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A Partial Ornithomimid Braincase from Ukhaa Tolgod (Upper Cretaceous, Mongolia)

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ABSTRACT

Among the dinosaurian remains recently discovered by the Mongolian Academy of Sciences–American Museum of Natural History expeditions at the Ukhaa Tolgod locality (Southeastern Gobi Desert, Mongolia) are a partial braincase and cervical vertebrae of an ornithomimid dinosaur (IGM 100/987). This specimen represents the first record of an ornithomimid from this rich locality, as well as the first discovery of such an animal in Djadokhta-like beds. Although broken and slightly distorted, the preserved portion of the braincase reveals new information on the anatomy of ornithomimids. The middle ear region is enlarged and is connected to three expansive tympanic pneu-

matic systems as in other advanced theropods. The hypoglossal nerve (cranial nerve XII) is divided into three branches, a feature otherwise known among nonavian coelurosaurs only in *Troodon formosus*. Several autapomorphies of the Ornithomimidae are preserved in IGM 100/987, including expansive pneumatization of the basioccipital–exoccipital region dorsal to the basal tubera and a large depression of the posterior face of the quadrate shaft. IGM 100/987 displays subtle differences from North American ornithomimid taxa and *Gallimimus bullatus*, but a more definite taxonomic assessment must await a thorough revision of ornithomimid phylogeny.

INTRODUCTION

In the summer of 1993 the Mongolian Academy of Sciences–American Museum of Natural History expedition collected an assemblage of small theropod remains as surface float at the Upper Cretaceous locality of

Ukhaa Tolgod, Southeastern Gobi Desert, Mongolia (Dashzeveg et al., 1995). This assemblage comprised the occipital portion of a braincase, several cervical vertebrae, and a cervicodorsal vertebra of an ornithomimid

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dinosaur (IGM 100/987), as well as the remains of a new troodontid taxon (Norell et al., in prep.). The remains of these two taxa are easily separated by diagnostic features as well as size; the ornithomimid is significantly larger than the troodontid. The cervicodorsal vertebra from the ornithomimid (probably the 10th or 11th presacral) is 33 mm long, whereas the length of the 1st dorsal vertebra of the troodontid (based on the presence of a large hypapophysis and the parapophysis being partially situated on the neural arch) is only 14.2 mm. Other comparable measurements include span of the paroccipital processes (well in excess of 40 mm in the ornithomimid and ca. 34 mm in the troodontid) and width across the postzygapophyses of the axis (24.3 mm in the ornithomimid but estimated to be only 12.5 mm in the troodontid).

Currently, there are five ornithomimid taxa known from the Cretaceous of Mongolia and Inner Mongolia. These include the primitive forms *Garudimimus brevipes* (Barsbold, 1981) and *Harpymimus okladnikovi* (Barsbold and Perle, 1984), as well as the more advanced ornithomimids *Archaeornithomimus asiaticus* (Gilmore, 1933), *Gallimimus bullatus* (Osmólska et al., 1972), and *Anserimimus planynychus* (Barsbold, 1988). The first two taxa are thought to be of Early Cretaceous age, whereas there is some uncertainty with regard to the age of the Iren Dabasu beds that yielded *Archaeornithomimus asiaticus*. Although these deposits have traditionally been interpreted as being of Cenomanian age (Berkey and Morris, 1927), recent reanalysis of the fauna and stratigraphy suggests that they may in fact be Campanian (Currie and Eberth, 1993). *Gallimimus bullatus* is known from a number of Upper Nemegt sites, and *Anserimimus planynychus* is from the Bugin Tsav locality, which has been considered a temporal equivalent of the Late Campanian to Maastrichtian Nemegt Formation (Jerzykiewicz and Russell, 1991). Jerzykiewicz and Russell (1991) listed the occurrence of an indeterminate ornithomimid from the Barun Goyot Formation without referral to a specific specimen or locality. Barun Goyotian localities listed by these authors extend over a considerable area, and their stratigraphic relationship to each other

and to other Djadokhta-like and Nemegt beds is unresolved. No other ornithomimids have been reported from Djadokhta or Djadokhta-like beds in Central Asia.

The ornithomimid braincase was only marginally treated by Parks (1928) and Russell (1972) but was treated in more detail by Osmólska et al. (1972) and Barsbold (1983). Currie and Zhao (1994a) revised several of the interpretations of braincase foramina presented in Osmólska et al. (1972). Descriptions of the ornithomimid IGM 100/987 will be supplemented with descriptions of an occipital portion of a braincase of *Struthiomimus altus* (AMNH 5355) when relevant to interpretation of structures in the former and also when assaying structural differences in ornithomimid braincases. Specimen 5355 was collected by an AMNH expedition in 1914 to the Dinosaur Park Formation (Campanian) of Alberta, Canada, but it has only been briefly discussed and figured by Russell (1972).

INSTITUTIONAL ABBREVIATIONS: **AMNH**—American Museum of Natural History (Vertebrate Paleontology Collection), New York; **IGM**—Institute of Geology, Mongolia, Ulaanbaatar; **ROM**—Royal Ontario Museum, Toronto; and **TMP**—Royal Tyrrell Museum of Palaeontology, Drumheller.

REFERRED MATERIAL: Derived characters of Ornithomimidae present in IGM 100/987 include a posteriorly excavated quadrate shaft (personal obs.), large subcondylar recesses (Witmer, 1997), a deep excavation below the ligament scar of the anterior face of the neural spine on the cervical vertebrae (Makovicky, 1995), and an expanded flange on the anterior face of the last cervical rib (personal obs.).

DESCRIPTION

Only the occipital region of the braincase is preserved in IGM 100/987, comprising the supraoccipital, both exoccipital-opisthotics, the basioccipital, the posteroventral part of the basisphenoid, the posterior part of the right prootic, and the shaft of the right quadrate with a sliver of the quadratojugal adhering to it (fig. 1A). The braincase is slightly distorted with the left exoccipital displaced dorsally relative to the right one. The basi-

sphenoid is disarticulated from, but in close association with, the basioccipital. Erosion of the anteromedial portion of the prootic exposes the inside of the floccular recess (fossa auricularis) and the internal aspect of the vestibular pyramid.

