the skull = 272 mm), and is substantially larger than most other troodontid species.

Only *Troodon formosus* appears to approach it in size. Differs from *Troodon formosus* in having a more ovoid-shaped foramen magnum, a posttemporal fenestra that is enclosed by an almost equal proportion of the exoccipital/opisthotic and squamosal (this same feature in *Troodon formosus* is formed almost entirely by the exoccipital/opisthotic), a deeper paroccipital process resulting in a different positon of the posttemporal fossa relative to the foramen magnum, and the lack of an

osseous signature of the ophthalmic branch of the trigeminal nerve (CN V) in the laterosphenoid.

Zanabazar junior (Barsbold, 1974)

HOLOTYPE: IGM 100/1, a skull and partial mandible, six sacral and 11 caudal vertebrae, and the distal part of the right hind limb. The skull is largely complete except for the left and right quadrate, quadratojugal, ventral part of the lacrimal, palatine, pterygoid, and ectopterygoid, and the left squamosal, postorbital, and jugal, posterior part of the right jugal, and the postdentary bones other than the splenials. The posterior part of the left nasal is reconstructed in plaster, as are small parts of the left maxilla anterior to the maxillary fenestra and dorsal to the interfenestral bar. Plaster covers the ventral surface of the bones roofing the antorbital fenestra. The mandible comprises only the dentaries and splenials. The right hind limb includes the distal end of the tibia with the coossified astragalus and calcaneum, a distal tarsal, and the proximal ends of MT II–IV.

TYPE LOCALITY AND AGE: As for *Zanabazar*.

DIAGNOSIS: As for *Zanabazar*.

REFERRED SPECIMENS: No new material of this species has been described, but two other troodontids have been described from the Nemegt Formation of Mongolia. *Borogovia gracilicrus* Osmólska, 1987, is known only from a partial hind limb from Altan Uul IV, and *Tochisaurus nemegtensis* Kurzanov and Osmólska, 1991, is known only from a metatarsus from the Nemegt area. Because the postcranial elements of *Zanabazar junior* do not include those parts diagnostic of the other two species, it is possible that one of the other two Nemegt Formation taxa is a junior synonym.

COMMENTS: We chose to construct the name *Zanabazar* for *Saurornithoides junior* based on the morphological differences between the holotype and that of *Saurornithoides mongoliensis* and the questionable monophyly of *Saurornithoides* as defined by the sister-taxon relationship of *S. mongoliensis* and *S. junior*. This decision also was influenced by the common practice in phylogenetic analyses of assuming monophyly by compositely coding taxa (especially "genera"). The differences between *Zanabazar junior* and *Saurornithoides mongoliensis* certainly merit coding these taxa separately. The temporal difference separating these specimens was not, and should not, be used to support taxonomic decisions.

DESCRIPTION

The bone is hard and very well preserved as is typical of vertebrates from the Nemegt Formation, and the skull is preserved uncrushed in three dimensions. Cranial sutures largely are indistinct due to maturity, and glue covers much of the outer surface.

SKULL

PREMAXILLA: In dorsal view the outline of the snout is distinctly rounded and U-shaped (fig. 22C). The nasal process of the premaxilla is dorsoventrally flat and forms the dorsal border of the elliptical nares. The caudal end of the external naris is positioned distinct anterior to the rostral margin of the antorbital fossa—a derived character shared with most dromaeosaurs, *Confuciusornis sanctus*, *Saurornithoides mongoliensis*, and other derived troodontids, but not *Mei long* and *Sinovenator changii* (Chiappe et al., 1999; Turner et al., 2007b). The flat nasal process (internarial bar) is long and extends posteriorly within a midline depression on the dorsal surface of the nasal to the level of the anterior margin of the maxillary fenestra. The premaxilla forms a broad shelf on the floor of the nares, which rises to form a longitudinal, midline ridge (as in IGM 100/972—a perinate troodontid; Bever and Norell, 2009). The premaxilla lacks a posterior process that excludes the ascending process of the maxilla from participation in the nares. The lateral surface of the premaxilla is pitted with small foramina similar to those of the maxilla. The premaxillae meet inside the oral cavity to form a vaulted secondary palate. This structure, however, is poorly exposed along the midline.

NASALS: The paired nasals form the roof of the elongate rostrum anterior to the orbits. The nasals meet the frontals posteriorly along a V-shaped suture where the frontals divide the nasals. The frontal-nasal contact begins at the level of the preorbital bar formed by the
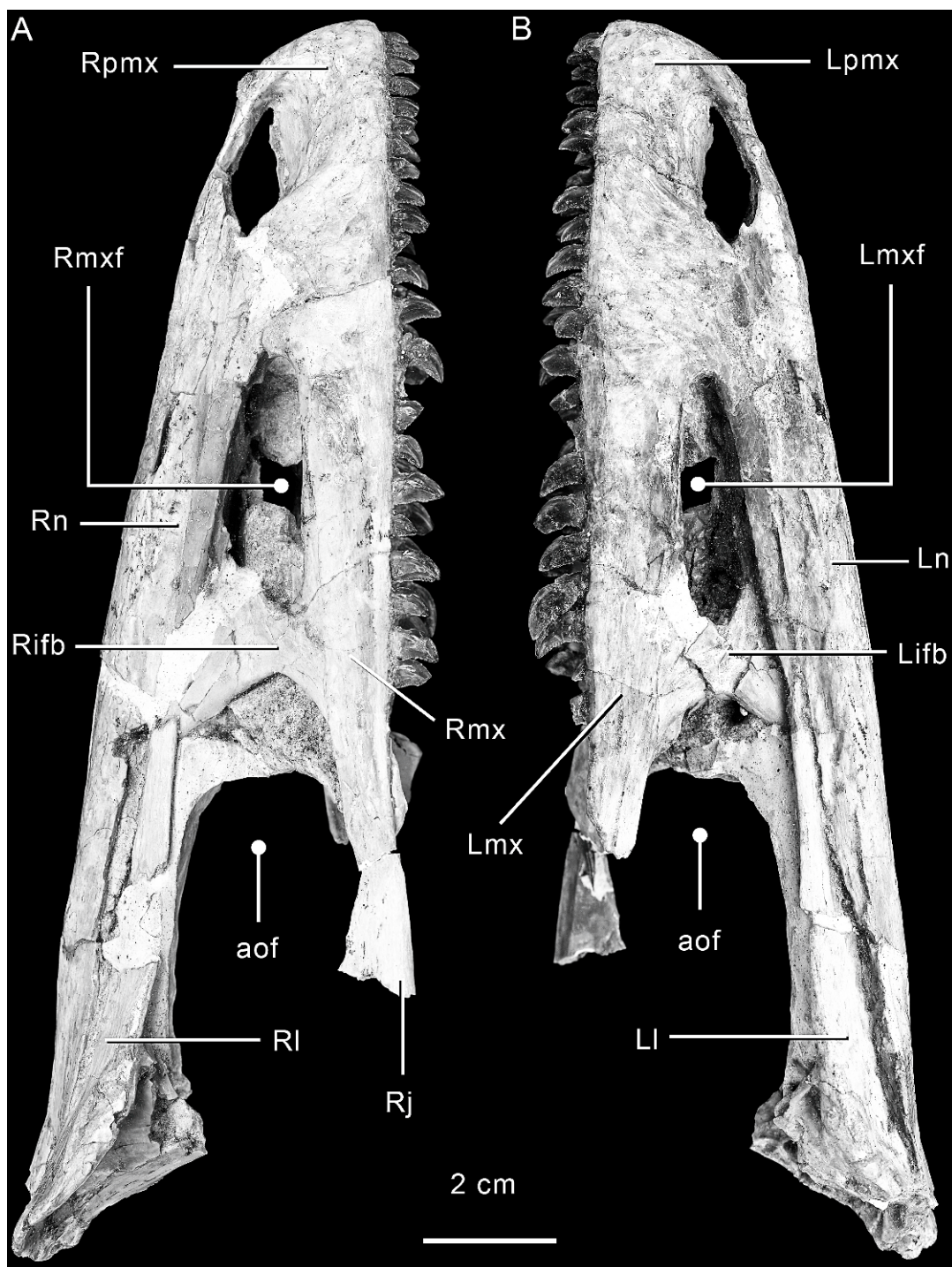
Fig. 22.   The rostrum of *Zanabazar junior* (IGM 100/1) in right lateral (**A**) and left lateral (**B**) views.
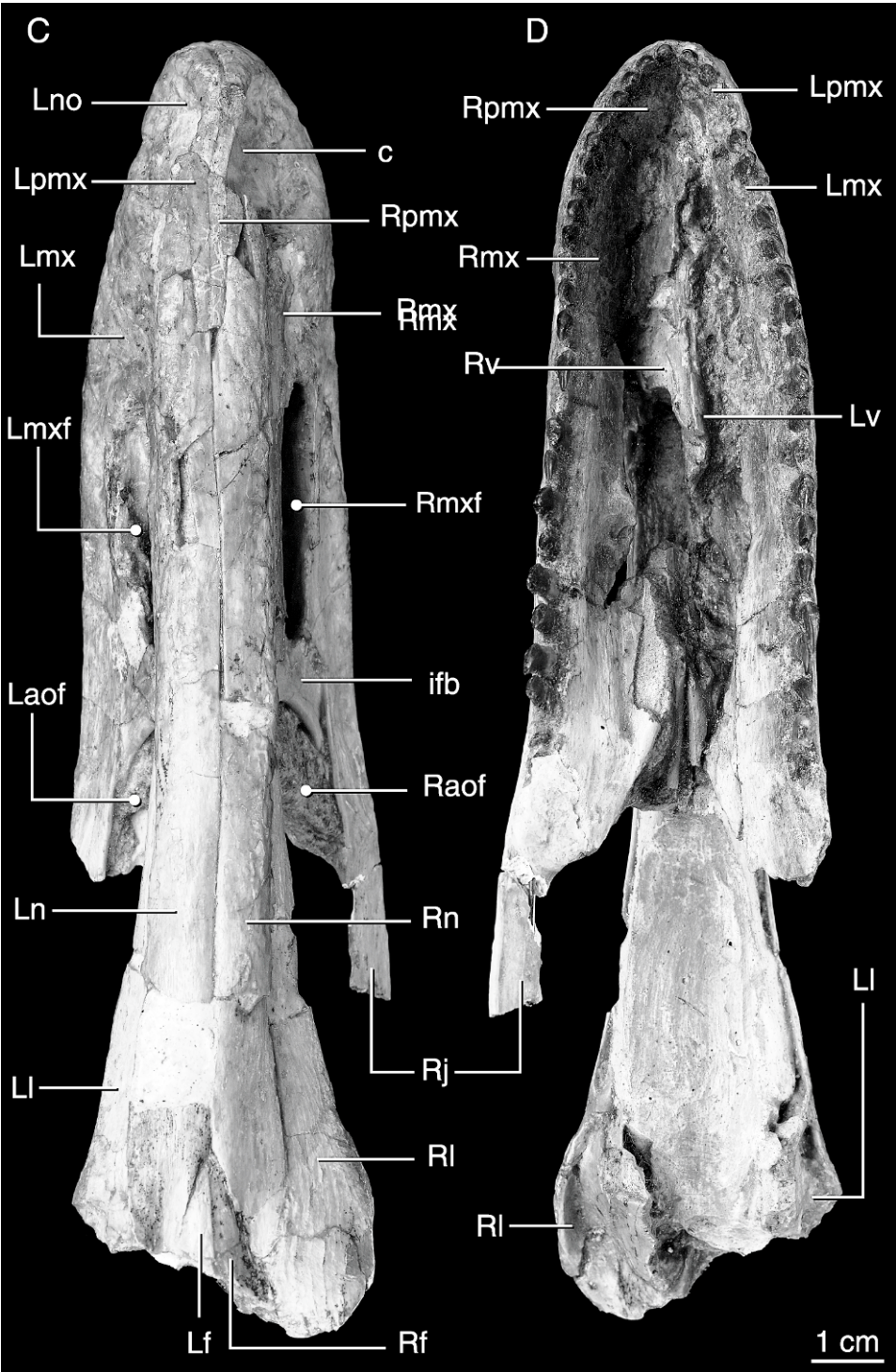
Fig. 22.   *Continued.* The rostrum of *Zanabazar junior* (IGM 100/1) in dorsal (**C**), and ventral (**D**) views.
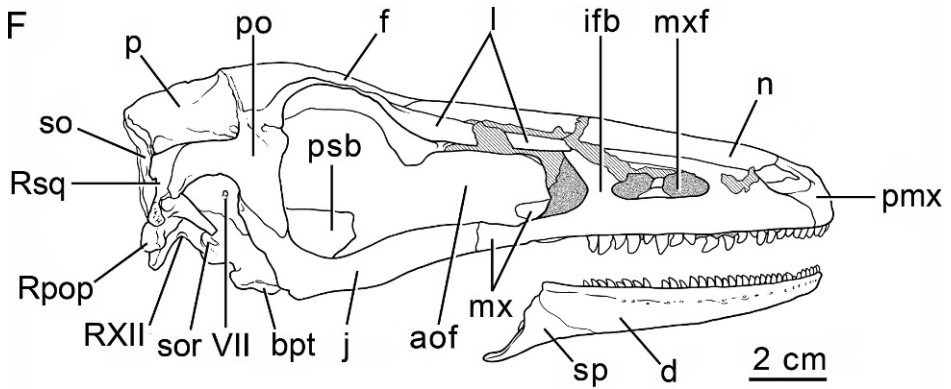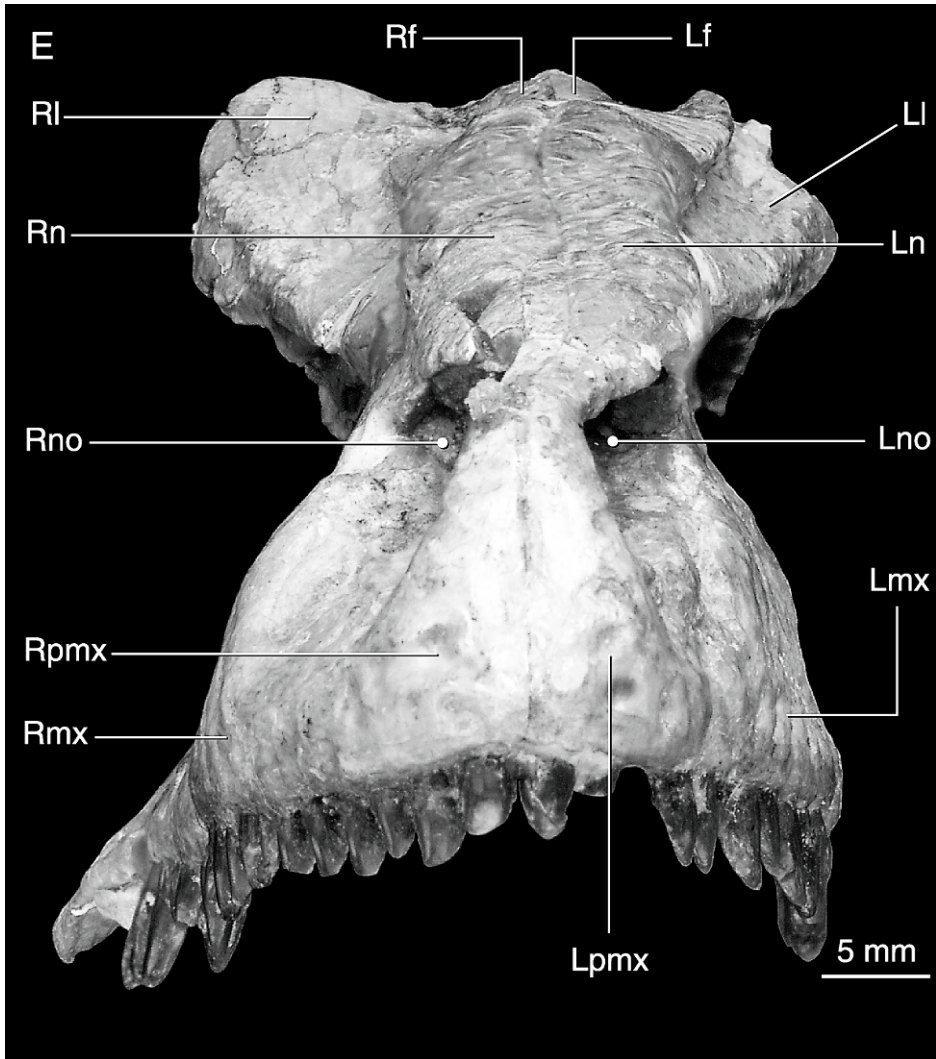
Fig. 22. *Continued.* The rostrum of *Zanabazar junior* (IGM 100/1) in anterior (**E**) view. Illustration of the holotype skull in right lateral view (**F**).

lacrimal. The nasals have parallel borders for nearly their entire length, until they taper at the narial margin. The nasals are L-shaped in cross section, a feature that gives the top of the rostrum a boxlike appearance. A shallow trough, parallel to the nasal-maxillary suture, lies on the anterolateral surface. Slight sculpturing covers the entire surface of the nasals.

