AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3545, 51 pp., 25 figures, 1 table December 7, 2006

A New Dromaeosaurid Theropod from Ukhaa Tolgod (Ömnögov, Mongolia)

MARK A. NORELL,[1] JAMES M. CLARK,[2] ALAN H. TURNER,[1] PETER J. MAKOVICKY,[3] RINCHEN BARSBOLD,[4] AND TIMOTHY ROWE[5]

ABSTRACT

We describe a new dromaeosaurid theropod from the Upper Cretaceous Djadokhta Formation of Ukhaa Tolgod, Mongolia. The new taxon, *Tsaagan mangas*, consists of a well-preserved skull and cervical series. This specimen marks only the second dromaeosaurid taxon from a formation that has otherwise yielded numerous specimens of *Velociraptor mongoliensis*, and *Tsaagan mangas* is the only dromaeosaurid known from Ukhaa Tolgod beyond sporadic occurrences of isolated teeth. *Tsaagan mangas* differs from other dromaeosaurids in the possession of a straight, untwisted, and pendulous paroccipital process, a large and anteriorly located maxillary fenestra, and a jugal–squamosal contact that excludes the postorbital from the margin of the infratemporal fenestra. The phylogenetic affinities of *Tsaagan mangas* are determined through a comprehensive phylogenetic analysis of Coelurosauria, confirming its position within Dromaeosauridae. This new specimen, coupled with CT imaging, provides new information on the skull and braincase anatomy of dromaeosaurids.

INTRODUCTION

Theropod dinosaur fossils are rare, and remains of the generally small dromaeosaurids are among the rarest. Twelve valid species have been described including several very fragmentary forms that are ambiguously dromaeosaurid (Norell and Makovicky,

---

[1] Division of Paleontology, American Museum of Natural History (MAN: norell@amnh.org; AHT: turner@amnh.org).
[2] Department of Biological Sciences, George Washington University, Washington, D.C. 20052. Research Associate, Division of Paleontology, American Museum of Natural History.
[3] Department of Geology, The Field Museum, Roosevelt Rd. at Lake Shore Drive, Chicago, Illinois 60605. Research Associate, Division of Paleontology, American Museum of Natural History.
[4] Institute of Geology, Mongolian Academy of Sciences, EnkhTaivani Gudamji, Ulan Bataar 210351, Mongolia.
[5] Vertebrate Paleontology Laboratory, Department of Geological Sciences, The University of Texas at Austin, Texas 78712.

ISSN 0003-0082

2004). Until recently the group was best known from the Cretaceous of Asia and North America, however in the last few years many new taxa have been discovered from Asia, North America, and South America (Norell and Makovicky, 2004; Makovicky et al., 2005). Among the most intriguing of these finds are specimens from the Lower Cretaceous Yixian Formation of Liaoning, China, preserved with epidermal features including feathers (Norell and Xu, 2005). Dromaeosaurids have been the focus of several recent studies because of their postulated close relationship to Avialae (Gauthier, 1986; Sereno, 1997; Holtz, 2000; Norell et al., 2001, Senter et al., 2004). Here we describe a new taxon of dromaeosaurid from the Upper Cretaceous Djadokhta Formation at Ukhaa Tolgod (Dashzeveg et al., 1995) in Mongolia and comment on aspects of dromaeosaurid phylogeny. This is only the second dromaeosaurid taxon reported from the Djadokhta Formation since *Velociraptor mongoliensis* was described in 1924 (Osborn, 1924), and it may occupy a more basal phylogenetic position within dromaeosaurids than *Velociraptor mongoliensis*.

METHODS

IGM 100/1015 was CT scanned at the University of Texas High Resolution X-Ray CT Facility in May 1998. The skull was scanned in air after final preparation was completed. Original scans were done in the sagittal plane with a slice thickness of 0.5 mm, an interslice spacing of 0.475 mm, and a field of reconstruction of 240 mm. The original slices were then digitally resliced to a 0.47 mm equivalent slice spacing using NIH Image software, and three-dimensional images were generated using VoxBlast. Subsequent manipulation and visualization of the dataset was done using ImageJ software.

Contrast in the CT imagery throughout much of the skull is weak. Nevertheless, internal contacts between bone and matrix can be discerned in many areas, and the internal morphology of the snout and right side of the braincase can be traced. Slices are available at www.amnh.org/vertpaleo/norell.html and at http://www.digimorph.org/. Abbreviations are listed in appendix 1.

SYSTEMATIC PALEONTOLOGY

THEROPODA MARSH, 1881

COELUROSAURIA HUENE, 1920

MANIRAPTORA GAUTHIER, 1986

DROMAEOSAURIDAE MATTHEW AND BROWN, 1922

Tsaagan mangas, new taxon

TYPE SPECIMEN: IGM 100/1015, a skull and mandible and anterior eight cervicals (fig. 1).

TYPE LOCALITY: Xanadu sublocality, Ukhaa Tolgod, Ömnögov Aimag, Mongolia (fig. 2).

FORMATION: Djadokhta Formation, Campanian (Dingus et al. in review).

ETYMOLOGY: *Tsaagan*, Mongolian for white; *mangas*, Mongolian for monster.

DIAGNOSIS: Referred to the Dromaeosauridae on the basis of the following derived characters: caudolateral overhanging shelf of the squamosal, large spike on medial inflected process of the articular, and large quadrate foramen (Currie, 1995; Norell and Makovicky, 2004). Differs from all other known dromaeosaurids in the following unique derived characters: paroccipital process pendulous and not twisted distally, basipterygoid process elongate and anteroventrally directed, maxillary fenestra large and located at the anterior edge of the antorbital fossa, jugal meets the squamosal to exclude the postorbital from the margin of the infratemporal fenestra.

DESCRIPTION

IGM 100/1015 comprises a skull with articulated mandibles and the eight anteriormost cervical vertebrae (figs. 1 and 3). The skull exhibits preburial wear on the outer bones, especially the dentaries and maxillae, indicative of prolonged subaerial exposure. The skull is laterally flattened and the rostral elements slightly displaced. The left postdentary bones and left lower temporal arch were separated from the main skull block in the laboratory to expose the braincase. Judging from the near obliteration of any trace of braincase sutures or sutures between the neural arches and the centra of the accompanying vertebrae, the specimen was an adult

Fig. 1. Holotype of *Tsaagan mangas* (IGM 100/1015) during initial preparation.

Fig. 2. View of Xanadu locality showing the location of holotype of *Tsaagan mangas* (IGM 100/1015). This view is looking toward the southeast.

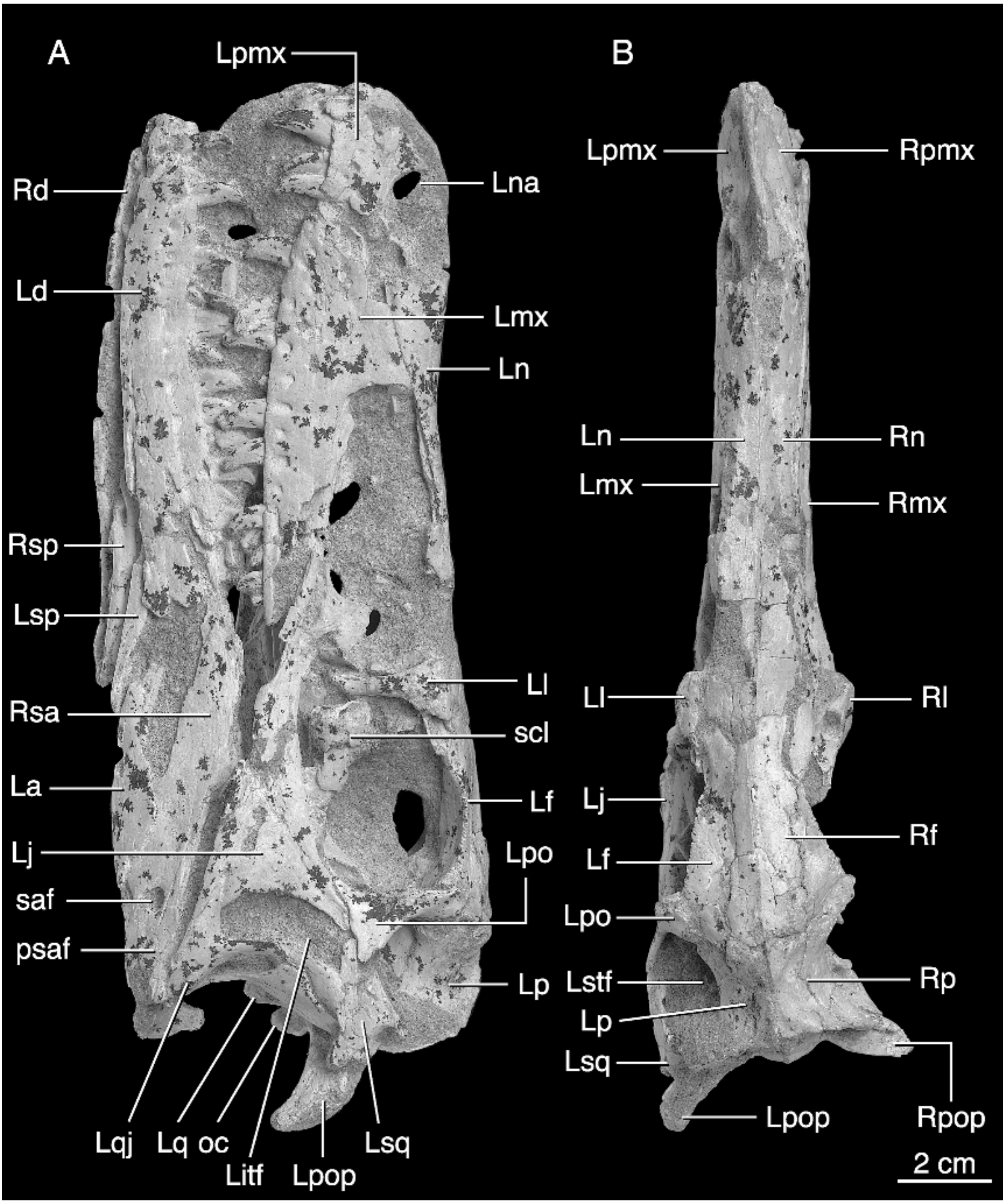


Fig. 3. **A**, Holotype of *Tsaagan mangas* (IGM 100/1015) in left lateral view. **B**, holotype of *Tsaagan mangas* (IGM 100/1015) in dorsal view. Abbreviations are in appendix 1.

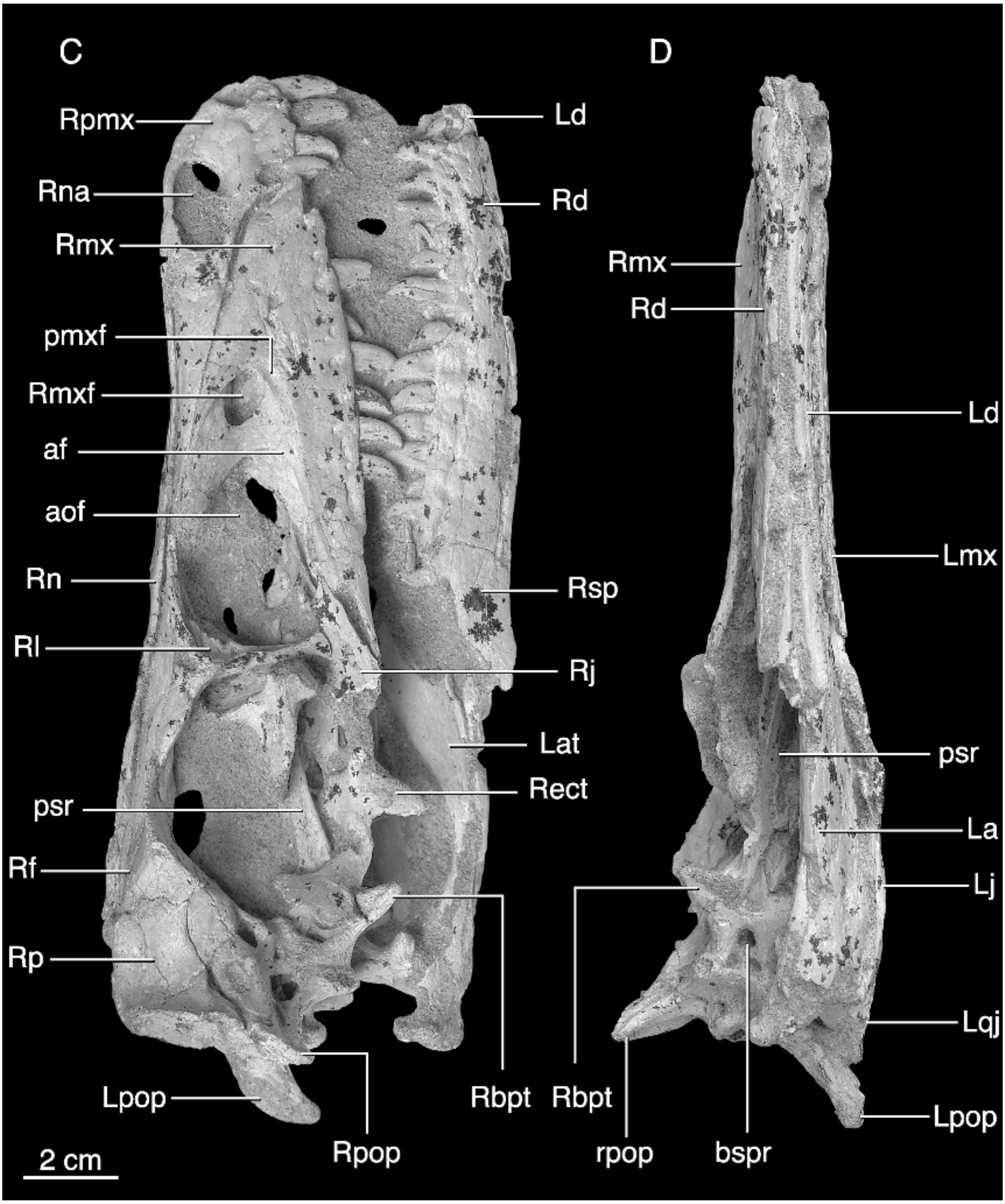


Fig. 3. (Continued). **C**, holotype of *Tsaagan mangas* (IGM 100/1015) in right lateral view. **D**, holotype of *Tsaagan mangas* (IGM 100/1015) in ventral view. Abbreviations are in appendix 1.

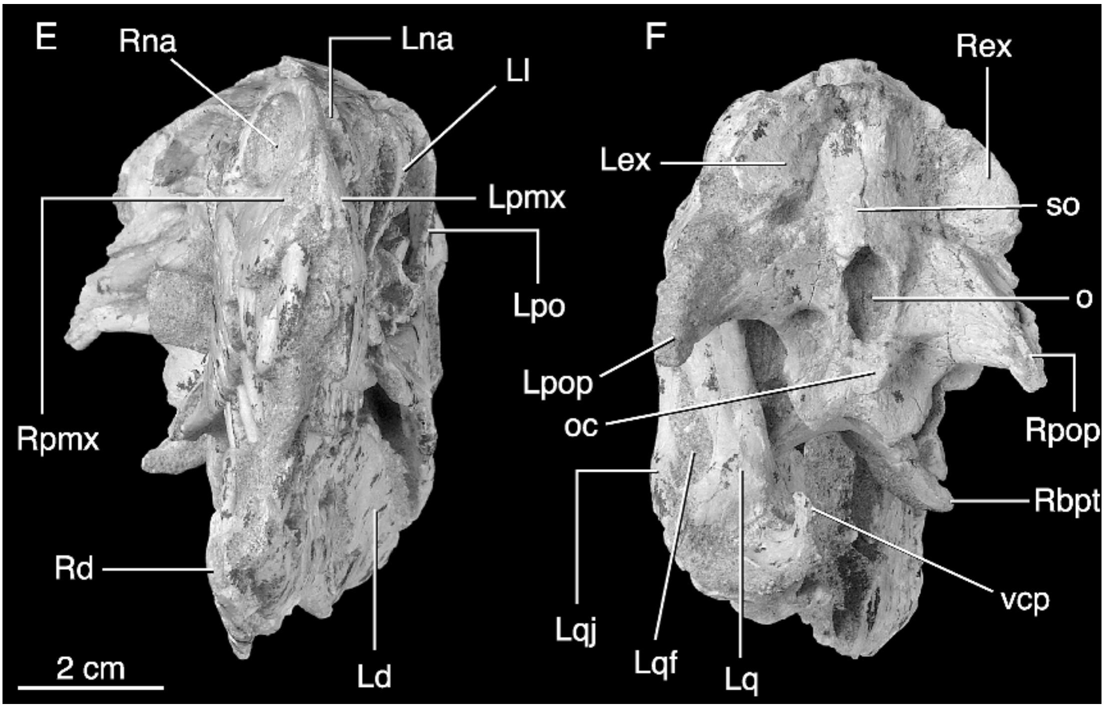


Fig. 3. (Continued). **E**, holotype of *Tsaagan mangas* (IGM 100/1015) in left anterior view. **F**, holotype of *Tsaagan mangas* (IGM 100/1015) in posterior view. Abbreviations are in appendix 1.

(Brochu 1992, 1996). A list of measurements is provided in table 1.

THE ROSTRUM

The rostrum is well preserved except for some mediolateral flattening (fig. 3). The snout is long, comprising 59% of the total length of the skull as measured from the preorbital bar. The nares are large and elliptical. As can be determined from CT data, the nasal chamber is separated from the maxillary sinus by an osseous floor (fig. 4). Therefore, the nasal canal is formed by the premaxilla anteriorly and the nasals and maxillae posteriorly as in the troodontid *Byronosaurus jaffei* (Norell et al., 2000; Makovicky et al., 2003) and presumably other basal coelurosaurs.

PREMAXILLA: The external nares, best preserved on the right side, are large and elliptical, longer than they are high. The maxillary process of the premaxilla is short, separating the anterior part of the nasal and the maxilla for only a short distance. It is relatively much shorter than in most specimens of *Velociraptor mongoliensis*. The nasal process is delicate, thin, and attenuate. It is more rodlike than straplike and is not T-shaped as in troodontids. It separates the nasals for the posterior three-quarters of the internarial bar. The nasal and maxillary processes are subparallel and project posteriorly rather than more vertically as in *Atrociraptor marshalli* (Currie and Varricchio, 2004). The body of the premaxilla is extensive and holds four premaxillary teeth as in all dromaeosaurids and the majority of toothed theropods. The floor of the narial chamber is smooth and there is no indication of a subnarial foramen. Scattered small neurovascular pits lie just dorsal to the tooth row on the labial surface.

MAXILLA: The maxilla is 103 mm long and 38 mm tall at its highest point and the tooth row is 90 mm long. The maxilla is more robust than in *Velociraptor mongoliensis* and borders a large antorbital fossa, which as in *Velociraptor mongoliensis* extends across two-

TABLE 1

Measurement of the Skull of the Holotype of *Tsaagan maangas* (IGM 100/1015)

All measurements are in millimeters and somewhat approximate as the skull has been mildly distorted.

Total skull length (occiput to distal end of premaxilla)	201
Length of maxilla	101
Maximum maxilla height	37
Nares length	20
Nares height	13
Premaxilla length	45
Premaxilla height	29
Length of maxillary fenestra	12
Height of maxillary fenestra	8
Length of antorbital fenestra	42
Height of antorbital Fenestra	28
Lacrimal exposure on skull roof	38
Nasal length	107
Frontal width across nares	24
Frontal length	45
Width of subtemporal fenestra	9.5
Height of suborbital fenestra	27
Jugal length	94
Jugal height	32
Height of quadrate foramen	18
Width of quadrate foramen	5
Braincase height (basipterygoid process to skull roof)	59
Width across basipterygoid processes	30
Mandible length	196
Width across basal tubera	16
Basal tubera to nuchal crest	48
Quadrate height	41
Width of quadrate articular surface	23
Dentary length	113
Maximum dentary height	20
Mandible width at retroarticular process	23

thirds of the length of the entire maxilla (Barsbold and Osmólska, 1999). The osseous floor of the fossa is relatively small, composed mostly of the interfenestral bar (interfenestral pila) because the antorbital fenestra is large and is adjacent to a very large maxillary fenestra at the anterior terminus of the fossa. This differs from the typical dromaeosaurid condition where (except in *Atrociraptor marshalli*) the maxillary fenestra lies posterior and dorsal to the anterior apex of the antorbital fossa (fig. 5). The posteroventral corner of the antorbital fossa is formed entirely by the jugal, which contacts the maxilla along an oblique overlapping joint. Dorsal to the antorbital fossa, the maxilla is exposed in lateral view ventral to the nasal, premaxilla, and lacrimal. A row of supralabial foramina is not bordered dorsally by an elevated ridge as reported in *Velociraptor mongoliensis* by Barsbold and Osmólska (1999), but this feature is variable in the latter species (personal obs.). Inside the large antorbital fenestra, an extensive osseous wall forms the medial border of the epiantral recess (Witmer, 1997) enclosing medially the caudal fenestra of the maxillary antrum as well as the antrum itself. Apparently this is an expansion of the postantral strut. Given the anterior placement of the maxillary fenestra and interfenestral bar (interfenestral pila of Witmer, 1997), the expanded postantral strut is visible laterally through the antorbital fenestra. This wall, however, apparently contacts the floor of the nasal chamber dorsal to the maxillary fenestra, as it does in some theropod taxa (e.g., *Albertosaurus libratus* [Lambe 1917], *Troodon formosus* [Currie 1985], *Byronosaurus jaffei* [IGM 100/983]). These ridges, which form the medial wall to the maxillary antrum, originate on the maxilla near its contact with the premaxilla, just posterior to the external nares, as can be determined from CT data. These sheets of bone fail to contact one another medially. Inside the antorbital fenestra on the dorsal surface of the right palatal shelf, a large palatine recess is present.

The promaxillary fenestra is a small slit entering the antrum rostrally from within a small pocket that lies just ventral to the anterior terminus of the antorbital fossa. A small ridge forms the promaxillary pila, which separates the promaxillary fenestra from the maxillary fenestra.

