Osteology of *Khaan mckennai* (Oviraptorosauria: Theropoda)

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OSTEOLOGY OF *KHAAN MCKENNAI* (OVIRAPTOROSAURIA: THEROPODA)

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CONTENTS

Abstract 4
Introduction 4
Material and Methods 8
  Material and Diagnosis of *Khaan mckennai* 8
  Geological Setting 10
  Mechanical Preparation 11
  CT Scanning 11
Cranial description 11
  Premaxilla 13
  Maxilla 16
  Nasal 17
  Frontal 18
  Parietal 19
  Lacrimal 23
  Jugal 24
  Postorbital 24
  Squamosal 25
  Supraoccipital 25
  Exoccipital 25
  Basioccipital 26
  Parabasisphenoid 26
  Quadratojugal 26
  Quadrate 27
  Laterosphenoid 27
  Prootic 28
  Inner Ear 28
Mandible 29
  Dentary 29
  Surangular 33
  Angular 33
  Prearticular 33
  Articular 34
  Splenial 34
  Hyoid 34
Postcranial Description 34
  Cervical Vertebrae 35
  Dorsal Vertebrae 38
  Sacral Vertebrae 40
  Caudal Vertebrae 40
  Chevrons 42
  Sternum 42
  Scapulocoracoid 43
  Furcula 45
  Humerus 45
  Ulna 46
  Radius 47
  Manus 48
  Ilium 51
  Pubis 53
  Ischium 54
  Femur 55

- Tibia 58
- Fibula 58
- Astragalus and Calcaneum 58
- Pes 60

Discussion 61
- Pneumaticity of the Narial Region 63
- Dorsal Frontal Sinus. 65
- Accessory Antorbital Fenestrae 67
- Trigeminal Foramen 69
- Maxillary Length 69
- Postcranium 70

Summary 71

Acknowledgments 72

References 72

Appendix 1: List of Taxa Used for Comparison in Analysis 76

Appendix 2: Anatomical Abbreviations 76

ABSTRACT

The monophyly of Oviraptoridae, a group of theropod dinosaurs, which share a uniquely bizarre morphology, has never been called into question due in large part to their unusual complex of characters. Despite a vivid recent history of discovery and broad public appeal the nature of their morphological diversity has not been explored extensively. Many previous descriptions of oviraptorid taxa are lost in the obscurity of hard-to-find journals, and many lack illustrations of what are now recognized as phylogenetically important characters. The primary goal of this paper is to provide a relatively comprehensive descriptive morphology and illustrations for one member of Oviraptoridae, namely *Khaan mckennai*, with an emphasis on characters that can be used to establish a phylogenetic hypothesis for the taxon and group as a whole. *K. mckennai* is a small-bodied, crestless oviraptorid that is known from pristine material that has been collected from the Late Cretaceous sediments of Mongolia. Similar to other oviraptorids, it shares a wide number of features in common with extant birds. However, when these characters are put in the context of Oviraptorosauria, including relatively new, more basal forms like *Incisivosaurus gauthieri* and *Caudipteryx zoui*, character states such as extreme pneumatization of the skull or the reduction in the number of caudal vertebrae are found to be either homoplastic for the two groups or plesiomorphic for a more inclusive clade.

INTRODUCTION

Members of the coelurosaurian group Oviraptorosauria encompass a wide range of body shapes and sizes from the morphologically bizarre, toothed forms *Incisivosaurus gauthieri* and *Caudipteryx zoui* to crested oviraptorids like *Citipati osmolskae* and even gigantic body sizes such as *Gigantoraptor erlianensis* (approximately 8 m in length; Xu et al., 2007). Members of this clade have been known for nearly 100 years, as reasonably complete specimens were first collected by the American Museum of Natural History Central Asiatic Expeditions in 1922 at the Late Cretaceous Shabarakh Usu (Flaming Cliffs) locality in the Mongolian Gobi Desert (Osborn, 1924). The circumstances surrounding this find (the fact that it was lying on top of a nest of presumed *Protoceratops* eggs) was only the beginning of inquiry and controversy surrounding the phylogenetic relationships among and paleobiology of oviraptorosaurian taxa (Osborn, 1924; Norell et al., 1995).