The supraoccipital forms the median dorsal border of the foramen magnum (fig. 1A). At the midline, the supraoccipital forms a transversely convex bulge that rises anterodorsally to meet the parietals. Unlike the supraoccipital of *Struthiomimus altus* (AMNH 5355) (fig. 2A), which bears a low median crest, the posterior surface of the supraoccipital is smooth in IGM 100/987 as it is in *Galimimus bullatus* (IGM 100/12). As in *Galimimus bullatus* (IGM 100/11; IGM 100/12) and *Dromiceiomimus samueli* (ROM 840), the dorsal border of the median bulge is horizontal, reflecting the flat morphology of the skull roof. On either side of the bulge, the supraoccipital levels out laterally and forms an expanded, but dorsally concave, shelf that sutures to the mediodorsal part of the exoccipital. Medially, a vertical pillar of bone forms the internal wall of the braincase dorsal to the prootic and anterior to the exoccipital. The supraoccipital contributes to the dorsal part of the vestibular pyramid. A large trough coursing posteroventrally along the base of the preserved part of the bone represents the dorsal wall of the floccular recess (figs. 1B, G). The anterior and lateral walls of the recess are lost; its ventral extremity is preserved on the prootic. The exact shape of the floccular recess cannot be determined due to relative displacement between the bones that form it.

As in other dinosaurs, the exoccipital and opisthotic form a single compound bone with no discernible border between centers of ossification (Currie, 1997). The exoccipital-opisthotics make up most of the foramen magnum border (fig. 1A). Ventrally, each exoccipital-opisthotic bears a posteroventrally directed process that rests upon the basioccipital and contributes approximately 20% of the occipital condyle. Above the pedicel that reaches the occipital condyle, the exoccipital boundary of the foramen magnum is emarginated into a thin edge. Adjacent to the foramen magnum, the exoccipital-supraoccipital suture is sinuous; a small convexity on

the exoccipital fits into a small concavity of the supraoccipital margin. Lateral to the foramen magnum, the posterior face of each exoccipital-opisthotic is shallowly concave but becomes convex farther laterally on the paroccipital process. The left paroccipital process is broken at its base, whereas the right one is missing only the distal tip. The latter fracture reveals that the interior of the paroccipital process is hollow. Its ventral surface is perforated by a large pneumatic foramen, which opens into the middle ear region and marks the entry of the posterior tympanic recess (fig. 1E). Posteromedial to this fossa, the exoccipital-opisthotic forms the metotic strut, which descends toward the basioccipital and forms the posterior wall of the middle ear chamber. Two large and three smaller foramina perforate the right exoccipital in the triangular region between the metotic strut, the suture with the basioccipital, and the occipital condyle on the posterior cranial surface (figs. 1A, F). The two larger foramina are lateral to the smaller ones. The dorsal of the two larger foramina passes through the metotic strut into the middle ear region and represents the vagus foramen (cranial nerve X and XI). The ventral foramen does not enter the braincase and is an accessory pneumatic feature termed the subcondylar recess by Witmer (1997). The hypoglossal nerve exits the braincase through the vertically oriented series of three smaller apertures near the base of the occipital condyle (fig. 1F).

The exoccipital-opisthotic forms a small portion of the interior braincase wall, posterior to the prootic and posteroventral to the supraoccipital. A tall, elongate depression is situated adjacent and parallel to the sharp edge bordering the foramen magnum (fig. 1F). A small depression is present in a similar position in *Dromiceiomimus samueli* (ROM 840), *Dromaeosaurus albertensis* (Currie, 1995), *Troodon formosus* (Currie and Zhao, 1994a), and *Velociraptor mongoliensis* (IGM 100/976). In *Struthiomimus altus* (AMNH 5355) this pit is situated on the border of the foramen magnum and opens posteriorly (fig. 2A). Currie (1995) identified this structure as the opening of the endolymphatic duct in *Dromaeosaurus albertensis*, but its position posterior to the metotic strut



Fig. 1.

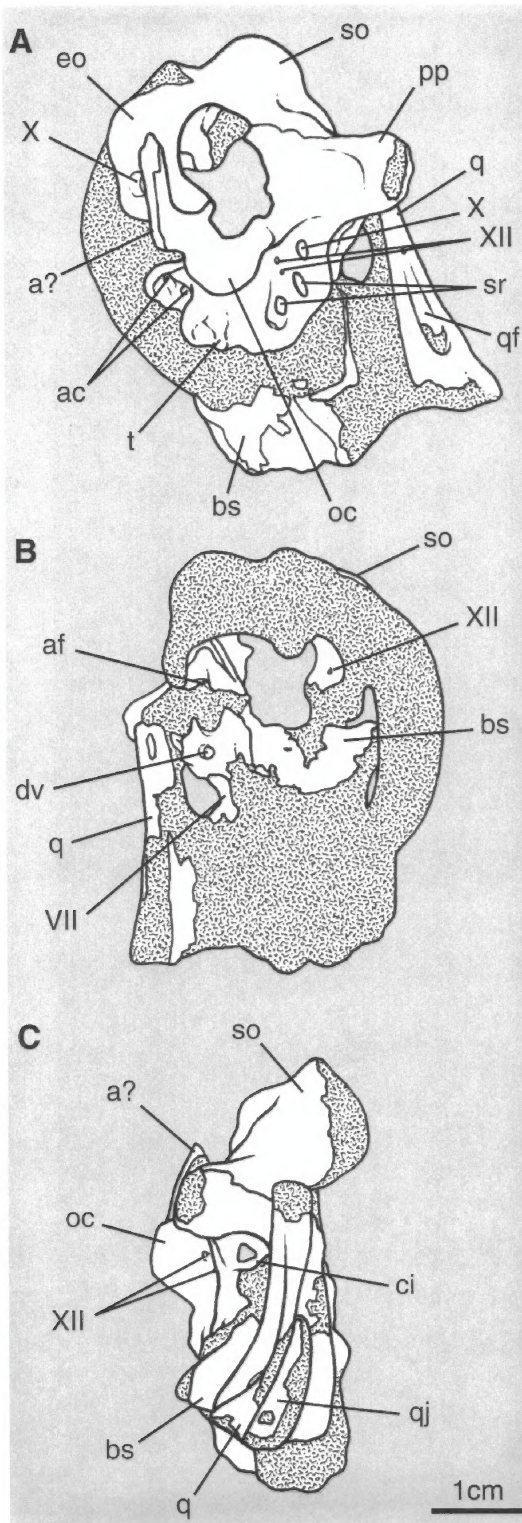


Fig. 1. (Continued)

clearly shows that it represents some other anatomical feature perhaps associated with the posterior cerebellar venous sinus (Sues, 1997). Anterior to this depression in IGM 100/987, the exoccipital forms the posteroventral portion of the vestibular pyramid. Erosion precludes positive tracing of the semicircular canals through this bone.