NASAL: As is typical for most theropod dinosaurs, the nasal is long, thin, and paired. In dorsal view the nasals together form an hourglass-shaped structure. Because they are wider anteriorly than in the midsection, they give the snout an unusual upturned appearance when mediolaterally crushed, as in this specimen and the holotype of *Velociraptor mongoliensis* (fig. 6). While the snouts of dromaeosaurids are slightly upturned at their tips, this characteristic pattern of crushing has led to many reconstructions of the *Velociraptor mongoliensis* skull with noses that are too far upturned (see Paul, 2002: 181). In

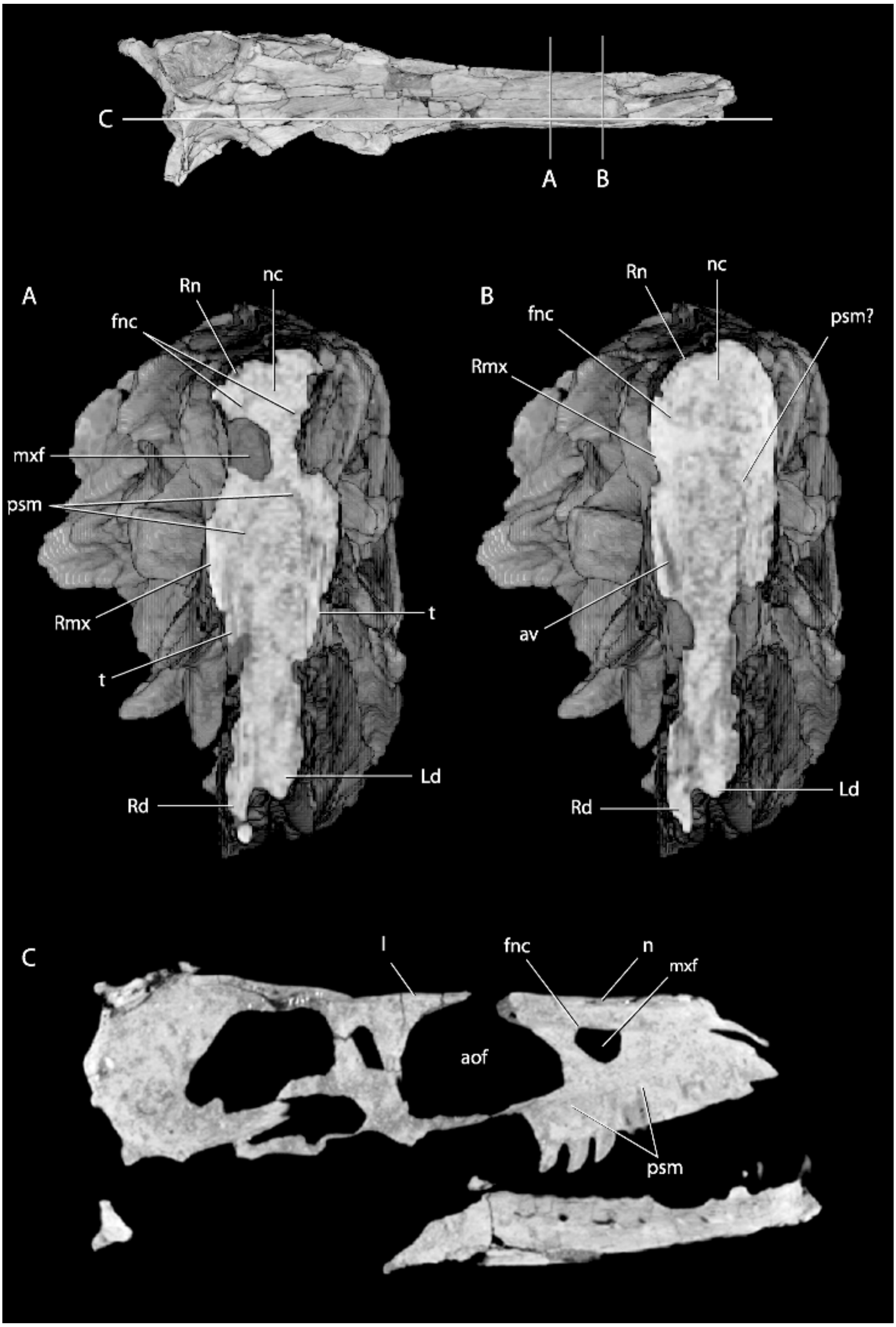


Fig. 4. CT slices through the skull of the holotype of *Tsaagan mangas* (IGM 100/1015). Image at top shows orientations of slices A, B, and C. **A** and **B**, anterior rostral coronal slices showing the well-defined palatal shelves and the separation of the nasal chamber from the maxillary sinus. **C**, a sagittal section showing the relationship of the nasal chamber to the antorbital fenestra and the maxillary fenestra. Abbreviations are in appendix 1.

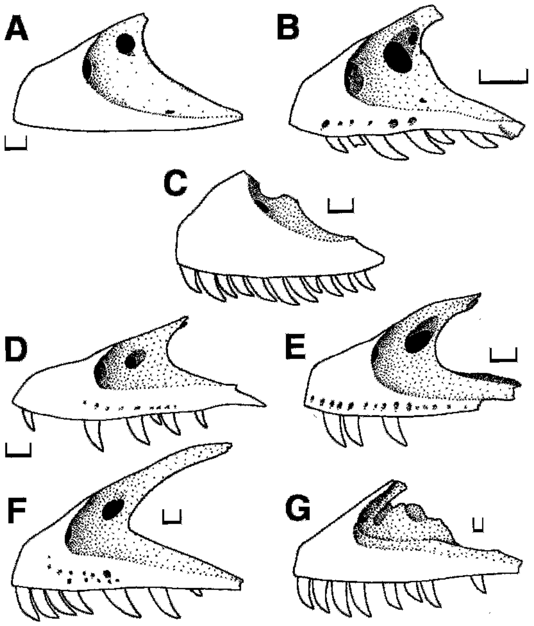


Fig. 5. The rostral area of a variety of dromaeosaurids. **A**, cf. *Bambiraptor feinbergorum* (MOR 553S-7.30.91.274); **B**, *Bambiraptor feinbergorum* (AMNH FR 30556); **C**, *Atrociraptor marshali* (TMP 95.166.1), reversed image of right maxilla; **D**, *Velociraptor mongoliensis* (IGM 100/25); **E**, *Saurornitholestes langstoni* (TMP 94.12.844), reversed image of right maxilla; **F**, *Deinoinychus antirrhopus* (YPM 5232); **G**, *Achillobator giganticus* (MNFUR 15). Reproduced from Currie and Varrichio (2004: 120).

cross section the nasals are L-shaped, forming a distinct dorsal and lateral surface. The dorsal surface diminishes anteriorly to an apex where the nasals contact the nasal process of the premaxilla. Anteriorly the concave border of the nasal forms the posterior margin of the nares. Laterally it contacts the maxilla and the lacrimal along a long straight suture. Posteriorly the nasal contacts the frontal along a transverse suture that lies just posterior to the preorbital bar. This is unlike the condition in the reconstructed skull of *Sinornithosaurus millenii* (Xu and Wu, 2001: 1742) or *Bambiraptor feinbergorum* (Burnham, 2004), where the frontal–nasal contact is at or anterior to the preorbital bar. A row of anteriorly projected foramina lies parallel to the contact with the maxilla as in *Velociraptor mongoliensis* (AMNH FR 6515) and *Deinonychus antirrhopus* (Ostrom, 1969).

LACRIMAL: The lacrimal is T-shaped as in other deinonychosaurs (dromaeosaurids and troodontids) and is not exposed as broadly on the roof of the skull as in *Velociraptor mongoliensis* (AMNH FR 6515, IGM 100/982) or the reconstructed skulls of *Sinornithosaurus millenii* (Xu and Wu, 2001) and *Bambiraptor feinbergorum* (Burnham, 2004). As preserved, the anterior ramus on the skull roof is about the same length as the posterior one, although the tip of the anterior ramus is broken on both sides of the specimen. Nevertheless, it is evident that the anterior ramus did form at least half the dorsal border of the antorbital fossa. The posterior ramus is more extensive in lateral view than the anterior ramus and its thick edge forms nearly half of the dorsal orbital boundary. The suture between the lacrimal, frontal, and nasal is concave rather than straight in dorsal view, with the narrowest exposure of the lacrimal corresponding to the level of the antorbital bar. A large lacrimal boss, or spike, at the dorsal margin of the preorbital bar as in *Velociraptor mongoliensis* (e.g., AMNH 6515, IGM 100/25), *Bambiraptor feinbergorum* (AMNH FR 30556), and *Utahraptor ostrommaysorum* (Kirkland et al., 1993) is absent. At the angle between the preorbital bar and the posterior ramus lies a lacrimal recess that houses a small lacrimal duct (fig. 7). A deep trough runs the length of the lacrimal anteriorly along the lacrimal contribution to the antorbital fossa. Ventrally the lacrimal expands slightly at its contact with the jugal. As in *Velociraptor mongoliensis* (IGM 100/25) and other dromaeosaurids except *Deinonychus antirrhopus* (Maxwell and Witmer, 1996) and *Sinornithosaurus milleni* (Xu and Wu, 2001), no evidence of a separate prefrontal ossification is present.

FRONTAL: As in other dromaeosaurids the frontals are paired and border the large orbits dorsally and the nasals and lacrimals anteriorly. The frontals are L-shaped in cross section, forming distinct dorsal and lateral surfaces. Cristae cranii extend ventrally to border the area that housed the narrow olfactory tracts of the brain, and their lateral surface is only slightly concave, a condition identical to other dromaeosaurids. The supraorbital rim of the frontal is rugose and slightly

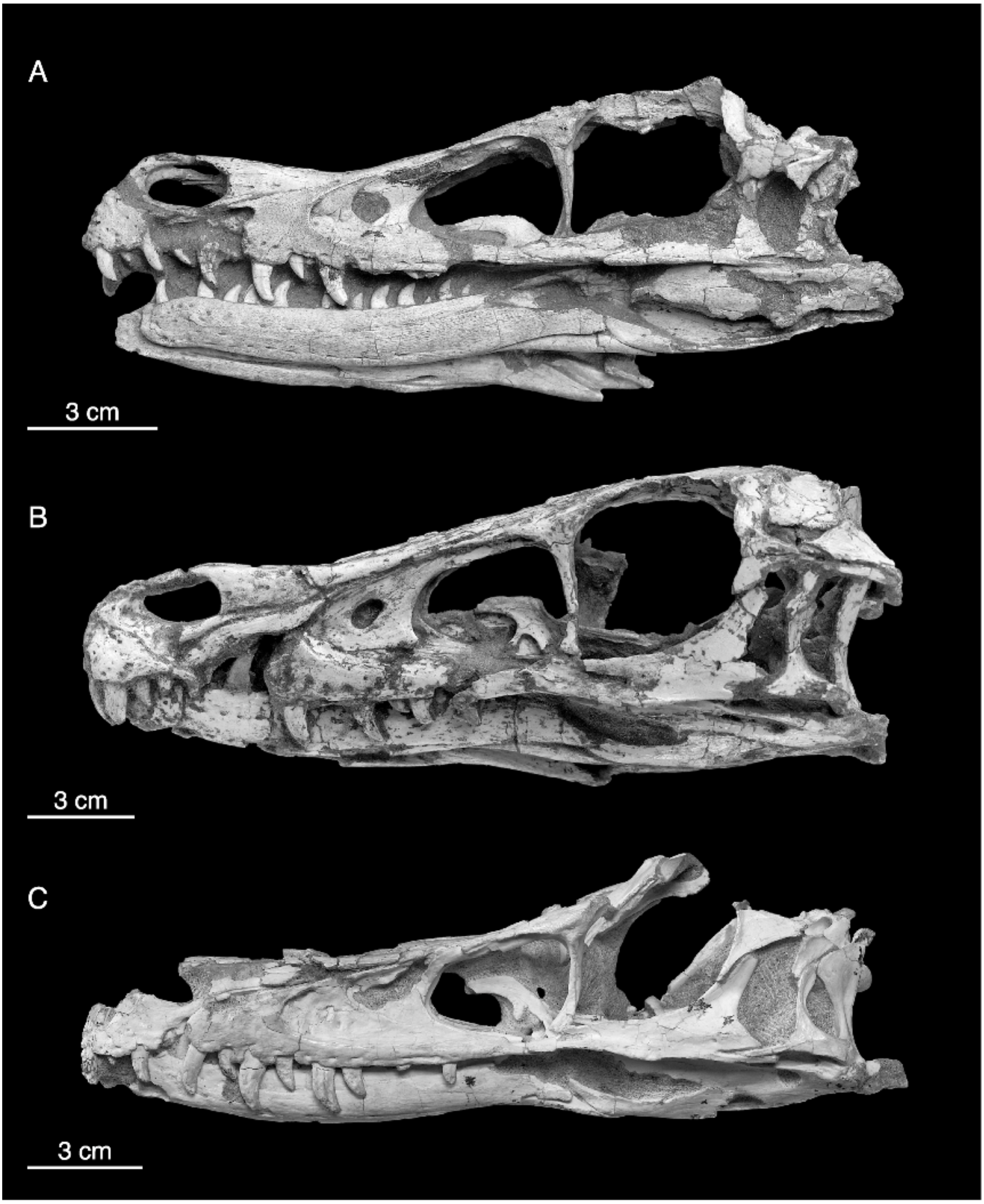


Fig. 6. Lateral views of the skulls of *Velociraptor mongoliensis* (AMNH FR 6516) and IGM 100/25 (the "Fighting Dinosaur" skull) and IGM 100/982.

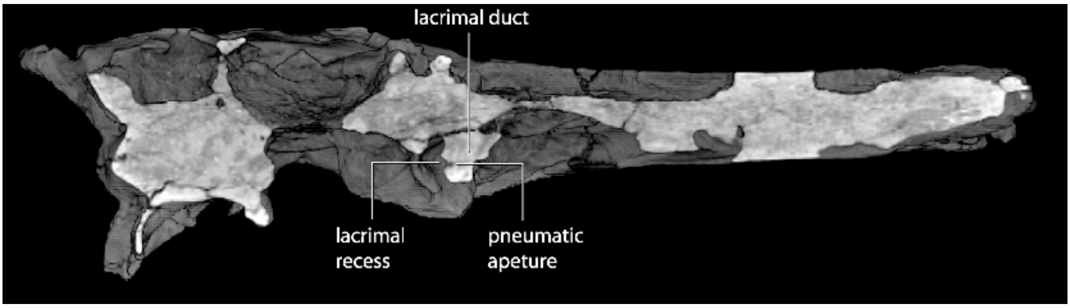


Fig. 7. Horizontal CT slice through the holotype skull of *Tsaagan mangas* (IGM 100/1015) showing the position of the lacrimal duct.

everted. Such a rugose supraorbital margin is also present in *Dromaeosaurus albertensis* (AMNH FR 5356), and Currie (1995) suggested it may possibly form the articulation point for a palpebral. However, several nearly complete dromaeosaurid skulls from Mongolia and China, including this one, provide no evidence for such an ossification. Like in *Dromaeosaurus albertensis* (Currie, 1995), the frontal lacks a pronounced pit along the anterior limit of the supratemporal fossa, on the postorbital process, as in *Velociraptor mongoliensis, Deinonychus antirrhopus*, and *Saurornitholestes langstoni* (Currie, 1995). *Tsaagan mangas* lacks the strongly sinusoidal anterior boundary of the supratemporal fenestra present in most other dromaeosaurids except for *Dromaeosaurus albertensis* (AMNH FR 5356). Posteriorly the frontal meets the parietal along a straight transverse suture and meets the postorbital posterolaterally. The postorbital processes are short, so the frontal lacks the strong T shape formed by long straight postorbital processes seen in other dromaeosaurids. CT imaging shows moderate-sized air spaces within the processes (fig. 8).

JUGAL: The jugal is deep and platelike, forming the majority of the postorbital bar and none of the preorbital bar. The jugal is roughly triangular and expands posteriorly in a sweeping arc to form the postorbital bar. Like other dromaeosaurids with the exception of *Bambiraptor feinbergorum* (AMNH FR 30556), the posterior expansion of the jugal begins midway through the orbit. The entire lateral surface is almost flat. The interior, or medial, surface is thick ventrally, where it defines a thin-walled fossa that runs along the internal dorsal surface of the element and is especially developed anteriorly. Unlike *Velociraptor mongoliensis* (IGM 100/25, AMNH 6515), but as in *Deinonychus antirrhopus* (Ostrom 1969), the jugal is not dorsoventrally concave anteriorly, nor does it have a longitudinal ridge running parallel to the ventral border of the postorbital process.

The right jugal is broken, exposing a solid internal structure devoid of pneumatic cavities—an observation corroborated by CT scans. The ventral margin of the jugal is nearly horizontal posteriorly, where it contains a thin attenuating trough that accommodates the anterior jugal process of the quadratojugal. The jugal, however, underlies the quadratojugal for its entire length to a point just anterior to the level of the mandibular articulation.

Anterior to contact with the lacrimal, the jugal tapers below the antorbital fenestra and contacts the maxilla along an anteriorly ascending diagonal suture. A small cuplike excavation, the jugal pneumatic recess (Witmer, 1997), forms the posteroventral corner of the antorbital fossa. Most of the postorbital bar is composed of the posteriorly sweeping and dorsally tapering postorbital process, which is not everted as in *Bambiraptor feinbergorum* (Burnham, 2004) and *Sinornithosaurus milleni* (Xu and Wu, 2001). The concave posterior surface of the jugal gives the infratemporal fenestra a kidney shape. The postorbital process of the jugal meets the squamosal to exclude the postorbital from the margin of the infratemporal fenestra, a condition that is unique among deinonychosaurs.

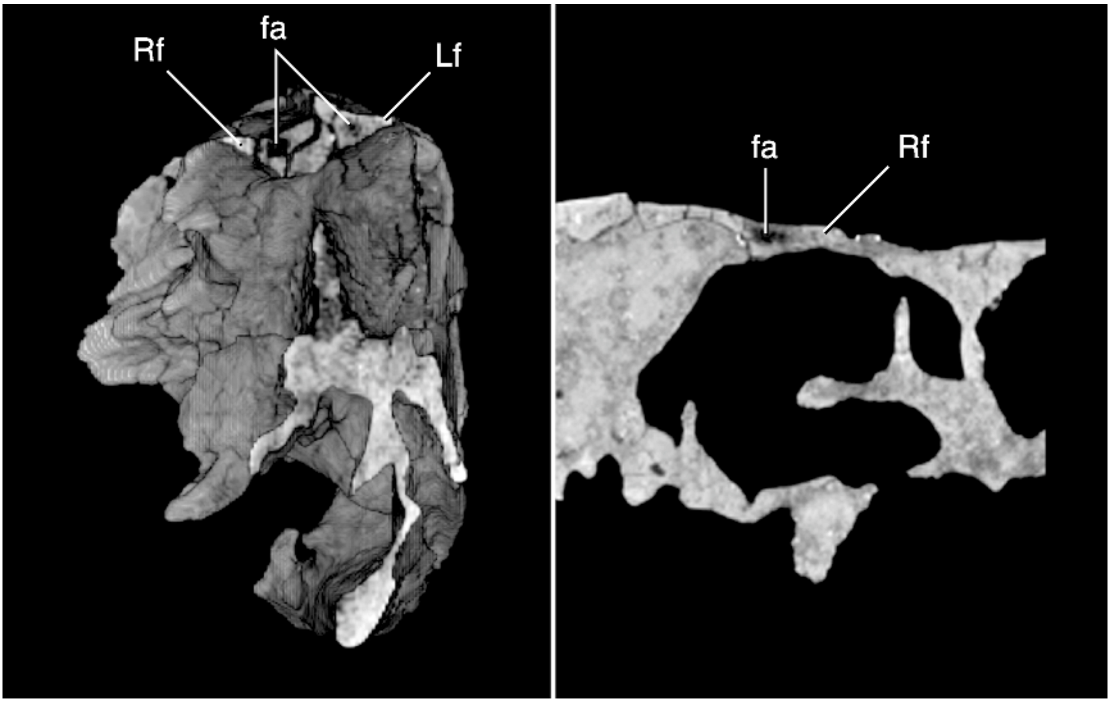


Fig. 8. CT slices of the holotype skull of *Tsaagan mangas* (IGM 100/1015) showing air spaces in the frontal. Abbreviations are in appendix 1.

POSTORBITAL: The postorbital is a small, triangular, and nearly flat bone. The tapering jugal ramus forms most of the posterior margin of the orbit, overlying part of the postorbital process of the jugal. The orbital margin of the postorbital is everted and slightly rugose as in other dromaeosaurids. Posteriorly the postorbital forms the anterior and anterolateral margin of the supratemporal fenestra. The postorbital curves to meet the frontal dorsally and the laterosphenoid ventrally just anterior to the parietal suture. Here, the bone is thick and smooth and forms the anterior edge of the supratemporal fenestra. It does not contribute to the supraciliary rim of the orbit. The posterior process is thick and forms the anterolateral wall of the supratemporal fenestra. A small notch on the posterior process accommodates the dorsal ramus of the postorbital process of the squamosal.

QUADRATOJUGAL: The quadratojugal is shaped as an inverted T and forms the lateral border of the large quadrate fenestra, as in other dromaeosaurids (Paul, 1988; Currie, 1995). Posteromedially it contacts the quadrate at its mandibular condyle. Like most other dromaeosaurids with the exception of *Microraptor zhaoianus* (Xu et al., 2000) and *Sinornithosaurus millenii* (Xu and Wu, 2001), the dorsal process is rodlike and extends dorsally to fit into a notch between the quadrate ramus of the squamosal and the rostrolateral flange of the quadrate. The ascending process of the quadratojugal is shorter than in *Velociraptor mongoliensis* and only makes up the ventral half of the infratemporal border.

SQUAMOSAL: The squamosal is a large, tetraradiate bone that forms the posterodorsal angle of the infratemporal fenestra (fig. 9). The descending process of the squamosal extends ventrally and slightly anteriorly to form the dorsal half of the posterior border of the infratemporal fenestra, contacting the quadratojugal ventrally. Anteriorly the postorbital process of the squamosal forks to accommodate the posterior process of the postorbital dorsal to the squamosal jugal contact. This isolation of the postorbital from infratemporal fenestra rim is a condition unique among dromaeosaurids. Although it is difficult to compare with many other dromaeosaurids because of a lack of material, a large floored fossa formed by a medial extension of the squamosal appears much more developed in *Tsaagan mangas* than in any other theropod. At the posterior end of the adductor chamber, the squamosal contacts the quadrate dorsally and the quadratojugal ventrally. Contact with the quadrate is extensive where the expanded rostrolateral flange of the quadrate overlies the descending, or quadratojugal, process of the squamosal. Apparently a small cleft in the dorsal surface accommodated the parietal at the posterior terminus of the supratemporal fenestra; however, this region is broken and slightly deformed. The squamosal has a large shelf (the quadrate shelf) that overhangs the quadrate, a derived character for the Dromaeosauridae (Currie, 1995, Barsbold and Osmólska, 1999).

QUADRATE: The quadrate is similar to other dromaeosaurids in that it has large distinct rami—the squamosal ramus, the articular ramus, the anterior flange, and a quadratojugal process. The quadrate is solid in the CT scans, although a small foramen or depression lies on the posterior surface at midshaft in the same position as the pneumatic foramen of some other archosaurs (Witmer, 1997). The anterior flange is triangular, and a shallow fossa lies on its medial surface. In posterior view, the lateral edge of the quadrate shaft is incised to form the medial margin of the large quadrate foramen, as in other dromaeosaurids. The squamosal ramus extends laterally above the foramen across the posterior surface of the descending process of the squamosal to contact the quadratojugal. As is probably primitive for theropods (Currie, 1995), the quadrate is broadly exposed laterally dorsal to the quadrate foramen. The dorsal articulation with the squamosal is obscured by matrix, but CT scans show it to be a simple single-headed ball-shaped process, an observation that is confirmed on the disarticulated right quadrate (fig. 10). The distal articulation surface is typical of dromaeosaurids in having two condyles that are slightly offset and divided by a sulcus. Lateral to the articular, the quadrate hooks anteriorly to form a well-defined process that contacts the quadratojugal laterally. The pterygoid flange of the quadrate is triangular and would have overlapped the quadrate ramus of the pterygoid.