Many oviraptorosaurs share convergent characters with avians (sensu Gauthier, 1986) such as a loss of teeth, extreme pneumatization and ornamentation of the skull, and reduction of the tail vertebrae to form a pygostyle (see Barsbold et al., 2000; Osmólska et al., 2004; Persons et al., 2011). Oviraptorosaur specimens also have been collected that preserve the remarkable behavior of brooding nests of eggs in the stereotypical posture of modern birds (Norell et al., 1995; Dong and Currie, 1996; Clark et al., 1999). These "birdlike" characters have led some to speculate that oviraptorosaurs are nested within Avialae (Osmólska et al., 2004; Paul, 2002). Although oviraptorosaurs have captured the imagination of the public, well-illustrated, easily accessible descriptions of these taxa are conspicuously absent from the literature with only a few notable exceptions (e.g., Sues, 1997; Ji et al., 1998; Barsbold et al., 2000; Zhou and Wang, 2000; Zhou et al., 2000; Clark et al., 2002; Vickers-Rich et al., 2002; Lü et al., 2004; Balanoff et al., 2009).

The monophyly of the group as a whole has remained relatively stable and most of the taxa positioned within the group are easily identified as oviraptorosaurs. Basal taxa include *Incisivosaurus gauthieri*, *Caudipteryx zoui*, *Avimimus portentosus*, and *Microvenator celer*. *Protarchaeopteryx robusta* has been hypothesized by Senter (2007) to be synonymous with *Incisivosaurus gauthieri*; however, this has yet to be rigorously tested. Named monophyletic groups within Oviraptorosauria include Caenagnathidae and Oviraptoridae, and these groups together have been designated Caenagnathoidea by Maryańska et al. (2002). We follow Sues (1997) for caenagnathid taxonomy. That paper gives the definition for Caenagnathidae as "*Chirostenotes pergracilis*, *Chirostenotes elegans*, an as yet unnamed large caenagnathid (Currie et al., [1993]; Triebold and Russell, 1995), ‘*Elmisaurus rarus,*’ *Caenagnathasia martinsoni*, and the most recent common ancestor of the aforementioned taxa” (Sues, 1997). Oviraptoridae is the largest of the node-based groups and includes a wide variety of taxa. Those referred to in this study include *Oviraptor philoceratops*, *Rinchenia mongoliensis*, *Nomingia gobiensis*, *Conchoraptor gracilis*, *Ingenia yanshini*, *Heyuannia huangi*, and *Khaan mckennai*. Maryańska et al. (2002) gives a stem-based definition for this taxon, which is defined as the most inclusive clade containing *Oviraptor philoceratops* Osborn, 1924, but not *Caenagnathus collinsi*.

The phylogenetic relationships among these oviraptorosaurs, however, are largely unresolved in that their relationships fail to remain congruent between analyses (e.g., Holtz, 1998; Maryańska et al., 2002; Lü et al., 2004; Osmólska et al., 2004; Lü, 2005; Senter, 2007; Turner et al., 2007b, Xu et al., 2010). Understanding relationships within Oviraptorosauria will provide needed insight into their many shared convergences with avians. Examining the acquisition of these characters within the oviraptorosaur lineage may shed light on the evolution of the same types of characters along the lineage leading to avialans. Whether Oviraptorosauria falls out as a basal member of Avialae (making it the most basal known clade among avialans to become secondarily flightless; see Maryánska et al., 2002; Paul, 2002; Osmólska et al., 2004) or as a nonavian theropod (see Holtz, 1998; Rauhut, 2003; Senter, 2007; Turner et al., 2007b, Xu et al., 2010), their relative position will have a large impact on the polarity of several characters in Avialae and their close nonavialan relatives.

Although our knowledge of more basal oviraptorosaurs has progressed extensively in the past several years (e.g., Currie and Russell, 1988; Kurzanov, 1981; 1987; Sues, 1997; Ji et al., 1998; Vickers-Rich et al., 2002; Xu et al., 2002; Balanoff et al., 2009), descriptive morphology of the node-based group Oviraptoridae has lagged behind. While many descriptions of these taxa have been produced (e.g., Barsbold, 1981; 1983; 1986), these historically have been published in journals not readily available to many scientists (in some cases in Russian) and almost all (with the exception of Clark et al., 2002) lack detailed figures of the specimens they describe.