Just over half of the occipital condyle is formed by the basioccipital. On each side of the condyle, the suture with the exoccipital descends ventrolaterally. The condyle is dorsoventrally flattened and not spherical as it is in troodontids (figs. 1A, 2A). A distinct neck between the condyle and braincase, as is present in troodontids, is not present in either IGM 100/987 or AMNH 5355 (figs. 1E, 2E). As in a majority of theropods, the dorsal surface of the condyle is transversely concave. Sues (1997) suggested that this concavity articulated with the dens or atlas centrum, but this is doubtful given the relative proportions of the dens and the occipital condyle in most nonavian theropods and the negative allometry of the occipital condyle to foramen magnum ratio within the group (Currie and Zhao, 1994b). Unlike the small tablike dens in Aves (Baumel and Witmer 1993), the atlas centrum is large and subspherical in ornithomimids (TMP 93.62.1). Rather, the con-

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Fig. 1. Braincase of ornithomimid indet. IGM 100/987 in (A) posterior, (B) anterior, (C) lateral views. Abbreviations: **VII** facial foramen; **VIIIc** exit for cochlear branch of vestibulocochlear nerve; **VIIIv** exit for vestibular branch of vestibulocochlear nerve; **X** vagus foramen; **XII** foramina for hypoglossal nerve; **a?** ?atlas fragment; **ac** accessory pneumatic connections; **af** floccular recess; **bo** basioccipital; **br** basisphenoid recess; **bs** basisphenoid; **bt** basal tuber; **ci** crista interfenestralis; **d** depression at suture between exoccipital and supraoccipital; **dtg** groove leading to dorsal tympanic recess; **dtr** dorsal tympanic recess; **dv** vestibule; **eo** exoccipital; **fm** foramen magnum; **hf** hypophyseal fossa; **mf** metotic fissure; **mo** middle ear opening; **ms** metotic strut; **oc** occipital condyle; **pp** paroccipital process; **pr** prootic; **ps** prootic recess; **ptr** posterior tympanic recess; **q** quadrate; **qf** quadrate fossa; **qj** quadratojugal; **so** supraoccipital; **sr** subcondylar recess; **ss** subotic recess; **t** tubercle.

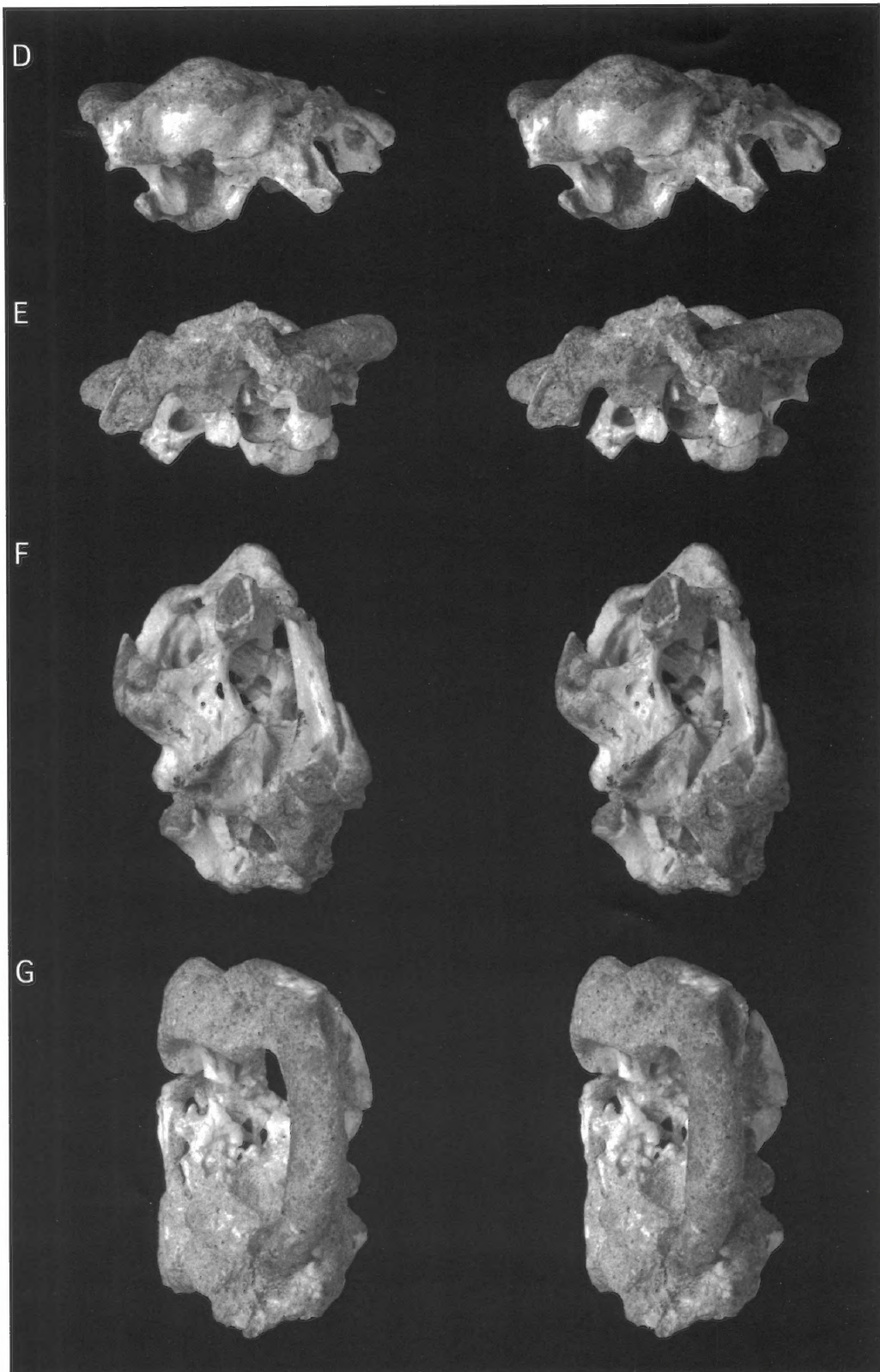


Fig. 1 (*continued*). Braincase of ornithomimid indet. IGM 100/987 in (D) dorsal, (E) ventral, (F) posteroventrolateral oblique, (G) anterolateral oblique views. See previous caption for abbreviations.