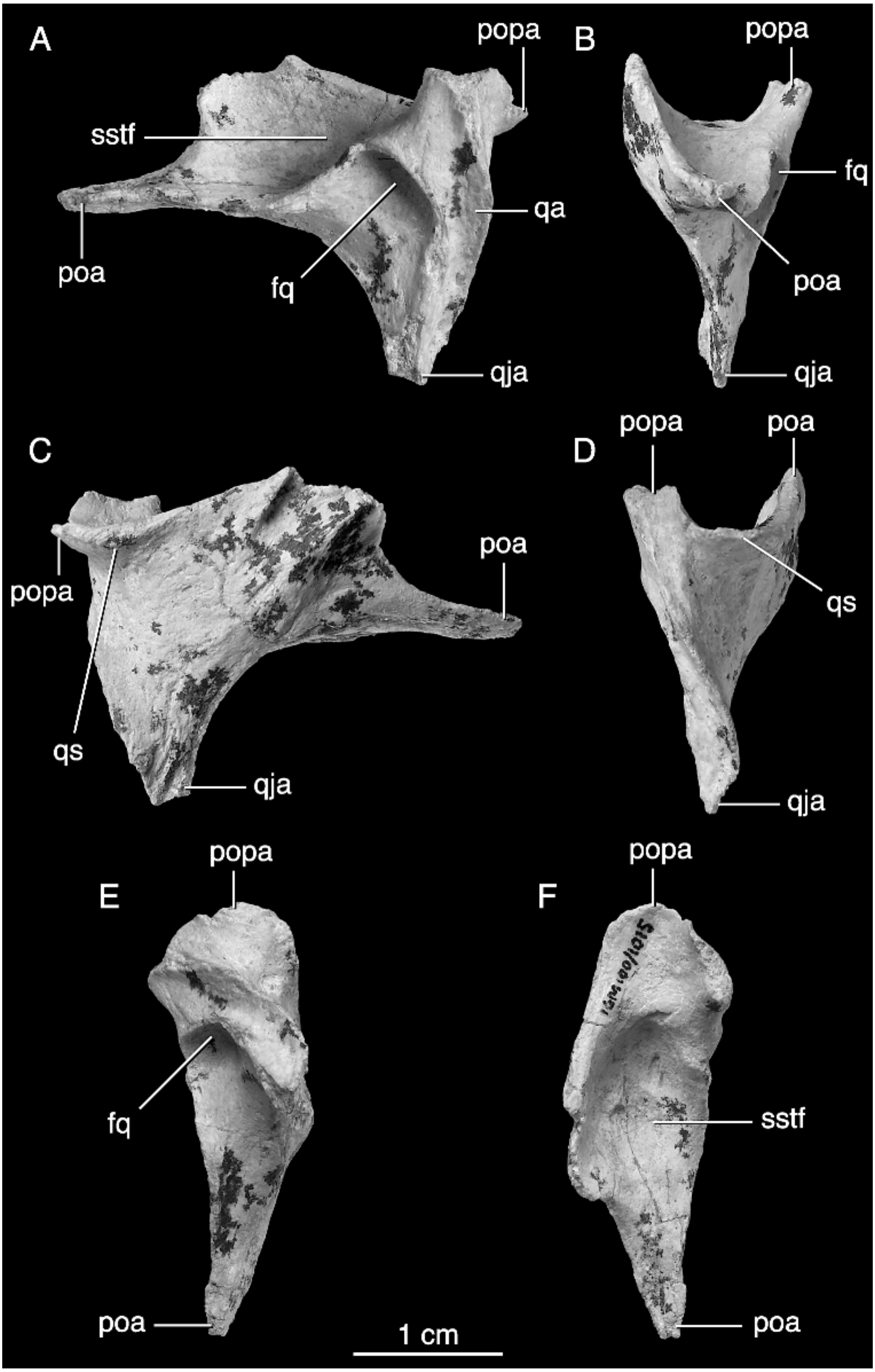
PALATAL ELEMENTS

Only a few palatal features can be ascertained, and there has been some deformation of the skull in this area. Also some of the bones are not found in articulation.

PTERYGOIDS: The pterygoids are well developed, with a large dorsoventrally expanded quadrate flange. The basipterygoid notch is apparently not as deep as in *Deinonychus antirrhopus* (Ostrom, 1969) and *Dromaeosaurus albertensis* (Currie, 1995), with which it also shares the lack of a pronounced pterygoid flange. A small shelf is present on the medial surface of the pterygoids, adjacent to the contact with the ectopterygoid, and is apparently an extension of the ectopterygoid recess. Anteriorly the pterygoids become very narrow, especially in the dorsoventral plane, and project forward as two parallel rods where they contact the vomers.

VOMERS: The paired vomers are barely visible; however, CT scans indicate that they form part of an extensive secondary palate along with the palatal shelves of the maxilla, as in *Velociraptor mongoliensis* (Norell and Makovicky, 1998). Unfortunately they cannot be examined anteriorly, so it is impossible to ascertain (even with CT scans) the degree of fusion or how far they extend anteriorly.

ECTOPTERYGOID: As in other dromaeosaurids, the ectopterygoids are large flat plates that form part of the posterior palate in place of the pterygoid flange. The ectopterygoid overlies the pterygoid medially as observed from the distal surface. Anterolaterally, the hooked jugal ramus of the ectopterygoid contacted the jugal in weak sutural connection and forms the posterior border of the suborbital fenestra. The "lateral flange" ramus of the ectopterygoid lies nearly vertical, and the medial surface is excavated by a deep fossa (the ectopterygoid recess *sensu* Witmer, 1997) as in


A
popa
sstf
poa
fq
qa
qja
B
popa
fq
poa
qja
C
popa
qs
qja
poa
D
popa
poa
qs
qja
E
popa
fq
poa
F
popa
sstf
poa
1 cm

other theropods (Gauthier, 1986). There is no recess on the dorsal surface of the ectopterygoid, and, like in *Dromaeosaurus albertensis* (but not *Deinonychus antirrhopus* and *Saurornitholestes langstoni*), this depression is not connected through pneumatopores with a dorsal recess (Sues, 1977; Currie, 1995). Barsbold and Osmólska (1999) also remarked that the dorsal ectopterygoid recess was not present in *Velociraptor mongoliensis*; however, this may have been due to poor preservation in their sample, as a dorsal recess is present in a *Velociraptor mongoliensis* specimen collected by American Museum–Mongolian Academy of Sciences teams (IGM 100/982).

Palatines: If preserved, the palatines are not visible, even in CT scans of IGM 100/1015.

The Braincase Roof

The roof of the braincase is composed primarily of the parietal with some participation of the frontal described above.

Parietal: The parietal is a single element with an hourglass-shaped dorsal surface that defines the medial boundaries of the supratemporal fossa. Anteriorly it contacts the frontal along a nearly straight suture just posterior to the postorbital process. Medially the parietals meet to form a well-developed sagittal crest. Posteriorly the parietal is inflected dorsally to form a very large nuchal crest. This crest is more developed than in any dromaeosaurid yet described. Even the largest known specimen of *Velociraptor mongoliensis* (IGM 100/25, the "fighting dinosaurs" skull), which is larger than the holotype of *Tsaagan mangas*, does not have such a strongly developed nuchal crest. The parietal tapers to a posterolateral point that extends laterally onto the paroccipital process.

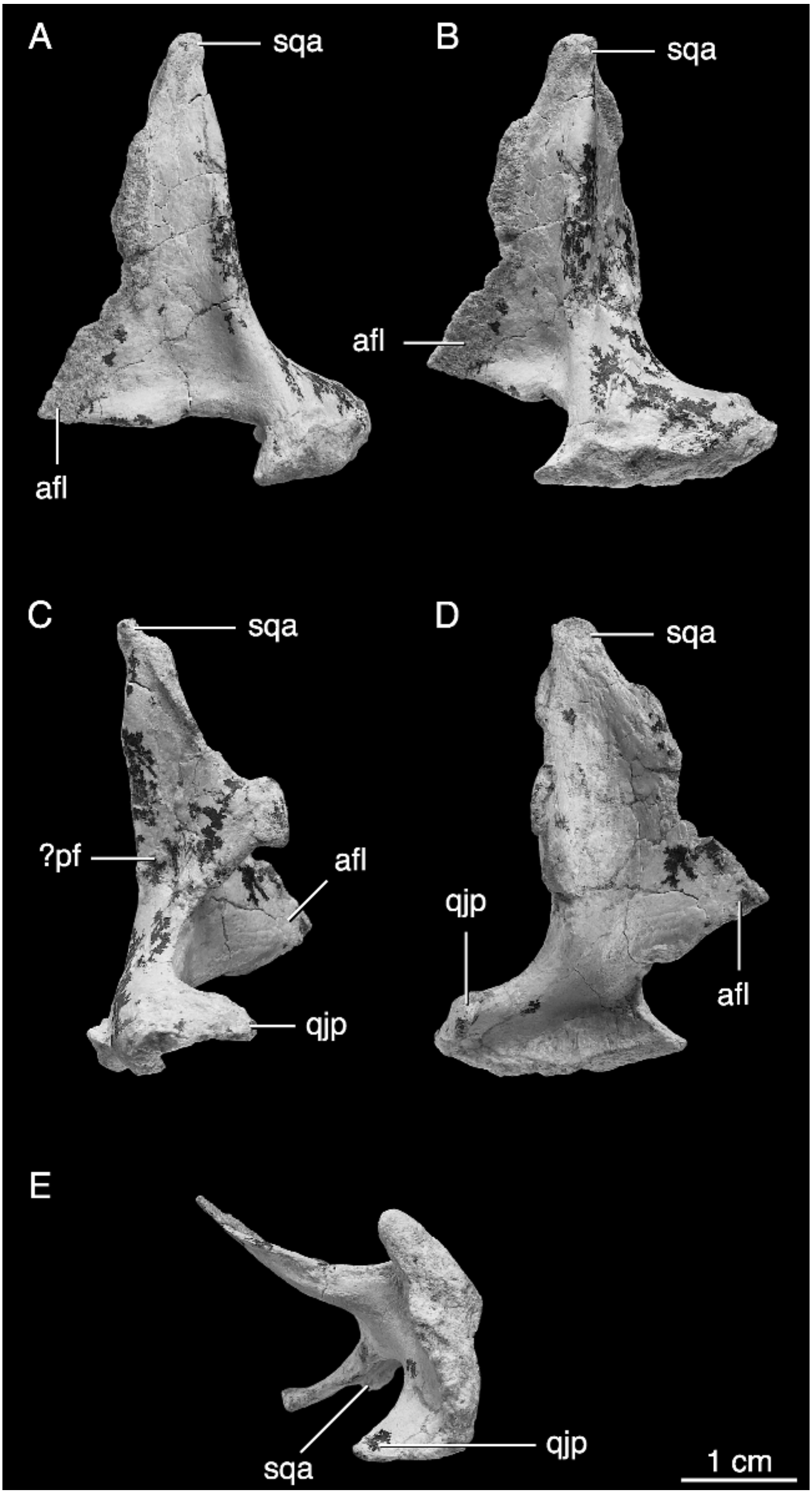
The Lateral Wall of the Braincase

The braincase is well preserved and the sutural boundaries between the elements are in some cases indistinct. This degree of fusion indicates that the animal had reached somatic maturity. The lateral wall of the braincase is divided into two distinct regions by a large pronounced ridge separating the more dorsal, dorsolaterally oriented surface from the lateral wall. This ridge runs posteroventrally from a point just dorsal to the trigeminal opening and terminates posteriorly on the paroccipital process at the same level as the distalmost excursion of the parietal on the paroccipital process (fig. 11). A small tuber defines the anterior extension of the crista prootica just anterior and ventral to the trigeminal opening. While the crista extends posteriorly to become confluent with the ridge defining the middle ear cavity, it does not extend out onto the paroccipital process. The dorsal surface of the lateral wall is composed primarily of a large smooth area that formed the medial surface of the supratemporal fenestra. Dorsomedially it is divided by a longitudinal suture separating the fronto-parietal complex from the ventral part of the neurocranial elements. Posteriorly, just anterior to the paroccipital process above the otic capsule lies a large dorsal tympanic recess as in specimens of *Velociraptor mongoliensis* (Norell et al., 2004) and reportedly in *Deinonychus antirrhopus* (Brinkman et al., 1998) and in most other basal coelurosaurs such as ornithomimids (Witmer, 1990; Makovicky and Norell, 1998; Makovicky et al., 2004). Such a recess is lacking in *Dromaeosaurus albertensis* (AMNH FR 5350) and is either reduced or absent in various troodontids (Makovicky et al., 2003; Makovicky and Norell, 2004). This recess opens dorsally and extends from the epiotic into the parietal.

The lateral wall of the braincase is traversed by several cranial nerves, and is also excavated by pneumatic cavities and the otic recess. Several of the passages for nerves and vessels typical of archosaurs, such as for the abducens (CN VI) and the anterior opening for the anterior canal of the middle

←

Fig. 9. The right squamosal of the holotype of *Tsaagan mangas* (IGM 100/1015) disarticulated from the skull in medial (**A**), anterior (**B**), lateral (**C**), posterior (**D**), dorsal (**E**), and ventral (**F**) views. Abbreviations are in appendix 1.


A
sqa
afl
B
sqa
afl
C
sqa
?pf
afl
qjp
D
sqa
qjp
afl
E
sqa
qjp
1 cm

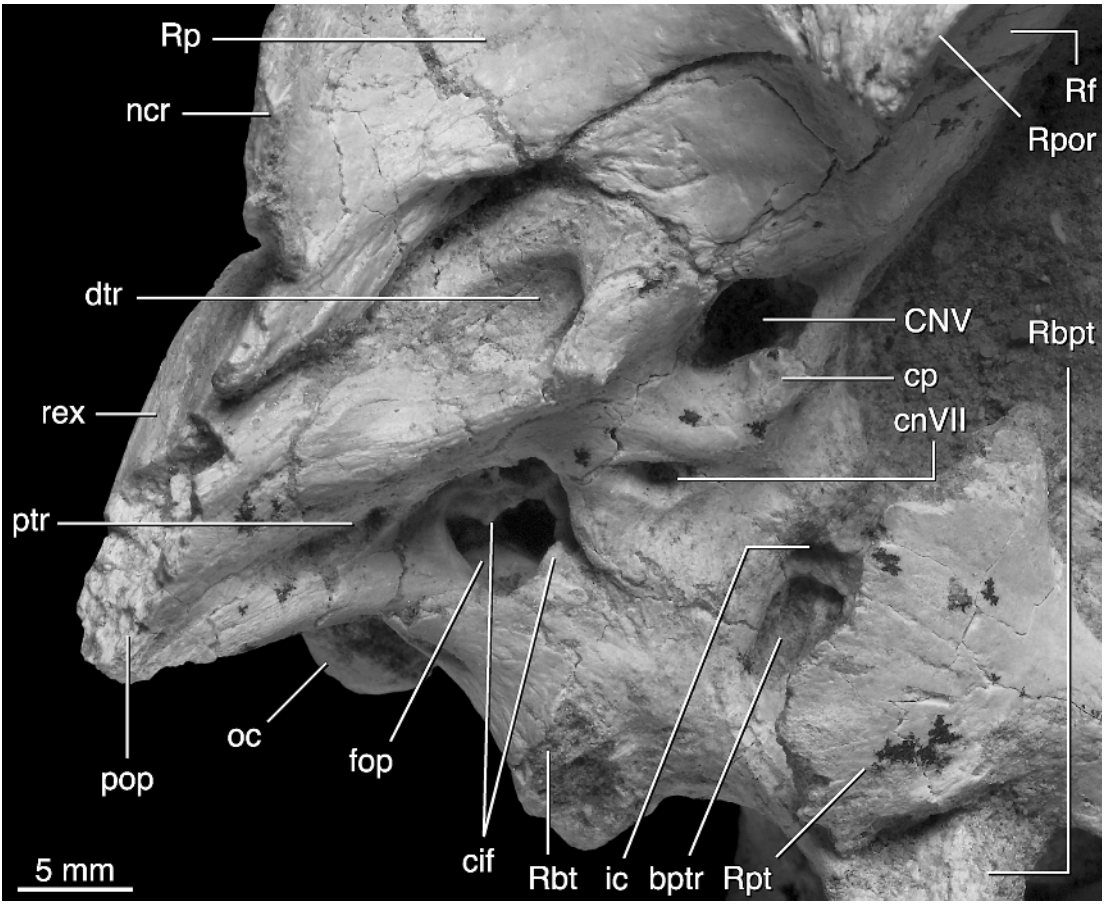


Fig. 11. Lateral wall of the braincase of the holotype of *Tsaagan mangas* (IGM 100/1015). Abbreviations are in appendix 1.

cerebral vein, cannot be positively identified. CT information provided little help in identifying many of these features due to insufficient contrast between matrix and fossil bone (fig. 12).

A large trigeminal foramen (CN V) lies along the anterior edge of the braincase. Just anterior to the trigeminal opening lies a vertical strut that demarks a flexure of the braincase between the lateral and anterior surfaces. The anterior surface of the laterosphenoid is nearly flat and continuous with the cristae cranii of the frontal. The laterosphenoid–frontal suture is marked by a small depression. The trigeminal foramen is obliquely oval and opens laterally. A large rugosity lies on its ventral surface and may indicate the position of the prootic–laterosphenoid suture. A low ridge, the crista prootica, separates the trigeminal exit from the opening of the facial nerve (CN VII), which lies posteroventral to it. The facial foramen opens posteriorly and leads to a shallow trough that extends posteriorly to the otic recess.

←

Fig. 10. The disarticulated right quadrate of the holotype of *Tsaagan mangas* (IGM 100/1015) in medial (**A**), posterior (**B**), lateral (**C**), anterior (**D**), and ventral (**E**) views. Abbreviations are in appendix 1.

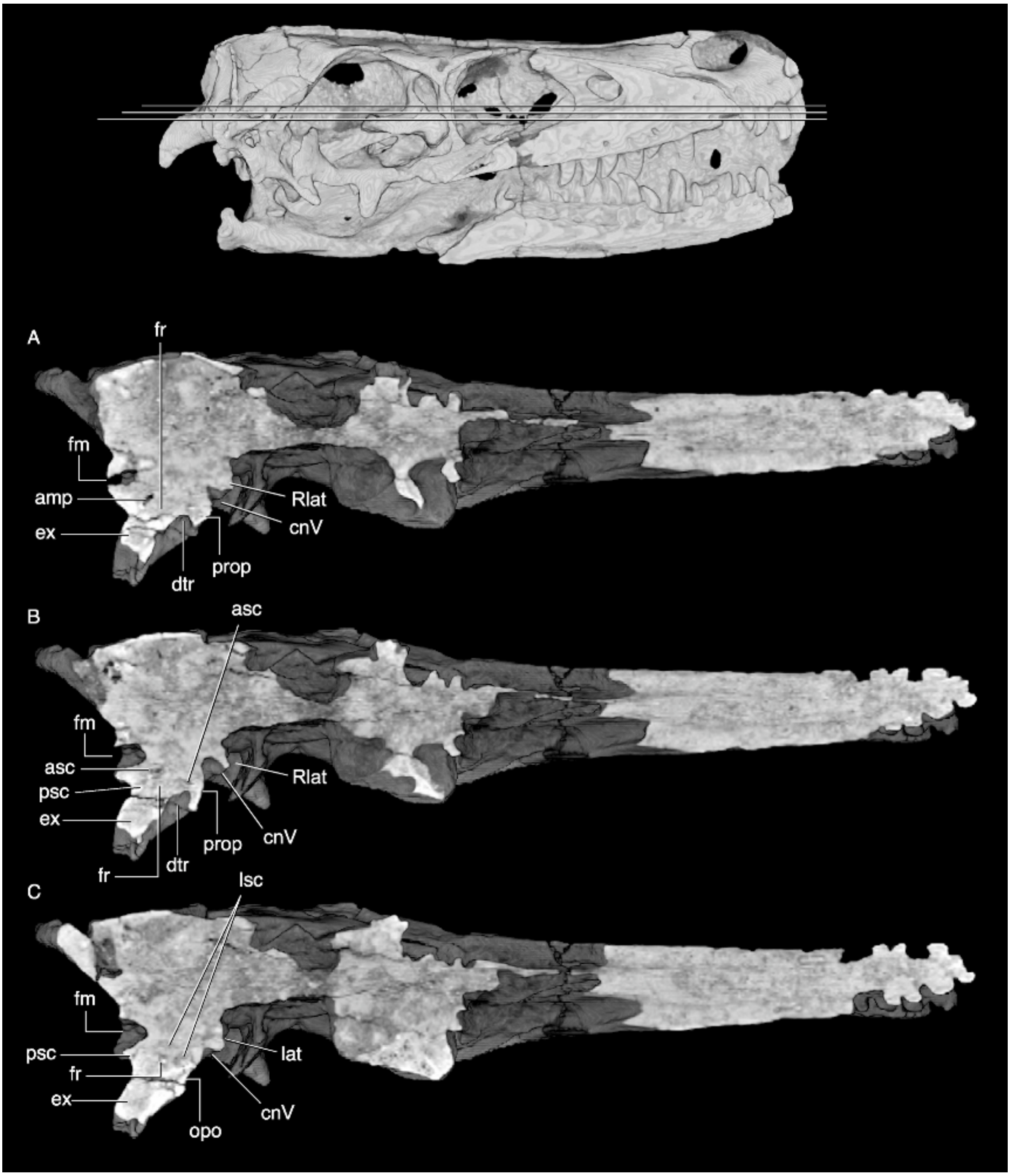


Fig. 12. Horizontal CT slices through the skull of the holotype of *Tsaagan mangas* (IGM 100/1015) showing the shape and proportions of the inner ear, including the semicircular canals and floccular recess. Image at top shows location and orientation of slices **A**, **B**, and **C**. Abbreviations are in appendix 1.

The ear region is inset, forming a distinct otic recess. The fenestrae ovalis and pseudorotunda are separated by a partial crista interfenestralis that is apparently incompletely preserved. A large foramen for the vagus nerve (CN X) pierces the metotic strut, which forms the posterior wall of the otic recess and connects the external auditory meatus with the occipital surface of the braincase. The fenestra ovalis is deep, and opposite it on the medial wall is a small foramen for the cochlear branch of the vestibulocochlear nerve (CN VIII). Dorsal to this opening is a depression in which the utriculus was housed. This depression is similarly sized in *Velociraptor mongoliensis* (IGM 100/976), being proportionally larger than the shallow depression of *Dromaeosaurus albertensis* (AMNH FR 5356).

A small posterior tympanic recess lies posterolateral to the opening of the middle ear and invades the anterior base of the paroccipital process. It is smaller than in *Velociraptor mongoliensis* (IGM 100/976). This recess did not invade the paroccipital process laterally to any great extent, and both CT scans and breakage indicate that the right paroccipital process is solid just adjacent to the opening of the posterior tympanic recess. Unlike *Velociraptor mongoliensis* (IGM 100/976), which has a prominent prootic recess, *Tsaagan mangas* (like *Dromaeosaurus albertensis*, AMNH FR 5356) has only a broad, gently concave surface ventral to the facial nerve (CN VII) foramen. All three taxa, however, bear a weakly developed otosphenoidal crest anterior to this region. An anterior (or prootic) tympanic recess is not present in *Tsaagan mangas* as in *Velociraptor mongoliensis* (IGM 100/976). Barsbold and Osmólska (1999) figure the wall of the braincase (their fig. 6) and their figures seem to indicate that there is some variation in the presence of the recess in *Velociraptor mongoliensis*. This figure is problematic in that their illustration of GIN 100/24 mislabels the prootic recess as the exit for CN VII. The illustration of the "Fighting Dinosaurs" skull (GIN 100/25), which shows no sign of an anterior tympanic recess, is difficult to reconcile with the actual specimen, where much of this region has been damaged.

A large basipterygoid recess lies at the base of the extensive basipterygoid process, as found in many tetanurans. On the anterior margin of this recess lies the posterior entrance of the carotid foramen. Just dorsal to this lies the small parabasisphenoidal recess. This recess lies at the posterior base of the long and tapering cultriform process, which is not inflated, but is very long and platelike. It tapers to its terminus about two-thirds of the way through the orbit. This is different form the condition in *Velociraptor mongoliensis* (Norell et al., 2004), where an anterior tympanic recess lies just anterior to the middle ear cavity and ventral to the opening for CN VII. In Velociraptor this recess is not as intimately associated with the carotid opening.

THE OCCIPUT

The occipital surface of the skull is slightly deformed due to mediolateral compression of the skull. The occipital surface is a mosaic of several bones, but sutural boundaries are often indistinct.