Oviraptoridae traditionally has been divided into two lineages, the crested Oviraptorinae (Barsbold, 1976) and those taxa that lack a developed crest, Ingeniinae (Barsbold, 1981). Whether these represent monophyletic taxa or not, gaining a better understanding of the morphology of both assemblages will shed light on the diversity and evolution of the larger lineage. Clark et al. (2002) provided an important contribution to the morphology of the cranial morphology of crested oviraptorids with their detailed description of *Citipati osmolskae*, which included comparisons with *Oviraptor philoceratops*. The remaining gap in our understanding of oviraptorids can be filled only by the further description of these taxa, especially with the addition of postcranial data. Once accomplished, such descriptions will present us with the opportunity to begin to make inferences about the evolution of morphological features in this group and allow direct comparison with other more completely described taxa like dromaeosaurids and basal avialans.

The goal of this study is to provide an in-depth osteological description of the oviraptorid *Khaan mckennai*, which lacks a well-developed cranial crest (Clark et al., 2001). To this end, descriptions including comprehensive illustrations and photographs are provided for three specimens of this taxon (Clark et al., 2001). The specimens of *Khaan mckennai* described here were collected from the Late Cretaceous Ukhaa Tolgod locality in the Gobi Desert, Omnogov Aimag, Mongolia (Dashzeveg et al., 1995; Dingus et al., 2008). In 1993 (the initial year of excavation at Ukhaa Tolgod), a single specimen (IGM 100/973) was collected by Mark Norell and James Clark. Two additional specimens of this taxon were found in close proximity to each other in 1995 (IGM 100/1002 and 100/1127)—affectionately referred to as Sid and Nancy after Sid Vicious of the Sex Pistols and his girlfriend, Nancy Spungen—which represent two of the most completely known skeletons of theropod dinosaurs collected to date. Film footage of some of the excavation and transport of these specimens is recorded in the National Geographic program “Dinosaur Hunters: secrets of the Gobi Desert”

Fig. 1. *Khaan mckennai* (IGM 100/1127, holotype).

(National Geographic, 1997). Interestingly, as the Ukhaa Tolgod assemblages have been shown to represent so-called "life" assemblages (where the animals were killed by the agents of their preservation—in this case, collapsed sand dunes; Loope et al., 1999; Dingus et al., 2008), this pair of animals were likely behaviorally interacting in life.

We place *Khaan mckennai* into a phylogenetic framework by making explicit comparisons with basal oviraptorosaurs such as *Incisivosaurus gauthieri* (cranial comparisons only; Xu et al., 2002; Balanoff et al., 2009), *Avimimus portentosus* (Kurzanov, 1981; 1987), and *Caudipteryx zoui* (Ji et al., 1998) as well as oviraptorids such as *Oviraptor*