LACRIMAL: Much of the lacrimal is missing; only the portions sutured to the skull roof and the base of the postorbital bars are preserved. As in other deinonychosaurs, the lacrimal is T-shaped with anterior and posterior processes dorsal to the preorbital bar. The anterior process, which forms the dorsal border of the antorbital fenestra, is longer than the posterior process and tapers to a point just dorsal to the interfenestral bar. The presence of an anterior lacrimal process that is longer than the posterior process is a derived character shared with *Saurornithoides mongoliensis*, *Troodon formosus*, and *Byronosaurus jaffei*. The length of the processes is approximately equal in most paravians including *Mei long* and *Sinovenator changii* (Turner et al., 2007b). The posterior process forms a ventrally concave shelf that overhangs the anterodorsal corner of the orbit as in *Troodon formosus* and *Byronosaurus jaffei* but in contrast to *Mei long* (Norell et al., 2000; Makovicky et al., 2003; Bever and Norell, 2009). A small, rugose boss lies on the dorsolateral edge of this shelf just above the preorbital bar. The lacrimal contacts the nasals anteromedially and the frontal posteromedially.

MAXILLA: The maxilla forms most of the lateral side of the rostrum (fig. 22A, B). Like the nasals, the lateral surface of the maxilla is heavily sculptured, and like the premaxilla, it is pitted above the dental margin. There are 20 tooth positions on both maxillae (see below). The ascending process just dorsal to the tooth row has a row of large pits ending at about the 13th tooth position. More posteriorly and ventral to the maxillary fenestra, the maxilla is dorsolaterally concave. Anterolaterally, the maxilla forms part of the narial opening. The maxilla meets the premaxilla inside the narial chamber to form part of this space's expanded floor. The maxillary contribution to this floor is especially apparent on the right side of the

skull where this region is relatively undistorted (fig. 22A).

Two large antorbital openings are bounded by the maxilla: the maxillary fenestra anteriorly and the antorbital fenestra posteriorly. The maxilla completely encloses the maxillary fenestra, whereas the antorbital fenestra is bounded anteriorly by the interfenestral bar and ventrally by the jugal ramus of the maxilla. Unlike most other theropods, the maxillary and antorbital fossae in troodontids lack an expanded osseous floor. Consequently, the antorbital fossa is not well delineated in bone outside the margins of the fenestrae. In IGM 100/1, as in *Saurornithoides mongoliensis*, these fenestrae are separated by a recessed interfenestral bar that is formed completely by the maxilla. The bar is roughly hourglass shaped in lateral view (fig. 22A, B), which is in contrast to the straight, vertical margins of the same bar in *Sinovenator changii*. The interfenestral bar is perforated posteriorly by two openings (fig. 23). The dorsal opening is an extension of the nasal passage (as in *Byronosaurus jaffei*; Makovicky et al., 2003) that may incorporate the caudal fenestra of the maxillary antrum (Bever and Norell, 2009). The ventral opening is the interfenestral canal that likely transmitted a neurovascular bundle containing the maxillary ramus of CN V from the antorbital to the maxillary fossa. As in *Saurornithoides mongoliensis* and in contrast to *Sinovenator changii*, there is no evidence of a promaxillary fenestra in *Zanabazar junior*.

Little of the palatal surface of the maxilla is exposed. The palatal region in general is extremely deep and vaulted. This vaulting combined with the extreme overbite of the rostrum over the mandible would have allowed the lower jaws to be nearly enclosed by the rostrum. The maxillary surface is nearly vertical adjacent to the tooth row medially. The maxillary surface flattens posteriorly, near the presumed contact with the palatine. This flattening is especially distinct posterior to the tooth row where the maxilla forms a broad, ventrally directed surface. Apparently, IGM 100/1 possessed a maxillary secondary palate, as in *Saurornithoides mongoliensis* and *Byronosaurus* (Norell et al., 2000; Makovicky et al., 2003; Bever and Norell, 2009). Although
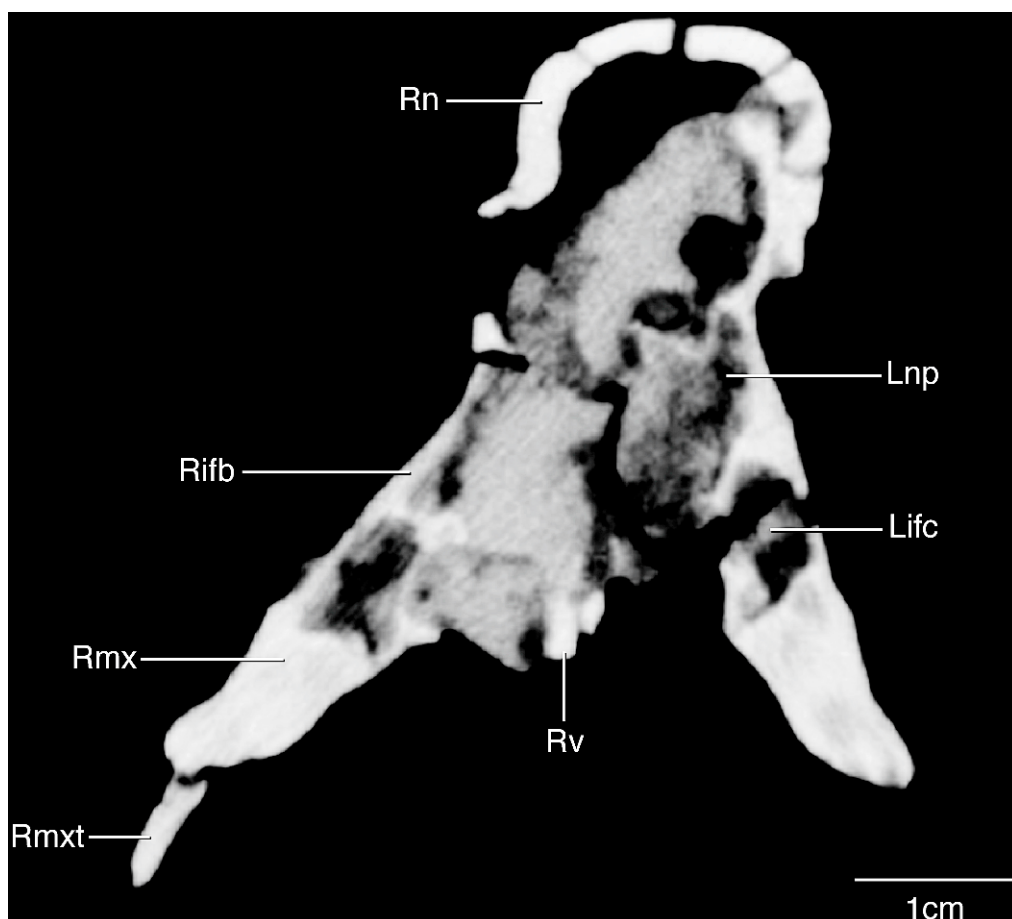
Fig. 23.   CT image of coronal slice (208) through the rostrum and interfenestral bar of *Zanabazar junior* (IGM 100/1). The bar is penetrated dorsally by a space confluent with the nasal passage (that may include the maxillary antrum) and ventrally by the interfenestral canal. The nasal lacks pneumatic fossa.

much of this region is not preserved, an enlarged palatal shelf that contacts the vomer is present on the right side of the palate just posterior to the premaxilla. Flat plates of bone contact the vomer below the maxillary fenestra, and the palatal shelves abut the paired, rodlike, bifid vomer posteriorly.

VOMER: The vomers are paired posteriorly (at the level of the last maxillary tooth). Their anterior and posterior connections are not preserved. Anteriorly, the vomers are preserved as adjacent and highly appressed rods approximately at the level of the anterior margin of the maxillary fenestra. The vomers lack the vertical depth seen in *Velociraptor mongoliensis* (IGM 100/986).

JUGAL: Only the right jugal is preserved, and its subtemporal process is broken (fig. 22; see also pl. 1 of Barsbold, 1974). The region in which the jugal articulates with the maxilla is reconstructed in plaster (supported medially by a wire), but the precise position of the contact cannot be determined. The contact indicated by the reconstruction is about midway beneath the antorbital fenestra, which is well anterior to the orbit and slightly anterior to the position of the same contact in other troodontids. The posterolateral surface of the jugal is marked by longitudinal striations where the quadratojugal would have overlapped it. The postorbital process has a broad anterior edge where it contacts the
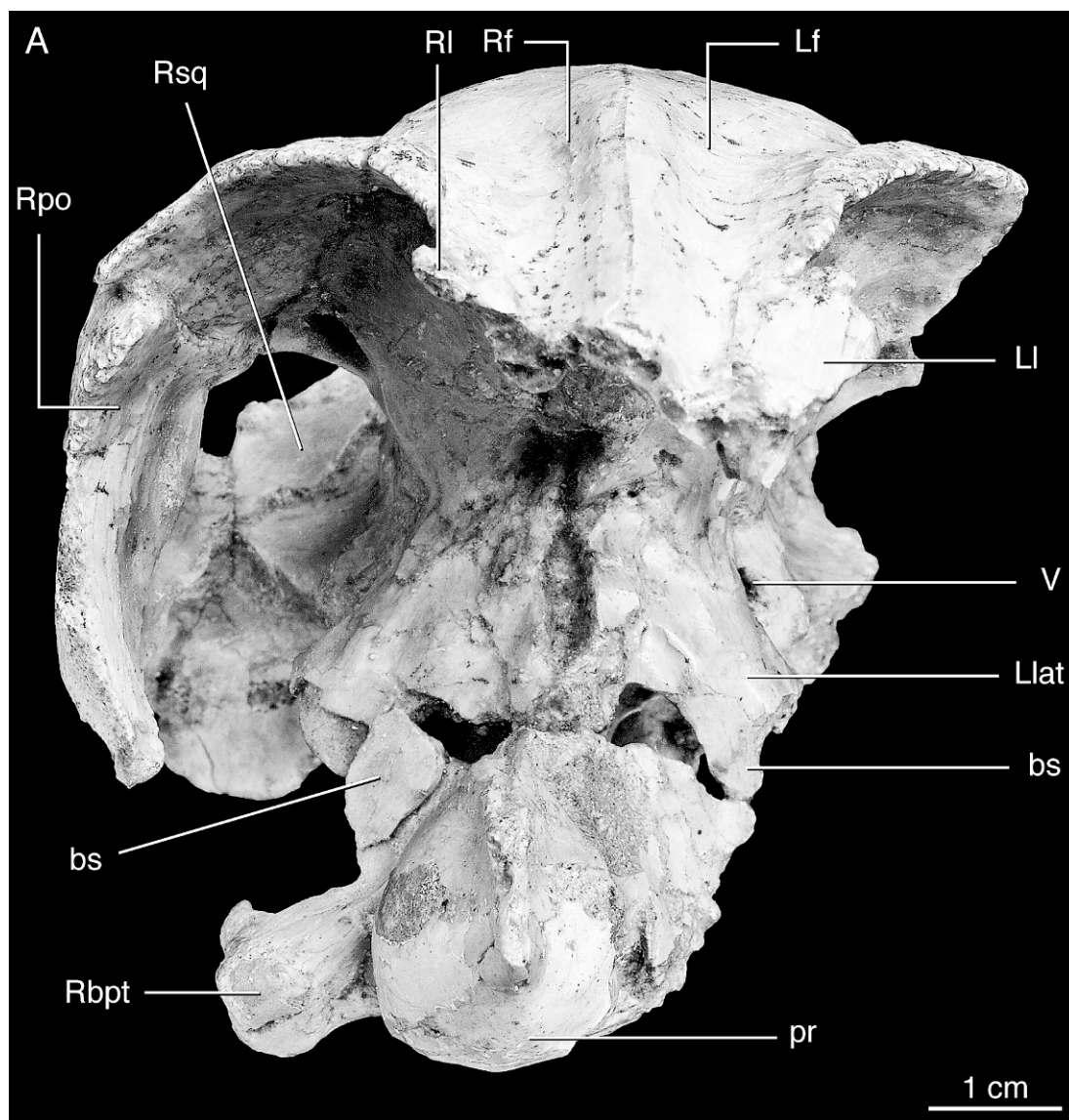
Fig. 24. The posterior dermal roof and braincase of *Zanabazar junior* (IGM 100/1) in anterior (**A**, above) and dorsal (**B**, opposite) views.

postorbital but becomes thin posteriorly. The postorbital process overall is triangular due to a vertical edge and an anterior edge that tapers to a point. The posteroventral corner of the orbital margin is rounded in lateral view, and the jugal gently rises and then falls anteriorly. As the jugal rises, it twists counterclockwise, so that the dorsal edge becomes more medial further anteriorly. In dorsal view, the jugal is convex medially, so that if the posterior part is parallel to the rest of the skull then the suborbital part curves anteromedially. The posterior section of the jugal is thin transversely, but the bone becomes much thicker where it rises in the bottom of the orbit. The inside of the jugal is hollow in this region, and this excavation exits anteriorly from a longitudinally elongate dorsal slit on the medial surface of the bone. This presumably was filled by a pneumatic diverticulum.