The foramen magnum is oval, with a long dorsoventral axis, although this shape may be exaggerated by mediolateral compression. Just ventral to the foramen magnum the occipital condyle is incompletely preserved. It is primarily composed of the basioccipital, although there is some dorsolateral participation by the exoccipitals/opisthotic. Dorsal to the foramen magnum, two large concavities are separated by the supraoccipital, perhaps accentuated in depth by mediolateral compression of the skull. Large convex exposures of the parietal lie lateral to these concave surfaces. Close inspection of the floor of these cavities (especially on the left) suggests that the epiotics were not completely fused to the supraoccipital and, during lateral compression, were displaced under the supraoccipital. A large, vertical ridge emanates from the dorsal margin of the foramen magnum and becomes sharper as it approaches the nuchal crest. Ridges extend laterally from the dorsal surface of the foramen magnum and define the bases of the paroccipital processes. The paroccipital processes are pendulous and project posteriorly, unlike those of other dromaeosaurids, which are straight and slightly twisted (e.g., *Dromaeosaurus albertensis*, AMNH FR 5356; *Velociraptor mongoliensis*, IGM 100/976; and *Deinonychus antirrhopus*, OMNH 50268). There is no indication of a posterior opening of the posterior tympanic recess on the occipital surface. Just lateral to the middle of the foramen magnum there are small depressions, as in *Velociraptor mongo-*

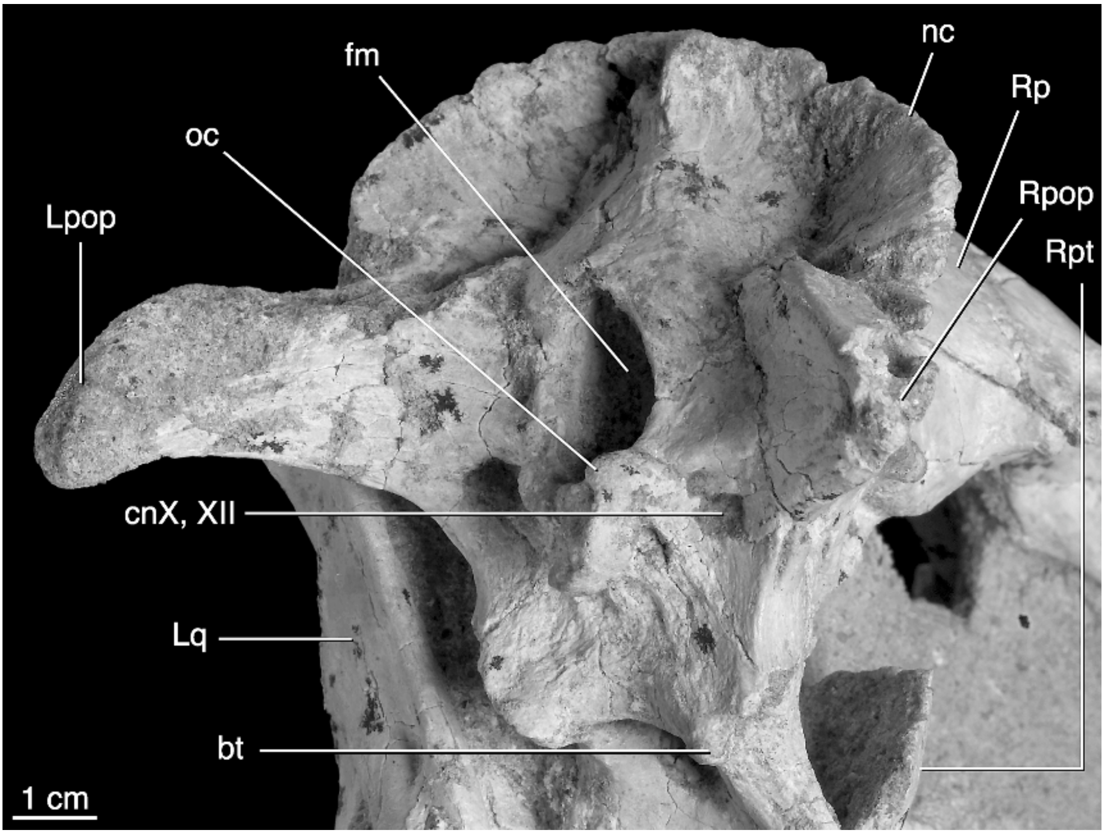


Fig. 13. Oblique view of the right occiput of the holotype skull of *Tsaagan mangas* (IGM 100/1015). Abbreviations are in appendix 1.

liensis (Norell et al., 2004). These are separated from large pits that house the openings of cranial nerves X, XI, and XII by a small horizontal ridge that extends to the base of the basipterygoid process (fig. 13). The single large pit housing the openings of the posterior cranial nerve foramina is also found in *Velociraptor mongoliensis* and *Deinonychus antirrhopus*, but not in other dromaeosaurids (Norell et al., 2004). The metotic strut, which defines the laterodorsal border of the occipital surface, lies just lateral to the foraminal pit. A slit-shaped depression extends obliquely across the metotic strut. The basioccipital tubera extend ventrolaterally. Their distal edges are slightly rugose and they are separated by a wide saddle. Just dorsal to this saddle a small depression lies at the ventral base of the basioccipital condyle.

The Ventral Surface of the Braincase

The ventral surface of the braincase is primarily composed of the basioccipital–basisphenoid complex. At the occipital end, the basicranium surface is delimited by the basal tubera and the saddle that connects them. The basioccipital recess is large (but not as large as in *Dromaeosaurus albertensis* AMNH FR 5356) and triangular with an anteriorly oriented apex. The floor of the basisphenoid recess has two foramina posteriorly and a single median opening anteriorly as in *Velociraptor mongoliensis* (IGM 100/982); *Dromaeosaurus albertensis* (AMNH FR 5356) is reported to have two posterior openings that enter into blind pockets (Currie, 1995). Only one of these (the left) is exposed, and it extends into the corresponding basal tuber as in *Tsaagan mangas*. Anteriorly, the basipterygoid processes project ventrolaterally for a distance equal to the breadth of the basisphenoid body, making them relatively longer than in any other dromaeosaurid. The bases of the basipterygoid processes are marked by large basipterygoid recesses as in *Bambiraptor feinbergorum* (Burnham, 2004) and *Velociraptor mongoliensis* (Barsbold and Osmólska, 1999).

SCLERAL OSSICLES

Scleral ossicles are present in the left orbit, but are somewhat disarticulated. At least seven elements are preserved, but most are poorly exposed. The best-exposed element is nearly twice as long as wide and almost flat, with only a slight lateral convexity.

INNER EAR AND INTERNAL WALL OF THE BRAINCASE

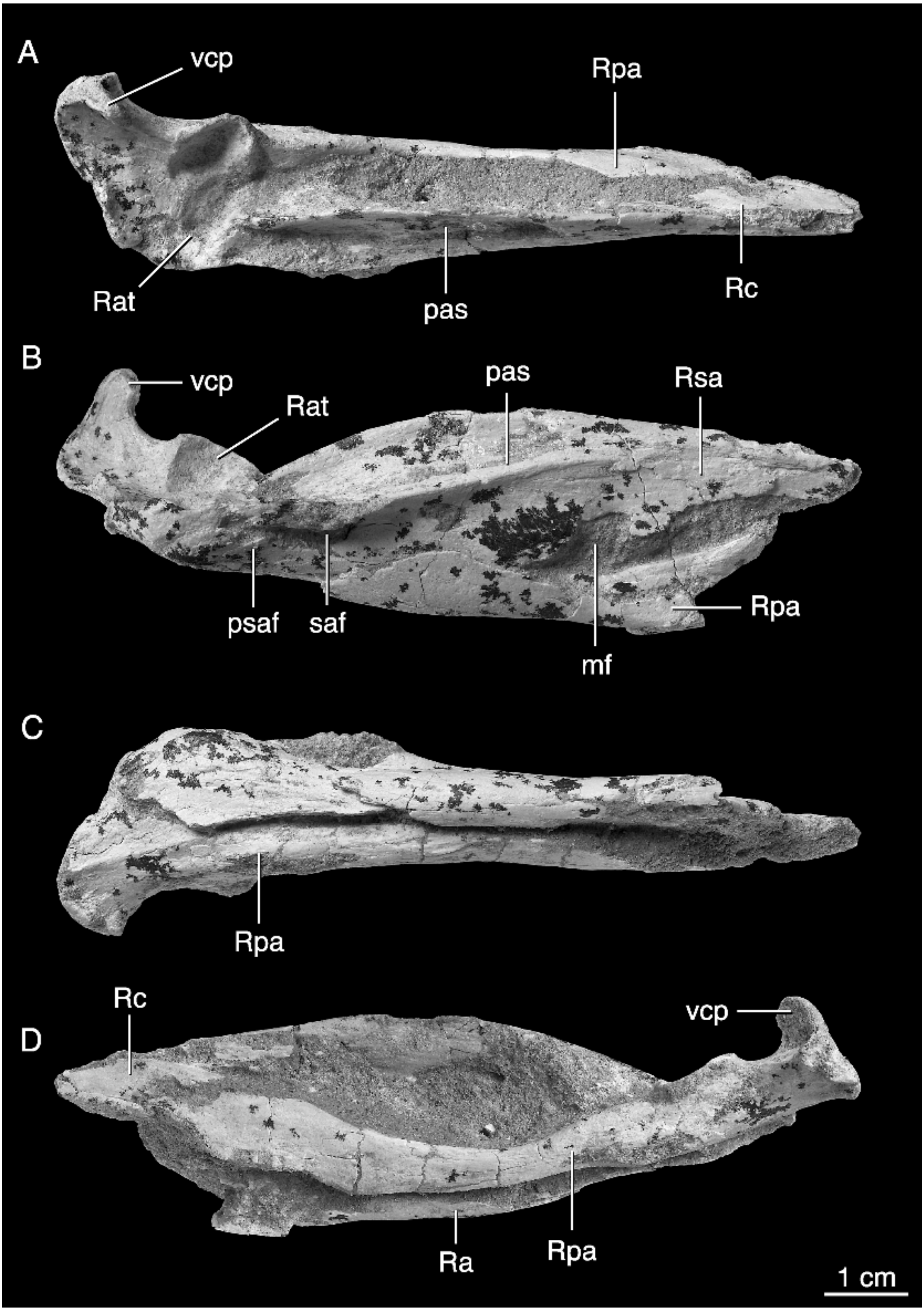
The posterior and anterior crurae of the anterior semicircular canal delimits the medial boundary of the floccular recess in *Tsaagan mangas* as well as other dromaeosaurids (e.g., *Dromaeosaurus albertensis*, AMNH FR 5356; *Bambiraptor feinbergorum*, AMNH FR 30554; *Velociraptor mongoliensis*, IGM 100/982). Although the contrast between bone and matrix in the CT scan is poor within the braincase, a rough outline of the floccular recess and the semicircular canals can be noted (fig. 12). The floccular recess is situated within the fused prootic and opisthotic, with the long axis of the recess oblique to the midline. The recess is large as in *Dromaeosaurus albertensis* (AMNH FR 5356) and *Velociraptor mongoliensis* (IGM 100/982). It is unclear if the recess extends into the exoccipital as it does in *Velociraptor mongoliensis*. Norell et al. (2004) noted that the anterior and posterior semicircular canals are rotated further posteriorly in *Velociraptor mongoliensis* (IGM 100/982) than in *Dromaeosaurus albertensis* (AMNH FR 5356). CT imaging confirms this observation in IGM 100/982 and reveals that a similar posterior rotation is present in *Tsaagan mangas*. The posterior semicircular canal is poorly defined in the CT data, but the ampulla and initial division of the anterior and posterior canals is evident (fig. 12A), as is the posteroventral crus (fig. 12B). As in other dromaeosaurids, the lateral semicircular canal floors the floccular recess (Currie, 1995; Norell et al., 2004) and is evident in CT scans (fig. 12C). The paths of the endolympathic duct and the cerebral veins are not sufficiently resolved to define their courses.

THE MANDIBLE

DENTARY: The dentary is deep with parallel dorsal and ventral margins as in *Deinonychus antirrhopus* (YPM 5210) and *Dromaeosaurus albertensis* (AMNH FR 5356). It is proportionally slightly deeper than in *Velociraptor mongoliensis*. A distinct longitudinal groove houses a row of elliptical mental foramina just ventral to the dorsal border of the dentary parallel to the tooth row, similar to but not as pronounced as in troodontids.

SPLENIAL: The splenial is a large platelike element that is only weakly attached to the medial surface of the mandible. Posteriorly, a triangular portion of the splenial is exposed on the lateral side of the mandible, spanning the intramandibular joint below the external mandibular fenestra, as in other deinonychosaurs. The anterior extent of the splenial cannot be observed. The anterior mylohyoid foramen can be seen on the right mandible and is a small elliptical notch on the anteroventral edge of the splenial and lies at the level of the ultimate tooth. On the right side, a small fragment of bone medial to the last tooth may represent part of a supradentary, as found in *Dromaeosaurus albertensis* (AMNH FR 5356). Apparently movable joints are formed between the dentary and surangular dorsally and between the splenial and angular ventrally. Unfortunately the boundaries of the internal mandibular fenestra between the splenial and the prearticular are so damaged that the extent of this fenestra cannot be determined.

SURANGULAR: The surangular (fig. 14) forms the entire dorsal and posterior margin of the relatively small, longitudinally elongate external mandibular fenestra. Anteriorly, it contacts the dentary at the intramandibular joint, and it contacts the angular ventrally


A
vcp
Rpa
Rat
pas
Rc
B
vcp
Rat
pas
Rsa
psaf
saf
Rpa
mf
C
Rpa
D
Rc
vcp
Ra
Rpa
1 cm

along a straight suture that becomes indistinct on the retroarticular process. On the medial surface of the mandible the surangular contacts the anterior process of the prearticular. Together, the prearticular (medially) and the angular and surangular (laterally) define a large and deep mandibular adductor fossa. A small surangular foramen, best preserved on the left side, lies just posterior to the external mandibular fenestra, and a more poorly preserved second surangular foramen appears to lie just anterior to the quadrate articulation, best preserved on the right side. The surangular continues posteriorly to participate in the retroarticular process and forms the medial surface of the quadrate articulation. A large and transversely concave prearticular shelf with a tall medial rim extends along the posterior half of the dorsal surface of the surangular as in other dromaeosaurids except for *Dromaeosaurus albertensis* (AMNH FR 5356). The lateral edge of this fossa overhangs the lateral surface of the mandible (fig. 15).

CORONOID: On the right mandible a small and very fragmentary ossification lies between the prearticular and the articular. This corresponds to the coronoid known in other dromaeosaurids. Because the element is so badly damaged it cannot be ascertained whether the bone was triangular or not. The "precoronoid" (*sensu* Currie, 1995), which is probably an anterior extension of the coronoid (see Brochu, 2003), cannot be observed.

PREARTICULAR: The prearticular is a large, curved bone that forms much of the medial surface of the posterior mandible as in other dromaeosaurids. Ventrally it contacts the angular and anteriorly the splenial. Posteriorly the prearticular contacts the articular, angular, and surangular at the retroarticular process. It is rodlike medially and flattens into a platelike structure anteriorly. Posteriorly, at the retroarticular process, it flattens in the horizontal plane.

ARTICULAR: The articular forms most of the quadrate articulation surface, which comprises two obliquely oriented, slightly overlapping depressions, running anteromedially to posterolaterally. The medial articular surface is larger and broader than the slightly narrow lateral depression. The prearticular appears to be fused to the articular medial to the glenoid. The dorsal surface of the retroarticular process forms a longitudinal, concave trough posterior to the glenoid. In dorsal view, the retroarticular process is fan-shaped with an everted margin that rises mediodorsally to form a large spine (the vertical columnar process; Currie, 1995), typical of dromaeosaurids. A small ventrally projecting tuberosity lies just posterior to the vertical columnar process.

DENTITION

PREMAXILLARY TEETH: As in other dromaeosaurids, the premaxillary teeth are labiolingually compressed and recurved, and are not D-shaped in cross section as in tyrannosaurids (Currie et al., 1990). The first and second premaxillary teeth are very large; however, the second is apparently slightly larger as in other dromaeosaurids except for *Dromaeosaurus albertensis* (Currie, 1995).

MAXILLARY TEETH: Thirteen tooth positions are preserved on the left maxilla. The teeth are relatively homodont, however tooth five appears slightly larger on both the right and left sides. This is unlike the heterodont condition of alternating large and small teeth reported by Barsold and Osmólska (1999) in *Velociraptor mongoliensis*, which probably represent alternating waves of tooth replacement (Zahnreihen). Posterior to the fifth tooth the teeth decrease in size, with the greatest decrease in teeth 9–13. The size of many of the teeth is accentuated by the fact that they have slid partway out of their alveoli, thus obscuring any patterns of replacement order.

The teeth are similar to other dromaeosaurid teeth in general form; all are slightly recurved (fig. 16). As in other dromaeosaur-

←

Fig. 14. The right postdentary bones removed from the cranium of the holotype of *Tsaagan mangas* (IGM 100/1015) in dorsal (**A**), lateral (**B**), ventral (**C**), and medial (**D**) views. Abbreviations are in appendix 1.

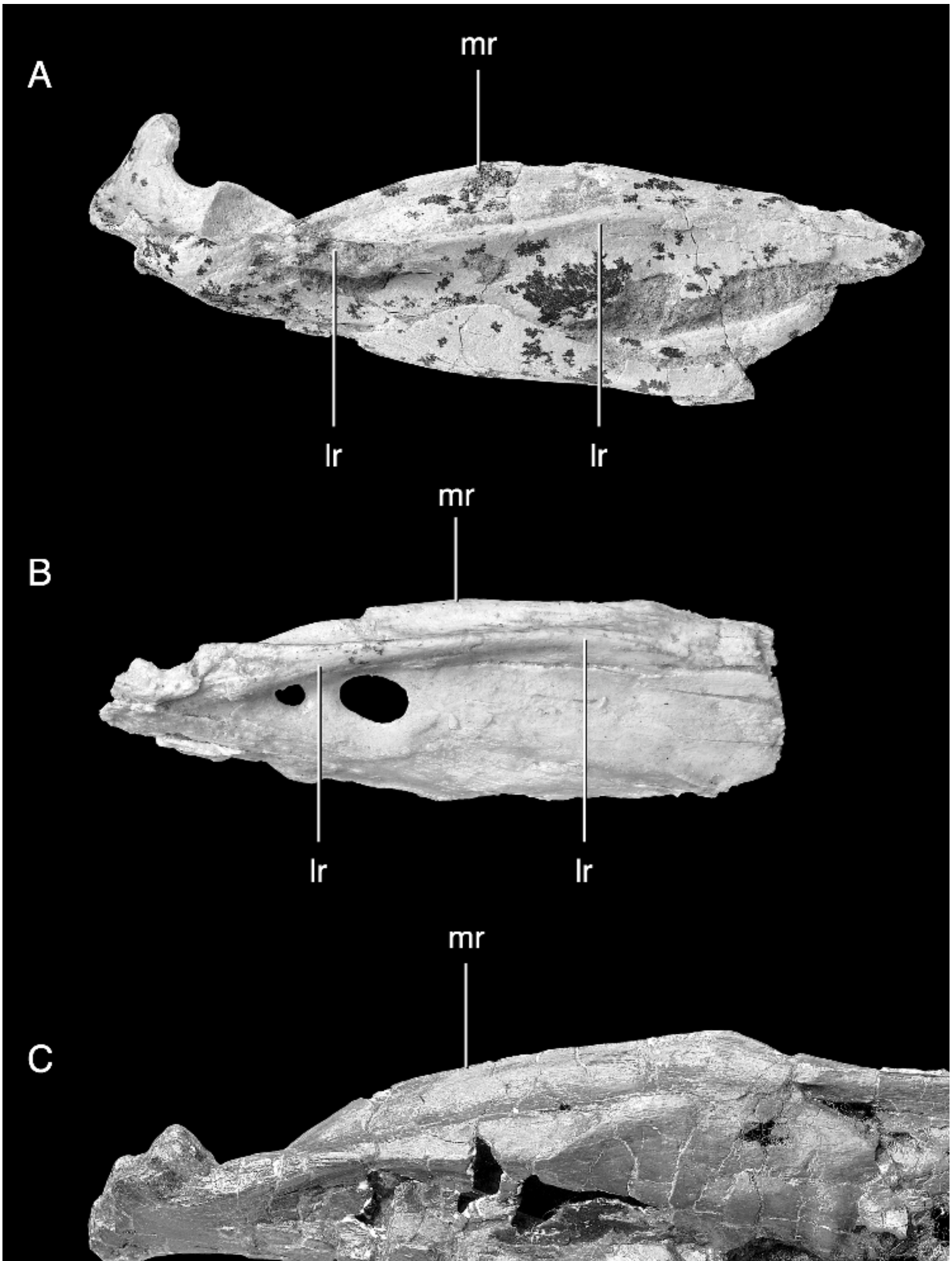


Fig. 15. Right postdentary bones in **(A)** *Tsaagan mangas* (IGM 100/1015), **(B)** an undescribed dromaeosaur from Khulson (IGM 100/981), and **(C)** *Dromaeosaurus albertensis* (AMNH FR 5356). Note the well-defined longitudinal trough on the dorsal surface of the surangular. Abbreviations are in appendix 1.

Fig. 16. Right maxillary tooth positions 6–8 and dentary tooth positions 9–11 of the holotype of *Tsaagan mangas* (IGM 100/1015). These teeth show the enlarged posterior denticles characteristic of dromaeosaurids.

ids, the teeth have a median constriction at the base, giving them a figure-8-shaped cross section. The constriction probably represents the track of the erupting replacement crown. The anterior carina is very rounded, dull, and completely devoid of denticles, even at the base and tips of teeth that are newly erupted. The posterior denticles increase in size distally and number 3–3.5 per mm towards the tip of the tooth. The denticles are uniformly straight and lack the distinctive hook shape seen in some other dromaeosaurids such as *Atrociraptor marshalli* (Currie and Varricchio, 2004).

DENTARY TEETH: Fourteen or 15 recurved teeth lie in the dentary, a number commensurate with other dromaeosaurids (Barsbold and Osmólska, 1999). The uncertainty is due to the poor preservation of the posterior alveoli. The dentary teeth are all nearly equivalent in size except for the last few teeth in the tooth row. Many of the teeth are very worn, with smooth and blunt apices. As with the maxillary teeth, there are apparently no serrations on the smooth anterior surface of the teeth, and the serrations on the lower teeth are slightly smaller than those of the maxillary teeth. On the posterior surface of the teeth, strong serrations (identical to those on the maxillary teeth) are preserved.

THE AXIAL COLUMN

CERVICAL VERTEBRAE: The entire cervical series from the atlas to the 10th cervical was recovered in articulation with the skull of IGM 100/1015, but most elements show varying degrees of arthropod scavenging. The atlas intercentrum is a low and flat element as in *Velociraptor mongoliensis* (fig. 17). Its ventral face is marked by a raised ridge that connects two lateral tubers, which may represent articulations for a pair of holocephalic atlantal ribs. An arcuate groove separates the ridge, from the concave posterior face of the intercentrum, which would have articulated with the axis intercentrum, and a similar ridge and groove morphology is observed on the altas of *Velociraptor mongoliensis* (IGM 100/ 976). Scavenging has destroyed the dorsal face of the atlas intercentrum, but both atlantal neurapophyses are preserved. The pedicel for articulation with the intercentrum is convex and slightly expanded in lateral view. The convex articulation is divided into a smaller ventral surface for articulation with the intercentrum, and a larger anterior surface that would have articulated with the occipital condyle. Dorsal to the pedicel, each neurapophyses broadens and curves medially to roof over the neural canal. Anteriorly, the canal portion is deep and terminates in a rounded medial point that would have approached, or contacted, its counterpart above the neural canal. This point is not recurved as in *Deinonychus antirrhopus* (Ostrom, 1969: fig. 26). The posterolateral end of each neurapophysis is drawn out into an elongate spur that is probably homologous with the epipophyses of the following cervicals. In medial view, a small postzygapophyseal articular facet occupies the base of this spur, as in *Deinonychus antirrhopus* and other theropods.

Two other elements were found associated with the atlas, but did not lie in articulation. They are identical mirror images and can therefore be considered a pair of structures (fig. 17). We interpret these as the proatlas, the first yet reported for deinonychosaurs.

The axis neural arch is fused to the centrum, as are the atlas centrum (odontoid) and axis intercentrum (fig. 18). In contrast to *Velociraptor mongoliensis* (IGM 100/976) and *Deinonychus antirrhopus* (YPM 5204), the axial centrum of *Tsaagan mangas* does not bear pneumatic foramina. A small parapophysis is present on either side of the anterior end of the centrum level with the top of the axial intercentrum, and a partial rib fragment lies close behind the left parapophysis. Several rodlike bone fragments are found in a similar position on the right side, but the more slender of these may derive from the atlantal rib pair. The axial neural spine is tall and slopes anteroventrally as in *Velociraptor mongoliensis*. The distal end is slightly expanded but not to the same degree observed in either *Velociraptor mongoliensis* or *Deinonychus antirrhopus*. As in other theropods, the prezygapophyses are formed as small oval facets projecting above and lateral to the neural canal. Expanded epipophyses overhang the postzygapophyses, as in other dromaeosaurids.