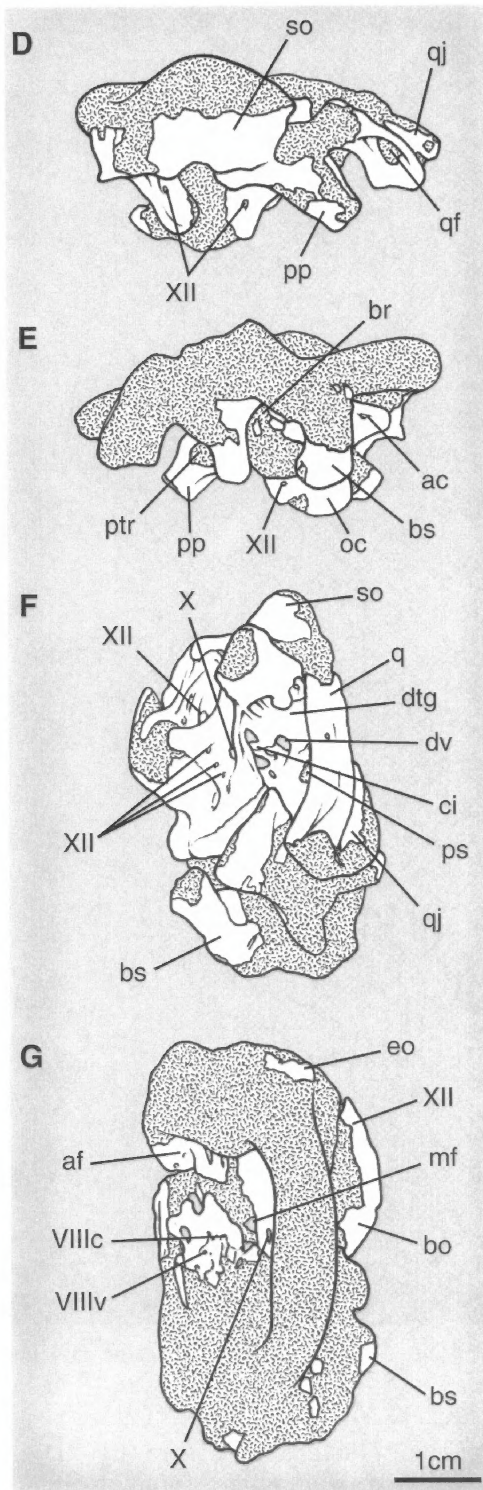


Fig. 1. (Continued)

cave surface of the condyle may have formed a floor for the medulla oblongata. The slightly rugose articular surface of the occipital condyle wraps onto the ventral surface of the condyle in IGM 100/987. A similar feature is developed in *Gallimimus bullatus* (IGM 100/11) and *Struthiomimus altus* (AMNH 5355) and indicates that the occipital condyle articulated posteroventrally with the atlas intercentrum. The basal tubera of IGM 100/987 are modest in size and ventrally rounded. A shallow depression for a ligament separates the two tubera. A small tubercle is present beneath this depression (fig. 1A) between the ventral extremities of the two tubera. Currie and Zhao (1994a) interpreted a small pit in this region in *Troodon formosus* as marking the attachment point for a ligament from the neck musculature. Dorsolateral to each basal tuber, the basioccipital is excavated by a large pneumatic pocket from which several foramina contribute to the subcondylar recess (Witmer, 1997).

The basisphenoid of IGM 100/987 is disarticulated and shifted a short distance away from the basal tubera. It is also broken along the median axis through the middle of the ventral recess. Although not fully preserved, this recess apparently was proportionately deep as in *Gallimimus bullatus* (IGM 100/11; Osmólska et al., 1972) and *Dromiceiomimus samueli* (ROM 840). The basisphenoid appears to be partially divided by a low, longitudinal ridge on the roof of the recess in *Struthiomimus altus* (AMNH 5355), but this character cannot be ascertained in IGM 100/987. The basisphenoid forms a large part of the braincase floor anterior to the basioccipital and exoccipitals. Three foramina perforate a lateral wing of the basisphenoid below the middle ear recess (fig. 1A, E), demonstrating that the series of pneumatic spaces in the basisphenoid (subotic recess of Witmer, 1997) is connected to the anterior pneumatic spaces of the anterior tympanic recess, as in *Troodon formosus* (Currie and Zhao, 1994a).

Internally, the prootic forms the lateroventral portion of the braincase wall (figs. 1B, 2D). Opposite the exoccipital-opisthotic, the posterior edge of the prootic defines the anterior rim of the middle ear. A small, finger-like process, which is broken dorsally and