Fig. 24. *Continued.*

C

Lptf

Rpo

fm

oc

Rsq

1 cm
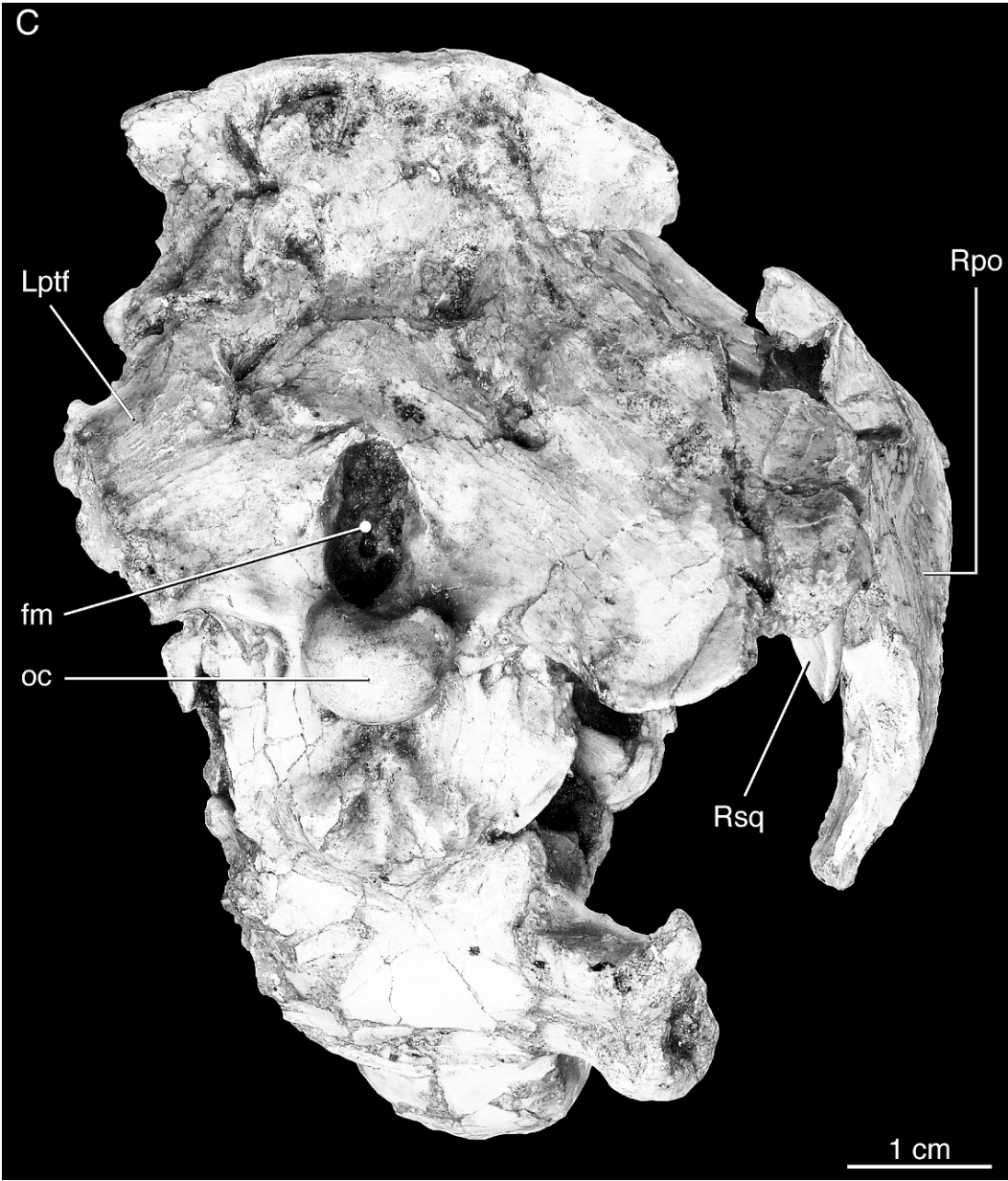
Fig. 24. *Continued.*

POSTORBITAL: Only the right postorbital is preserved (figs. 22D, 24E). This triradiate element forms the postorbital bar and much of the temporal arcade. Its medial extent is not clear, but it does not appear to reach the parietal. The postorbital ramus is thick and nearly vertical. The orbital surface is rugose and a small tubercle projects into the orbit along the orbital margin just ventral to the frontal suture. As in *Saurornithoides mongoliensis* and other derived coelurosaurs, the postorbital lacks a prominent anterior process
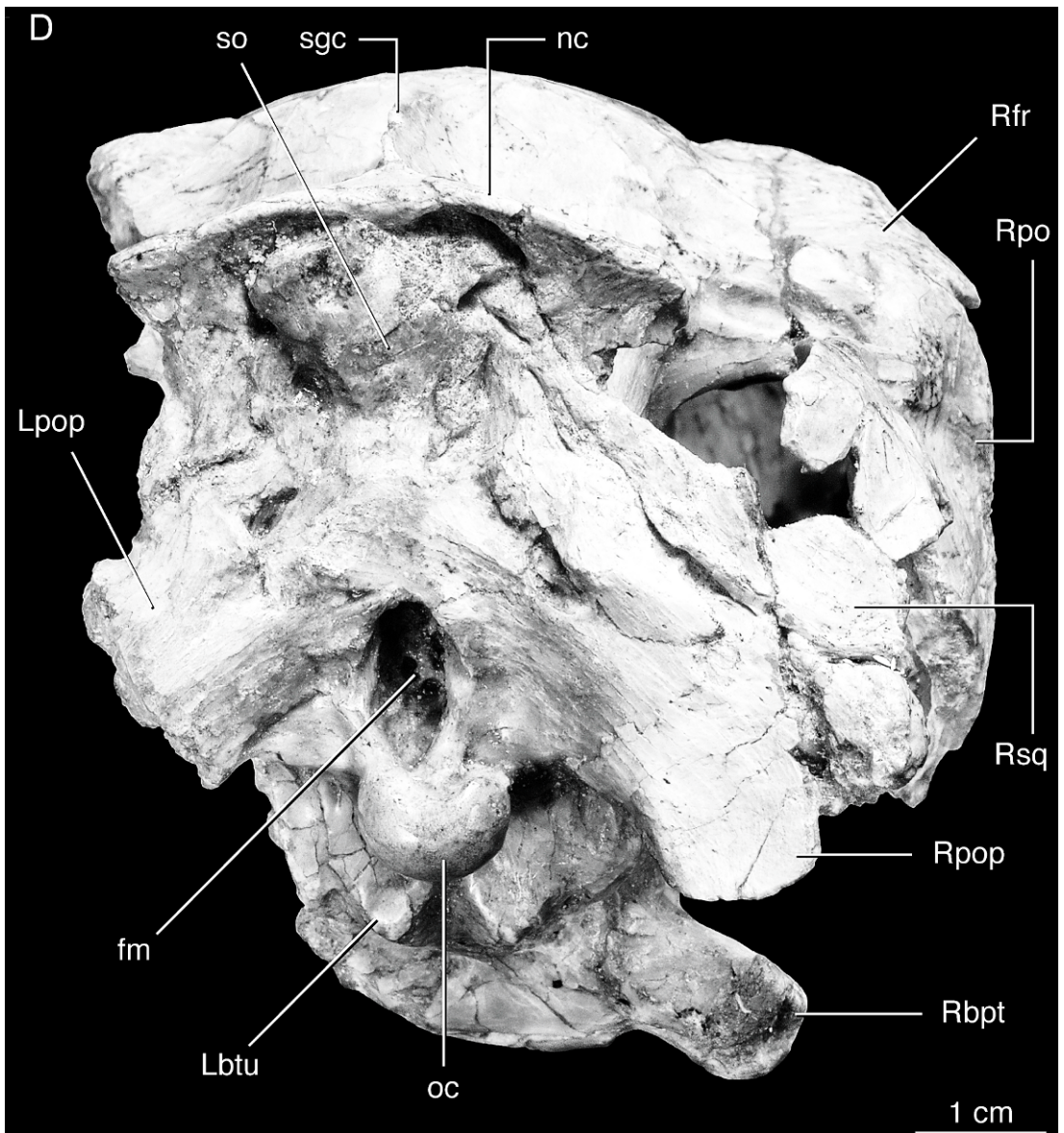
Fig. 24. *Continued.* The posterior dermal roof and braincase of *Zanabazar junior* (IGM 100/1) in posterior (**C**, opposite) posterodorsal (**D**, above) views.

that projects into the orbit as in tyranno-saurids. The postorbital tapers to a point ventrally as it contacts the postorbital process of the jugal posteriorly along a butt joint. The transition between the supratemporal and frontal process ascends markedly as is typical of other maniraptorans (Barsbold and Osmólska, 1999). The frontal process curves anterodorsally as in other derived maniraptorans (Turner et al., 2007b). The supratemporal process of the postorbital forms the anterior and entire ventral margin of the supratemporal arcade. The supratemporal process is concave dorsally, tapers posteriorly, descends posteroventrally, and overlaps the squamosal laterally. The process terminates just anterior to the occipital plane.
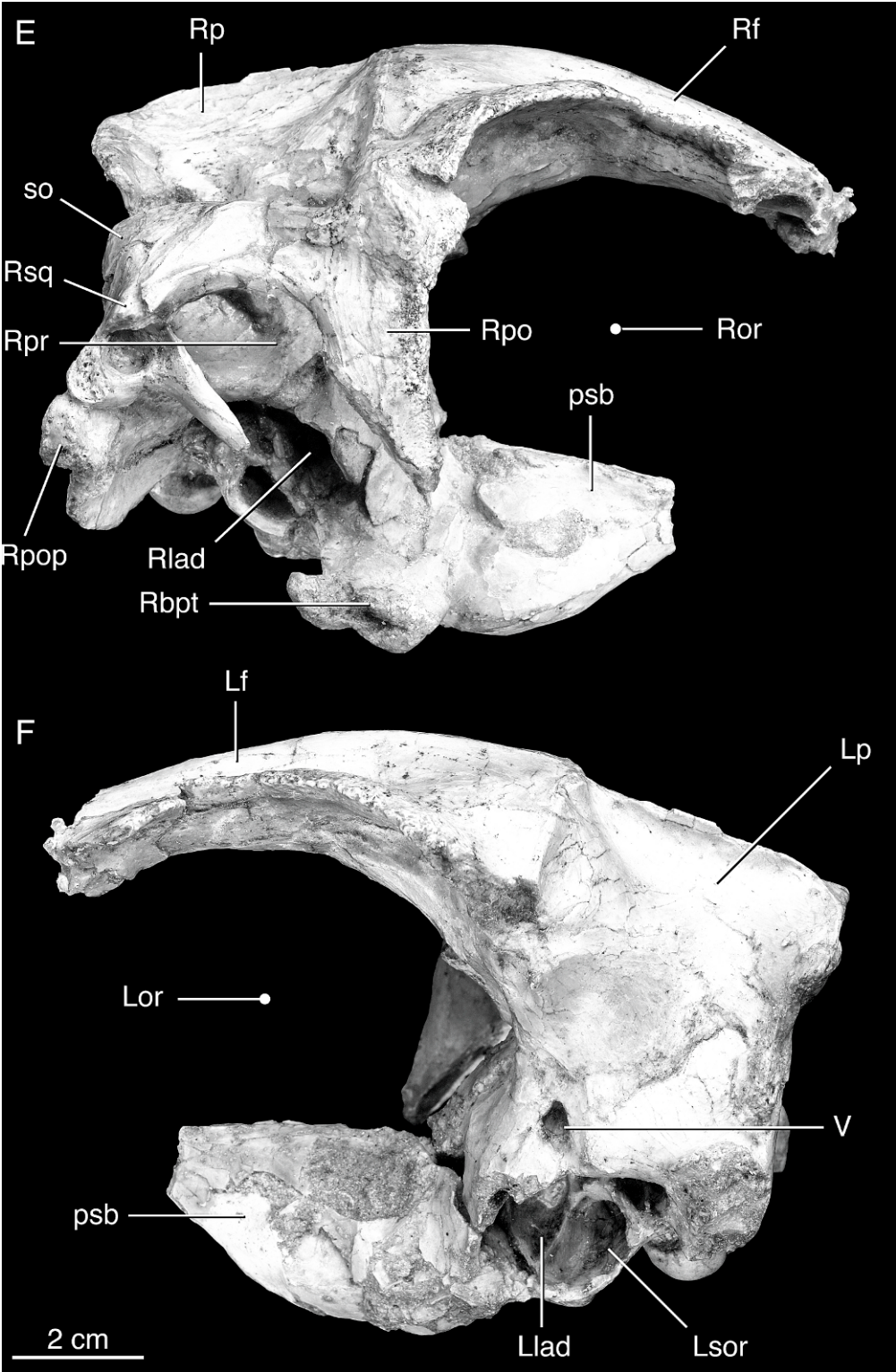
Fig. 24.   *Continued.*
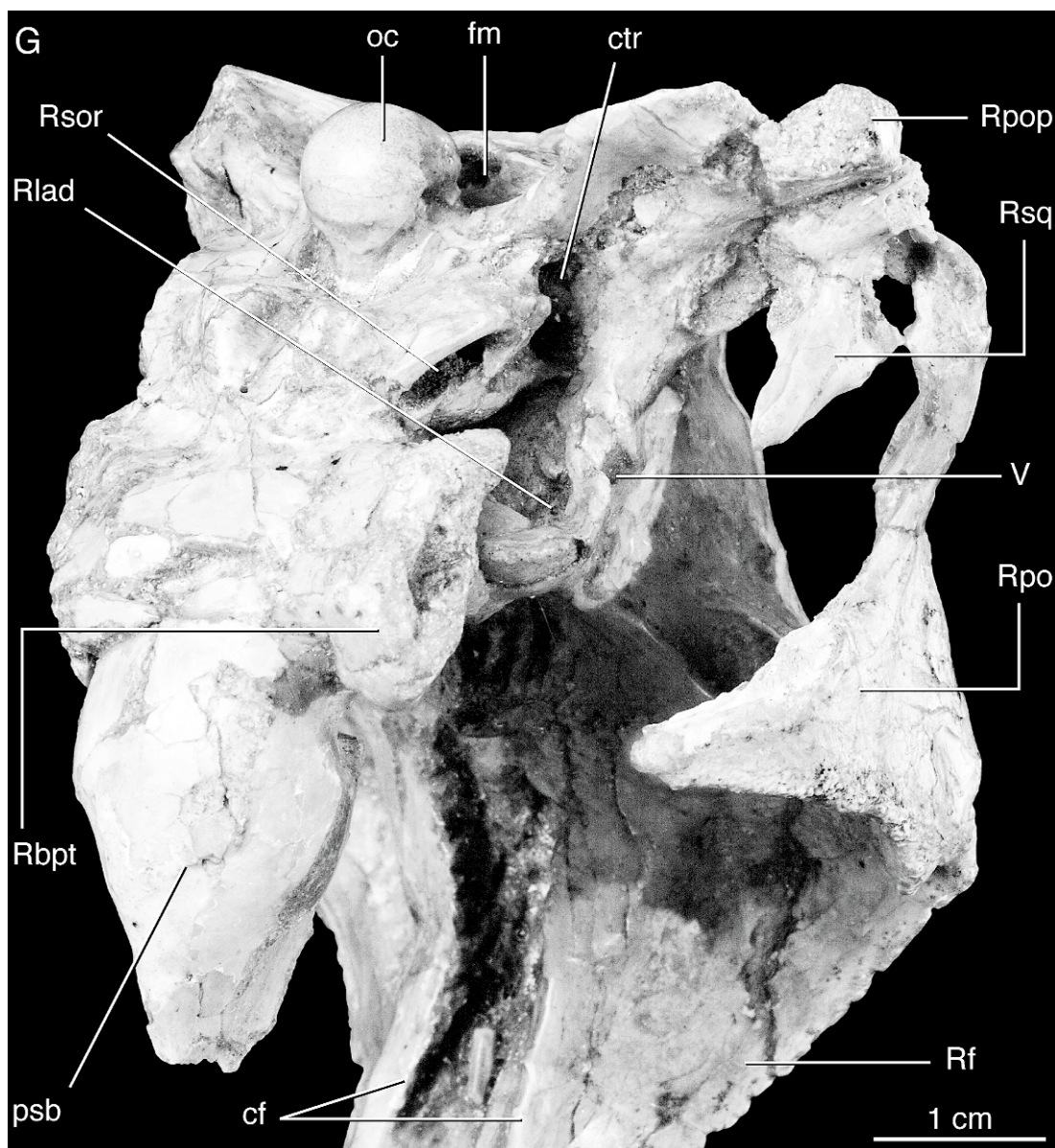
Fig. 24. *Continued.* The posterior dermal roof and braincase of *Zanabazar junior* (IGM 100/1) in right lateral (**E**) and left lateral (**F**) views (opposite page), and in right ventrolateral (**G**) view (above).

FRONTALS: The frontals (fig. 24) are paired and similar in shape and proportion to those preserved in *Troodon formosus* ("*Stenonychosaurus inequalis*," AMNH 6147 [fig. 25], and RTMP 82.19.23; see Currie, 1985). The frontals attenuate anteriorly between the lacrimals and the nasals forming a triangular point—in agreement with *Troodon formosus*

and *Byronosaurus jaffei* but in contrast to *Mei long* and *Sinovenator changii* in which the nasal-frontal suture is oriented transversely. The frontals form the posterodorsal corner and dorsal border of the large, circular orbits. The orbital border of each frontal is striated and pitted forming an elevated supraciliary rim above the orbit. The orbital margin
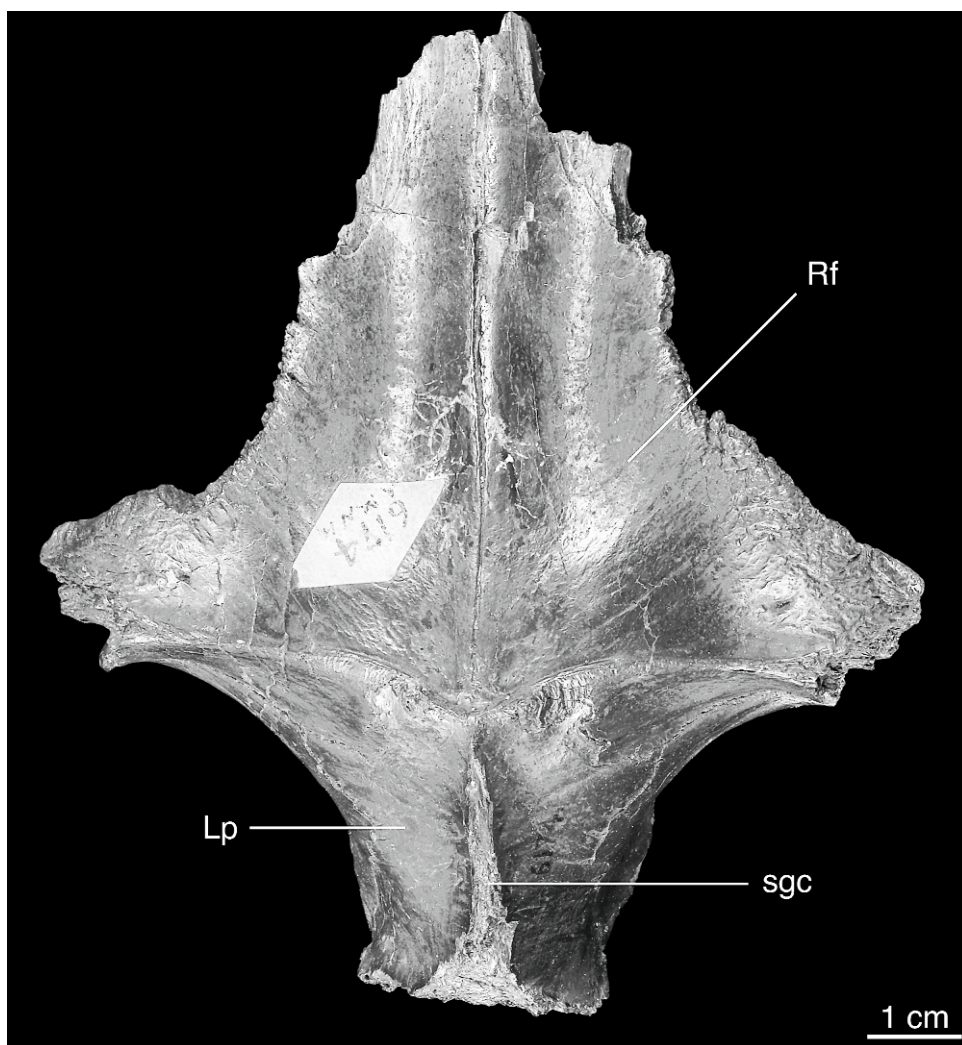
Fig. 25.   Dorsal view of the posterior dermal roof of *Troodon formosus* (AMNH 6174).

appears to be intact and we find no evidence that any of this margin posterior to the lacrimal is formed by a separate prefrontal ossification (contra Currie, 1985). Along the midline lies a large longitudinal ridge separated from the supraciliary rim by an elongate trough that terminates at the level of the anterior surface of the preorbital bar. Posterior to these structures, the frontals are bulbous and expanded dorsally above the cerebral hemispheres. A well-developed transverse ridge that extends medially at the posterior margin of the postorbital borders this expansion posteriorly. This ridge defines the anterior margin of the supratemporal fossa. A small depression is present anterior to this transverse ridge at the lateral apex of the frontal. All of these features are also found in *Troodon formosus* (fig. 25).