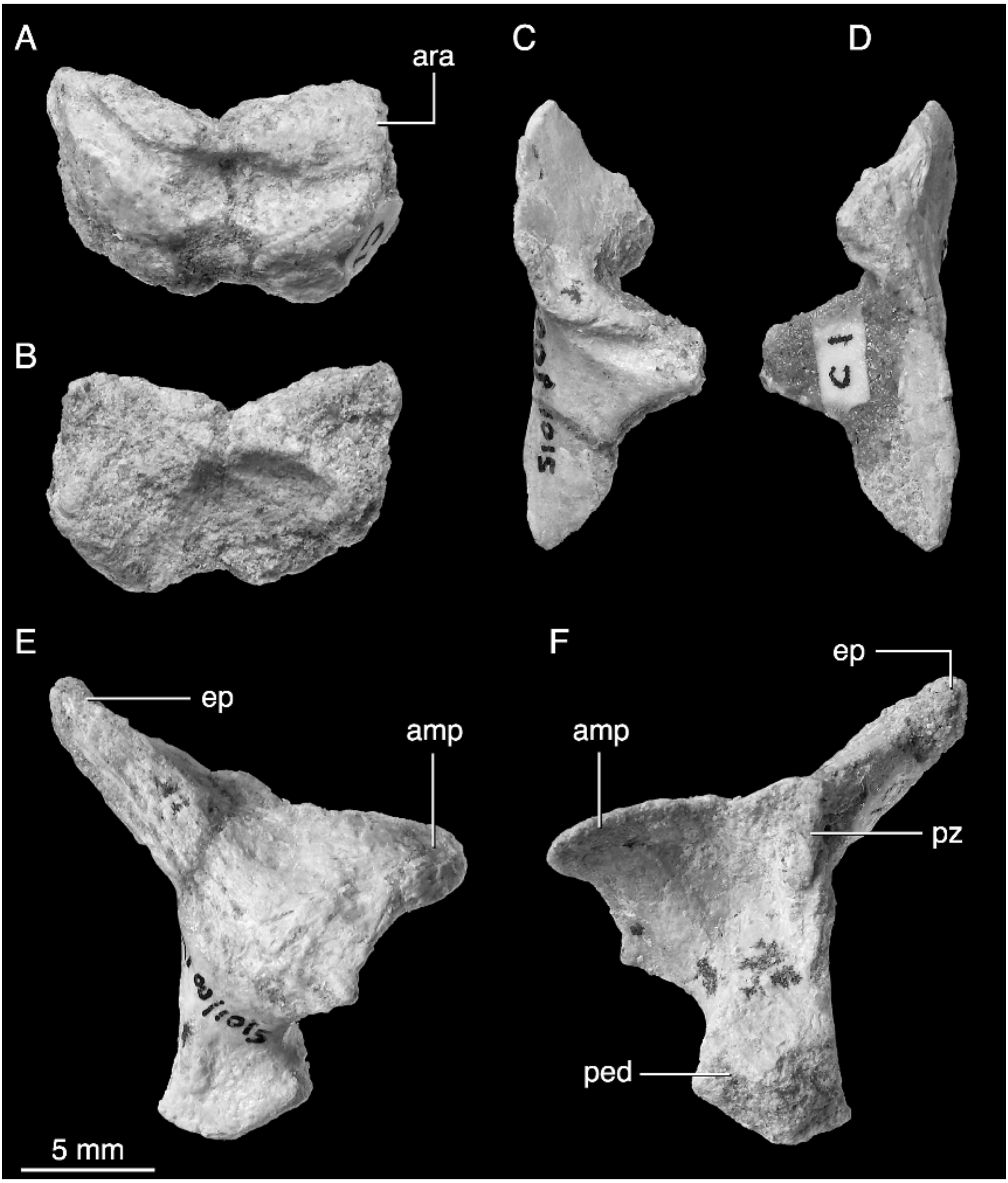


Fig. 17. Atlas, right neurapophysis, and proatlus of the holotype of *Tsaagan mangas* (IGM 100/1015). The atlas intercentrum in ventral (**A**) and dorsal (**B**) views. Right proatlus in lateral (**C**) and medial (**D**) views; right neurapophysis in lateral (**E**) and medial (**F**) views. Abbreviations are in appendix 1.

All the remaining cervical centra have relatively short and wide centra, as is typical for dromaeosaurids (figs. 19 and 20). No centrum is complete, however, due to scavenging, which predominantly affected the intercentral faces. Anterior intercentral articulations on cervicals 3–5 appear to have been strongly directed anteroventrally, as in other

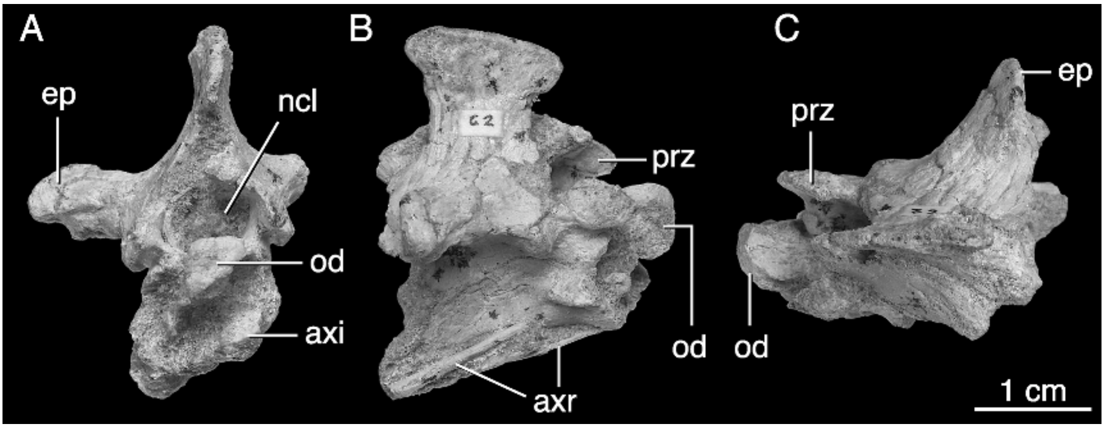


Fig. 18. Axis of the holotype of *Tsaagan mangas* (IGM 100/1015) in anterior (**A**), right lateral (**B**), and dorsal (**C**) views. Abbreviations are in appendix 1.

dromaeosaurids (Ostrom, 1969; Senter, 2004). Central pneumatic foramina are observed on the fifth and the seventh through eighth cervicals. Their presence or absence cannot be determined with certainty on the other cervicals, except for cervical 10, in which they appear to be absent. The ventral midline region of cervicals 8 and 9 is raised between the parapophyses and is suggestive of development of either carotid processes, as observed in troodontids (Makovicky and Norell, 2004), *Microraptor zhaoianus* (Hwang et al., 2002), and alvarezsaurids, or a raised ventral lip, as in *Velociraptor mongoliensis* (IGM 100/ 986) and cf. *Saurornitholestes langstoni* (MOR 660). Unfortunately, the anterior intercentral faces are too scavenged to allow for definitive observations of such structures.

Neural arches are broad and quite square in dorsal view in the third through sixth cervicals. These elements also bear relatively tall neural spines, which diminish in height caudally through the series. Epipophyses are well developed throughout the cervical series, but not to the degree observed in either *Velociraptor mongoliensis* (IGM 100/ 976) or *Deinonychus antirrhopus* (Ostrom, 1969), in which they overhang the postzygapophyseal facets posterolaterally. Like the neural spines, they diminish in size caudally through the cervical series. Infrazygapophsyeal laminae and pneumatic recesses are well developed throughout the cervical vertebrae, with the

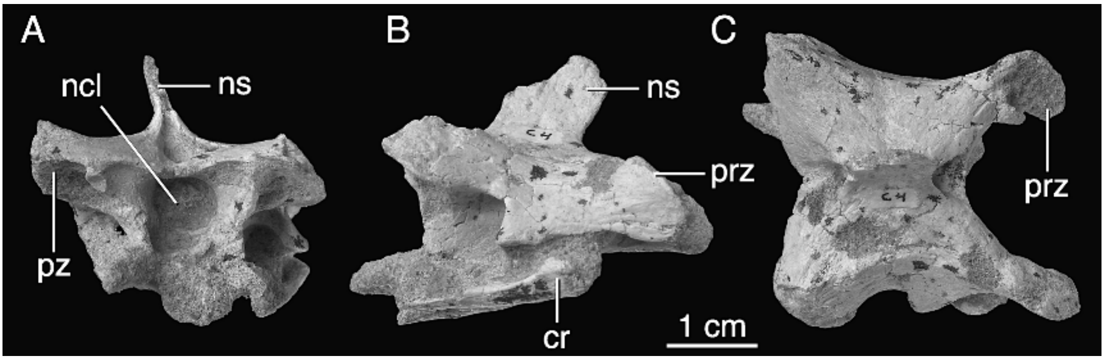


Fig. 19. Fourth cervical vertebra of the holotype of *Tsaagan mangas* (IGM 100/1015) in posterior (**A**), right lateral (**B**), and dorsal (**C**) views. Abbreviations are in appendix 1.

infradiapophyseal pocket being especially prominent. Anterior and posterior pedicular fossae are not present, however, in contrast to *Deinonychus antirrhopus* (Ostrom, 1969), but like *Velociraptor mongoliensis* (IGM 100/ 976). Cervical ribs are associated with most of the vertebrae, but do not appear to have been fused to the vertebrae except perhaps in cervicals 7 to 9. Preservation is too poor to ascertain whether fusion really had occurred. Fusion between cervical ribs and centra is observed in the seventh through ninth cervicals of a mature specimen of *Velociraptor mongoliensis* (IGM 100/ 976).

Cervical 10 is transitional between the cervical and dorsal series. Its centrum is more cylindrical, with parallel anterior and posterior intercentral articulations. The neural arch is reduced and the zygapophyses are closer to the midline than in the cervical vertebrae. A ventral keel is developed along the ventral aspect of the centrum, but no hypapophysis is present, in contrast to many other maniraptorans.

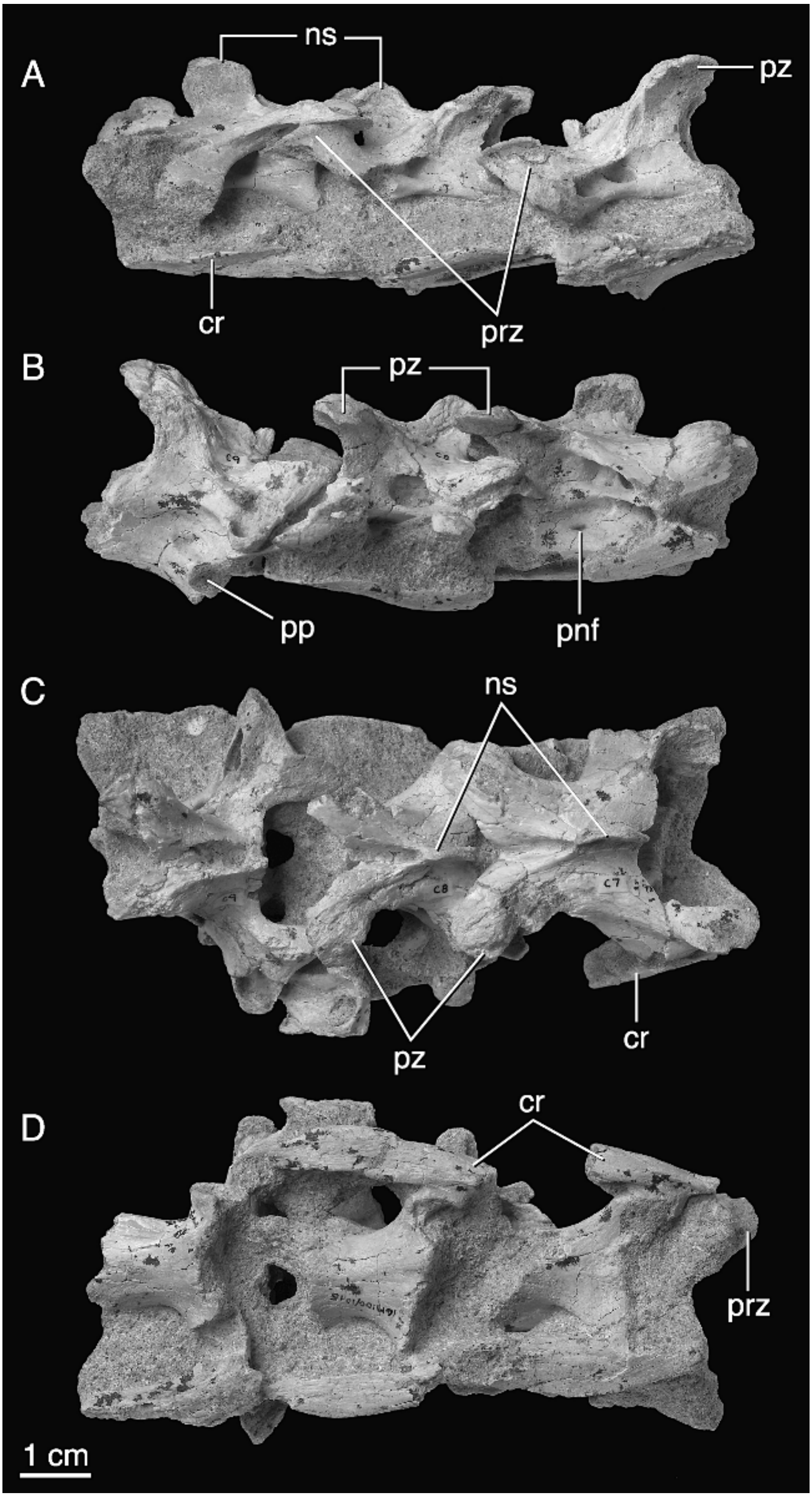
The Pectoral Girdle

Scapulacoracoid: A partial left scapulocoracoid was preserved in association with the vertebral series of IGM 100/1015 (fig. 21). Neither element is complete; the scapula is missing most of its shaft as well as the anterodorsal edge of the acromion process. Most of the coracoid plate anterior to the coracoid foramen and ventral to the coracoid tuber is missing. The glenoid is excavated by a large arthropod burrow. The scapula and coracoid adhere tightly to each other, but preservation is not good enough to evaluate whether they had fused. The scapula is similar to that of other dromaeosaurs in having an everted acromion process (Norell and Makovicky, 1999) and a laterally directed glenoid (Novas and Puerta, 1997; Xu et al., 1999).

The coracoid differs from most other dromaeosaurids such as *Velociraptor mongoliensis* (IGM 100/ 986; IGM 100/ 25), *Deinonychus antirrhopus* (YPM 5236), *Sinornithosaurus milleni* (IVPP V 12811), and *Bambiraptor feinbergorum* (AMNH FR 30556) in having a low coracoid tuber and a weak subglenoid shelf (*sensu* Norell and Makovicky, 1999). Such a shelf is well defined and transversely flat or concave in the majority of dromaeosaurid taxa, but not in *Tsaagan mangas*. The posterior wall of the coracoid foramen, which probably transmitted the supracoracoid nerve, is well preserved. Its tract forms a dorsomedial–ventrolaterally oriented channel just in front of and above the coracoid tuber. This dorsoventral orientation is also unusual among theropods, where the coracoid foramen is usually a simple perforation of the coracoid plate. A similar canalization of the coracoid foramen is present in *Deinonychus antirrhopus* (YPM 5236).

DISCUSSION

Tsaagan mangas is only the second dromaeosaurid taxon reported from Djadokhta Formation and equivalent beds (see remarks in Norell and Makovicky, 2004, concerning *Hulsanpes perlei*), even though numerous specimens of *Velociraptor* have been discovered from such beds (Norell and Makovicky, 1997, 1999; Barsbold and Osmólska, 2000; Tsogtbaatar, 2004). So far, *Tsaagan mangas* represents the only dromaeosaurid skeleton (aside from teeth) identified from Ukhaa Tolgod, in spite of more than a decade of collection. A second, as yet undescribed species of dromaeosaurid, which differs from *Tsaagan mangas* in frontal morphology, is known from the nearby locality of Zos Wash. The Zos Wash locality shares an undescribed troodontid species (Hwang et al., 2004), the multituberculate *Kryptobaatar*, the basal therian *Zalambdalestes*, and several lizards. The ubiquitous *Protoceratops andrewsi* (personal obs.) and the alvarezsaurid *Shuvuuia deserti* (personal obs.) are also faunal elements shared with Ukhaa Tolgod, suggesting that this second dromaeosaurid species was possibly sympatric with *Tsaagan mangas*. Dromaeosaurid taxa are sympatric in other localities such as *Dromaeosaurus albertensis* and *Saurornitholestes langstoni* in the Dinosaur Park Fm. of Alberta (Eberth, 1997) and several dromaeosaurids in the Yixian Formation (Norell and Xu, 2005). Note that while *Utahraptor ostrommaysorum* and *Deinonychus antirrhopus* both occur in the Cedar


A
ns
pz
cr
prz
B
pz
pp
pnf
C
ns
pz
cr
D
cr
prz
1 cm

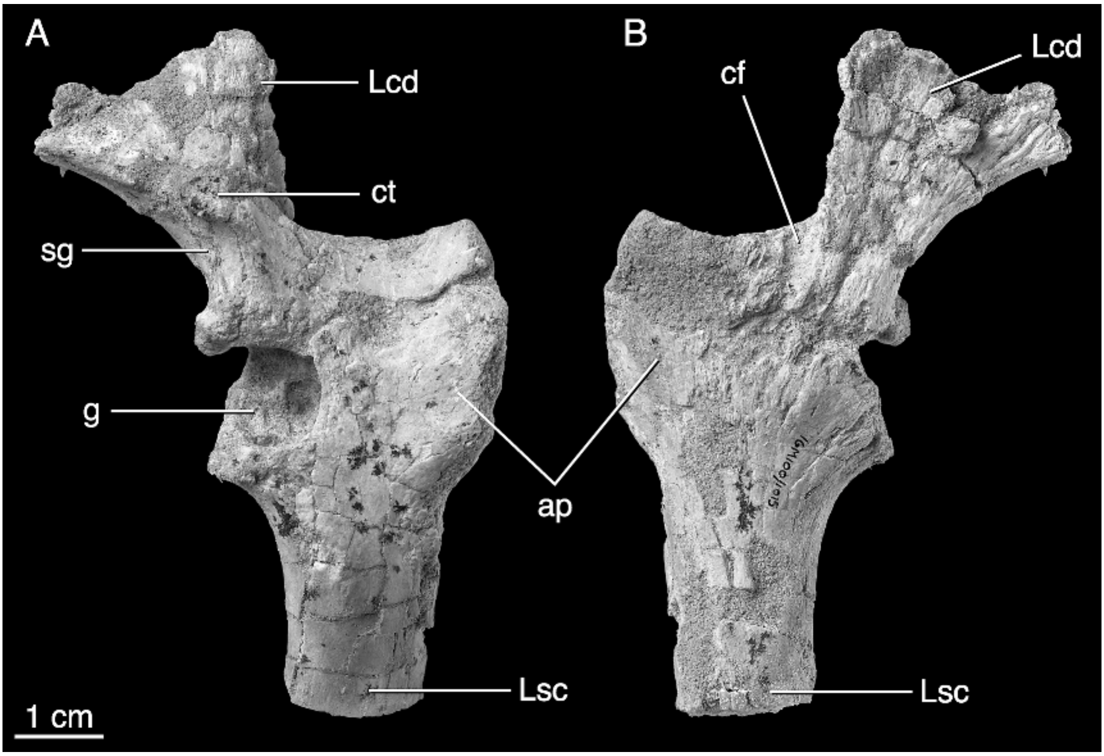


Fig. 21. Left scapulocoracoid of the holotype of *Tsaagan mangas* (IGM 100/1015) in lateral (**A**) and medial (**B**) views. Abbreviations are in appendix 1.

Mountain Fm. of Utah (Kirkland, 2005), they are from different units and are not temporally contemporaneous (Kirkland et al., 1999). The rarity of dromaeosaurid skeletons and correspondingly weak evidence for sympatric taxa at Ukhaa and nearby localities is surprising, however, given the general abundance of theropod remains and evidence for sympatry of at least two oviraptorids (Clark et al., 1999) and three troodontid species (Norell and Hwang, 2004; Hwang and Norell, 2004). Whether this discrepancy represents actual rarity or a taphonomic bias is unclear, but it is noteworthy that the more abundant taxa are either small (troodontids, alvarezsaurids) or frequently found brooding nests (Norell et al., 1995; Clark et al., 2000).

Tsaagan mangas differs from all other dromaeosaurids with known cranial remains in a suite of characters, some of which are unique to this taxon. It differs from *Velociraptor mongoliensis* in various aspects of its cranial anatomy, especially the more massive proportions of its jaws and its less pneumatic braincase and pendulous paroccipital processes. *Tsaagan mangas* resembles *Dromaeosaurus albertensis* (AMNH FR 5356) somewhat in the reduced nature of the anterior and posterior tympanic recesses and its more massive jaw proportions. However, they differ in detail: For example, *Dromaeosaurus albertensis* (AMNH FR 5356) lacks any trace of a dorsal tympanic recess (Currie, 1995), but one is still present, albeit

---

←

Fig. 20. Cervical vertebrae 7, 8, and 9 of the holotype of *Tsaagan mangas* (IGM 100/1015) in left lateral (**A**), right lateral (**B**), dorsal (**C**), and ventral (**D**) views. Abbreviations are in appendix 1.

reduced, in *Tsaagan mangas*. Differences also exist in dental morphology. Because our understanding of the interrelationships among dromaeosaurids is still in flux (see below) and we lack information on a wide range of taxa, it is uncertain whether the reduced tympanic recesses are indicative of a close relationship between *Tsaagan mangas* and *Dromaeosaurus albertensis* or represent a more widely distributed (and possibly homoplastic) trait.

DEINONYCHOSAURIAN PHYLOGENY

Tsaagan mangas exhibits numerous dromaeosaurid synapomorphies: a posterior process of the premaxilla excluding the maxilla from participation in the nares, a large spike on the medial inflected process of the articular, and a large quadrate foramen formed in part by a triangular flange on the quadrate and a squamosal shelf extending posterior to the quadrate head. It is therefore clearly referable to the Dromaeosauridae. To determine the phylogenetic relationships of *Tsaagan mangas*, the taxon was integrated into a phylogenetic analysis using the most recent version of the Theropod Working Group (TWiG) matrix. Character codings for a number of taxa have been changed and/or updated from the Makovicky et al. (2005) version (see appendix 2). Both the current data matrix (*matrix 2006.1*) and character descriptions are available at http://research.amnh.org/vertpaleo/norell.html. *Tsaagan mangas* has been included in previous versions of the TWiG matrix (e.g., Norell et al., 2001; Clark et al., 2002; Hwang et al., 2002; Xu et al., 2002; Makovicky et al., 2005) under its specimen number IGM 100/1015.

The dataset was treated with equally weighted parsimony analysis implemented in TNT v. 1.0 (Goloboff et al., 2003). A heuristic tree search strategy was conducted performing 1000 replicates of Wagner trees (using random addition sequences) followed by TBR branch swapping (holding 10 trees per replicate). The best trees obtained at the end of the replicates were subjected to a final round of TBR branch swapping. Zero length branches were collapsed if they lack support under any of the most parsimonious reconstructions.