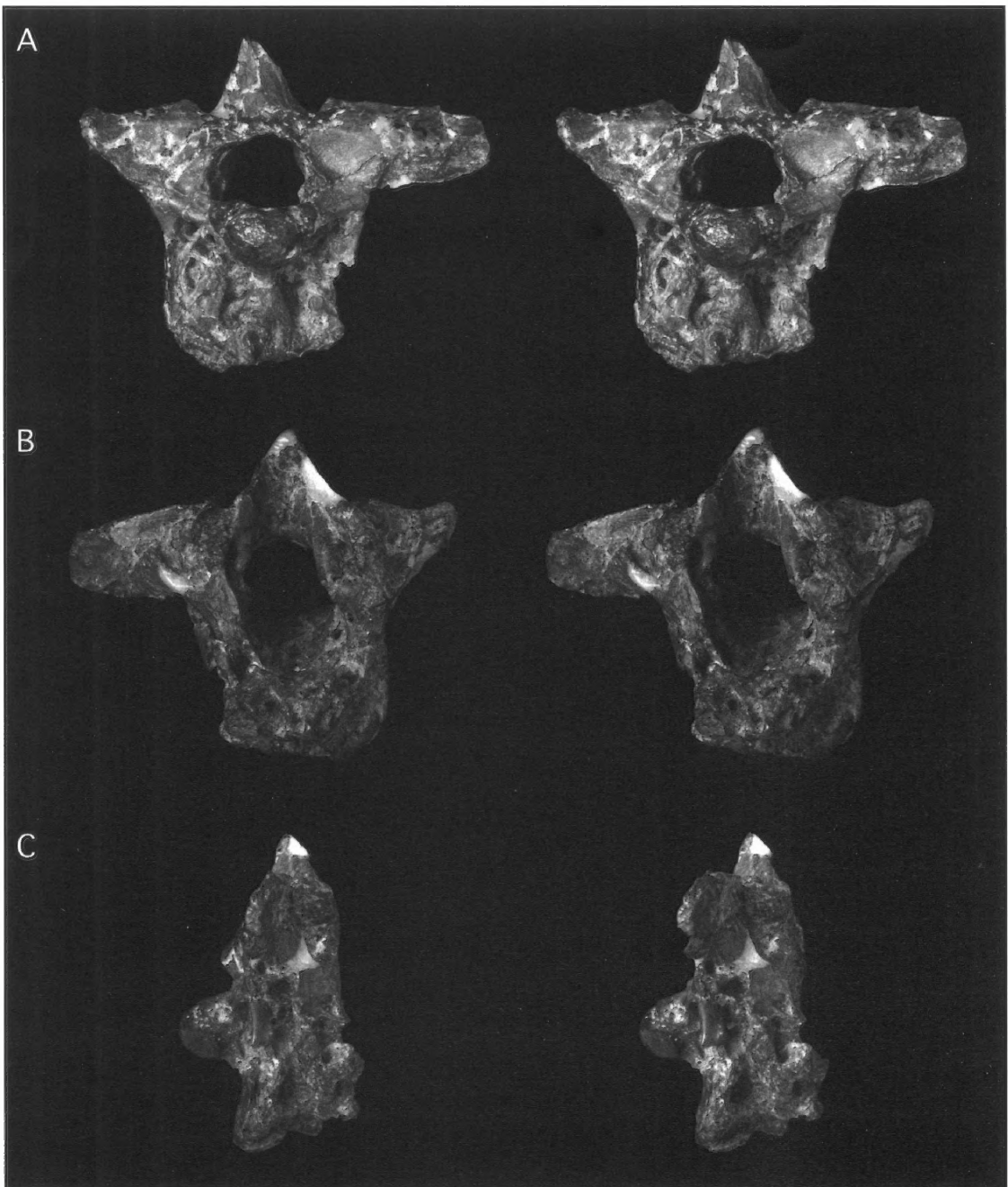


Fig. 2. Braincase of *Struthiomimus altus* (AMNH 5355) in (A) posterior, (B) anterior, (C) lateral views. See fig. 1 for abbreviations.

crosses horizontally across the top of the middle ear, may represent the dorsal part of the crista interfenestralis or promontorium (fig. 1C, F). The exit of the cochlear branch of cranial nerve VIII is found anterior and medial to this process at the preserved an-

terior rim of the metotic fissure (fig. 2D). Absence of a perilymphatic foramen indicates that the anterior rim is not fully preserved. In the troodontid (IGM 100/983) collected together with IGM 100/987, the perilymphatic opening is located on the anterior rim

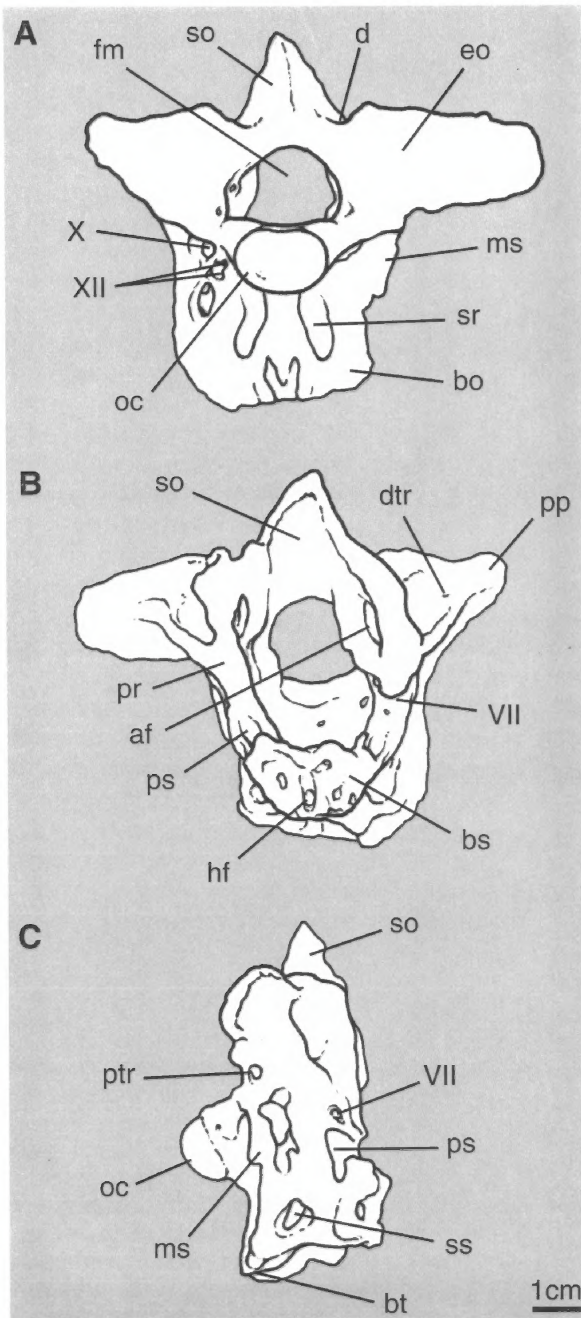


Fig. 2. (Continued)

of the metotic fissure and opens toward the posterior. The opening into the vestibule lies anterolateral to the cochlear exit of the vestibulocochlear nerve, and the vestibule itself courses anterodorsally beneath the vestibular pyramid. A circular cross section of the vestibule is exposed in anterior view by the frac-

ture that runs through the prootic (fig. 1B). This cross section is visible just beneath the ventral border of the floccular recess. A thin lamina of bone forms the anterior wall of the floccular recess. The space anterior to this lamina may have been a pneumatic recess, as seen in *Troodon formosus* (Currie and Zhao, 1994a: fig. 2). A large prootic recess (Witmer, 1997), which is part of the anterior tympanic system, is present on the lateral face of the prootic anteroventral to the acoustic fossa (fig. 1F). A similar depression is found in *Velociraptor mongoliensis* (IGM 100/976), *Gallimimus bullatus* (IGM 100/11), *Struthiomimus altus* (AMNH 5355), and in troodontids (Currie and Zhao, 1994a).

A shallow groove that begins near the opening of the inner ear courses dorsolaterally away from the middle ear and approaches the base of the paroccipital process (fig. 1F). It leads to the dorsal tympanic recess and marks a pneumatic connection between the middle ear and a pneumatic fossa anterodorsal to the paroccipital process. Although not preserved in IGM 100/987, such a depression is well developed in *Dromiceiomimus samueli* (ROM 840), *Struthiomimus altus* (AMNH 5355), and *Gallimimus bullatus* (IGM 100/10; 100/11; 100/12) and extends from the dorsal part of the prootic above the facial foramen on to the opisthotic, where it excavates the base of the paroccipital process anteriorly (fig. 2B, G). Dorsal tympanic recesses are also encountered on the prootic and opisthotic of some other advanced theropods (Witmer, 1997), including oviraptorosaurs (IGM 100/42), avialans (Walker, 1985), and some, but not all, troodontids (present in IGM 100/983 but absent in *Troodon formosus* [Witmer, 1997]).