The frontal contact with the parietal is complex and again similar to that of *Troodon formosus*. The suture is confluent at the sagittal midline with the transverse ridge. Laterally, the parietal descends posteroventrally and the frontal contacts the laterosphenoid. This gives a small portion of the frontal a near-vertical exposure inside the fossa. On this surface lies a shallow depression or fossa.
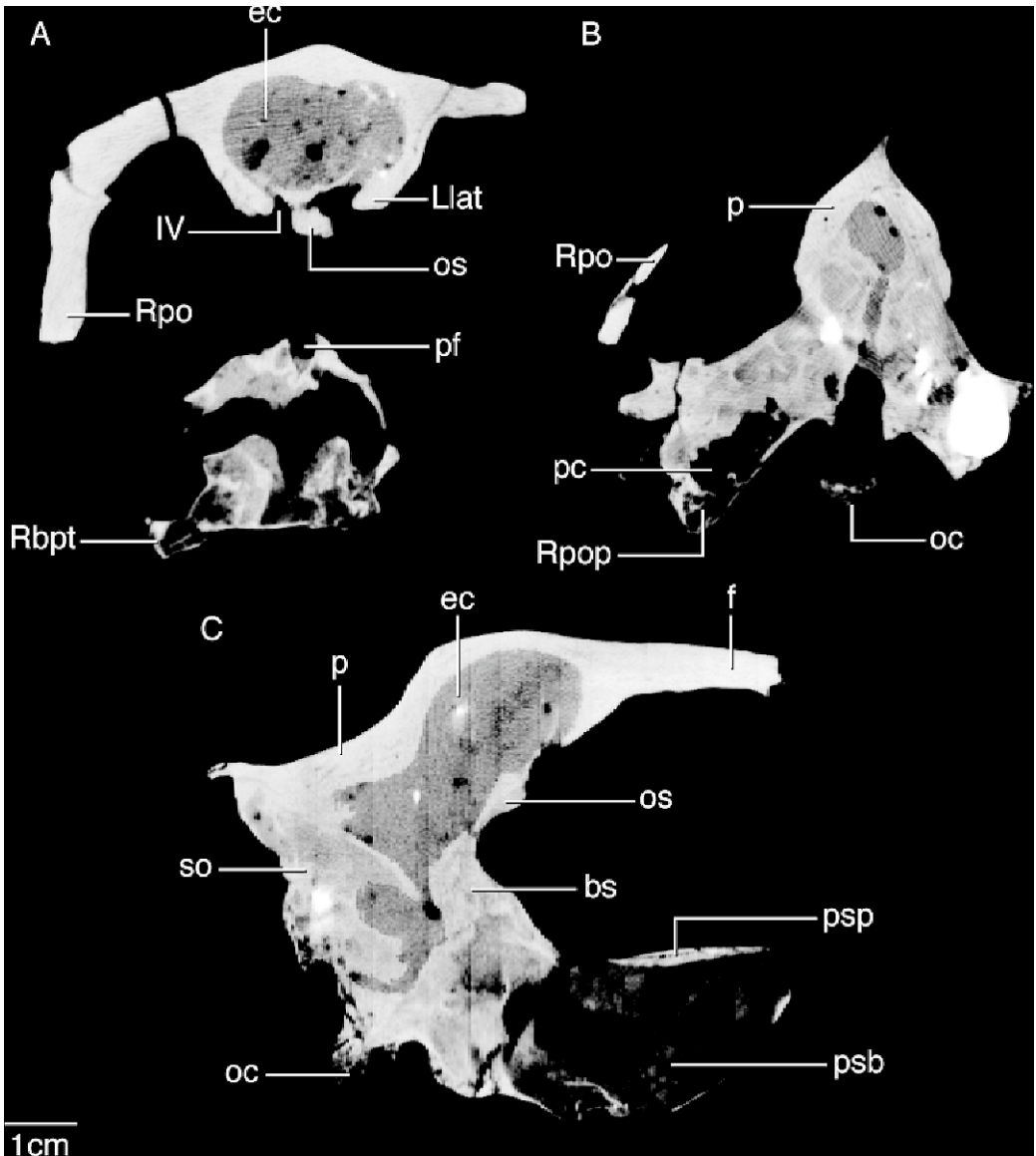
Fig. 26. CT slices through the braincase of *Zanabazar junior*. **A.** Coronal slice (507) showing the presence of a distinct orbitosphenoid ossification at the anteroventral margin of the endocranial space (medial to the paths of the paired trochlear nerve CN IV). **B.** Coronal slice (578) through the occipital plate showing a distinct cavity within the paroccipital process. The cavity is inferred to result from investment of the process by pneumatic diverticula from the caudal tympanic recess. **C.** Sagittal slice (187) near the cranial midline showing the expanded and hollow parasphenoid bulla.

Ventrally, a shallow, irregularly shaped fossa lies just medial to the postorbital and anterior to the laterosphenoid on the inside of the orbit. Anterior to this fossa lies a broad, but shallow, depression that presumably held the oculomotor musculature (Barsbold, 1974).

This area is somewhat deeper than in *Troodon formosus* (AMNH 6174). Medially, the cristae calvarii frontalis define a deep trough for the olfactory bulbs. These cristae are separated posteriorly by a mass of bone, which may represent a separate orbitosphenoid ossifica-

tion or separate extensions of the laterosphenoids. CT scans reveal a pair of midline ossifications that are separate from the main body of the laterosphenoid (fig. 26A). This trough is wide and deep posteriorly, constricts anteriorly, and then is shallow and expanded at the anteriormost end (presumably for the olfactory bulbs). The ventral contact with the anterior rostral bones largely is obscured by plaster added during preparation. Only a longitudinal ventrolateral contact with the left lacrimal is visible.

PARIETAL: The parietals are fused as in other troodontids (in contrast to the unfused parietals of basal avialans and some dromaeosaurs; Turner et al., 2007b). The parietals are dorsally convex with a tall, midline sagittal crest that terminates anteriorly at a transverse ridge along the frontoparietal suture and posteriorly at the nuchal crest. This sagittal crest defines the medial margins of the supratemporal fenestrae. The dorsally convex shape and presence of a tall sagittal crest are shared with *Troodon formosus* but differ from the flattened parietal table of *Mei long* and the low sagittal crest of *Sinovenator changii*. The sharp nuchal crest forms the posterior boundary of the medial portion of the supratemporal crest and the posterior terminus of the skull table. Lateral to the sagittal crest, the parietal descends rapidly where it meets the laterosphenoid along a straight parasagittal suture. A short anterolateral process of the parietal is wedged between the supratemporal surface of the frontal and the base of the postorbital process of the laterosphenoid. Although the exact sutural boundaries are indistinct, the parietal forms the dorsal border of the occipital surface.

SQUAMOSAL: Only the right squamosal is preserved and posteriorly it is fragmented (fig. 24). The squamosal formed the posterolateral component of the temporal arcade and the posterodorsal surface of the supratemporal fenestra. The squamosal meets the parietal posteromedially, with which it forms the nuchal crest. Ventrally, the squamosal sits atop the paroccipital process of the exoccipital/opisthotic. The lateroventral surface of the squamosal bordering the rectangle-shaped infratemporal fenestra forms a concave surface with the postorbital (fig. 24C). A large

cavity or fossa lies at the base of the anteroventrally projecting quadrate process. The quadrate process itself tapers ventrally. Its anterior surface is transversely concave, forming a broad furrow that runs the length of the process. The medial surface is flat and probably was appressed against the quadrate shaft. Ventrally, the squamosal contacts the prootic along a transverse suture. The fossa for articulation for the quadrate (the quadrate cotyle) lies at the anterior terminus of this suture at the base of the quadrate process. This fossa is deep and cup shaped and extends onto the opisthotic and perhaps the prootic (Currie and Zhao, 1993). Less than half of the fossa is within the squamosal.

EXOCCIPITAL/OPISTHOTIC: The fused exoccipital-opisthotics form much of the occipital plate. The right element is nearly complete and the left is broken distally. The exoccipitals form the lateral margin of the foramen magnum, which is strongly elliptical along the dorsoventral axis (as in *Byronosaurus jaffei* and *Sinovenator changii* but in contrast with the circular foramen magnum of *Troodon formosus*). Although this shape may be somewhat accentuated by postmortem deformation (the right exoccipital/opisthotic is displaced medially), the left exoccipital/opisthotic is intact and undisplaced. Just lateral to the foramen magnum lies a shallow depression defined ventrally by a lateral ridge emanating from the occipital condyle.

The paroccipital processes are relatively short, but very deep—as in other troodontids and basal avialans. The processes do not twist distally as they do in dromaeosaurids. As can be determined by the broken left paroccipital process and erosion of the thin bone on the anterior surface of the right element, the paroccipital process of *Zanabazar junior* is hollow—at least at its base (fig. 26B). This morphology presumably is due to pneumatization from the caudal tympanic sinus as is typical of maniraptorans (Witmer, 1997); however, the presence of a caudal tympanic recess and associated pneumaticity generally is considered only to be present in *Mei long* and *Sinovenator changii* among troodontids (see Bever and Norell, 2009). Unlike other troodontids, the process is pendant with its distal
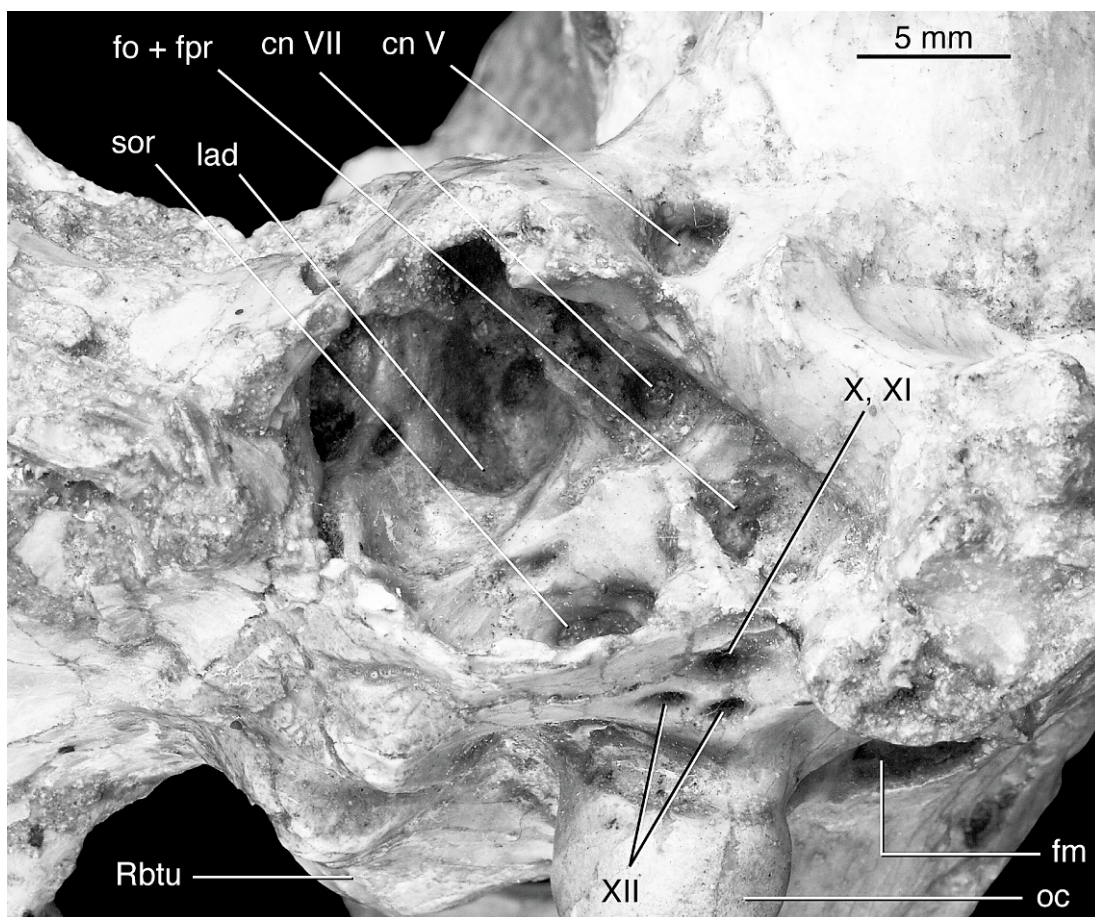
Fig. 27.   Posteroventral view of the left lateral depression of the braincase in *Zanabazar junior* (IGM 100/1). Anterior is to the top of the page.

end lying at the level of the ventral edge of the occipital condyle. The exoccipital/opisthotics contact the squamosal on the occipital plate along a lateroventrally running suture. A parallel raised ridge lies medial to the suture. The small, transversely oval posttemporal fenestra is positioned between the exoccipital/opisthotic and squamosal suture. Unlike in *Troodon formosus* where the posttemporal fenestra is enclosed predominately by the exoccipital/opisthotic, the boundary of this fenestra in IGM 100/1 is formed by an almost equal participation of the squamosal and exoccipital/opisthotic. The great depth of the paroccipital process positions the fenestra far dorsal to the level of the dorsal border of the foramen magnum. This is in contrast to

Troodon formosus where the posttemporal fenestra lies at the same level as the top of the foramen magnum (Currie and Zhao, 1993).

The anterior surface of the paroccipital process is slightly concave dorsoventrally. A small notch lies between the base of the paroccipital process and the prevagal strut (see Gower and Weber [1998] regarding the prevagal [metotic] strut). Dorsally, the exoccipital/opisthotic may have participated in a deep quadrate facet along with the squamosal and the prootic. This facet was the contact with the quadrate and also is found in *Troodon* (Currie and Zhao, 1993) and the perinate *Byronosaurus* (Bever and Norell, 2009), but not in dromaeosaurids and most other thero-

pods. As in RTMP 86.36.457, this facet is pitted, suggesting that it was covered by connective tissue in life.

Contacts between the exoccipital/opisthotic and the supraoccipital and parietal are difficult to ascertain. It will suffice to point out that the supraoccipital suture lies at the level of the dorsal border of the foramen magnum and continues lateral to a complex of ill-defined sutural boundaries. The posterior canal for the middle cerebral vein lies in this region.

Lateral and ventral to the basioccipital condyle lies a small posterolaterally oriented surface that is defined dorsally by the lateral ridge emanating from the occipital condyle and laterally by the prevagal strut, which forms the posterodorsal wall of the lateral depression. This surface is perforated by three small openings. The posterior pair is the exits for CN XII, whereas the more anterior vagus foramen transmitted CN X and XI (CN IX is inferred to have exited anterior to the prevagal strut through the fenestra pseudorotunda; Currie, 1997). Because the braincase sutures are fused, the exact relationship between the exoccipital/opisthotics and the basioccipital/basisphenoid ventral to the foramen magnum cannot be determined even in CT scans.