The most parsimonious distribution of 236 morphological characters recovers *Tsaagan mangas* within an unresolved clade of dromaeosaurids comprised of *Velociraptor mongoliensis, Deinonychus antirrhopus, Adasaurus mongoliensis, Dromaeosaurus albertensis, Achilllobator giganticus, Saurornitholestes langstoni*, and *Utahraptor ostrommaysorum* (fig. 22A). Relationships within the Dromaeosauridae are similar to that recovered by Makovicky et al. (2005). A basal split is present between an Unenlagiinae clade and a large clade comprised of all other dromaeosaurids. *Sinornithosaurus millenii* and *Microraptor zhaoianus* are recovered as sister taxa within this larger clade. Unlike Makovicky et al. (2005), the strict consensus of the most parsimonious trees from the current analysis failed to recover a *Velociraptor mongoliensis, Deinonychus antirrhopus*, and *Tsaagan mangas* clade sister to a *Utahraptor ostrommaysorum, Achillobator giganticus, Dromaeosaurus albertensis, Adasaurus mongoliensis*, and *Saurornitholestes langstoni* clade. An Adams consensus (fig. 22B) indicates that *Saurornitholestes langstoni* is liabile among the unresolved large-bodied dromaeosaurids. The Adams consensus, however, identifies underlying tree structure similar to that recovered by Makovicky et al. (2005). *Tsaagan mangas* is depicted in a clade with *Velociraptor mongoliensis* and *Deinonychus antirrhopus*. These taxa are united by three unambiguous synapomorphies: The posterior opening of the basisphenoid recess is divided into two openings (char. 10-1), basipterygoid recesses are present on dorsolateral surfaces of basipterygoid processes (char. 15-1), and exits for CN X–XII are located together in a bowl-like basisphenoid depression (char. 19-1).

Topological support is weak throughout the dromaeosaurid clade with bootstrap values below 50% in all cases. This poor support is likely due to a combination of conflict and missing data. Nonoverlap between preserved skeletal regions of different species accounts for much of the irresolution. Taxa such as *Dromaeosaurus albertensis* and *Tsaagan mangas* are predominantly known only from cranial material, whereas other taxa like *Unenlagia comahuensis* are described from postcranial remains, thus not allowing for

Fig. 22. Phylogenetic placement of *Tsaagan mangas*. **A**, strict consensus of 144 most parsimonious reconstructions of coelurosaurian interrelationships found in our phylogenetic analysis of 236 characters and 57 coelurosaurian taxa. *Tsaagan mangas* is indicated in boldface. The most parsimonious trees (length = 710, CI = 0.401, RI = 0.728) were found in 693 of the 1000 replicates of TBR followed by an additional round of TBR on the retained MPTs. **B**, detail of dromaeosaurid topology in the Adams consensus of same tree set.

direct comparisons and phylogenetic placement relative to each other. In previous analyses the Mongolian taxon *Adasaurus mongoliensis* represented a wildcard taxon that occupied a sister group relationship with a variety of dromaeosaurids, but lacked synapomorphies tying it to any taxon in particular. In those cases it could be deleted from the analysis without any change in tree length (Norell and Makovicky, 2004), yielding a more resolved tree, in which *Tsaagan mangas* was in a clade with *Velociraptor mongoliensis and Deinonychus antirrhopus*, as in the Adams consensus of the current analysis. Other taxa could not and cannot readily be deleted without incurring changes in tree length, which suggests that their wildcard behavior is at least partly due to character conflicts (Kearney, 2002). This observation indicates that techniques such as the reduced consensus (Wilkinson, 1994, 1995a, 1995b) cannot be applied to our dataset without incurring the risk of settling on consensus solutions that are incompatible with all character data at hand. It furthermore suggests that taxon deletion based simply on relative proportions of missing data (e.g., Senter et al., 2004) may achieve greater levels of resolution through deletion of conflicting, but informative, character state observations as well as through the omission of missing data. We caution against the unwarranted application of such heuristic techniques for increasing resolution in consensus trees, without due consideration of the underlying reasons for the polytomies resulting from primary analysis of the data (Kearney, 2000; Kearney and Clark, 2003).

A detailed study of deinonychosaurian monophyly and interrelationships is currently under way. It will suffice to say here that there are several issues concerning dromaeosaurid phylogeny, their relationship to other deinonychosaurs, and even deinonychosaur monophyly that have recently arisen due to the discovery of very primitive dromaeosaurids (Xu et al., 2000, 2003; Xu and Wu, 2001; Hwang et al., 2002) and troodontids (Xu et al., 2002; Xu and Norell, 2004). Some of the specimens in question display interesting mosaics of derived and primitive characters, shared with troodontids, avialans, or even more inclusive clades of maniraptorans (Hwang et al., 2004). Incorporation of these taxa, along with undescribed Mongolian and Chinese material, is crucial to the accurate representation of the phylogeny of this group, but lies beyond the scope of this paper.

Recently Currie and Varricchio (2004) examined the phylogenetic relationship among six dromaeosaurid taxa in their study of a newly discovered dromaeosaurid taxon, *Atrociraptor marshalli*, recovering a remarkably well-resolved single most parsimonious solution. The character set used by Currie and Varricchio (2004) includes 43 cranial characters and samples most of the "traditional" cranial characteristics used to diagnose dromaeosaurid taxa. It therefore provides an interesting, albeit limited, basis for discussion, as well as a further means of comparing *Tsaagan mangas* to other dromaeosaurid taxa. The characters used by Currie and Varricchio (2004) are commented upon and revised when necessary (see appendix 3). We added *Tsaagan mangas* and the basal dromaeosaurids *Sinornithosaurus millenii* (Xu et al., 1999) and *Microraptor zhaoianus* (Xu et al., 2000) to the revised Currie and Varricchio (2004) dataset and reran the analysis to explore what effects the addition of these two taxa have on the analysis. We did not include several taxa such as *Microraptor gui, Utahraptor ostrommaysi, Adasaurus mongoliensis*, and *Achillobator giganticus* because of the paucity of published information on these taxa.

The consensus of two trees is congruent with the phylogeny proposed by Currie and Varricchio (2004) and the additional taxa are only placed on their topology (fig. 23). It shows the Early Cretaceous dromaeosaurid *Microraptor zhaoianus* to be the most primitive dromaeosaurid followed by *Tsaagan mangas*. Another Liaoning dromaeosaurid, *Sinornithosaurus milleni*, is more closely related to the more derived dromaeosaurids, with the difference between the two fundamental trees simply being the swapping of positions between *Sinornithosaurus milleni* and *Dromaeosaurus albertensis*. The paraphyletic occurrence of the two Liaoning taxa stands in contrast to the monophyletic grouping of them recovered by Norell and Xu (2004) and Senter (2004), who dubbed this clade Microraptoria, and also to a previous analysis that found *Microraptor* and *Sinornithosaurus* to be paraphyletic, but basal to all other dromaeosaurids (Hwang et al., 2001).

Two other issues with the Currie and Varricchio dataset concern outgroup choice. In their analysis they assert a monophyletic Dromaeosauridae as suggested originally by

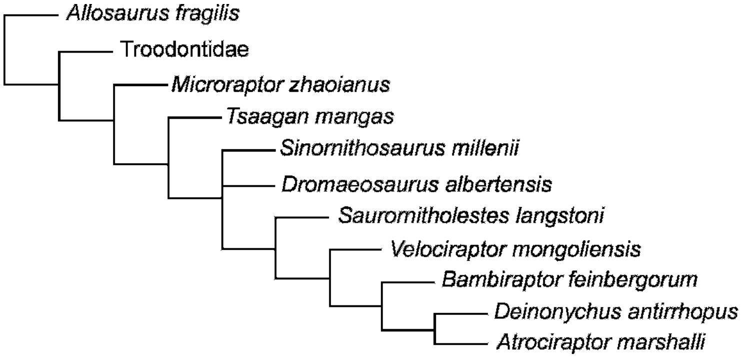


Fig. 23. The phylogenetic result of incorporating *Tsaagan mangas* into the revised dataset of Currie and Varrichio (2004). A strict consensus shows the results of a branch-and-bound search conducted in PAUP* (v. 4.0b10). Two most parsimonious trees of length 64 (CI = 0.7344, RI = 0.7733) were found. See the text for tree shape details.

Gauthier (1986). This is also an empirical result that has been found in a number of other independent cladistic analyses (Gauthier, 1986; Sereno, 1999; Holtz, 1998; Norell and Makovicky, 2004; Xu and Norell, 2004). All recent quantitative phylogenetic analyses have indicated a close relationship between deinonychosaurs and avialans, with this group nested within Coelurosauria along with taxa such as ornithomimosaurs, oviraptorosaurs, and *Ornitholestes hermanni.* Greater precision in determining the character conditions at the base of the deinonychosaur node requires that these outgroup taxa be added to the analysis.

Another issue is the composite scoring of Troodontidae. Troodontids have recently been shown to be a diverse group (Xu et al., 2003; Hwang et al., 2004; Makovicky and Norell, 2004; Xu and Norell, 2004). The distribution of character states (e.g., tooth serrations and contact of the quadratojugal and the squamosal) within troodontids is poorly understood and requires the introduction of several troodontids into a more global analysis to accurately determine character polarities at the base of Dromaeosauridae. As we note in appendix 3, a number of codings employed by Currie and Varricchio (2004) are based on the derived troodontid *Troodon formosus*, but do not reflect the character states present in the most basal members of the clade such as *Sinovenator changii* (Xu et al., 2002). For further details about the difficulty in using composite taxa, see Norell et al. (2001).

Recently, Senter et al. (2004) proposed another phylogeny of dromaeosaurids. In this analysis, a modest sample of coelurosaur taxa and characters were used to determine relationships. There is much that we disagree with in this paper regarding character choice and state delimitation. A critique of this paper is part of a much larger project, now under way. As an example of problematic characters, we point to character 2. This character as defined by Senter et al. states that "Anterior border of premaxilla- (0) subperpindicular *(sic)* to long axis of skull, (1) slanted posteriorly, 50°–70°, (2) slanted posteriorly, greater than 45°." Confirming Senter et al.'s published scorings proves problematic. For instance, *Velociraptor mongoliensis* and *Bambiraptor feinbergorum* are scored as having a 50°–70° slanting premaxilla border (state 1), while *Ornitholestes hermanni* was scored for the subperpendicular condition (state 0). These three taxa share a very similar morphology in the anterior border of the premaxilla. What is considered by Senter et al.'s (2004) character 2 as a large and phylogenetically informative difference between these taxa proves to be generally subtle differences between skulls of markedly different preservational conditions.

Many of Senter et al.'s characters are postcranial and cannot be scored on *Tsaagan mangas*. If *Tsaagan mangas* is included in the Senter et al. (2004) matrix (appendix 5) as

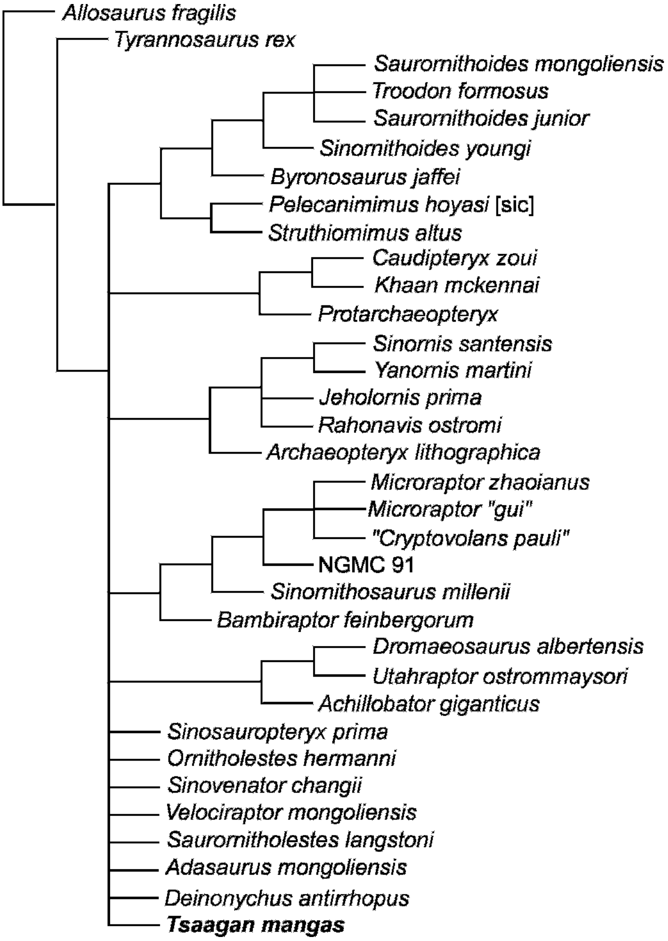


Fig. 24. The phylogenetic result of incorporating *Tsaagan mangas* into the dataset of Senter et al. (2004). A strict consensus shows the results of a heuristic search conducted in PAUP* (v. 4.0b10). One thousand replicates of random sequence addition followed by TBR branch swapping recovered 189 most parsimonious trees of length 230 (CI = 0.4826, RI = 0.7927). See the text for tree shape details.

a heuristic exercise, we recover an unexpected result (fig. 24), which does not place *Tsaagan mangas* as a dromaeosaurid. Additionally, the consensus of the most parsimonious tree set fails to recover a monophyletic dromaeosaurid clade (in both the traditional sense and that employed by Senter et al.). It is unusual that Senter et al.'s (2004) dataset is unable to recover a dromaeosaurid clade with the inclusion of *Tsaagan mangas*, which exhibits clear dromaeosaurid cranial synapomorphies. This is even more unusual in light of the fact that even the largely incomplete taxa *Unenlagia comahuensis, Hulsanpes perlei*, and *Pyroraptor olymipius* were placed in a dromaeosaurid clade. This suggests that the limited dataset size of Senter et al.'s analysis (101 characters) is not sufficient to sample the necessary, and currently recognized, synapomorphies of the Dromaeosauridae.

We maintain that the large-scale analysis of the broad sample of coelurosaur taxa presented above (fig. 22), while failing to provide resolution within Dromaeosauridae, best reflects our current understanding of the available data. Restricted analyses with limited taxon and character sampling and composite scoring (e.g., Troodontidae), while interesting

Fig. 25. A reconstruction of *Tsaagan mangas*. Courtesy of Nick Frankfurt.

as preliminary exploratory exercises, do not take into account the complexity of character distribution and may achieve resolution at the expense of accuracy.

CONCLUSIONS

Although carnivorous dinosaurs are relatively common in the Mongolian Late Cretaceous, the diversity of dromaeosaurids is limited (Osmólska, 1980; Norell and Makovicky, 2004). This diversity is probably underestimated, as the remains of dromaeosaurid teeth are common at several localities that lack material identifiable at a lower taxonomic level and the presence of several undescribed dromaeosaurid taxa awaiting study (personal obs.).

Here we present *Tsaagan mangas* (fig. 25), a new component of dromaeosaurid diversity. Its presence at Ukhaa Tolgod and the absence of any specimens at this locality that are definitively assignable to *Velociraptor mongoliensis* suggest that there were regional differences among Djadokhta localities in regards to its dromaeosaurid fauna.

ACKNOWLEDGMENTS

Collection and study of this specimen was supported by NSF grants DEB-9300700 and ATOL 0228693. We thank the Mongolian Academy of Sciences, D. Dashzeveg, and the members of the 1993 expedition. This specimen was prepared by Amy Davidson. The figures were skillfully constructed by Mick Ellison and the reconstruction is by Nick Frankfurt.

REFERENCES

Barsbold, R., and H. Osmólska. 1999. The skull of *Velociraptor* (Theropoda) from the Late Cretaceous of Mongolia. Acta Palaeontologica Polonica 44: 189–219.

Brinkman, D.L., R.L. Ciffelli, and N.J. Czaplewski. 1998. First occurrence of *Deinonychus antirrhopus* (Dinosauria:Theropoda) from the Antlers Formation (Lower Cretaceous: Aptian-Albian) of Oklahoma. Oklahoma Geological Survey Bulletin 146: 1–27.

Brochu, C.A. 1992. Ontogeny of the postcranium in crocodylomorph archosaurs. Unpublished M. A. thesis, University of Texas at Austin.

Brochu, C.A. 1996. Closure of neurocentral sutures during crocodylian ontogeny: implications for maturity assessment in fossil archosaurs. Journal of Vertebrate Paleontology 16: 49–62.

Brochu, C.A. 2003. Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high-resolution computed tomographical analysis of the skull. Society of Vertebrate Paleontology Memoir 7: 1–138.

Burnham, D.A. 2004. New information on *Bambiraptor feinbergi* (Theropoda: Dromaeosauridae) from the Cretaceous of Montana. *In* P.J. Currie, E.B. Koppelhus, M.A. Shugar and J.L. Wright (editors), Feathered Dinosaurs: 67–111. Bloomington: University of Indiana Press.

Burnham, D.A., K.L. Derstler, P.J. Currie, R.T. Bakker, Z.-H. Zhou, and J.H. Ostrom. 2000. Remarkable new birdlike dinosaur (Theropoda: Maniraptora) from the Upper Cretaceous of Montana. University of Kansas Paleontological Contributions 13: 1–14.

Chiappe, L.M., M.A. Norell, and J.M. Clark. 2002. The Cretaceous, short-armed Alvarezsauridae: *Mononykus* and its kin. 87–120, *In* L.M. Chiappe and L. Witmer (editors), Mesozoic Birds: Above the Heads of Dinosaurs. Berkeley: University of California Press.

Clark, J.M., A. Perle, and M.A. Norell. 1994. The skull of *Erlikosaurus andrewsi*, a lete Cretaceous "Segnosaur" (Theropoda: Therizinosauridae) from Mongolia. American Museum Novitates 3115: 1–39.

Currie, P.J. 1985. Cranial anatomy of *Stenonychosaurus inequalis* (Saurischia, Theropoda) and its bearings on the origin of birds. Canadian Journal of Earth Sciences 22: 1643–1658.

Currie, P.J. 1995. New information on the anatomy and relationships of *Dromaeosaurus albertensis* (Dinosauria: Theropoda). Journal of Vertebrate Paleontology 15: 576–591.

Currie, P.J., J.K. Rigby, and R.E. Sloan. 1990. Theropod teeth from the Judith River Formation of Southern Alberta, Canada. *In* P.J. Currie and K. Carpenter (editors), Dinosaur systematics: approaches and perspectives: 107–125. Cambridge: Cambridge University Press.

Currie, P.J., and X.-J. Zhao. 1993. A new carnosaur (Dinosauria, Theropoda) from the Jurassic of Xinjiang, People's Republic of China. Canadian Journal of Earth Sciences 30: 2037–2081.

Currie, P.J., and D.J. Varricchio. 2004. A new dromaeosaurid from the Horseshoe Canyon Formation (Upper Cretaceous) of Alberta, Canada. *In* P.J. Currie, E.B. Koppelhus, M.A. Shugar and J.L. Wright (editors), Feathered Dinosaurs: 112–132. Bloomington: Indiana Press.

Dashzeveg, D., M.J. Novacek, M.A. Norell, J.M. Clark, L.M. Chiappe, A. Davidson, M.C. McKenna, L. Dingus, C. Swisher, and Perle, A.. 1995. Unusual preservation in a new vertebrate assemblage from the Late Cretaceous of Mongolia. Nature 374: 446–449.

Dingus, L.D., D. Loope, C. Swisher, MinjinM.J. Novacek, and M.A. Norell. In review. New stratigraphic subdivision, depositional environment and age estimate for the upper Cretaceous Djadokhta Formation, Southern Ulan Nur basin, Mongolia: American Museum Novitates.

Eberth, D.A. 1997. Judith River Wedge. *In* Encyclopedia of Dinosaurs, P.J. Currie and K. Padian (editors), 379–385. San Diego: Academic Press.

Gauthier, J.A. 1986. Saurischian monophyly and the origin of birds. Memoirs of the California Academy of Sciences 8: 1–55.

Goloboff, P.A., J.S. Farris, and K. Nixon. 2003. TNT : tree analysis using new technologies. Program and documentation available from the authors and at http://www.zmuc.dk/public/phylogeny.

Holtz, T.R., Jr. 2000. A new phylogeny of the carnivorous dinosaurs. Gaia 15: 5–61.

Hwang, S.H., M.A. Norell, Q. Ji, and K.-Q. Gao. 2002. New specimens of *Microraptor zhaoianus* (Theropoda: Dromaeosauridae) from northeastern China. American Museum Novitates 3381: 1–44.

Hwang, S., M.A. Norell, and Q. Ji. 2004. A new troodontid from the Lower Yixian formation of China and its affinities to Mongolian troodontids. Journal of Vertebrate Paleontology 24(3 suppl.): 73A.

Kearney, M. 2002. Fragmentary taxa, missing data, and ambiguity: mistaken assumptions and conclusions. Systematic Biology 51: 369–381.

Kearney, M., and J.M. Clark. 2003. Strategies for resolving ambiguity resulting from missing data in the phylogenetic analysis of extinct and living taxa: a critical review. Journal of Vertebrate Paleontology 23: 263–274.

Kirkland, J.I. 2005. Utah's newly recognized dinosaur record from the Early Cretaceous Cedar Mountain Formation: Utah Geological Survey, Survey Notes 37(1): 1–5.

Kirkland, J.I., D. Burge, and R. Gaston. 1993. A large dromaeosaur (Theropoda) from the Lower Cretaceous of eastern Utah. Hunteria 2(10): 1–16.

Kirkland, J.I., R.L. Cifelli, B.B. Britt, D.L. Burge, F.L. DeCourten, J.G. Eaton, and J.M. Parrish. 1999. Distribution of vertebrate faunas in the Cedar Mountain Formation, east-central Utah. Pp. 201–217, *In* D.D. Gillette (editor), Vertebrate Paleontology in Utah: Utah Geological Survey Miscellaneous Publications 99–1.

Lambe, L.M. 1917. The Cretaceous theropodous dinosaur *Gorgosaurus*. Canadian Geological Survey Memoir 100: 1–84.

Madsen, J.H., Jr. 1976. *Allosaurus fragilis*: a revised osteology. Utah Geological Survey Bulletin 109: 1–163.

Makovicky, P.J., S. Apesteguía, and F.L. Agnolían. 2005. The earliest dromaeosaurid theropod from South America. Nature 437: 1007–1011.

Makovicky, P.J., Y. Kobayashi, and P.J. Currie. 2004. Ornithomimosauria, *In* D.B. Weishampel, P. Dodson and H. Osmolska (editors), The Dinosauria, 2nd ed.: 137–150. Berkeley: California University Press.

Makovicky, P.J., and M.A. Norell. 1998. A partial ornithomimid braincase from Ukhaa Tolgod (Upper Cretaceous, Mongolia). American Museum Novitates 3247: 1–16.

Makovicky, P., and M.A. Norell. 2004. Troodontidae, *In* D.B. Weishampel, P. Dodson and H. Osmolska (editors), The Dinosauria, 2nd ed.: 184–195. Berkeley: California University Press.

Makovicky, P.J., M.A. Norell, J.M. Clark, and T. Rowe. 2003. Osteology and relationships of *Byronosaurus jaffei* (Theropoda: Troodontidae). American Museum Novitates 3402: 1–32.

Makovicky, P.J., and H.D. Sues. 1998. Anatomy and phylogenetic relationships of the theropod dinosaur *Microvenator celer* from the Lower Cretaceous of Montana. American Museum Novitates 3240: 1–27.

Matthew, W.D., and B. Brown. 1922. The family Deinodontidae, with notice of a new genus from the Cretaceous of Alberta. Bulletin of the American Museum of Natural History 46: 367–385.

Maxwell, D.W., and L.M. Witmer. 1996. New material of *Deinonychus* (Dinosauria: Theropoda). Journal of Vertebrate Paleontology 16(3 suppl.): 51A.

Norell, M.A., J.M. Clark, L.M. Chiappe, and D. Dashzeveg. 1995. A nesting dinosaur. Nature 378: 774–776.

Norell, M.A., J.M. Clark, and P.J. Makovicky. 2001. Phylogenetic relationships among coelurosaurian theropods. *In* J. Gauthier and L.F. Gall (editors), New perspectives on the origin and early evolution of birds: 49–68. New Haven: Peabody Museum of Natural History, Yale University.

Norell, M.A., J.M. Clark, P.J. Makovicky, R. Barsbold, and T. Rowe. In prep. A revision of *Saurornithoides*: American Museum Novitates.

Norell, M.A., and S. Hwang. 2004. A troodontid dinosaur from Ukhaa Tolgod (Late Cretaceous Mongolia). Novitates 3446: 1–9.

Norell, M.A., and P.J. Makovicky. 1998. A revised look at the osteology of the dromaeosaurs: evidence from new specimens of *Velociraptor*. Journal of Vertebrate Paleontology 18(3 suppl.): 66A.