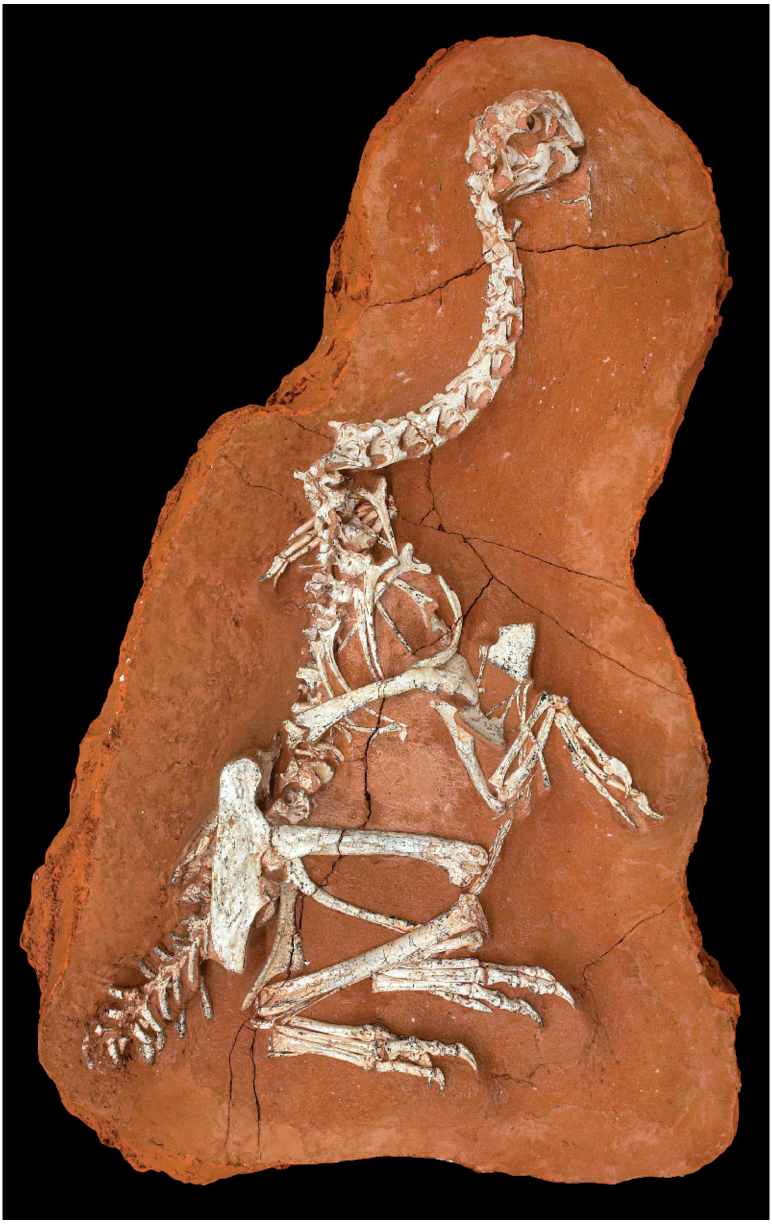


Fig. 2. *Khaan mckennai* (IGM 100/1002, referred specimen).

philoceratops (Osborn, 1924), *Conchoraptor gracilis* (Barsbold, 1976), *Gigantoraptor erlianensis* (Xu et al., 2007), and *Citipati osmolskae* (Clark et al., 2002) (appendix 1). This framework will allow us to make preliminary inferences about the evolution of morphological features along the oviraptorosaur lineage. These hypotheses can be further tested in future analyses that include an expanded taxon sampling. We currently are in the process of compiling a comprehensive phylogenetic analysis of Oviraptorosauria that will elucidate the nature and order of acquisition of avianlike characters in this group.

A list of anatomical abbreviations is provided in appendix 2.