PROOTIC: Both prootics are well preserved, forming the lateral wall of the braincase anterior to the fenestra ovalis and posterior to the trigeminal opening (fig. 27). Sutural contact with surrounding bones is indistinct as the sutures are closed. The prootic forms the anterior border of the fenestra ovalis and thus forms the anterodorsal and ventral parts of the middle ear cavity. As in other derived troodontids, a well-defined otosphenoidal crest on the anterior edge of the prootic forms the anterodorsal border of a deep lateral depression and continues ventrally onto the basisphenoid. The lateral depression of *Zanabazar junior* is oval along a posterodorsal-anteroventral axis. The circular opening to the middle ear cavity lies at the posterodorsal apex of the lateral depression. Large pneumatic recesses lie anterior and ventral to the middle ear cavity and represent the prootic and subotic recess, respectively. The prootic recess is separated from the middle ear cavity

by a thick bar, whereas a relatively thin bar defines the subotic recess dorsally—a vertical ridge separates these recesses from each other. Numerous subchambers further divide each recess. The presence of a subotic recess is likely a derived feature shared by all troodontids with the exception of *Sinovenator changii* and *Mei long*. There is no clear indication of a pneumatic recess above the trigeminal fenestra on the prootic of *Saurornithoides mongoliensis*, *Byronosaurus jaffei*, and *Sinovenator changii* (Turner et al., 2007b).

The anterior border of the prootic recess is formed by the arching otosphenoidal crest, which is a composite of the prootic, laterosphenoid, and basisphenoid. CN VII exits the braincase inside the lateral depression on the posterior wall of the otosphenoidal crest, as in *Saurornithoides mongoliensis*. Discussing this feature, Currie and Zhao (1993: 2242) cited Barsbold's (1974) description of this position for the foramen in *Zanabazar junior*, but then noted that this nerve opens outside the depression in *Troodon* and stated that this was the condition "in troodontids." Contrary to their implication, Barsbold's description is accurate, making the position of this foramen seemingly a clear synapomorphy supporting the sister-taxon relationship between *Saurornithodes mongoliensis* and *Zanabazar junior*. Complicating this issue is the fact that despite the description and braincase reconstruction of Currie and Zhao (1993: fig. 4) for *Troodon formosus*, which clearly indicate that CN VII exits the braincase at a position outside the lateral depression, the photograph of the same *Troodon* specimen (Currie and Zhao, 1993: fig. 2) shows the facial foramen lying within the lateral depression. This latter position is corroborated by an earlier description of a different *Troodon* specimen (Currie, 1985: figs. 4 and 5) and the morphology of additional specimens of *Troodon formosus* (D. Varricchio, personal commun.). A facial foramen that lies within the lateral depression, therefore, appears to be a derived character supporting the monophyletic status of a *Troodon-Saurornithodes-Zanabazar* clade.

LATEROSPHENOID: The laterosphenoid forms the anterior and anterodorsal walls of the braincase. It articulates with the parietal along a convex suture on the near-vertical wall of the

supratemporal fossa. Sutural contact with the exoccipital/opisthotic and prootic is oblique, extending along an anteroventral-posterodorsal axis. The anterior face of the laterosphenoid is nearly perpendicular to the lateral face and forms the anterior surface of the enlarged braincase. The laterosphenoids nearly meet anteriorly above the hypophyseal fossa. Above the flexure between the anterior and lateral faces and just proximal to the contact with the postorbital, the lateral process of the laterosphenoid bears a large ventral depression, a derived feature also present in *Troodon formosus* (AMNH 6174) and *Sinovenator changii* (Xu et al., 2002). A large trigeminal exit is present at the posterior border of the laterosphenoid. There is no evidence of a separate osseous path within the laterosphenoid for the opthalmic branch of CN V as described in *Troodon formosus* (Currie and Zhao, 1993) and birds. This morphology suggests that the gasserian ganglion was positioned extracranially as inferred for *Saurornithoides mongoliensis*, *Byronosaurus jaffei*, and most nonavian theropods (Makovicky et al., 2003; Bever and Norell, 2009). In the latter taxon, only a single trigeminal exit is visible on the interior wall of the braincase, but the trigeminal branches within the laterosphenoid, and the ophthalmic branch exits through a slitlike foramen on the rostral face of the laterosphenoid, anterior to the flexure that divides this bone into anterior and lateral surfaces. This region is covered by thick glue in *Zanabazar junior* hampering our observations. Pneumatic sinuses may be present within the laterosphenoid near the trigeminal opening as in *Troodon formosus* (Currie and Zhao, 1993), but the laterosphenoid's contact with the basisphenoid is not clear and they may lie within that bone.

ORBITOSPHENOID: A small midline ossification between the laterosphenoids is presumably a remnant of the orbitosphenoid(s). This part of the skull is covered by thick glue, and sutures are difficult to make out. The best evidence for a separate orbitosphenoid ossification is that a distinct moiety of bone, marked as the "presphenoid" by Barsbold (1974), appears to separate the common exit for the optic nerves (CN II) from the olfactory tracts dorsal to it. This moiety appears unconnected with the laterosphenoid in CT section (fig. 26A). The orbitosphenoid of *Sinraptor dongi* (Currie and Zhao, 1993) and tyrannosaurids bears a ventral lamina that separates the optic nerves of the left and right side, but such a structure is either absent or lost in *Zanabazar junior*. The orbitosphenoid may reach the edge of the exit for CN III laterally, although breakage and glue make this difficult to ascertain.

BASIOCCIPITAL: The basioccipital forms the posteroventral surface of the braincase and the ventral part of the occipital surface. The occipital condyle is formed entirely of basioccipital. It is separated from the back of the skull by a constricted neck. A constricted neck also is present in *Troodon formosus* in contrast to the elongate neck of most paravians including *Sinovenator changii*. The dorsal surface of the basioccipital is concave where it forms the foramen magnum and braincase floor. Ventral to the basioccipital condyle is a recessed area that is flanked ventrally by the small ventrolaterally projecting basioccipital (basal) tubera. Like in other troodontids (Norell et al., 2000), the basal tubera are separated by a small inverted, V-shaped trough into which the basisphenoid extends. Contact with the basisphenoid lateral to this extension is along a straight suture just anterior to the basal tubera. No foramen between the basal tubera is apparent. The basioccipital forms the posteroventral wall of the lateral depression. Inside the lateral depression, the basioccipital is invaded by pneumatic spaces (subotic recesses). As reported for *Troodon formosus* (Currie and Zhao, 1993), these spaces are portioned by struts that are somewhat bilaterally asymmetric. Nevertheless, each of these invades the base of the basal tubera and expands dorsomedially into an area ventral to the basioccipital condyle.

BASISPHENOID: As in other troodontids, the basisphenoid is large and hollow, presumably enclosing pneumatic cavities. Sutural contact with adjacent bones, aside from the posterior contact with the basioccipital, is obscured by fusion. The basipterygoid processes and the parabasisphenoid rostrum are remarkably large. The basipterygoid process (preserved only on the right side) is hollow and projects
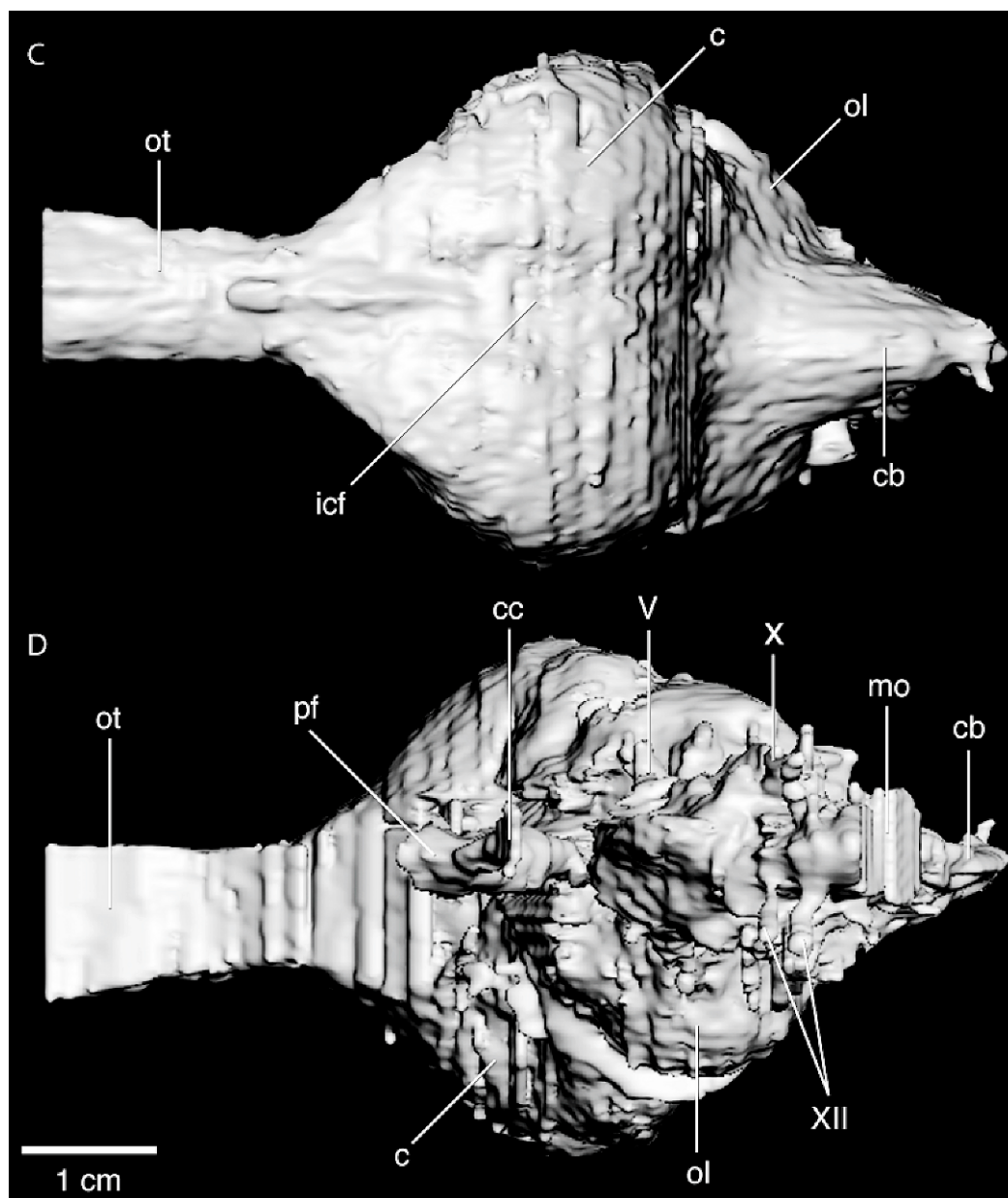
Fig. 28.   Isosurface rendering of the endocranial cast of *Zanabazar junior* (IGM 100/1) in left lateral (**A**) and right lateral (**B**) views (opposite) and in dorsal (**C**) and ventral (**D**) views (above).

ventrolaterally rather than anteroventrally, both of which are derived features in Coelurosauria that are shared by ornithomimids and all troodontids besides *Mei long* and *Sinovenator changii* (Turner et al., 2007b). The process expands distally, and a posteriorly projecting hook lies at its terminus. There is

no evidence of a basisphenoid recess—the lack of which is a derived character shared with other troodontids and avialans (Turner et al., 2007b).

The parabasisphenoid is large and bulbous, forming an onion-shaped bulla. The presence of a pneumatized parasphenoid bulla is a

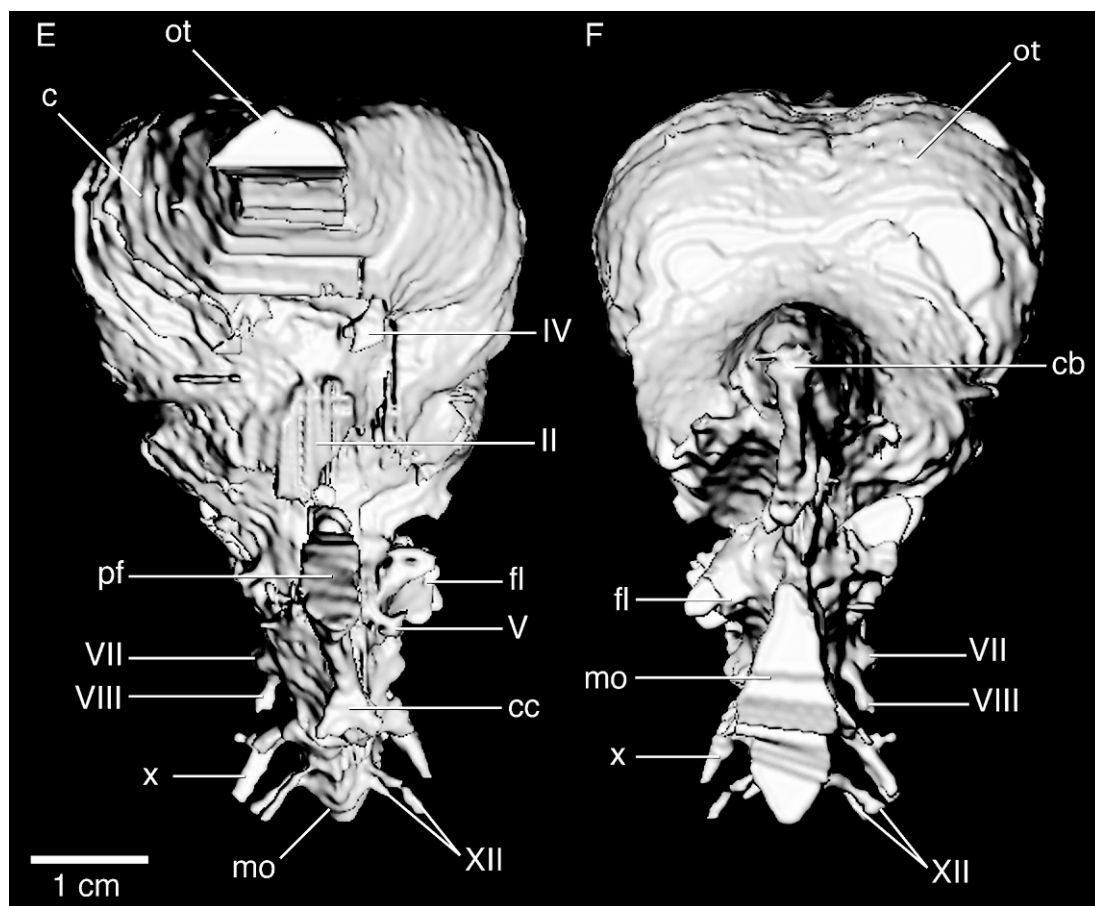Fig. 28. *Continued.* Isosurface rendering of the endocranial cast of *Zanabazar junior* (IGM 100/1) in anterior (**E**) and posterior (**F**) views.

derived feature present in *Saurornithoides mongoliensis*, *Zanabazar junior*, *Troodon formosus*, neonate *Byronosaurus*, and ornithomimids, but not *Mei long* or *Sinovenator changii* (Turner et al., 2007b; Bever and Norell, 2009). It is oriented horizontally in lateral view, in contrast to the anteroventrally descending orientation of the bulla reconstructed in *Troodon formosus* (Currie and Zhao, 1993: fig. 4a). The parasphenoid expands rostral to a constricted area just anterior to the basipterygoid processes. In anterior view, the dorsal and lateral portions of the parabasisphenoid rostrum are swollen, whereas the dorsal surface is keeled. The bulla ends anteriorly in a mediolaterally compressed, solid process that is broken at its base. The process is continuous with a ridge along the straight (in

lateral view) dorsal edge of the bulla. As determined from CT scans (fig. 26C), the bulla is hollow. Near its base where it is joined by the basipterygoid processes, the bulla is partitioned internally by struts that form numerous internal chambers around a central, hollow channel.

ENDOCRANIAL CAST: The exceptional preservation of the braincase of IGM 1/100 allowed us to complete a nearlyundistorted digital endocranial cast (fig. 28). The endocranial cavity has a length of 7.2 cm from the anterior extent of the olfactory tracts to the posterior border of the cerebellum. The greatest width of the endocast is 3.9 cm across the cerebral hemispheres. The total volume is approximately 28.0 cm^3. This volume differs considerably from the 45 cm^3 and 49 cm^3

previously estimated for *Troodon formosus* (Currie and Zhao [1993] and Russell [1969], respectively)—a taxon whose overall cranial length is slightly smaller than that of *Zanabazar junior*. This relatively high endocranial volume for *Troodon formosus* suggests this taxon had an autapomorphically large index of endocranial volume to body size (encephalization quotient; Jerison, 1973) among troodontids. Much of the endocasts of *Troodon formosus* that formed the bases for these volumetric assessments were reconstructed from specimens with incomplete endocranial cavities. The disparity in preservational quality and methodology (CT versus physical reconstructions) complicates the direct comparison of these data. For example, the cerebellum in *Zanabazar junior* is considerably narrower than that reconstructed for *Troodon formosus* (Currie and Zhao, 1993; Russell, 1969). This difference, whether accurate or exaggerated, likely is a major contributor to the volumetric disparity between these taxa.