Norell, M.A., and P.J. Makovicky. 2004. Dromaeosauridae. *In* D.B. Weishampel, P. Dodson and H. Osmólska (editors), The Dinosauria, 2nd edition: 196–209. Berkley: University of California Press.

Norell, M.A., P. Makovicky, and J.M. Clark. 2000. A new troodontid from Ukhaa Tolgod, Late Cretaceous, Mongolia. Journal of Vertebrate Paleontology 20(1): 7–11.

Norell, M.A., P.J. Makovicky, and J.M. Clark. 2004. The braincase of *Velociraptor*. *In* P.J. Currie, E.B. Koppelhus, M.A. Shugar and J.L. Wright (editors), Feathered Dinosaurs: 133–143. Bloomington: University of Indiana Press.

Norell, M.A., and X. Xu. 2005. Feathered dinosaurs. Annual Reviews of Earth and Planetary Sciences 33: 8.1–8.23.

Novas, F.E., and D. Pol. 2005. New evidence on deinonychosaurian dinosaurs from the Late Cretaceous of Patagonia. Nature 433: 858–861.

Novas, F.E., and P.F. Puerta. 1997. New evidence concerning avian origins from the Late Cretaceous of Patagonia. Nature 387: 390–392.

Osborn, H.F. 1924. Three new Theropoda, *Protoceratops* zone, central Mongolia. American Museum Novitates 144: 1–30.

Osmólska, H. 1980. The Late Cretaceous vertebrate assemblages of the Gobi Desert, Mongolia. Memoires Societe Geologique France 139: 145–152.

Ostrom, J.H. 1969. Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. Bulletin Peabody Museum of Natural History 30: 1–165.

Paul, G. 1988. Predatory dinosaurs of the world. New York: NY Academy of Sciences.

Paul, G. 2002. Dinosaurs of the air: the evolution and loss of flight in dinosaurs and birds. Baltimore: Johns Hopkins, 460 pages.

Raath, M.A. 1985. The theropod *Syntarsus* and its bearing on the origin of birds. *In* M.K. Hecht, J.H. Ostrom, G. Viohl and P. Wellnhofer (editors), The beginning of birds: 219–227, Freunde des Jura–Museums Eichstätt: Eichstätt.

Rauhut, O.W.M. 2003. The interrelationships and evolution of basal theropod dinosaurs. Special Papers in Palaeontology 69: 1–213.

Russell, D.A., and Z.-M. Dong. 1993. A nearly complete skeleton of a new troodontid dinosaur from the Early Cretaceous of the Ordos Basin, Inner Mongolia, People's Republic of China. Canadian Journal of Earth Sciences 30: 2163–2173.

Senter, P., R. Barsbold, B. Britt, and D.A. Burnham. 2004. Systematics and evolution of Dromaeosauridae (Dinosauria, Theropoda). Bulletin of Gunma Museum of Natural History 8: 1–20.

Sereno, P. 1997. The origin and evolution of dinosaurs. Annual Review of Earth and Planetary Sciences 25: 435–489.

Sereno, P.C. 1999. The evolution of dinosaurs. Science 284: 2137–2147.

Sues, H.-D. 1977. The skull of *Velociraptor mongoliensis*, a small Cretaceous theropod dinosaur from Mongolia. Paläontologische Zeitschrift 51: 173–184.

Sues, H.-D. 1997. On *Chirostenotes*, a Late Cretaceous oviraptorosaur (Dinosauria: Theropoda) from western North America. Journal of Vertebrate Paleontology 17: 698–716.

Tsogtbaatar, K. 2004. Fossil specimens prepared in Mongolian Paleontological center 1993–2001. Hayashibara Museum of Sciences Research Bulletin 2: 123–128.

Tykoski, R.S. 1998. The osteology of *Syntarsus kayentakatae* and its implications for ceratosaurid phylogeny. Unpublished Masters thesis, University of Texas at Austin, 217 pp.

Wilkinson, M. 1994. Common cladistic information and its consensus representation: reduced Adams and reduced cladistic consensus trees and profiles. Systematic Biology 43: 343–346.

Wilkinson, M. 1995a. More on reduced consensus methods. Systematic Biology 44: 436–440.

Wilkinson, M. 1995b. REDCON 2 0, reduced consensus programs and documentation: School of Biological Sciences, University of Bristol.

Witmer, L.M. 1990. The craniofacial air sac system of Mesozoic birds (Aves). Zoological Journal of the Linnean Society 100: 327–378.

Witmer, L.M. 1997. The evolution of the antorbital cavity of archosaurs: a study in soft-tissue reconstruction in the fossil record with an analysis of the function of pneumaticity. Memoirs of the Society of Vertebrate Paleontology, Journal of Vertebrate Paleontology 17(Suppl. to 1): 1–73.

Witmer, L.M., and W.D. Maxwell. 1996. The skull of *Deinonychus* (Dinosauria:Theropoda): new insights and implications. Journal of Vertebrate Paleontology 16(3: Suppl.): 73A.

Xu, X., and M.A. Norell. 2004. A new troodontid dinosaur from China with avian-like sleeping posture. Nature 431: 838–841.

Xu, X., M.A. Norell, X.-L. Wang, P.J. Makovicky, and X.-C. Wu. 2002. A basal troodontid from the Early Cretaceous of China. Nature 415: 780–784.

Xu, X., X.-L. Wang, and X.-C. Wu. 1999. A dromaeosaurid dinosaur with a filamentous integument from the Yixian Formation of China. Nature 401: 262–266.

Xu, X., and X.-C. Wu. 2001. Cranial morphology of *Sinornithosaurus millenii* Xu et al. 1999 (Dinosauria: Theropoda: Dromaeosauridae) from the Yixian Formation of Liaoning, China. Canadian Journal of Earth Sciences 38: 1739–1752.

Xu, X., Z. Zhou, and X. Wang. 2000. The smallest known non-avian theropod dinosaur. Nature 408: 705–708.

Xu, X., Z. Zhou, X. Wang, X. Kuang, F. Zhang, and X. Du. 2003. Four-winged dinosaurs from China. Nature 421: 335–340.

APPENDIX 1

Abbreviations

Institutional

AMNH FR	American Museum of Natural History Fossil Reptiles and Amphibians
GIN	Institute of Geology, Mongolian Academy of Sciences
IGM	Institute of Geology, Mongolian Academy of Sciences
MNU	Mongolian National University

MOR	Museum of the Rockies
OMNH	Oklahoma Museum of Natural History
TMP	Tyrell Museum of Paleontology
UA	Université d'Antananarivo
YPM	Yale Peabody Museum

Anatomical

Uppercase L and R as prefixes signify left and right.

a	angular
af	antorbital fossa
afl	anterior flange of quadrate
amp	ampullae
aof	antorbital fenestra
ap	acromion process
ara	atlantal rib articulation?
asc	anterior semicircular canal
at	articular
axi	axial intercentrum
axr	axial rib
av	alveolus
bpt	basipterygoid process
bptr	basipterygoid recess
bspr	basisphenoidal recess
bt	basal tuber
c	coronoid
cd	coracoid
cf	coracoid foramen
cif	crista interfenestralis
CN V	trigeminal foramen
CN VII	facial foramen
CN X	vagus foramen
CN XII	hypoglossal foramen
cp	crista prootica
cr	cervical rib
ct	coracoid tuber
d	dentary
dtr	dorsal tympanic recess
ect	ectopterygoid
ep	epipophysis
ex	exoccipital
f	frontal
fa	frontal air spaces
fm	foramen magnum
fnc	floor of the nasal chamber
fop	fenestrae ovale and pseudorotundum
fq	facet for articulation on squamosal
fr	floccular recess
g	glenoid
ic	internal carotid
itf	infratemporal fenestra
j	jugal
l	lacrimal
lat	laterosphenoid
lr	lateral ridge
lsc	lateral semicircular canal
mf	mandibular fenestra
mr	medial ridge
mx	maxilla
mxf	maxillary fenestra
n	nasal
na	nare
nc	nasal chamber
ncl	neural canal
ncr	nuchal crest
ns	neural spine
o	occiput
oc	occipital condyle
od	odontoid
opo	opisthotic
p	parietal
pa	prearticular
pas	prearticular shelf
ped	pedicel
pf	pneumatic foramen
pmx	premaxilla
pmxf	promaxillary foramen
pnf	pneumatic foramen
po	postorbital
poa	postorbital articulation
pop	paroccipital process
popa	paroccipital process articulation
por	postorbital process
pp	parapophysis
prop	prootic/opisthotic
prz	prezygapophysis
psaf	posterior surangular foramen
psc	posterior semicircular canal
psm	palatal shelf of maxilla
psr	parasphenoid rostrum
pt	pterygoid
ptr	posterior tympanic recess
pz	postzygapophysis
q	quadrate
qa	quadrate articulation
qf	quadrate foramen
qj	quadratojugal
qja	quadratojugal articulation
qjp	quadratojugal process of quadrate
qs	quadrate shelf
sa	surangular
saf	surangular foramen
sc	scapula
scl	scleral ossicles
sg	subglenoid shelf
so	supraoccipital
sp	splenial
sq	squamosal
sqa	squamosal articulation
sstf	squamosal supratemporal fossa
stf	supratemporal fenestra
t	tooth
vcp	vertical columnar process

APPENDIX 2

Data Matrix Used in Phylogenetic Analysis

Characters are derived from the Theropod Working Group Matrix. This matrix is *matrix 2006.1* and is available at http://research.amnh.org/vertpaleo/norell.html. Character definitions follow from Makovicky et al. (2005) and are in turn based largely on the recent work of Makovicky and Sues (1998), Norell et al. (2001), Xu et al. (2002), Makovicky et al. (2003), and Hwang et al. (2004). Characters 9, 16, 17, 18, 27, 37, 39, 40, 68, 76, 113, 157, 164, 169, 174, 182, 184, and 220 represent potentially nested sets of character states or include presence/absence states. Ordering of these characters affects the tree length (721 instead of 710), and 271 most parsimonious trees are recovered instead of 144. These differences are due to an increased lack of resolution in the topology of oviraptorsaurians more derived than *Incisivosaurus gauthieri*.

Character states enclosed between brackets represent conditions found to be variable within a terminal taxon (i.e., polymorphic scorings). Multiple states enclosed in braces indicate uncertainty or ambiguity in the condition of a terminal taxon (among these states, but not among the remaining character states). Following Makovicky et al., (2005), we considered *Neuquenraptor argentinus* a junior synonym of *Unenlagia comahuensis* and combined the morphological information of this taxa in the analysis.

Character codings listed below represent modifications to those from Makovicky et al. (2005). In the process of preparing this manuscript a number of revisions to the codings were made based on newly available data or because previous codings were either incorrect or inconsistent with the character descriptions. Revised character codings are discussed below and indicated by boldface type in the matrix.

The palate of *Mei long* is not exposed; therefore character 26 was rescored as uncertain (?) instead of state 1. No taxa were coded for the derived state of character 31. Reexamination of the ingroup taxa, however, indicates that *Struthiomimus altus, Gallimimus bullatus*, and *Ornithomimus edmonticus* depict state 1. *Velociraptor mongoliensis* was previously coded as uncertain (?) for characters 43 and 77. Reexamination of available material for *Velociraptor mongoliensis* (AMNH FR 6515, IGM 100/25, IGM 100/976, IGM 100/982) indicates that the taxon possesses state 1 for character 43 and state 1 for character 77. *Buitreraptor gonzalezorum* was erroneously coded as possessing an edentulous maxilla (character 82-1); this was changed to the toothed state 0. *Conchoraptor gracilis* was erroneously coded as possessing state 3 for character 110. No such character state is present; instead *Conchoraptor gracilis* depicts state 2 (i.e., 8 or more sacral vertebrae). *Sinraptor dongi, Mononykus olecranus, Shuuvia deserti*, and *Confuciusornis sanctus* were erroneously coded as possessing state 2 for character 128. No such character state exists; instead these four taxa depict state 1 (i.e., presence of fused sternal plates). Optimization of this character was not affected by this error because previously no taxa were scored as possessing state 1. The scapula and coracoid in *Rahonavis ostromi* (UA 8656) are not fused, and character 135 was rescored as state 0 to reflect this. Codings for character 150 and 151 were reversed in *Archaeornithomimus asiaticus. Microraptor zhaoianus* was recoded as possessing state 2 (i.e., pubic shaft curves posteriorly with an anteriorly convex curvature) based on Hwang et al. (2002) and Xu et al. (2003).

A new character used in Makovicky et al. (2005) coded for the derived presence of prominent lateral tubercle about halfway down the lateral shaft of the pubis (character 231-1). This character state is found exclusively in the Yixian Formation dromaeosaurids *Microraptor* and *Sinornithosaurus* (see Supplemental Data for Makovicky et al., 2005). *Archaeopteryx lithographica* was erroneously coded as possessing this state as well. Thus character 231 was recoded as state 0 to reflect this (see berlin, eichstatt, solenhofen and WDC specimens). Following the publication of a new *Archaeopteryx lithographica* specimen (Mayr et al., 2005), revisions to previous character codings could be made. According to the newly available data, characters 35, 63, 128, 197, 200, and 205 were recoded as states 0, 0, inapplicable, 1, 0, and 0/1, respectively. Lastly, Makovicky et al. (2005) expanded character 166 of Xu and Norell (2004) as well as previous versions of the TWG matrix into three separate characters (chars. 166, 167, 168) describing morphology of the shaft of the ischium. The proper coding of these revised and expanded characters was not incorporated for all taxa in the data. Codings for *Ingenia yashani, Citipati osmolskae*, "*Oviraptor*" *mongoliensis, Chirostenotes pergracilis, Velociraptor mongoliensis, Achillobator giganticus, Sinornithosaurus millenii, Ornitholestes hermanni, Avimimus portentosus, Caudipteryx zoui, Confuciusornis sanctus, Saurornithoides mongoliensis, Sinornithoides youngi, Sinovenator changii, Segnosaurus galbinensis, Shenzhouraptor orientalis*, and *Buitreraptor gonzalezorum* were updated to reflect changes made by Makovicky et al. (2005).

Allosaurus fragilis

?11000?00000001000110010001000001110110010??
000000000010001000000000001000100000000000001
01010010000000100100000000000001000000?01????
0000000000000000?000001000000100000001000000
000000?100000110000001000000000000000000010
0000000000?0?000?00

Sinraptor dongi

?11000??00?00010001000000010?0000010110010
?00?00000000000010000?00000100?10?0000000001
0101001000000010010000000000000??????????**1**?00?
0?0??00??0???????000010000?010??0000100000000?
001000000?000000100000000000000?000?000?00?00
0000?0?000?00

Ingenia yanshani

?01?0?????????????????1?1?????1??????????????????????
???????????21120?01000?0111?1????????????????????
??????1???01????2?00???0011110011??00000??100000
0100021??????01**01**2010011010?11101101?0000?000
10?000000000??0000??11?2000?000?0?001000

Citipati osmolskae

?011001001001??221000101111?01011?0001021000
1100000110001000110121120?0100010111?1???????
??1011101100101111001??201??002100111?011110
0110100100?1100000001000211001??01**01**2010??101
01111?2101000000000?000000000000000000001102
0000000?0?001000

"Oviraptor" mongoliensis

?01?0????0?????????0111?1???1?11?00010??00???000
?0??????00??1?12112??01000??111?1?????????????????
?????????????0?????210?????????1??1???00?0???10??00
01000?1?????1???????????????1?????????0????0??0?0???
????0??00??001??2?00?????????????

Oviraptor philoceratops

?01?0??????01?1????0??1??111?1011???0???1?0?11????
0?1?0???0?11?121120?01?00?01?1?1?????????????????
?????????????0???????????????11??1?????00???1?0??00?
00??1??0??????**?**????????????????????0????0????0??0???
??00?00000???2?00?0???????????

Conchoraptor gracilis

?0110??????????1???00111?1???1?11?000??21000110?
000?????1?0????121120?010?0?0111?1???????????????
??010??1?01**2**?110??1?????0??1???1?10011000010????
????0010002100010101?0??10???01001?1?11010?0???
?0??0?0000??0?0??000?001102?0?0000?0?001000

Incisivosaurus gauthieri

?01?0???1??01?????1000?1101001001?010?1?0000110
00?11010110101111210100001001?1?000210??00?0
??
??
??????00??00??01?0??0?0?????????

Microvenator celer

??
?????????21?20?0?????????????????????011?0?11000111
100???0?1?1002?????????????00?000?11000??????00100
02???0000?????????????0110??0101100?0000010??????
?0??0???00??11?20?0??00???0?1??0

Chirostenotes pergracilis

?????1??01?01101??0???1?110?0?????????????????????
??01010??????21120?00000?01???1?????????????????11
01?11????1?12???0?????????????????01?1???????????00?
10002??00?0?01**21**20101110?011???0?????????00?100
?00200000??000?0?1??20?0?000?0?00100?

Dromaeosaurus albertensis

?0??0010000000000010??0???0?01??01110???1111??
??10001?1001100??0000001001111000?000010100
1???
????????????1???
???1??????00??????00?0?00??1????????

Deinonychus antirrhopus

?0110????1???????1??0000?011100011100011??????
0?1????0?00?110100000?0100111?1000?0100101000?
110001100?1111011???00110111121??????1?110111
00100111000000100221110101010220?01111?0120
1?1111000000000010001101001000?000001100000?0
0010?001000

Velociraptor mongoliensis

?011001001000012011200001011100011100012 11**1**
?10?010001000011101000000001001111**1**000101001
0100001100011001111101111100011011012111001
110111111001001110000000100221110111 01**02**2010
11112112011111?000000000101011010010 0000000
0110000000011?001000

Utahraptor ostrommaysorum

?????????????????????0???????????????001???????????????
??????????????????????????0????0101??1????????????1?????
??????0??011??????????????????????????????0?0?????????
??????????????10?????0??????????00?0????0?????????????
???????????????????

Adasaurus mongoliensis

??
?????????????????????????0?0??0?????????????????????????

???1?22111?10
?01?0201?1?1?21?0?1????????????????????01???0??????
0????0???????1??0010??

Achillobator giganticus

????????????????????????01?1????????????????????????
??????????????????????????0000101??????0?01100?111
10???????0??011?11??????????101?????????????00??102
20??11010**0**0**2**101?011010?001?21110?0????00?000?1
01????0???????1???0????001??001000

Tsaagan mangas

?01100100100001201120000101010001?10001211?1
10001000??00001?0??000000100?111100010100101
00001100??1????????????????????????????????11?11???
???
??????????? ????0??00??00?0?00???????????

Saurornitholestes langstoni

??111??????????
????11????0?????????????????100101?00?110001100111
11011011100?1011?111?????????????????????????0001
????????????1?**?**??????????????????????????????????0????0
???00?0????00??000010?001000

Sinornithosaurus millenii

0011??????0??????????00???1110????1000111100?1???
0?01???????????00?00100??1????010100??100????????
1??1???????0???00?1??1???????0111?11011110?0????0
?0000?00?201?01?1110**2**3?1?111021?2?1???1?????????
110001?1100?0?00010001??0000???0110111100

Microraptor zhaoianus

0?????????????????100????????????????????????????????
??????????0??010?0?1????0?01000000?????001?1??01?
1000?01???0110?12?2111?01?101?1?111010??100100
0011012111??01110?3?1?1110211**2**01?11111??00?00
01?10111110?100??000?11?000????1010111100

Rahonavis ostromi

??
????????????????????????????0???????????????01?111???1
?01?011112?12???????????**0**??11??011???????0?01111?1
0111110?3?1012?01??21??211?0001??0??10001101?0
100????0??1????????10001011111

Mononykus olecranus

??????00???????112????????????????????????????????????
??100????????????????????????2????0????????1?1?111010
01?????10?2???????1???**1**000?000200030110?11220110
0??1????1??000?0?1?????2??0???21010011101121100
0030000001??00???1??0?0??00?0?0???00

Shuuvia deserti

?0110100000000?112011000?0?0?0?111?110
0210000101010010010???1?10010101000002100?10
211??000??0111111011101?0??1?201012012110100?
1000?0002000301 1??1122011000?1??011?2000?0?10
021022?0???2101001110112110000300000001100000
1100000010000?00??00

Patagonykus puertai

???
???1?011?110???
?12[01]10?2????????????????00200??0110???????1????1
????1??0?????10????21101??1100?000100001110??0???
?0?1??0?0?1???00????????0010?0

Alvarezsaurus calvoi

???
??100?????????
?2?10?2?12?????????????0?0?00?????????0??????0011??0
??2????????????????????1?00???0??0??10000000???0????
????1???0????00???????0?

Ornitholestes hermanni

?0100???0?0?00?1???0?010?01110001?100001?0??100
000001?01011????0000001000?0?000010?00101001?
????011?010110000???000?0010??1???????????????01?
00??????????00001??1?0?0[**01**]**0**0100000001??0?1?????
??0????????00?00???00000?0010?00?0?0000?0?0000?0

Archaeopteryx lithographica

101?0000??000??112010010??1110?011**0**00012100?1
0?0000?0??100111?**0**?000001000002?00000200??001
00?1?1???00?0??0?0?0???0021012211000?**?**??1011111
111000?11000000000112111010?1100301012?021?21
2?111100000?000**1**01**0**0000{**01**}0?000000000110000
0??00**?**00011001

Avimimus portentosus

?01?0???10011?00??0??1?1????????1???1?????00?11
??0?00100110???????2?1???00?0??0111?????????????011
010110101?0?00??100?????????????????????????0100???
????????00?211?01??01**01**201010?010?0?1000100?0
???00011110020???00??0?0?01?02?000000?0?001000

Caudipteryx zoui

00110??????????????0?111??10?0001?10???21000???0?
00???????????????21120?0?????????0?1??0?????00????0??0
0?????????0???01?????20?????0???0??0???0??0???100000
0?000?1???????01**01**201???1????101?11?????0????01000
??1?00?0?000000?1102000??00?0?001000

Confuciusornis sanctus

10110??????????????1?000?00??0001???0??2??0??0??0
10???01???????000010000?10?0001?1?????????0??????
????101??0?2???0?2????2??111?**1**1010??1?111400?1111
10000001121?1?1??11**00**0?1?111022?21?12??10??11?
?12011101001 0?0000000001102000??00?0101??11

Struthiomimus altus

?01010?110??0??1010210001011101?110000
0000000000001?0??0001?01??0001000001020001?1?
????????001?10110000100000101000000001001001?
????01120002000000?1010010000001100001010 01
000000000100000110001000100000203?000011111
110121110000?0?001000

Gallimimus bullatus

?01010?110110101010210001011?0**1**?110000000000
0000001000000001?010000000000001020001?1??????
??0011101100001000001?1000000000100100??????01
12000200000?0?101001000000110000101001000 00
010010000011000100010000020 3?000001111111012
1110000?0?001000

Garudimimus brevipes

?010?????01101?????2?000101010 00??000?00?00?0?
000??????0001??1?0??0??0??0?02?0?1?1??????????????
????????0???1??0???????????????????????????????????
???0?0???1???0?0????????0??0?1???????0????????00000
000?0??01??1?1??2?1?0?00?0?0??000

Pelecanimimus polydon

?01???????1?????????2?00????100?????????0??0????????
??????????????00?0000???????000211??0001???????????
?????????????????????????0?00????2?????00??00?1010??
??
001110????0?????0?????0????

Harpymimus okladnikovi

?0??????????????????2?0???????????????????????????????
????????????0??00?00?????????200??1???????????????????
??0???????????????????????????????2?00?00000010?10??0
???????010?????00????0????????????????????000000???0?0
01011????1?0???00?0?0???00

Troodon formosus

???1?1112?1101000001???0?011?0??????202200002
10?00?1?01100????0?10??001??????????0111010100??
?111110010110111 1?1000?1020??11??????????????1?0
10????0?000010???????????0?3?2?10?11000?0??011110
00???00010000021??01????000??1?0??010???1??0??0?

Saurornithoides mongoliensis

?01??1?1??1101???0?110001?1000?????????2??????????
?????????1?010?100?0010??1????0001110101?????????
1???0??0?????100??1??????????????????????????????????
?????????????01**01**2010?010??10?1?11110????????????0??
?10?01??????0??1?0?????????????010??