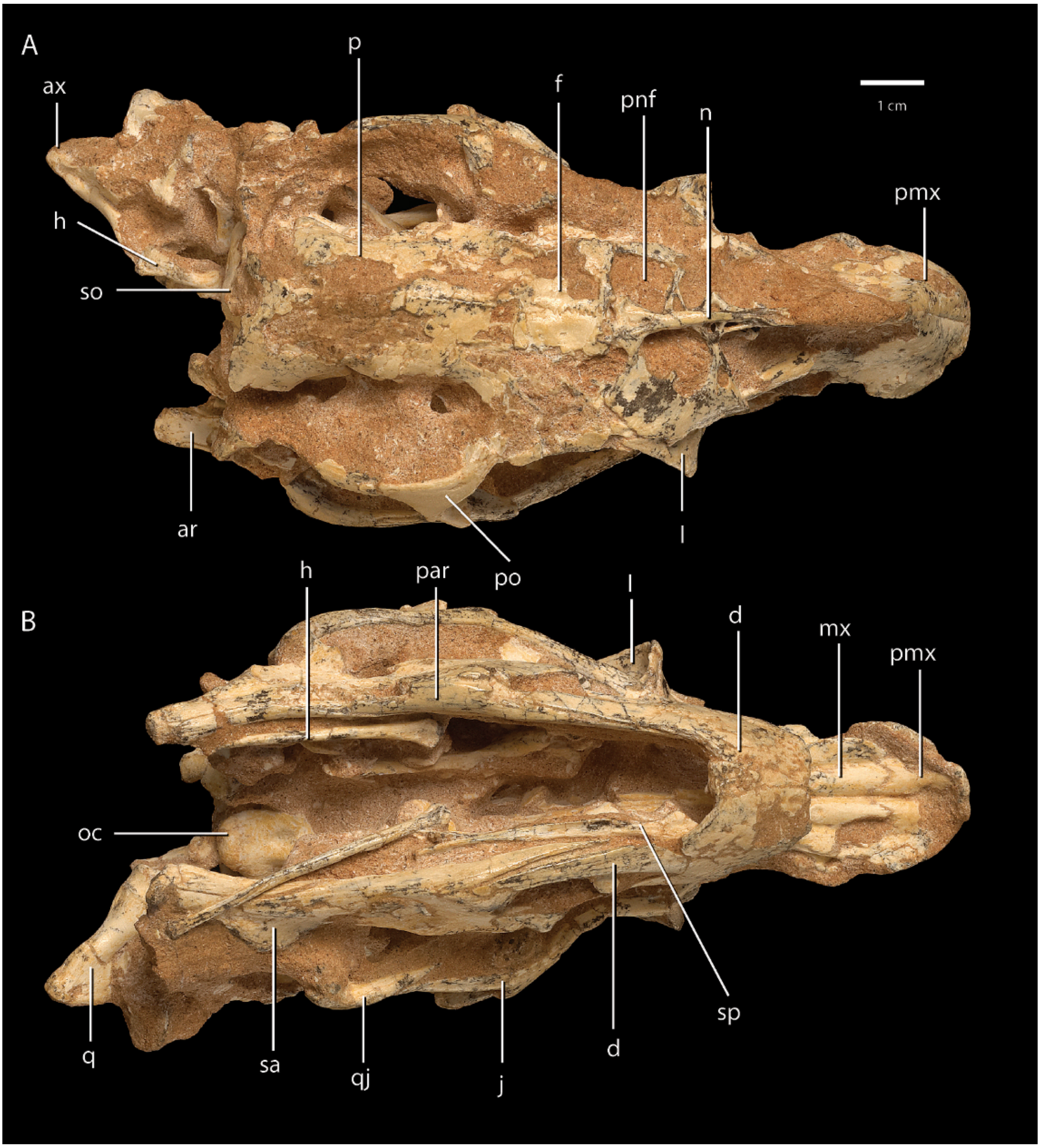


Fig. 3. Skull of *Khaan mckennai* (IGM 100/973, referred specimen): **A,** dorsal and **B,** ventral (above). **C,** right lateral and **D,** left lateral (opposite page). **E,** anterior and **F,** posterior views (following page).

MATERIAL AND METHODS

MATERIAL AND DIAGNOSIS OF *KHAAN MCKENNAI*

Clark et al. (2001) named and provided a brief description of *Khaan mckennai*. The description provided here is based on the three specimens referred to in that publication (figs. 1–3). The holotype of *Khaan mckennai* (fig. 1; IGM [Geological Institute, Mongolian Academy of Sciences] 100/1127) and IGM 100/1002 (fig. 2; referred specimen) are nearly complete, articulated specimens. The final specimen (fig. 3; IGM 100/973; referred