Features of the forebrain that are identifiable on the endocast of *Zanabazar junior* include the olfactory tracts, cerebral hemispheres, pituitary body, and CN II and IV. The olfactory tract makes up the anteriormost portion of the endocast (fig. 28). The absence of the bones that enclosed the ventral portion of the olfactory bulbs and tract makes the exact length and shape of this region impossible to determine; therefore, the digital endocast begins at the anterior extent of the frontal. Posterior to the olfactory tracts, the cerebral hemispheres are pyriform in shape—similar to those of *Archaeopteryx lithographica* (Dominguez-Alonso et al., 2004) and *Troodon formosus* (Russell, 1969). The same region in more basal theropods, such as *Acrocanthosaurus atokensis* (Franzosa and Rowe, 2005) and *Tyrannosaurus rex* (Brochu, 2000; Larsson et al., 2000), lacks distinctive expansion and is instead tubular in shape (Larsson et al., 2000). The optic nerves (CN II) exit the braincase through a single midline opening between the paired laterosphenoids, and are represented on the endocast as a large midline stucture. The pituitary body lies anteroventral to the level of the optic nerve exit (fig. 28). The overall orientation of the pituitary body is oblique to the angle of the endocast as a whole. The paired internal carotid canals penetrate the basisphenoid, anastomose, and enter the posteroventral end of the pituitary fossa through a single opening.

The only portions of the midbrain that are observable on the endocast are the optic lobes and trochlear nerves (CN IV). The lateral exposure of the optic lobe is located posteroventral to the expanded cerebral hemispheres. The posteroventral displacement of the optic lobes and their relative degree of development again is more similar to the condition in modern birds than in most nonavian theropods (Larsson et al., 2000; Dominguez-Alonso et al., 2004). This degree and direction of development of the optic lobes, however, is present in some other nonavian coelurosaur lineages, such as ornithomimosaurs and oviraptorosaurs (Balanoff et al., 2007). The cerebellum is expanded anterodorsally and overlies the dorsal surface of the optic lobes. The transverse distance across both optic lobes is nearly the same length as across the cerebral hemispheres (fig. 28; compare to fig. 3 in Dominguez-Alonso et al., 2004). The trochlear nerves (CN IV) exit between the orbitosphenoid and laterosphenoid and are visible on the endocast on the ventral surface of the cerebral hemispheres approximately midway along their length (fig. 28). A pair of foramina for the exit of the oculomotor nerves (CN III) lies between the laterosphenoid and orbitosphenoid just posterior and ventrolateral to the foramen for the optic nerve. The paths of these foramina are not readily apparent on the endocast.

The prominent features of the hindbrain that are identifiable on the endocast include the cerebellum, floccular lobes, and medulla oblongata. The majority of the cranial nerves of this region also are visible. These include the trigeminal (CN V), facial (CN VII), vagus canal (CN X–XI), and hypoglossals (CN XII). Unfortunately, important features of the inner and middle ear, such as the semicircular canals and cochlear canal, are not visible on the endocast. The absence of these features is due to damage in this region and a lack of adequate contrast between matrix and bone.

The cerebellum is compressed mediolaterally and lacks the lateral expansion present in
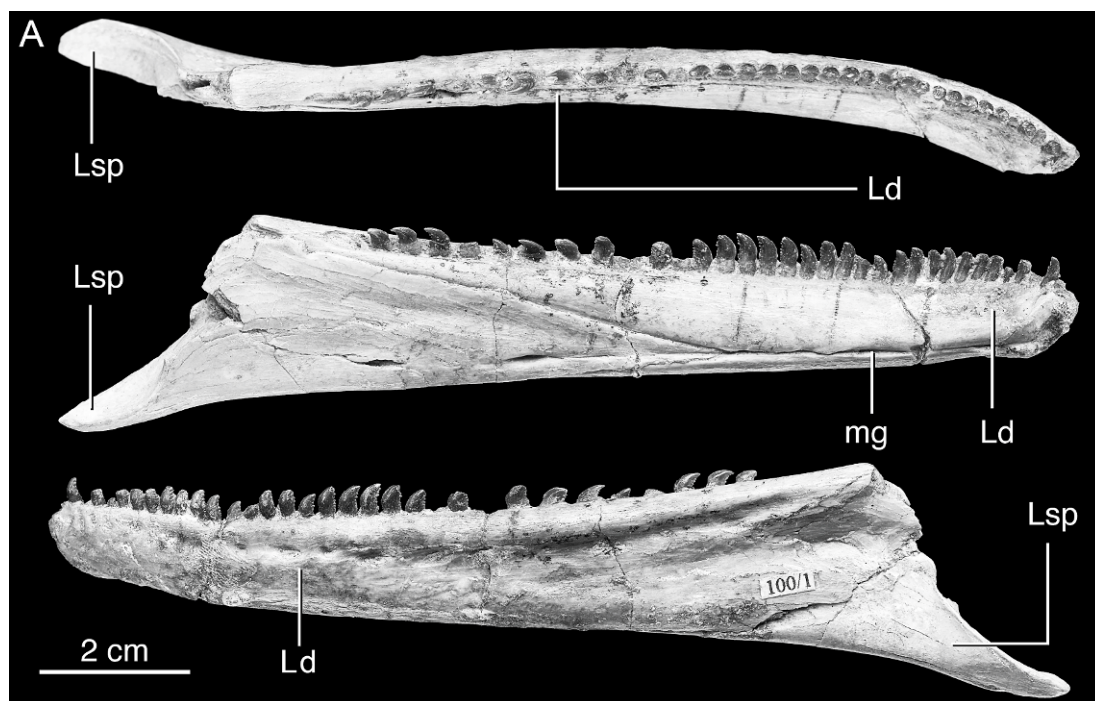
Fig. 29. The mandible of *Zanabazar junior* (IGM 100/1). **A,** above. Left mandible in dorsal, medial, and lateral views. **B,** opposite. Right mandible in dorsal, medial, and lateral views.

avialans (Dominguez-Alonso et al., 2004; Kurochkin et al., 2005). There also is no apparent folding of the cerebellum as in avialans (Kurochkin et al., 2005) and oviraptorosaurs (Kundrát, 2007; Balanoff et al., 2007). Lateral to the cerebellum are the paired floccular lobes (fig. 28). These structures protrude from the endocast in a ventrolateral direction and are surrounded by the bones that enclose the semicircular canals. In this specimen, only the right floccular lobe is distinguishable because of a concentration of dense minerals in this area on the left side of the skull (only the base of the left floccular lobe can be identified). Only a short length of the medulla oblongata is visible on the endocranial cast, but this portion is mediolaterally compression as in most other theropods (Balanoff et al., 2007).

The trigeminal nerve (CN V) exits the braincase through a foramen lying between the prootic and laterosphenoid, and the path of this nerve is prominent on the endocranial cast. In contrast to *Troodon formosus* and avians where the gasserian ganglion typically is positioned intracranially with separate openings for the ophthalmic and maxillomandibular branches of the trigeminal nerve (Baumel and Witmer, 1993; Currie and Zhao, 1993), this nerve appears to exit the braincase of *Zanabazar junior* before branching (as in *Saurornithoides mongoliensis*, *Bryonosaurus jaffei*, and most nonavian theropods; Makovicky et al., 2003; Bever and Norell, 2009). The abducens nerve (CN VI), which typically extends through the basisphenoid to exit the braincase lateral to the pituitary fossa, is not visible. The facial nerve (CN VII) exits the braincase posteroventral to the trigeminal nerve within the lateral depression (fig. 27), an apparently derived condition shared only with *Saurornithoides mongoliensis*. The path of the facial nerve on the right side cannot be determined because of damage to this region. The direct paths of the branches of the vestibulocochlear nerve (CN VIII) are difficult to follow. The foramina for the posteriormost cranial nerves are located posteroventral to the lateral depression. Three prominent structures are visible in this region
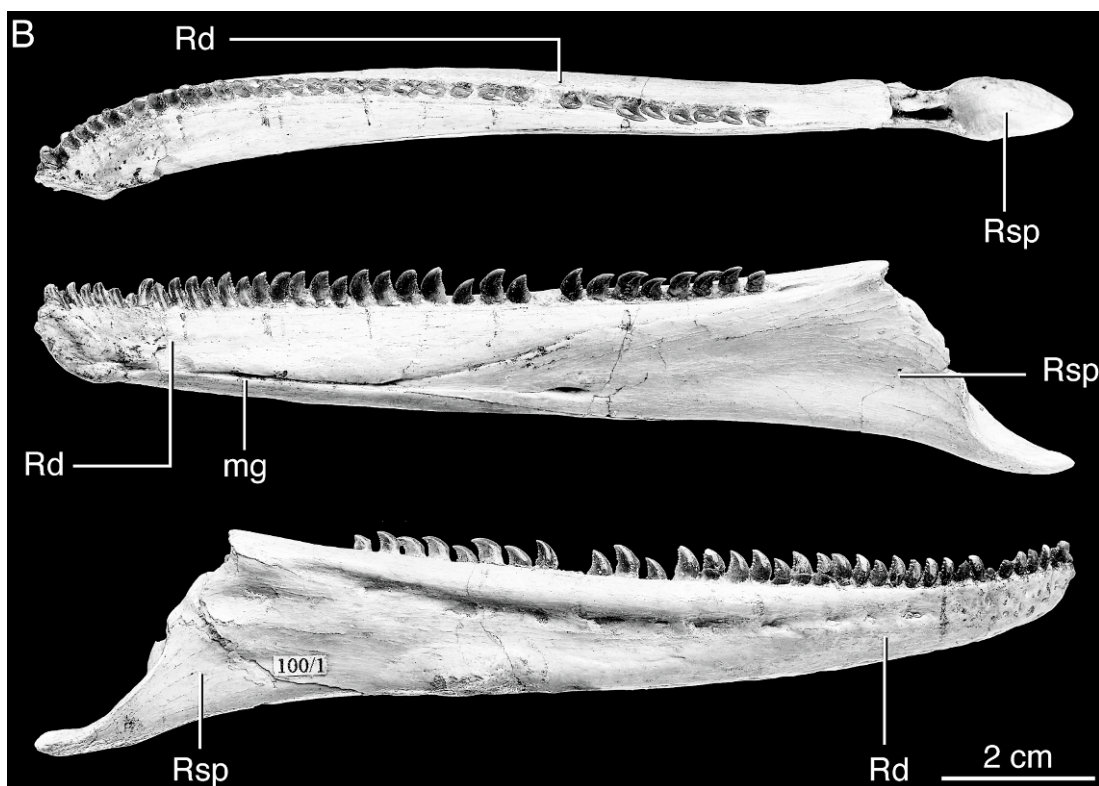
Fig. 29. *Continued.*

posteroventral to the floccular lobe. The largest is the cast of the vagus foramen, which transmits CN X–XI. A small branch exits dorsal to the vagus canal and may represent the glossopharyngeal nerve (CN IX). The glossopharyngeal nerve also may exit with CN X and XI or it may exit the metotic fissure through the fenestra pseudorotunda, as generally is assumed in theropods (Currie, 1997). The two smaller median foramina represent exits for branches of the hypoglossal nerve (CN XII).

MANDIBLE

The mandible of IGM 100/1 is incomplete and only the splenials and dentaries are preserved. In lateral view it is triangular in shape without a prominent coronoid prominence, while viewed ventrally or dorsally it is gently sigmoid (fig. 29).

DENTARY: The dentary is triangular in lateral view, which is a derived shape among paravians that is shared with other troodontids and a small number of other taxa (e.g., *Confuciusornis sanctus*, *Buitreraptor gonzalozorum*; Chiappe et al., 1999; Makovicky et al., 2005). There are 35 tooth positions on the right dentary (which appears to be complete) and 35 on the left. A large, shallow, triangular fossa lies on the posterolateral surface of the dentary and roughly parallels the shape of the bone. A row of nutrient foramina lies in a shallow groove just ventral to the tooth row as in other troodontids, *Buitreraptor gonzalorum*, and *Shanag ashile* (Makovicky et al., 2005; Turner et al., 2007a). On the lateral surface of the dentary just dorsal to the splenial, lies a small, rugose tubercle. A row of shallow, slitlike depressions extend anteriorly from the tubercle and for nearly the entire length of the dentary. This groove becomes more pronounced posteriorly. In dorsal view, the anterior end of the dentary is slightly recurved medially giving the articulated mandibles a U-shaped appearance in dorsal view (as in *Saurornithoides mongoliensis* and *Troodon for-*
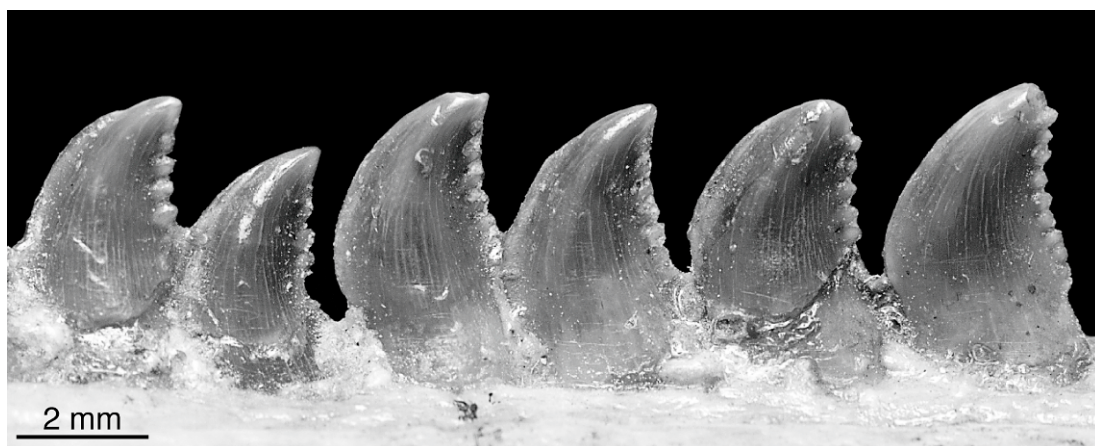
Fig. 30.   Lateral view of closely appressed teeth in the left dentary of *Zanabazar junior* (IGM 100/1).

mosus). A thin, but distinct, groove positioned adjacent and medial to the tooth row anteriorly becomes confluent with the tooth row posteriorly. The dentary is expanded anteriorly forming a sloping shelf medial to the tooth row. Anterior to the splenial, a shallow, but distinct, Meckelian groove extends to the symphysis.

SPLENIAL: The splenial is visible on the lateral surface of the mandible as a large triangular bone. The splenial meets the dentary along a suture that is diagonal on the lateral surface of the mandible. The posteroventral border of the splenial in lateral view projects ventrally. This is accompanied by a general transverse expansion of this element's posterior end. This transverse expansion, together with the medially curving dentary, gives the mandible a sigmoidal shape in ventral view (fig. 29). The lateral margin of the splenial along this boundary is everted and bounds a deep concave fossa posteriorly, as in *Dromaeosaurus albertensis*. This fossa accommodated the angular, which is not preserved, forming a flexible joint between the spleniodentary and the remaining, more posterior, elements of the mandible. This fossa is directed dorsomedially in posterior view and its lateral edge is higher than its medial (as in most theropods but in contrast to dromaeosaurs; Currie, 1987). The splenial fossa constricts to a point posteriorly, while it forms a deep groove along the dorsal suture of the ventral part of the bone anterodorsally. As in other deinonychosaurs, the splenial is broadly exposed on the medial surface of the dentary as a long, tapering triangular element. The anterior terminus of the splenial reaches a point that is well into the anterior one-half of the dentary. Anteroventrally, the splenial is perforated by a slitlike anterior mylohyoid foramen.

TEETH

The teeth of *Zanabazar junior* are similar to those of *Saurornithoides mongoliensis*. The teeth are all closely packed and the tooth apices all curve posteriorly, although in the premaxillary teeth this curvature is not as pronounced. Denticles generally are present— as in *Troodon formosus*, *Sinornithoides youngi*, and *Sinovenator changii* but in contrast to unserrated teeth of *Byronosaurus jaffei* and *Mei long*—but on the posterior edge only. The denticles are relatively large, being similar in proportion to those of *Saurornithoides mongoliensis*, *Troodon formosus*, and *Sinornithoides youngi* and larger than those of most paravians including *Sinovenator changii*. The teeth are constricted between crown and root as in *Saurornithoides mongoliensis* and other troodontids and in contrast to most dromaeosaurs.