Saurornithoides junior

?01101?12?110100?001?000??100000????2022000?21
??0????11100??????100?001???1????0001110101 00???
?????????????????1?1000?1020?1???????????????????????
????????????????????1????????????????????????????????01?????
2???????????00??00???11????????0??

Byronosaurus jaffei

?????101???101?11001100010 11?0???????20220??????
????????100??????0000001??11????000211??01?0?0???
????010110?????????0??02????????????????????????????????
????????????????????????????????????1????0?0??0????????2
1??????????0????0????1???????????

Sinornithoides youngi

?0??01??????????????1?000??1??0????00???2????????1?0?
??????????????00??0010????????0001110?01??????11??00
1???????????0011?10112101????1?00?1?101?0???1000
000????21??01??01?**?**30???11?0??001??1110?????0????
?000110001?0??0?0?1??00?0???0???0010?0

Sinovenator changii

?0???0002?00001111001010 1?1110?011?0???2??0011
???011?10100??????000?001??????0000011110?1?????
11?1010001101 0?001000110221?1??????????110111??
?????1000?0?????211?010111{**02**}0301?1110211201?
11110000??1101000011 1??110?00?000???000011000
10001100

Mei long

?0??????????????????11010?**?**???0?11?000012100001?10
?110??100??????00010010??1?0000?021???01?001101
1100011?1010?01???0110221111?11????111?11100?0
?1?1000000 1??12111?1??1100301?1110211???01111
00?0101101?00??110011?0?0000???00000??000100?1
??0

EK troodontid (IGM 100/44)

?????0012???1??
0????????????????1??11???????????1??????0??????????????
??????????????????????????????????????10?00000?????????
??????????????????????????????????????01?1?001???00??
????0?0??1??????????0?

Segnosaurus galbinensis

??
??????????1??10?0000?000???01000001???????????????

????????0????????????????????11???00????????010?1002
1?0000?110**0**211?0?1020?0?????????00??0?00??0000?
21?0??00????1??0?0???00?0?00??0?

Erlikosaurus andrewsi

?0110??02?0?1?0??1010011100??0001?100000100
001000?0??00000??11112100100000020001?001000
001???0??
??
0?00?0??????00??01??00?0?00???????????

Alxasaurus elesitaiensis

??
?????????210?100????????????100?001??????????0?0100
0000?1?000??02?0?1???????????????00000?100?000011
0021?00?01010?211?021?2??????01????00????????000
00210000??00??1??00?0??00?0?00??00

Tyrannosaurus rex

?10000?01100001002100000101010000000001100001
0211000010010001?000000000100110010000000001
010110100000?00001010000000100000?001000??1????
?000000010000??0??100010010001000000001011011
0000001?010010000?000100000200000000100000000
000000000?0?001000

Albertosaurus libratus

?10000?00?0???????100000101?100000000110000??21
100?010010001????000000100?100100000000010101
10100000??0001010000000100000000100000?10001000
000001000000000?010001001000100000000101100100
00001001000000001000100000200000000100000000000
000?000?0?001000

Shenzhousaurus orientalis

???0?????????????????210001?10?0??1???000??00?000?0
0?????????????0?00000000??0??0?1?12?0??1????????????
0????0???0???00000???0??????????????????????????????0010
000001??110?000**0**10??000000100??00001?0??????????
??????????0??1??1?0011?????00???0010??

Ornithomimus edmonticus

?01010?110?101?10102100010101010**1**011000000000
00000001000000000??????000000000010?1001?1???????
0?001?10110000100000101000000000100100 1?????0
1120002000000 0?102001000000110000101001000 0
0010010000001100010001000000203?00?0111111101
21110000?0?001000

Archaeornithomimus asiaticus

??
???00?101100001000
001?100000000?0??????????01?200?20000?0010**0**{**12**
}0???000?110000101001?00?001001000001?0001000
1000000?0?00001?11??10??1?1??00?00?001000

Anserimimus planinychus

??
??0?????
?????????????0???????????1???0?2????000?102001000000
11000010100????000?001?????????????????00002?3?00
????11??10??1?1??00?0?001000

Huaxiagnathus orientalis

?01?0????????????????0001???1???0?????00??0???????????
?????????????00?0010????????00010?1010?00??0???1??
??????0??????00???0?100010????000000000?00??0010
000000020?0??000000100?000011?0???0??????0??0?0
10000000?0?011??000???00?0??00?0?0010?0

Sinosauropteryx prima

001?0????????????????0001???1???0?????0000??????00??1
10????????????00??01?????????0001001010?00??01??10
0????1?0?0???00?110010001 0?????00000000?10??00
11000?00020??????0000100?000?11?0?1?00?0??000?0
?0100000000?011??0000??000?0??00?0?000??0

Compsognathus longipes

?01?0?????????????????????1???????00000?????11?????
??00??????????0000010??1?????0001001010100??01??0
0?????0?0?????000???0010001??????0?000000?10???0?
??00??0??????????0000100?000?01?0???????????00?0???0
000000000001100?00????0?????00?0?001000

Buitreraptor gonzalozorum

?0110?????????????????00001011?00???????????100?10??0
011?0???????????00??001??????????**0**210??100?00101111
00111?010???100011012?121???????01101111010?1?
10??0???????11?101??11{**02**}**2**???01???1?120???11?0??
0??1?011?0?1110000????????1????????11010001100

Neuquenraptor + Unenlagia

??
??1111111
[12]?10???1????1?????????????0??1001??????????????01111
?1011111002?10110?111202011?10000??0?000??1111
00000????0??11????0??110110?110?

APPENDIX 3

DISCUSSION OF THE CHARACTERS IN CURRIE AND VARRICHIO (2004)

The character descriptions follow the wording used by Currie and Varricchio (2004) exactly. The numbers preceding the descriptions correspond to Currie and Varricchio's numbers, except when changes are specified with a bracketed number.

1. Articular, vertical columnar process on retroarticular process: 0, absent; 1, present (Currie, 1995). Accepted without comment.

2. Basipterygoid process: 0, moderately long; 1, very short. *Velociraptor mongoliensis* (IGM 100/982) preserves basipterygoid processes that are moderately long (see Norell et al., 2004: fig. 5.2c). The character state was rescored from uncertain (?) to state 0.

3. Braincase, endocranial cavity: 0, typical size; 1, enlarged, but temporal musculature extends onto frontals. This character is used here in its current wording; however, it is worth noting that the character state "typical size" does not define a particular morphology. A more quantitative description of what is the "typical size" theropod braincase is needed in order to truly delimit the character state.

4. Braincase, trigeminal nerve, separation of ophthalmic branch: 0, no; 1, incipient; 2, complete (Bakker et al. 1988). The composite-coded supraspecific taxon Troodontidae is scored as having a completely separated ophthalmic branch of the trigeminal nerve (state 2). While this is indeed present in the derived *Troodon formosus*, all other troodontids we have seen (*Byronosaurus jaffei* and *Saurornithoides junior*) that preserve the CN V exit have a single foramen, suggesting an undifferentiated trigeminal nerve in these taxa.

5. Dentary: 0, thick when compared to height, deep Meckelian groove; 1, thin and high with shallow MG and dental shelf (Currie, 1995). Although not explicitly stated in the character definition, the primitive condition refers to a mediolaterally broad dentary (i.e., "thick"). The depth of the Meckelian groove does not necessarily covary with the height/width ratio of the dentary, however. While most dromaeosaurids have a thin and high dentary with a shallow, broad Meckelian groove (Currie, 1995), *Sinornithosaurus milleni* has a deep Meckelian groove even though the dentary is high-sided and narrow (Xu and Wu, 2001). Reference to the depth of the Meckelian groove was not considered when scoring this character in the current analysis.

6. Dentary, lateral view: 0, tapers conspicuously anteriorly; 1, upper and ventral margins subparallel (Currie, 1995). Accepted without comment.

7. Ectopterygoid, ventral recesss: 0, absent; 1, present and comma shaped; 2, present and subcircular. No taxa in the Currie and Varricchio (2004) dataset were scored for an absence of the ventral ectopterygoid recess (state 0). Indeed, this character is present in most of the Theropoda (Witmer, 1997). Therefore, absence of such a recess is of limited utility in resolving coelurosaurian relationships. *Bambiraptor feinbergorum* was rescored for this character in the present analysis. Currie and Varricchio (2004) scored a ventral ectopterygoid recess as unknown (?) in *Bambiraptor feinbergorum*. However, examination of the ectopterygoid of *Bambiraptor feinbergorum* (AMNH FR 30554) clearly demonstrates that a recess was indeed present. However, due to crushing of the element, the exact shape of the recess cannot be determined. To reflect this, the character is rescored in the present analysis as "either state 1 or state 2".

8. Exoccipital–opisthotic, paroccipital processs: 0, no pneumatization; 1, pneumatized in proximal part. This character appears to reference the invasion of the caudal tympanic recess into the paroccipital process present in some theropod taxa. A caudal tympanic recess is not evident in *Allosaurus fragilis* (Madsen, 1976) or *Sinraptor dongi* (Currie and Zhao, 1993), while most coelurosaurs (e.g., dromaeosaurids, ornithomimosaurs, *Erilikosaurus andrewsi* [Clark et al., 1994], *Sinovenator changii*) have a caudal tympanic recess on the anterior face of the paroccipital process. *Archaeopteryx lithographica* and *Tyrannosaurus rex* have a recess that is on the opisthotic, deep to the paroccipital process, opening just dorsal to the fenestra ovalis (an area topologically equivalent to the collumellar recess). Currie and Varricchio (2004) score *Coelophysis* as lacking a pneumatic paroccipital process. Raath (1985) described *Syntarsus rhodesiensis* as having a caudal tympanic recess, medially placed on the paroccipital process. However, *Piatnitzkysaurus floresi* (Rauhut, 2003) does not have a clear caudal tympanic recess; Rauhut (2003) interprets a groove on the paroccipital process as the jugular vein track. Tykoski (1998) interprets a similar groove on *Syntarsus kayentakae* to be for the jugular vein as well (contra Raath's interpretation). We follow the codings of Currie and Varricchio (2004) in the current analysis, with the exception of *Deinonychus antirrhopus*. Currie and Varricchio (2004) code

Deinonychus as uncertain (?). The *Deinonychus antirrhopus* braincase described by Brinkman et al. (1998), however, has pneumatic paroccipital processes. Consequently, this was rescored as present (state 1) in the current analysis.

9. Exoccipital–opisthotic, paroccipital process: 0, occipital surface of distal end oriented more posteriorly than dorsally; 1, conspicuous twist in the distal end oriented more dorsally than proximal end (Currie, 1995). *Bambiraptor feinbergorum* was scored as having a conspicuous twist in the distal end oriented more dorsally than the proximal end (state 1). Reexamination of the holotype material of *Bambiraptor feinbergorum* (AMNH FR 30554) reveals that the distal extremities of the paroccipital processes are damaged. Consequently, we were unable to repeat Currie and Varricchio's (2004) observation, and this character's scoring in *Bambiraptor feinbergorum* was changed to uncertain (?) to reflect this.

10. External auditory meatus: 0, does not extend beyond level of intertemporal bar of postorbital and squamosal; 1, ventrolateral process of squamosal and lateral extension of paroccipital process beyond head of quadrate (Currie, 1995). As stated, this character is confusing because it does not maintain a consistent reference frame; state 0 refers directly to the placement of the external auditory meatus relative to, presumably, the posterior margin of the intertemporal bar, while state 1 refers to the morphology of the squamosal and paroccipital process. Therefore, the character states are ambiguous and not necessarily mutually exclusive (e.g., an extreme anterior placement of the quadrate head would result in satisfying both character states 0 and 1). We interpret this character as referring to the anteroposterior placement of the external auditory meatus. Consequently, we restate this character as an external auditory meatus that does (state 1) or does not (state 0) extend beyond the posterior border of the intertemporal bar of the postorbital and squamosal. This rewording does not change the current coding of this character.

11. Frontal: 0, anterior margin of supratemporal fossa straight or slightly sinuous; 1, sinusoidal with deep pit (Currie, 1995). Accepted without comment.

12. Frontal, anterior part: 0, relatively broad and square with obtuse or W-shaped suture with nasals; 1, dorsal and ventral sutural surfaces connected by a vertical slot (Currie, 1995). Accepted without comment.

13. Frontal, lacrimal-prefrontal contacts: 0, sutures on lateral, dorsal, and/or ventral surfaces; 1, dorsal and ventral sutural surfaces connected by a vertical slot (Currie, 1995). This character is ambiguous in its current wording. It is unclear if this is referencing a notch present in the lateral surface of the frontal or the medial surface of the lacrimal. Currie (1995) indicates that the notch is in fact in the frontal. We follow the coding of Currie and Varricchio (2004) here, but note that the scoring of this character's states in *Tsaagan mangas* does not impact its phylogenetic position.

14. Frontal, supratemporal fossa: 0, limited extension onto dorsal surfaces of frontal and postorbital; 1, covers most of frontal process of the postorbital and extends anteriorly onto dorsal surface of frontal (Currie, 1995). Accepted without comment.

15. Interdental plates: 0, present and separate; 1, fused together; 2, absent (Currie, 1995). Accepted without comment.

16. Jugal: 0, does not particulate in margin of antorbital fenestra; 1, participates in antorbital fenestra. Accepted without comment.

17. Jugal, pneumatic: 0, no; 1, yes. That is, a pneumatic recess in the jugal is present or absent.

18. Lacrimal shape in lateral view: 0, L-shaped; 1, T-shaped (Currie, 1995). Accepted without comment.

19. Lacrimal, dorsal ramus: 0, dorsoventrally thick; 1, pinched and narrow; 2, absent. It is unclear if any dromaeosaurid or troodontid taxa have a dorsally directed ramus on the lacrimal. We therefore interpret this character to reference the *anterior* ramus of the lacrimal. The coding of this character by Currie and Varricchio (2004) is retained here, although we note that character state 2 (absence of a dorsal (*anterior*) ramus) is not scored for any taxa in the analysis.

20. Maxilla, anterior ramus size: 0, absent; 1, shorter anteroposteriorly than dorsoventrally; 2, as long or longer anteroposteriorly. We are unsure what the "anterior ramus" of the maxilla is. Theropod maxillae possess a distinct dorsal process and subantorbital process. We, therefore, interpret the "anterior ramus" of the maxilla as the region of the maxilla anterior to the dorsal process. We do not, however, espouse the use of this term.

21. Maxilla, palatal shelf: 0, narrow; 1, wide and forms part of secondary bony palate (Makovicky and Sues, 1998). Accepted without comment.

22. Maxilla: 0, no maxillary fenestra; 1, maxillary fenestra occupies less than half of the depressed area between the anterior margins of the antorbital fossa and the antorbital fenestra; 2, maxillary fenestra large and takes up most of the space between the anterior margins of the antorbital fossa and fenestra.

We differ from Currie and Varricchio (2004) in the scoring of this character. *Allosaurus* was scored as having no maxillary fenestra (state 0). However, *Allosaurus fragilis* (Madsen, 1976) certainly possesses a maxillary fenestra, as well as a "concealed" promaxillary fenestra (see Witmer, 1997). Presence of a maxillary fenestra is generally regarded as a tetanuran (Gauthier, 1986) or neotetanuran (Sereno, 1997) synapomorphy. In its current wording, what constitutes the second derived state is unclear. The cut-off for what takes up "most" of the space between the anterior margins of the antorbital fossa and fenestra is not specified and could be anywhere from 51% to 100%. However, state 1 uses the phrase "occupies less than half of the depressed area" to evaluate the size of the fenestra. Presumably, the two derived states were intended to consider the entire range of potential variation in maxillary fenestra size. Therefore, we interpret state 1 to be when the maxillary fenestra occupies half or less of the depressed area between the anterior margins of the antorbital fossa and the antorbital fenestra and state 2 to be when the maxillary fenestra occupies more than half of that same area. *Allosaurus fragilis* would therefore be scored as having state 2. Furthermore, *Atrociraptor marshalli*, originally scored as uncertain (?), is rescored here as having state 2 as well. The ventral portion of the interfenestral strut (pila interfenestralis sensu Witmer, 1997) is preserved in the holotype of *Atrociraptor marshalli* (Currie and Varricchio, 2004) and indicates a narrow strut that is less than half the width of the maxillary fenestra.

23. Orbit, length: 0, subequal to or longer than antorbital fenestra length; 1, shorter than antorbital fenestra length. Accepted without comment.

24. Orbit, margin: 0, smooth; 1, raised rim. Accepted without comment.

25. Palatine, recesses; 0, absent; 1, present. Accepted without comment.

26. Palatine, subsidiary fenestra between pterygoid and palatine: 0, absent; 1, present (Sues, 1997). Accepted without comment.

27. Parietal, dorsal surface: 0, flat with ridge bordering supratemporal fossa; 1, parietals with sagittal crest (Russell and Dong, 1993). Accepted without comment.

28. Prefrontal: 0, well exposed dorsally; 1, reduced or absent. *Bambiraptor feinbergorum* (AMNH FR 30554) lacks a distinct prefrontal ossification or sutural indication on the frontal. Thus, the scoring of *Bambiraptor feinbergorum* was changed from uncertain (?) to absent (1).

29. Premaxilla, palatal shelf: 0, absent; 1, broad (Sues, 1997). IGM 100/982 and IGM 100/976 demonstrate that a broad palatal shelf formed by palatal processes of the premaxillae is present in *Velociraptor mongoliensis*. Furthermore, *Byronosaurus jaffei* (and probably *Sinovenator changii*) demonstrate that a similar palatal shelf was present in (at least) some basal troodontids. Although the skull is broken, fragments and breakage indicate that a palatal shelf was also present in *Saurornithoides mongoliensis* (Norell et al., in review). Consequently, Troodontidae and *Velociraptor* were rescored as possessing a broad premaxillary palatal shelf (state 1).

30. Premaxilla, subnarial depth: 0, shallow; 1, higher than long. Restated, the subnarial portion of the premaxilla is either dorsoventrally narrow or dorsoventrally broad.

31. Premaxilla, subnarial-maxillary process: 0, distal end separated from maxilla by nasal; 1, distal end separates nasal and maxilla; 2, no subnarial contact between premaxilla and nasal (Currie, 1995). State 0 was not scored by Currie and Varricchio (2004) in any of the included taxa. This character would be better worded as "Maxillary process of premaxilla present, premaxilla contacts nasal ventral to external nares (0) or process absent, no contact between premaxilla and nasal ventral to external nares (1)". Taxa in the current analysis are rescored to reflect this change. Additionally, Troodontidae was changed from uncertain (?) to possessing the derived state (1) of lacking a maxillary process of the premaxilla with the nasals failing to contact the premaxilla below the external nares.

32. Pterygoid flange: 0, includes major contribution from pterygoid; 1, is formed mostly by ectopterygoid. Accepted without comment.

33. Quadratojugal: 0, L-shaped; 1, Y- or T-shaped (Currie, 1995). Accepted without comment.

34. Quadratojugal–squamosal (qj-sq) contact: 0, tip of dorsal ramus of quadratojugal contacts tip of lateroventral ramus of squamosal; 1, dorsal ramus of qj does not contact squamosal; 2, broad contact between dorsal ramus of qj and lateroventral ramus of sq. The character was rescored as polymorphic in Troodontidae for states 1 and 2. Derived troodontids have a broad contact between the quadratojugal and squamosal; however, basal troodontids like *Mei long* (Xu and Norell, 2004) lack any squamosal/quadratojugal contact. It is unclear which character state optimizes as plesiomorphic for Troodontidae.

35. Splenial, forms notched anterior margin of internal mandibular fenestra: 0, absent; 1, present.

Presumably, the primitive state refers to a smooth splenial forming the anterior margin of the internal mandibular fenestra.

36. Splenial: 0, limited or no exposure of splenial on lateral surface of mandible; 1, conspicuous triangular process on external surface of mandible between dentary and angular (Currie, 1995). Accepted without comment.

37. Surangular, horizontal shelf on lateral surface anterior and ventral to the jaw articulation; 0, absent or faint; 1, prominent and lateral; 2, prominent and pendant. This character pertains to the presence/absence and shape of the surangular shelf dorsal to the posterior surangular foramen in theropods. Presumably, state 1 "prominent and lateral" refers to a prominent and *horizontal* shelf considering that, when present, all surangular shelves are *lateral*. This rewording would thus distinguish it from the "prominent and pendant" shelf (state 2) found in *Allosaurus fragilis*.

38. Teeth, maxillary, mandibular: 0, anterior and posterior denticles not significantly different in size; 1, anterior denticles, when present, significantly smaller than posterior denticles (Ostrom, 1969). Accepted without comment.

39. Teeth, maxillary: 0, 13 to 15; 1, 11 or 12; 2, 8 to 10; 3, 16 or more; 4, none. It is unclear what basis was used to subdivide an apparently continuously varying character. Moreover, the number of maxillary teeth is known to be highly variable within particular taxa. *Allosaurus* was scored by Currie and Varricchio (2004) as having 13 to 15 maxillary teeth (state 0); however, Madsen (1976) noted that the number is known to vary from 14 to 17. This encompasses both state 0 and state 3. Currie and Varricchio (2004) scored *Velociraptor* as having 11 or 12 maxillary teeth (state 1). The holotype of *Velociraptor mongoliensis* (AMNH FR 6515; Sues, 1977), however, only has 9 or 10 maxillary teeth (state 2). This character was therefore excluded from the current analysis.

40 [39]. Teeth, maxillary: 0, almost perpendicular to jaw margin; 1, teeth inclined strongly posteroventrally. This character was newly defined by Currie and Varricchio (2004) to describe the distinct posterior inclination of the maxillary teeth in the holotype of *Atrociraptor marshalli* and *Bambiraptor feinbergorum* (AMNH FR 30554).

41 [40]. Teeth, maxillary: 0, tooth height highly variable with gaps evident for replacement; 1, almost isodont dentition with no replacement gaps and with no more than a 30% difference in height between adjacent teeth. Accepted without comment.

42 [41]. Teeth, premaxillary tooth #1, size compared with crowns of premaxillary teeth 2 and 3: 0, slightly smaller or same size; 1, much smaller (Currie, 1995). Accepted without comment.

APPENDIX 4

REVISED AND EXPANDED CHARACTER DATASET BASED ON CURRIE AND VARRICCHIO (2004) WITH THE ADDITION OF *TSAAGAN MANGAS*

A=either 1 or 2; B=polymorphic.

		1	11111	11112	22222	22223	33333	33334	4
	12345	67890	12345	67890	12345	67890	12345	67890	1
Allosaurus fragilis	01020	01000	00000	01001	02100	00000	10021	02000	0
Coelophysis bauri	00000	01000	000?0	00000	00100	00000	10010	00000	?
Atrociraptor marshalli	?????	1????	????1	????1	?21??	???11	0????	1?111	?
Bambiraptor feinbergorum	10101	1A??1	11111	10111	1101?	?1110	0110?	11110	1
Deinonychus antirrhopus	1???1	11111	1??11	11111	1101?	1?111	01101	11110	1
Dromaeosaurus albertensis	11101	12111	00111	10110	1?001	1?11?	01121	11000	0
Saurornitholestes langstoni	1?1?1	12??1	11111	1???2	1101?	???10	01121	11100	1
Velociraptor mongoliensis	101?1	12111	11111	11112	1101?	11110	01101	11100	1
Troodontidae	00120	02100	01002	10100	12011	11110	100B0	10001	0
Tsaagan mangas	10101	12101	0111?	1012?	1201?	?1110	0112?	11100	0
Sinorhithosaurus millenii	1?1?1	1?1??	10?1A	1?1??	11011	?1110	1111?	11100	0
Microraptor zhaoianus	????0	1????	?????	1????	?A???	?????	1????	1?101	?

APPENDIX 5

CODINGS FOR THE HOLOTYPE OF *TSAAGAN MANGAS* FOR THE CHARACTERS OF SENTER ET AL. (2004)

?1011	00002	01002	10001	00000	000??
?????	?????	?????	?????	?????	?????
?????	?????	?????	?????	?????	?????
?????	?????	?			