The posterior wall of the exit for the facial nerve (cranial nerve VII) is visible on the preserved anterior rim of the right prootic (fig. 1B). By comparison with AMNH 5355, two foramina on the internal face of the acoustic fossa of IGM 100/987 are here interpreted as the internal exits of the cochlear and vestibular branches of cranial nerve VIII (N. vestibulocochlearis). The two foramina are almost level with each other, as in AMNH 5355, and are situated posterior and slightly dorsal to the opening for the facial nerve. Damage to this region in IGM 100/

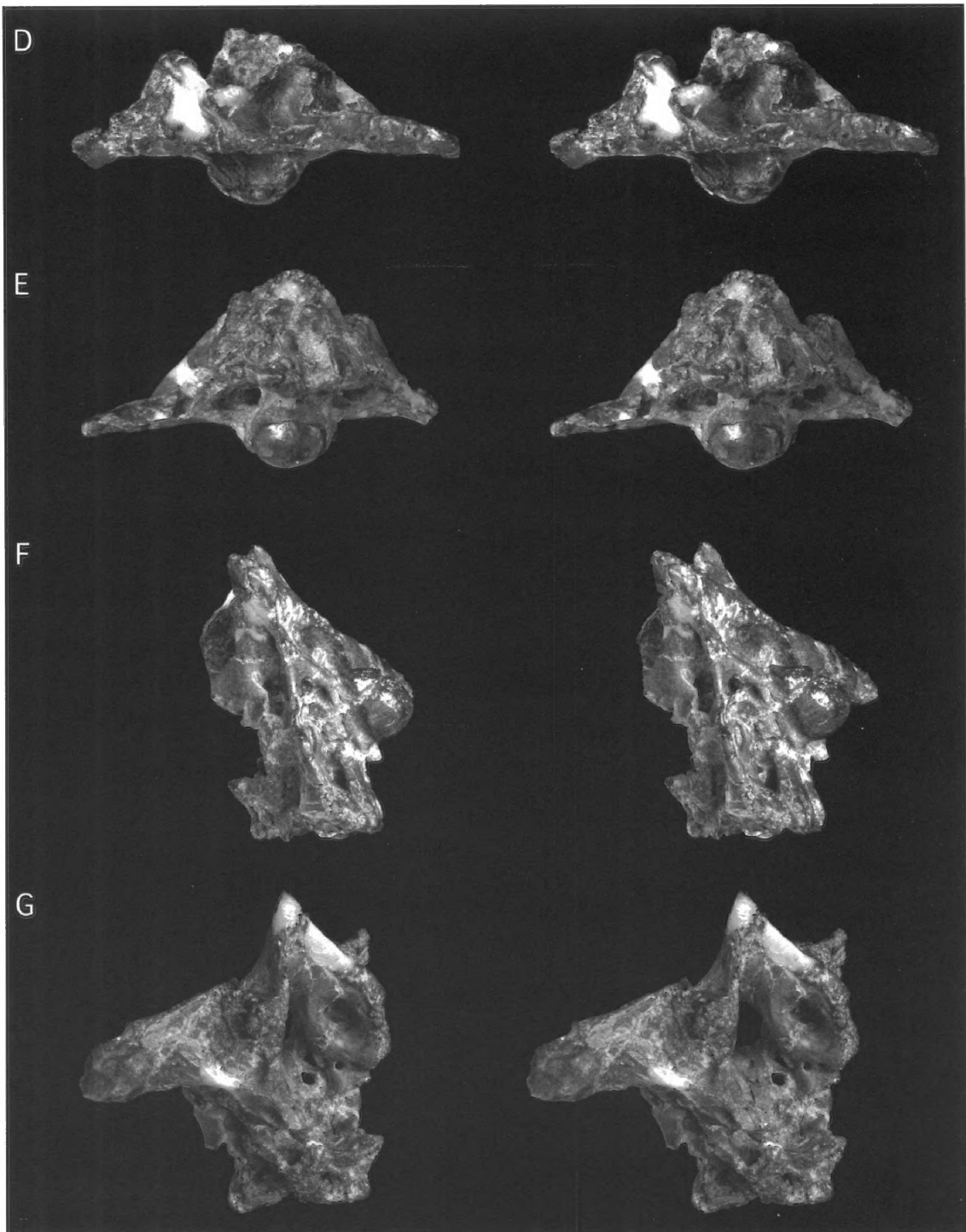


Fig. 2 (continued). Braincase of *Struthiomimus altus* (AMNH 5355) in (D) dorsal, (E) ventral, (F) posteroventrolateral oblique, (G) anterolateral oblique views. See fig. 1 for abbreviations.