The right and left premaxilla (fig. 22E) contains four teeth, although on the left side the posterior two and the crown of the second are broken. The premaxillary teeth are approximately uniform in size and significantly smaller than the teeth of the midmaxillary
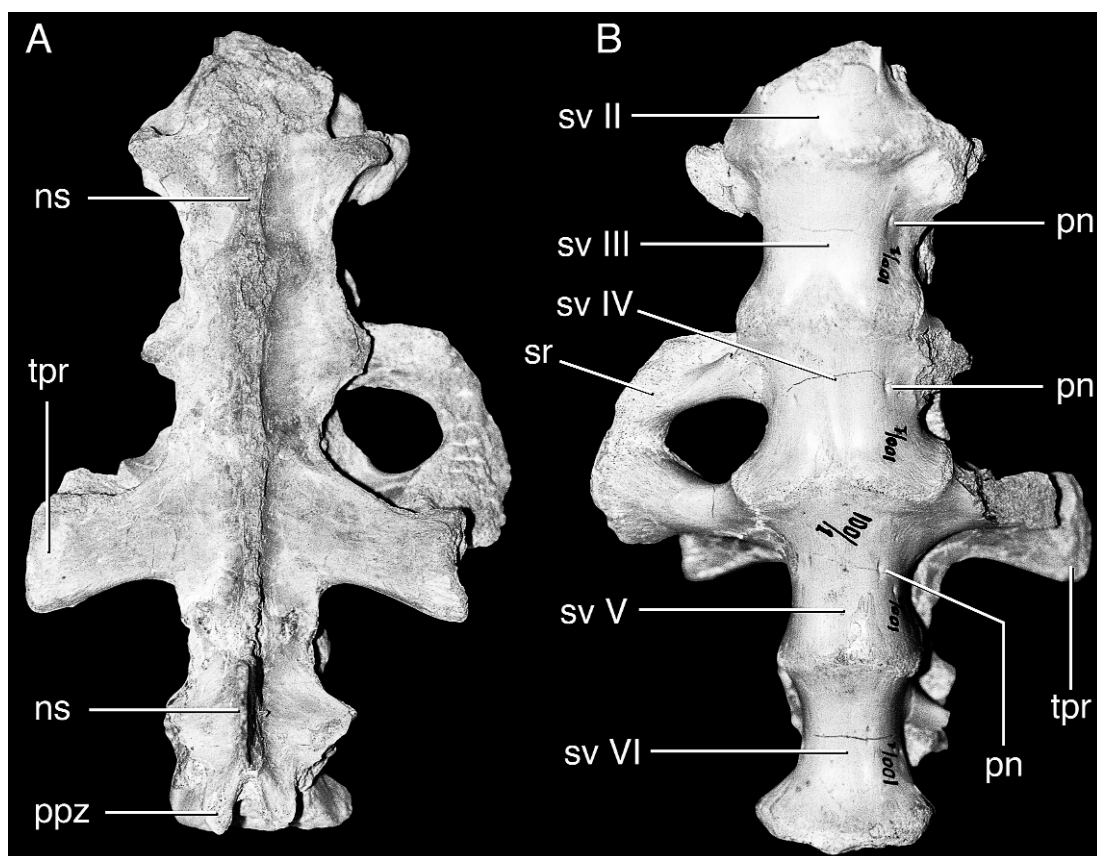
Fig. 31.   The five preserved sacral vertebrae of *Zanabazar junior* (IGM 100/1) in dorsal (**A**) and ventral (**B**) views.

tooth row. The anteriormost two teeth are D-shaped in cross section, with a flat lingual surface. The premaxillary teeth are all similar in size and lack denticles.

There are 20 teeth in the right maxillary and 19 in the left, but the 3rd, 11th, and 19th on the left side and the 11th on the right are missing their crowns. The teeth increase in size posteriorly, with the exception that the last two teeth are slightly smaller than those succeeding them. Maxillary tooth height is more variable than in *Saurornithoides mongoliensis*. The CT scans demonstrate that the roots of the larger teeth are bilobate in cross section. The teeth are set into a vertical groove in the middle on the lingual and labial sides. The first four or five teeth are not strongly recurved, but curvature becomes stronger posteriorly, and the larger teeth are strongly recurved.

There are 35 tooth positions in the left dentary, but the crowns of the 2nd, 22nd, 24th, and 29th are missing. The dentary teeth become more closely appreased in the anterior end of the jaw (fig. 30)—a derived condition shared by all troodontids. There is a slight increase in tooth size posteriorly accompanied by an increase in recurvature of the crown (fig. 30). The crowns are similar in both size and shape to those of the maxillary and premaxillary teeth that they oppose.

VERTEBRAE

SACRAL VERTEBRAE: The cervical and dorsal vertebral series are not preserved, whereas six sacral vertebrae (SV) are present (fig. 31). This number is in agreement with the sacral series of most paravians, including both *Saurornithoides mongoliensis* and *Troodon for-*
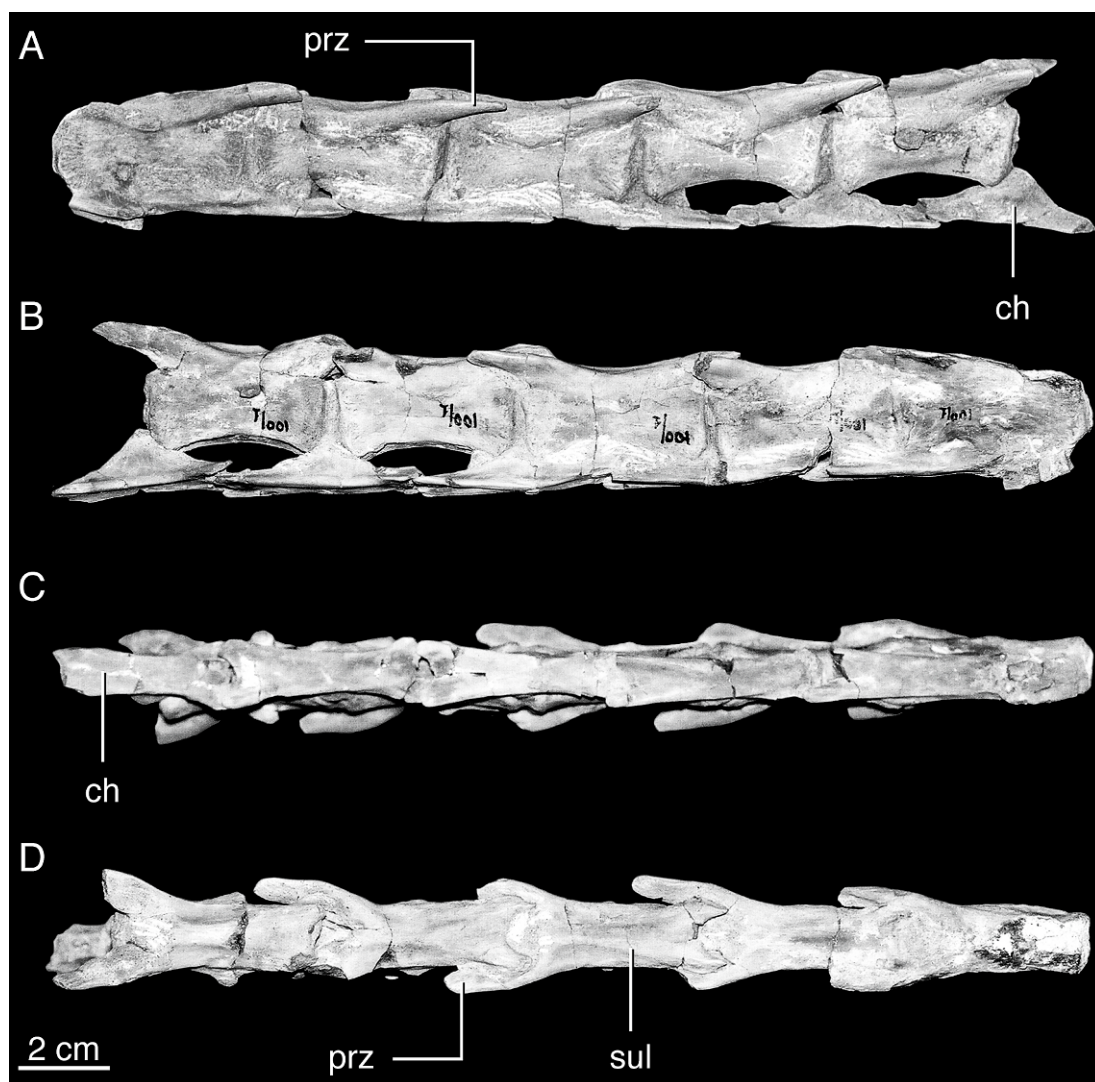
Fig. 32.   Series of five articulated distal caudal vertebrae of *Zanabazar junior* (IGM 100/1) in right lateral (**A**), left lateral (**B**), dorsal (**C**), and ventral (**D**) views.

mosus. It should be noted, however, that only five sacrals are present in *Mei long* and *Sinovenator changii*.

The ventral surface of each sacral vertebra is flat with a slight sulcus present on the intercentral sutures. The neural spines are broken in all but SVVI, where the spine is tall. The neural spines of SVII and III are ankylosed near their base. It is possible that neural spines of SVII–V were fused into a spine lamina as in many other theropods. The intercentral surface between SVV and VI is

less expanded laterally than those of the other sacral vertebrae. The lateral surfaces lying between the sacral ribs of SVII–IV are perforated by paired pneumatic foramina, each of exhibits a similar depth. The sacral ribs, in general, are not well preserved, although the 5th sacral rib is nearly complete on both sides. This rib is deep with an expanded lateral margin. The 4th and 5th sacral ribs are fused distally, so that a fenestra is enclosed between them. The transverse processes of SVVI are broken. The neural

canal, as exposed anteriorly (SVII) and posteriorly (SVVI) is dorsoventrally compressed resulting in a rectangular cross-sectional shape.

CAUDAL VERTEBRAE: Fourteen caudal vertebrae were figured in Barsbold (1974). It is unclear, however, whether they represent a continuous series (Barsbold, 1974). The anteriormost three caudals remain in articulation and apparently derive from just behind the sacrum. Their centra are subquadrangular in anterior and posterior views and are slightly concave ventrally in lateral view. The ventral surfaces of the centra are smooth and lack keels. The zygapophyses are inclined at a high angle. The transverse processes extend from the lateral surface of the centrum at a relatively dorsal position that corresponds to the position of the neural canal. The neural spines are broken but, like the transverse processes, appear to have been long and robust. The neural spines overlie the caudal halves of the centra. Long, rodlike haemal arches are attached to the posterior two of these caudals.

Two separate caudals from a more distal position in the tail have zygapophyses set at a lower angle. The neural spines are dorsoventrally lower but anteroposteriorly longer (the spines extend further forward above the centra) than in the first three caudal vertebrae. The transverse processes are relatively short, directed ventrally, and positioned at about the midlength of the centrum. The ventral surface of each centrum bears a pair of faint longitudinal ridges connecting proximal and distal chevron facets. A triangle-shaped chevron is preserved attached to the more posterior of these two vertebrae.

A single vertebra from the transitional section of the tail is preserved. The zygapophyses of this vertebra lie at a low angle—similar to that of the just-decribed pair of caudals. The prezygapophyses project anterolaterally and taper distally. A prominent hemal canal is incised between strong longitudinal ridges on the ventral surface of the centrum. The anterior intercentral face is subcircular whereas the posterior face is quadrangular. The transverse process is small and projects lateroventrally. The neural spine is absent and replaced by paired ridges that diverge

posteriorly and extend onto the postzygapophyses (as in the posterior caudals of other troodontids; Russell, 1969). The postzygapophyses are much shorter than the prezygapophyses and do not project laterally.

Five articulated distal caudals are preserved (fig. 32). All have long, low centra with concave ventral faces. The ventral surface of the vertebrae has strong lateral ridges that define a flat medial surface. A neural spine is absent on all vertebrae, and its place is taken by a shallow sulcus set between paired low ridges that connect the pre- and postzygapophysis of each side (as in *Troodon formosus*, *Byronosaurus jaffei*, *Mei long*, and *Sinovenator changii*, but not *Sinornithoides youngi*; Turner et al., 2007b). The prezygapophyses are not strongly reduced as in *Mei long*, some dromaeosaurs, and basal avialans. Diminutive transverse processes become smaller and are absent after the third vertebra in the series—the transverse process on the latter element is only a small nubbin. The terminal vertebra is pathologic. The chevrons associated with these elements are low and elongate and overlap one another. In ventral view, the chevrons each form a flattened plate with bifid anterior and posterior ends that articulate with the anterior and posterior surfaces of the adjacent chevrons.

HIND LIMB

Very little of the appendicular skeleton is preserved—only elements from the distal right hind limb. The distal end of the right tibia is preserved along with a coossified astragalus and calcaneum (fig. 33). The fibula is absent. The astragalo-calcaneum is not fused to the tibia and is slightly dislocated from it. There is a large striated fossa on the lateral surface of the tibia that would have accepted the distal end of the fibula. A large crest bounds this fossa posteriorly. Although broken, the ascending process of the astragalus evidently was very tall, and covered the entire anterior surface of the tibia distally. A pronounced bump lies in the middle of the ascending process (fig. 33A). The medial condyle of the astragalus is larger than the lateral condyle. The condyles are connected by an intercondylar ridge, posterior to which lies a small depression. This depression is part of a longer
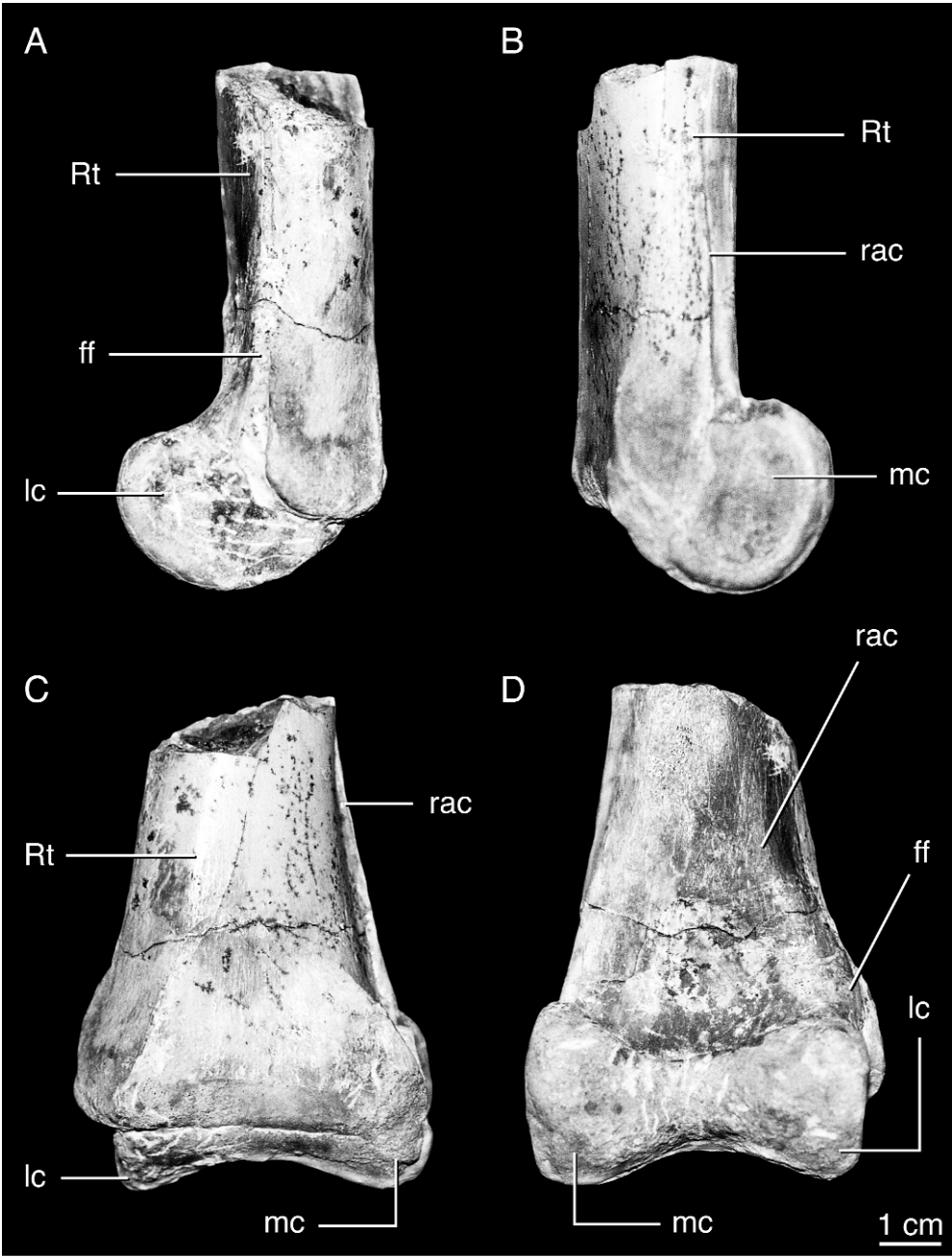
Fig. 33.   Distal end of the right tibia with coossified astragalus and calcaneum of *Zanabazar junior* (IGM 100/1) in lateral (**A**), medial (**B**), posterior (**C**), and anterior (**D**) views.
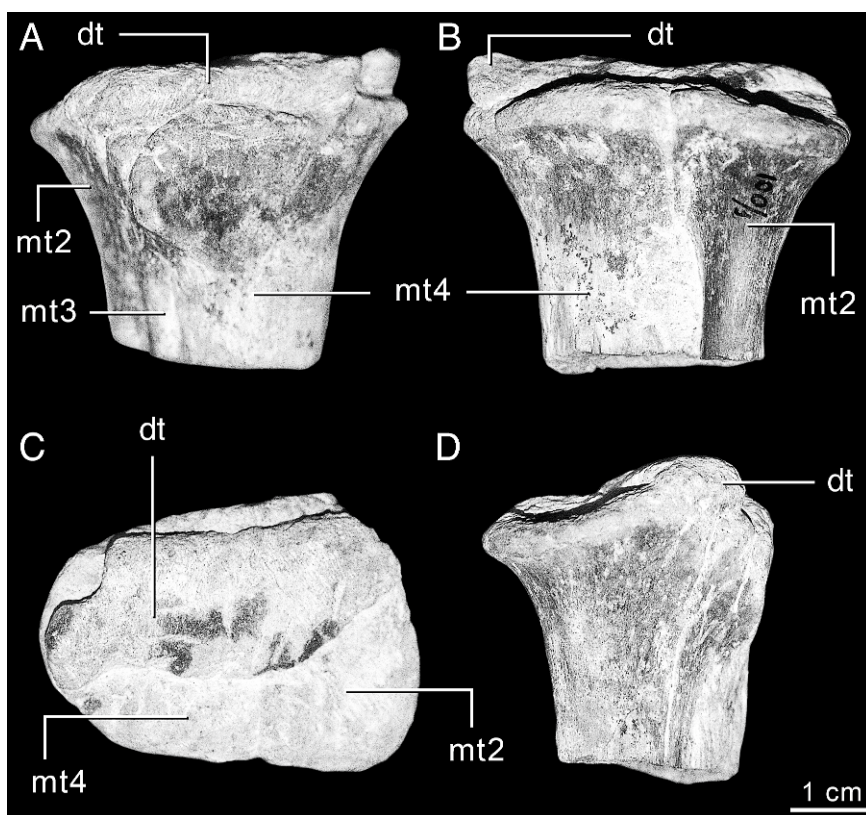
Fig. 34. Proximal end of right metatarsus with fused distal tarsal in *Zanabazar junior* (IGM 100/1) in posterior (**A**), anterior (**B**), dorsal (**C**), and medial (**D**) views.