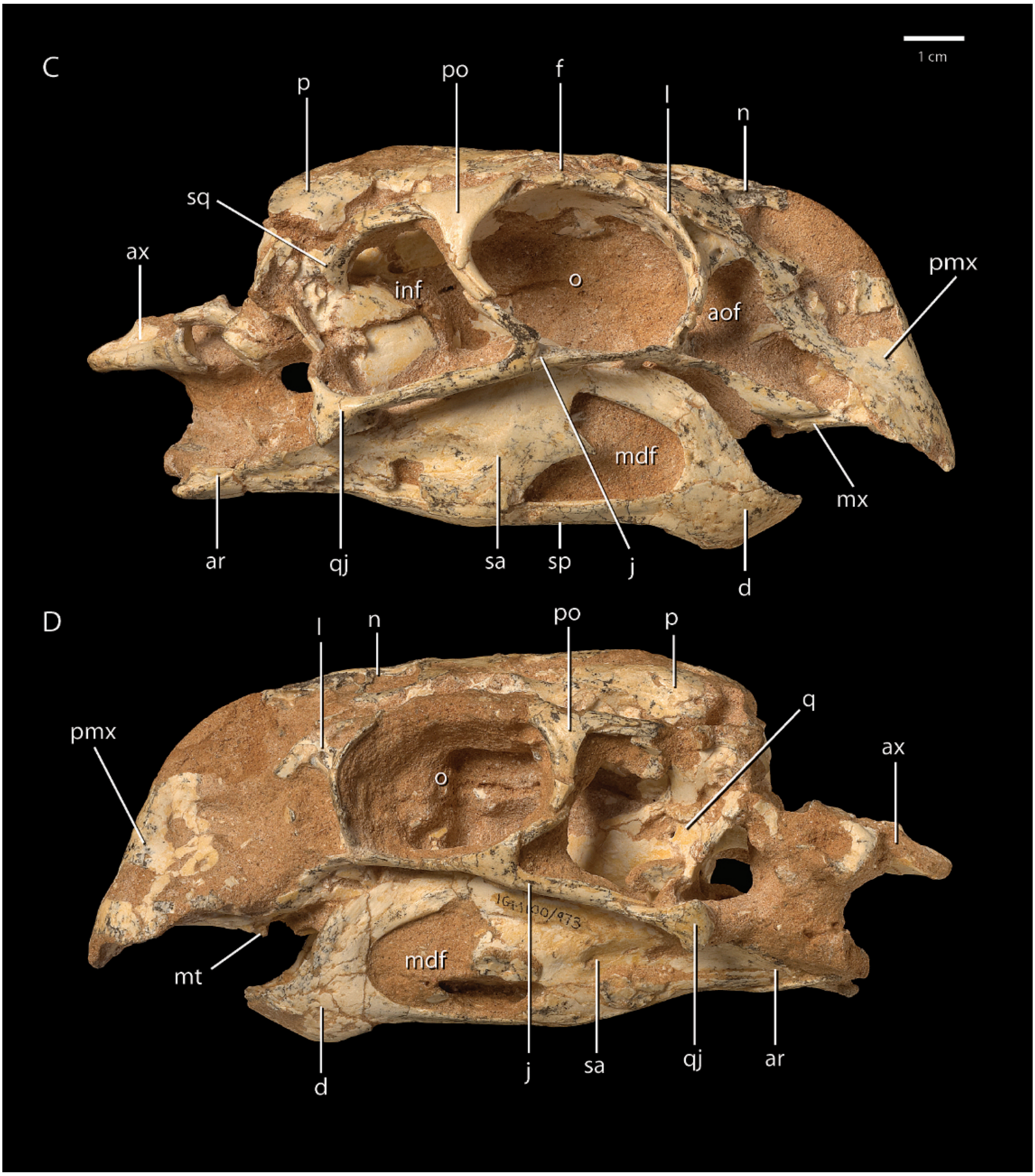


Fig. 3. Continued.

specimen) has been prepared completely out of the matrix. Many of the three-dimensional observations of the skeleton are taken from this specimen. Because the skull of IGM 100/973 has also been prepared out of a larger block, we were able to scan it using high-resolution X-ray computed tomography (CT), enabling this study to access additional data on the internal anatomy of the cranium.

These three specimens of *Khaan mckennai* share numerous derived features that diagnose them to the successively nested clades Oviraptorosauria, Caenagnathoidea (Oviraptoridae + Caenagnathidae), and Oviraptoridae

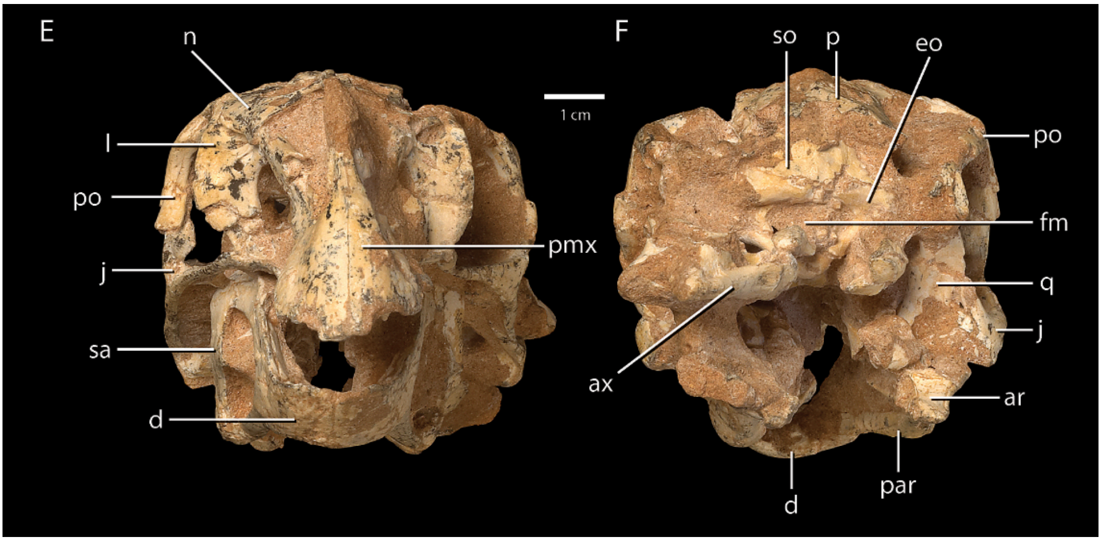


Fig. 3. Continued.