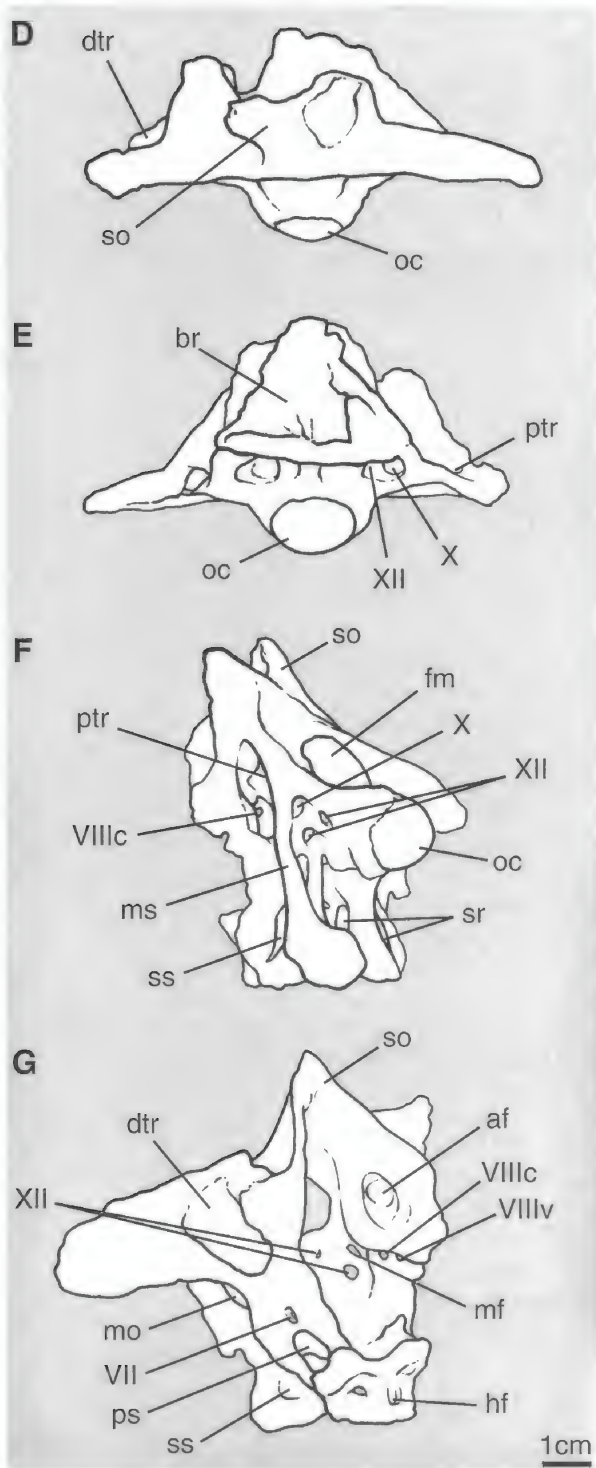


Fig. 2. (Continued)

987 obscures much of the anatomy, but in AMNH 5355 the openings for the facial and vestibulocochlear nerves lie within a shallow acoustic fossa on the inner wall of the braincase (fig. 2G). The exit for the facial nerve is set in a deep fossa on the lateral braincase wall in AMNH 5355, as in other theropod taxa.

Neither the head nor the condyle of the quadrate are preserved. The posterior margin of the preserved section of the shaft is gently bowed anteriorly (fig. 1C). It is transversely narrow and slender in comparison with the quadrates of adult specimens of *Gallimimus bullatus* (IGM 100/11; IGM 100/12), although a juvenile specimen referred to the same taxon has a transversely compressed quadrate shaft (IGM 100/10). The proportions of the shaft and condyles of the ornithomimid quadrate are tall and narrow in comparison with those of dromaeosaurids (AMNH 5616) and oviraptorids (Maryańska and Osmólska, 1997). A short section of the pterygoid wing is preserved in IGM 100/987. In cross section, the quadrate shaft is subtriangular with the anterior apex formed by the pterygoid wing. Posteriorly, a large teardrop-shaped depression is situated near the distal end of the quadrate (fig. 1C, F). Broken surfaces reveal that the quadrate is hollow, and a slitlike foramen near the dorsal end of the depression may represent a pneumatic connection into the quadrate interior. As is typical in archosaurs, the quadrate apparently formed a portion of the anterolateral wall of the external auditory meatus in ornithomimids. A small sliver of bone adhering to the lateral face of the quadrate shaft is the only preserved piece of the quadratojugal.

An elongate piece of bone adhering to the left, disarticulated side of the occipital condyle may be part of the proatlas or atlas (fig. 1A). It has no distinct features that allow positive identification.

DISCUSSION

IGM 100/987 represents the first evidence of an ornithomimid in the Ukhaa Tolgod assemblage and adds yet another taxon to an already astounding diversity of theropod dinosaurs from this locality (Norell et al., 1996). In some localities such as Iren Da-

basu, ornithomimids are numerous and occur in bone beds. Elsewhere, as in the Dinosaur Park Formation, ornithomimids are usually found individually, but their skeletal remains are still more numerous than those of other small theropods. This appears not to be the case at Ukhaa Tolgod, where discoveries of oviraptorids, dromaeosaurids, avialans, and troodontids outnumber the single ornithomimid occurrence represented by IGM 100/987. The presence of an ornithomimid in Djadokhta-like beds at Ukhaa Tolgod demonstrates once again that faunal differences between Djadokhta and Nemegt beds are more a matter of frequency than composition.

Several characters of IGM 100/987 have relevance to the study of other advanced theropods. Three tympanic recesses connect to the middle ear in IGM 100/987, as in avialans (Whetstone, 1983; Walker, 1985; Witmer, 1990) and dromaeosaurids (Norell et al., 1992). Unlike avialans and troodontids (Chiappe et al., 1996), however, the posterior tympanic recess invades the base of the paroccipital process through a large foramen (fig. 1E) instead of being confined to the columellar recess. This condition is primitive for coelurosaurs (Witmer, 1997) and is encountered in tyrannosaurids, dromaeosaurids (Chiappe et al., 1996), oviraptorosaurs (IGM 100/42), and *Erlicosaurius andrewsi* (Clark et al., 1994) as well as ornithomimids. Although the part of the prootic that bears the depression for the dorsal tympanic recess is not preserved in IGM 100/987, a groove leads from the tympanic region toward this region in IGM 100/987 and *Struthiomimus altus* (AMNH 5355). Furthermore, a deep depression is present on the anterodorsal part of the paroccipital process in *Gallimimus bullatus* (IGM 100/11), *Struthiomimus altus* (AMNH 5355), and *Dromiceiomimus samueli* (ROM 840). The dorsal tympanic recess of ornithomimids is proportionately large in comparison with the same structure in troodontids (IGM 100/983), *Velociraptor mongoliensis* (IGM 100/976), and *Archaeopteryx lithographica* (London specimen; Walker, 1985).

The anterior tympanic recess is also well developed in ornithomimids. Structures relating to it include the prootic recess ventral

to the foramen for the facial nerve (figs. 1F, 2C, G), a feature encountered widely among coelurosaurs. In dromaeosaurs and ornithomimids the prootic recess of the anterior tympanic recess is positioned directly ventral to the exit of the facial nerve (Witmer, 1997). Oviraptorids have a disproportionately elongate braincase, and the prootic recess lies anterior, rather than ventral, to the exit for the facial foramen (IGM 100/42). In troodontids this pocket is greatly expanded and confluent with the subotic recess and other air spaces within the basisphenoid (Currie and Zhao, 1994a: fig. 4; Norell et al., in prep.). The invasion of the basisphenoid (subotic recess) and basioccipital by air spaces in ornithomimids is similar to, but less expressed than, the condition found in troodontids (Currie and Zhao, 1994a). The anterior tympanic recess enters the interior of the para-basisphenoid mainly by way of the basisphenoidal recess or median pharyngeal system (Witmer, 1997) and to a lesser degree via lateral connections from the pneumatic space within the basisphenoid (Currie and Zhao, 1994a), although such connections are evident in IGM 100/987. In troodontids, the basisphenoid recess is lost, or ventrally enclosed as in ornithurine birds, and the parasphenoid bulla is connected exclusively with the anterior tympanic recess (Currie and Zhao, 1994a).