transverse groove that separates the asending process of the astragalus from its condylar portion. A swollen area on the anterior surface of the astragalus buttresses the medial condyle from above. The outer surfaces of both condyles are concave. The intercondylar groove does not extend onto the surface of the tibia.

The proximal end of the right metatarsus is preserved (fig. 34). A large quadrangular distal tarsal lies on the anterior part of the proximal surface of MT II–IV, but mainly on MT III and IV. Barsbold (1974) considered the large distal tarsal to represent a pair of partially fused tarsals (his T_3 and T_4). We acknowledge that the original interpretation may be the correct one; however, in a second examination of the specimen, we failed to see any separation between the left and right "halves." We therefore adopt the empirical conclusion that the element represents a single

tarsal. MT II is small and expands proximally. MT III is tiny and is wedged between MT II and IV. The proximal shaft of MT III is pinched in an arctometatarsal condition (Novas and Pol, 2005), which is in agreement with *Troodon formosus* but in contrast to the subarctometarsal condition of *Sinornithoides youngi*, *Mei long*, and *Sinovenator changii*. MT IV is the largest and is subtriangular in proximal view. A flattened anterior surface just distal to proximal end of MT IV overhangs the metatarsal shaft.

DISCUSSION

COMPARISON OF *SAURORNITHOIDES MONGOLIENSIS* WITH *ZANABAZAR JUNIOR*

Saurornithoides mongoliensis and *Zanabazar junior* are similar in overall morphology, but a majority of these similarities probably

are plesiomorphic—being shared with other troodontids, especially *Troodon formosus*. Although the distinctiveness of *Zanabazar junior* from *Saurornithoides mongoliensis* was questioned (Gauthier, 1986), there is little doubt that the two are distinct species. The most obvious difference is the larger size of *Saurornithoides junior* (*Saurornithoides mongoliensis* midline skull length is 189 mm, versus 272 mm for *Zanabazar junior*). This comparison, of course, is based only on single specimens of each species; however, each specimen is an adult based on neurocentral fusion in the preserved vertebrae. Among the characters that separate the two taxa is the presence of a pneumatic recess on the lateral surface of the prootic dorsal to the trigeminal fenestra in *Saurornithoides mongoliensis*. This recess is absent in both *Zanabazar junior* and *Troodon formosus* but likely is plesiomorphic for *S. mongoliensis* as it is present in the other known troodontids (e.g., *Byronosaurus jaffei* and *Sinovenator changii*). The complex curvature of the jugal beneath the orbit in *Zanabazar junior* is a character that is absent in *Saurornithoides mongoliensis*. Finally, the tooth counts are slightly different in the two taxa (although not as different as described by Barsbold, 1974), with 19 maxillary and 31–33 dentary teeth in *Saurornithoides mongoliensis* and 19–20 maxillary and 35 dentary teeth in *Zanabazar junior*. The shared number of maxillary teeth (approx. 19) is a possible synapomorphy supporting a sister-taxon relationship between these taxa. The polarity of this number, however, is questionable as the two most likely outgroups to the *Troodon-Saurornithoides-Zanabazar* clade (*Byronosaurus* and *Sinornithoides*) exhibit 30 and 18 maxillary teeth, respectively. An additional concern regarding the use of relatively subtle differences in tooth number to diagnose a clade is the presence of what may be significant transformations in maxillary tooth number during the postnatal ontogeny of troodontids (Bever and Norell, 2009).

Postcranial overlap between the specimens is limited to the sacral and anterior caudal vertebrae and slight overlap of metatarsals. An observed difference between the two specimens is the absence of distinct foramina on the sacral vertebrae in *Saurornithoides mongoliensis*. Three of the sacrals in *Zanabazar junior* bear small lateral foramina, probably of pneumatic nature (Barsbold, 1974; Howse and Milner, 1993), although pneumatic features are known to be highly variable in the postcranium of theropods. The proximal shafts of the metatarsals preserved with *Zanabazar junior* overlap slightly those preserved on the foot of *Saurornithoides mongoliensis*; however, as noted by Barsbold (1974), these lack significant comparative morphology to be informative. Another specimen of a large Djadokhta troodontid from Ukhaa Tolgod (Norell and Hwang, 2004) preserves a proximal metatarsal with a distal tarsal fused to it as in *Zanabazar junior*, however, such a morphology is found in a variety of theropod taxa and may be at least partially related to skeletal maturity in coelurosaurs.

The monophyly of *Saurornithoides mongoliensis* + *Zanabazar junior* generally has not been questioned, but character support for this priviledged relationship is not readily apparent. This may be due in part to the poor preservation of *Saurornithoides mongoliensis*. The position of the facial foramen outside of the lateral depression in other troodontids (e.g., *Troodon formosus* and *Byronosaurus jaffei*) in the context of our large-scale analyses of coelurosaur relationships (e.g., Makovicky et al., 2003; Norell et al., 2006; Turner et al., 2007b) indicates this condition is derived within Troodontidae.

The *Saurornithoides mongoliensis* + *Zanabazar junior* group is one of the few sister species (or at least very exclusive clades) that occur in both the Djadokhta and Nemegt formations. The Nemegt Formation overlies the Barun Goyot Formation in most areas in which it is exposed, and there does not appear to be a depositional hiatus between them. The precise lithostratigraphic relationship between the Barun Goyot and Djadokhta formations is unclear, because the two formations are not exposed in contact in any area. The fauna of the Barun Goyot is very similar to that of the Djadokhta (Gao and Norell, 2000). The difference in age between the Djadokhta and Barun Goyot formations, on the one hand, and the Djadokhta and Nemegt formations on the other is probably not large, and the faunal

differences are more likely due to the different depositional environments represented by these sediments.

PHYLOGENETIC RELATIONSHIPS

Troodontid interrelationships are treated in detail by Makovicky et al. (2003) and Makovicky and Norell (2004), and the following discussion refers to clades and diagnostic characters found in those studies. *Saurornithoides mongoliensis + Zanabazar junior* is a highly derived maniraptorans that exhibit the following troodontid synapomorphies (Makovicky et al., 2003): a subtriangular dentary (Currie, 1987), groove on the labial surface of the mandible housing the mental foramina, numerous tightly packed small teeth in the anterior part of the lower tooth row (Currie, 1987), flat internarial bar, basioccipital tubera closely spaced and separated only by a small V-shaped notch, absence of a basisphenoid recess (Witmer, 1997; shared with basal avialans), and an asymmetrical foot with the second metatarsal shorter and narrower than the fourth. *Saurornithoides mongoliensis* and *Zanabazar junior* share the presence of a subotic recess with a clade of troodontids excluding *Sinovenator changii* and *Mei long* (Xu and Norell, 2004). *Saurornithoides mongoliensis*, *Zanabazar junior*, and other Late Cretaceous troodontids form a clade to the exclusion of an unnamed Early Cretaceous troodontid from Mongolia (Barsbold et al., 1987) diagnosed by enlarged and distally hooked serrations on the teeth (Makovicky et al., 2003). *Saurornithoides mongoliensis* and *Zanabazar junior* are united with *Troodon formosus* in a clade diagnosed by anteromedially deflected dentaries that have a U-shaped symphysis and especially large denticles on the teeth (Currie and Dong, 2001). Denticle size appears to evolve gradually within Troodontidae, although it is complicated by several independent losses of serrations (Makovicky et al., 2003; Xu and Norell, 2004; Bever and Norell, 2009). Serrations are small in *Sinovenator changii* (Xu et al., 2002) and the unnamed Early Cretaceous troodontid (Barsbold et al., 1987) but are relatively large in *Sinornithoides youngi* (Currie and Dong, 2001) and reach their relatively largest development in the *Troodon-Saurornithoides-Zana-bazar* triad. An additional character that appears to diagnose this clade is the presence of an expanded otosphenoidal crest that surrounds the external facial foramen within the lateral depression of the braincase. The discovery of several small- to medium-sized troodontids in recent years (reviewed by Makovicky and Norell, 2004) has shifted our previous interpretation of several features as diagnostic of all troodontids to being synapomorphies of more exclusive clades within Troodontidae. This is especially the case with a number of braincase, mandibular, and dental features originally recognized and discussed by Russell (1969), Barsbold (1974), and Currie (1985, 1987). The gradual evolution of enlarged denticles was already discussed, and similar trends may characterize the evolution of neurocranial pneumatic features (see also Bever and Norell, 2009). For example, a bulla and lateral depression are absent in *Sinovenator changii* and the latter feature is reportedly also absent in the unnamed Early Cretaceous taxon (Barsbold et al., 1987). The lateral depression is defined by an expanded otosphenoidal crest in more derived troodontids. Expansion of the otosphenoidal crest is most developed in the large-bodied Late Cretaceous taxa *Troodon formosus*, *Saurornithoides mongoliensis*, and *Zanabazar junior*, in which the crest extends dorsal to the exit foramen of the facial nerve. This progressive character transformation may correlate with body size, although more data on basal, small-bodied taxa is required to address this hypothesis. Whether formation of a bulla relates to body size in a similar fashion is unknown as this region is not well preserved in most small troodontids, although it is notably absent in *Sinovenator changii*.

Xu et al. (2002) also pointed to a number of character states in derived troodontids that could be interpreted as size-related changes from the generalized paravian condition. Among these are the propubic condition of the pelvis, relatively short and wide centra in the trunk vertebrae, and relative development of the cervical epipophyses as seen in *Troodon formosus* (P.J.M., personal obs.). These latter features also are seen in large-bodied dromaeosaurids and represent potential size-related parallelism.

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APPENDIX 1

ABBREVIATIONS

INSTITUTIONAL

AMMH FR	American Museum of Natural History Fossil Reptiles and Amphibians, New York
IGM	Institute of Geology, Mongolian Academy of Sciences, Ulan Bator
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Beijing
RTMP	Royal Tyrell Museum of Paleontology, Drumheller

ANATOMICAL

Uppercase L and R as prefixes signify left and right

a	angular
aof	antorbital fenestra
arm	rim of acetabulum
bpt	basipterygoid process
bs	basisphenoid
btu	basal tubera
c	cerebrum
cb	cerebellum
cc	cerebral carotid canal
cf	crista calvarii frontalis
ch	chevron
cm	centrum
CN	cranial nerve
ctr	caudal tympanic recess
cv1	caudal vertebra I
cv2	caudal vertebra II
cv3	caudal vertebra III
cv4	caudal vertebra IV
d	dentary
df	dorsal fossa
dt	distal tarsal
ec	endocranial cavity
ect	ectopterygoid
ex-op	exoccipital/opisthotic
f	frontal
fl	flocculus
fe	femur
ff	fibular fossa
fh	femoral head
fm	foramen magnum
fo	fenestra ovalis
fpr	fenestra pseudorotunda
i	ischium
iai	iliac articulation of ischium
iap	iliac articulation of pubis
icc	internal caroid canal
icf	intercerebral fissure
ifb	interfenestral bar
ifc	interfenestral canal
ipp	ischiac process of pubis
is	ischiac symphysis
j	jugal
l	lacrimal
lad	lateral depression of braincase
lat	laterosphenoid
lc	lateral condyle
lrf	lateral ridge of femur
mc	medial condyle
mg	Meckelian groove
mo	medulla oblongata
mps	palatal shelf of maxilla
mt	metatarsal

mt1	metatarsal I
mt2	metatarsal II
mt3	metatarsal III
mt4	metatarsal IV
mx	maxilla
mxf	maxillary fenestra
mxt	maxillary tooth
n	nasal
na	external naris
nc	nuchal crest
np	nasal passage
ns	neural spine
obp	obturator process of ischium
oc	occipital condyle
ol	optic lobe
or	orbit
os	orbitosphenoid
ot	olfactory tract
otc	otosphenoid crest
p	parietal
pai	pubic articulation of ischium
pal	palatine
pb	pituitary body
pc	pneumatic cavity
ph1-1	phalanx I-1
ph1-2	phalanx I-2
ph2-1	phalanx II-1
ph2-2	phalanx II-2
ph2-3	phalanx II-3
ph3-1	phalanx III-1
ph3-2	phalanx III-2
ph3-3	phalanx III-3
ph4-1	phalanx IV-1
ph4-2	phalanx IV-2
pmx	premaxilla
pn	pneumatic foramen
po	postorbital
pop	paroccipital process
ppz	postzygapophysis
pr	prootic
prz	prezygapophysis
ps	pubic shaft
psb	parasphenoid bulla
psp	parasphenoid process
pt	pterygoid
ptf	posttemporal fenestra
pu	pubis
q	quadrate
qf	quadrate fossa of squamosal
rac	ascending process of astragalus
sa	surangular
sgc	sagittal crest
so	supraoccipital
sor	subotic recess
sos	scleral ossicle
sp	splenial
sq	squamosal
sr	sacral rib
sul	sulcus
sv1	sacral vertebra I
sv2	sacral vertebra II
sv3	sacral vertebra III
sv4	sacral vertebra IV
sv5	sacral vertebra V
sv6	sacral vertebra VI
t	tibia
tg	greater trochanter (femur)
tl	lesser trochanter (femur)
tp	posterior trochanter (femur)
tpr	transverse process
udv	ultimate dorsal vertebra
v	vomer
II	optic canal
IV	trochlear foramen
V	trigeminal fenestra
VII	facial foramen
VIII	acoustic foramen
X, XI	vagus foramen
XII	hypoglossal foramina