The relative positions of the foramina for cranial nerves VII and VIII on the internal aspect of the braincase appear to vary among coelurosaurs. The internal foramen of the facial nerve lies anteroventral to those of the vestibulocochlear nerves in AMNH 5355 and IGM 100/987. The vestibular branch of cranial nerve VIII is positioned anterior and only slightly ventral to the exit of the cochlear branch. By contrast, the facial nerve exits the braincase directly ventral to the vestibular exit of cranial nerve VIII in the holotype of *Dromaeosaurus albertensis* (AMNH 5516; Currie, 1995; fig. 6) and in *Itemirus medullaris* (Kurzanov, 1976; Currie, 1995). A unique condition is present in *Troodon formosus*, where the vestibular branch of cranial nerve VIII does not appear to have a separate exit but passes through the braincase together with the facial nerve (P. Currie, personal commun.). In the Ukhaa Tolgod troodontid, however, the two branches of the ves-

tibulocochlear are separate from the facial nerve, as in ornithomimids. *Tyrannosaurus rex* also displays three separate openings in the acoustic fossa (Osborn, 1912), but, when the braincase is oriented with the foramen magnum facing posteriorly, the configuration is that of a triangle where the exit of the facial nerve lies anterior to the openings for cranial nerve VIII, with the vestibular and cochlear branches of the latter nerve exiting dorsoposterior and ventroposterior, respectively, to the facial nerve. The two openings for cranial nerve VIII are situated posterior to the exit for cranial nerve VII in *Chirostenotes pergracilis* (Sues, 1997).

Citing a personal communication from S. Chatterjee, Currie and Zhao (1994a) stated that the vagus foramen is directed anterolaterally in ornithomimids, but it is directed anteromedially in both IGM 100/987 and *Struthiomimus altus* (AMNH 5355), as it is in troodontids and *Dromaeosaurus albertensis* (AMNH 5516). IGM 100/987 displays a third small foramen for a branch of the hypoglossal. Such a foramen is present in some extant birds but has not been reported widely in other theropods, although it is present in *Troodon formosus* (Currie and Zhao, 1994a). The number of hypoglossal exits is indeterminate in *Struthiomimus altus* (AMNH 5355). The number of hypoglossal foramina is highly variable in extant archosaurs, displaying even interspecific variability.

In many respects, ornithomimid braincase anatomy is similar to that of troodontids. Common derived features include a bulbous parabasisphenoid (not preserved in IGM 100/987), expansion of the anterior tympanic recess to invade the basisphenoid (also in *Velociraptor mongoliensis* [IGM 100/967]), the relative positions of the facial and vestibulocochlear nerve (also in Avialae [Witmer, 1990] and *Velociraptor mongoliensis* [IGM 100/967] but not *Dromaeosaurus albertensis*), and three exits for the hypoglossal (also in some extant avialans). These similarities contrast with substantial differences in the postcranial skeleton, where troodontids display many maniraptoran apomorphies not present in ornithomimids.

A number of features of the ornithomimid braincase region are potentially autapomorphic, including the presence of pneumat-

ic subcondylar recesses that open posteriorly on the basioccipital and exoccipital, just dorsal and lateral to the basal tubera. The presence of a large depression on the posterior face of the quadrate shaft is also unique to ornithomimids among coelurosaurian dinosaurs. The quadrate is hollow, and a slitlike foramen in the depression may have connected the interior to the tympanic pneumatic systems, as in birds (Witmer, 1990) and some nonavian theropods such as troodontids (Currie and Zhao, 1994a), tyrannosaurids (Molnar, 1985), and oviraptorids (Maryańska and Osmólska, 1997). Examination of other ornithomimid skulls (ROM 851; ROM 840) has not revealed such a connection to the exterior, however, and this feature may be either an artifact or a derived character of IGM 100/987.

IGM 100/987 differs from preserved cranial material of other advanced ornithomimids in a number of subtle features. The basal tubera of IGM 100/987 are shallow and widely separated with a small tubercle occupying the center of the cleft between them. By contrast, the basal tubera of *Struthiomimus altus* (AMNH 5355) are deeper, and separated by only a narrow cleft. In *Gallimimus bullatus* (IGM 100/12) the basal tubera are also proportionately deep, but preservation does not permit a determination of the extent of their separation. Another difference between *Struthiomimus altus* and IGM 100/987 is the absence of a midline ridge on the supraoccipital of the latter taxon, a similarity it shares with *Gallimimus bullatus* (Osmólska et al., 1972; IGM 100/12). IGM 100/987 differs from the holotype of *Gallimimus bullatus* (IGM 100/11) in having a proportionately narrower quadrate shaft with a more developed posterior fossa. The quadrate fossa is well developed in *Dromiceiomimus samueli* (ROM 840) and *Ornithomimus edmontonicus* (ROM 851). These differences clearly indicate that IGM 100/987 cannot confidently be referred to any known ornithomimid taxon.

Phylogenetic assessments are further complicated by possible ontogenetic changes in cranial characters. In a juvenile specimen referred to *Gallimimus bullatus* (IGM 100/10) the quadrate fossa is situated more proximally than it is in other known specimens,

and the quadrate shaft appears relatively narrow. It is currently not possible to assess whether these quadrate features display ontogenetic changes. Another difference between the juvenile specimen IGM 100/10 and other ornithomimid skulls is the presence of a large foramen on the posterior face of the paroccipital process. Such a foramen is not widely distributed among advanced theropods but is encountered in some, although not all, dromaeosaur specimens (IGM 100/967).

Advanced ornithomimid taxa are currently diagnosed mainly by different proportions between limb bones (Russell, 1972; Barsbold and Osmólska, 1990) and the form of the manual unguals, elements not recovered for the Ukhaa Tolgod ornithomimid. Furthermore, braincase anatomy remains undescribed or unknown in a majority of named ornithomimid taxa, so it is possible to refer IGM 100/987 only to Ornithomimidae indeterminate. A more exact taxonomic placement of IGM 100/987 must await description of new material and, above all, a reevaluation of ornithomimid phylogeny based on discrete osteological characters.

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