(fig. 4) using a recent iteration of the Theropod Working Group (TWiG) phylogenetic analysis (Turner et al., 2007b). These specimens are unambiguously assigned to Oviraptorosauria based on an extensively pneumatized narial region, ventrally curved (pendant-shaped) paroccipital processes, crenulate margin on the buccal edge of the premaxilla, an elongate dorsal process of the dentary, slender, elongate retroarticular process, and no distinct transition point in the caudal vertebral series. An unambiguous diagnosis can be made to the clade composed of Oviraptoridae and Caenagnathidae based on the following characters: a palatal shelf with ventral "toothlike" projections and an anteriorly concave pubic shaft. Several synapomorphies diagnose these specimens to Oviraptoridae. These characters are an external mandibular fenestra that is subdivided by a rostral spinelike process of the surangular, an ectopterygoid fossa with a constricted opening (visible in CT slices and diagnostic only in DELTRAN optimization), and a mandibular articular surface that is two times or more as long as the quadrate surface. Clark et al. (2001) provides a detailed diagnosis of *Khaan mckennai*. The diagnostic features of this taxon are metacarpal III not expanding dorsally and not contacting the distal carpals.

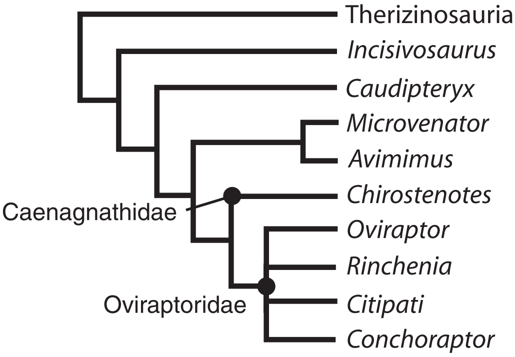


Fig. 4. Proposed hypothesis for the relationships within Oviraptorosauria based on Norell et al. (2006).

GEOLOGICAL SETTING

The holotype of *Khaan mckennai* (IGM 100/1127) was found at Mark's Second Egg locality in Ukhaa Tolgod (Gurvan Tes Somon, Omnogov Aimak, Gobi Desert, Mongolia; Clark et al., 2001) in 1995. The specimen IGM 100/1002 was found adjacent (about 20 cm away and in the same bedding plane) to IGM 100/1127. IGM 100/973 was found about a kilometer away at the Granger's Hill sublocality of Ukhaa Tolgod in 1993. Further information concerning the geological provenance of these specimens can be obtained from Dingus et al. (2008).

MECHANICAL PREPARATION

IGM 100/973, IGM 100/1002 and IGM 100/1127 were prepared at the American Museum of Natural History by Amy Davidson (IGM 100/1127, IGM 100/1002) and Ed Pederson (IGM 100/973). All preparation records are held in the American Museum of Natural History Division of Paleontology database. Matrix was removed with hand tools, and specimens were consolidated with Butvar® B-76 (Monsanto Company), a terpolymer of vinyl butyral, vinyl alcohol, and vinyl acetate monomers. Joins were made with Paraloid® B-72 (Rohm and Haas Company), an ethyl methacrylate and methyl acrylate copolymer. A missing portion of the nasal crest of IGM 100/973 was reconstructed initially with gray epoxy putty that was later removed and replaced with a cement of pulverized matrix mixed with Butvar® B-76. On IGM 100/1002, the lower margin of the right orbit was carved from the original matrix, and the ungual of right forelimb digit I was reconstructed in plaster. Preparation of IGM100/1127 involved reconstruction of the anterior premaxilla and the ungual of right forelimb digit III with a cement of pulverized matrix and Butvar® B-76. The cut edges of both jackets were stuccoed over with the same cement and the sides painted orange for an exhibition on Mongolian dinosaurs in 2001.

CT SCANNING

The cranium and attached mandible of IGM 100/973 was scanned at the University of Texas High-Resolution X-ray Computed Tomography Facility using the high-energy scanning source on 3 September 2009. The specimen was scanned along its coronal axis for a total of 913 slices. The specimen was too long to be accommodated in one pass in the high-energy system, which has a limit of 15 cm. Therefore, it was scanned in two passes and the slices digitally reassembled. The interslice spacing was equal to 0.1637 mm with a field of reconstruction of 78 mm. The resolution of the resulting images was 1024 × 1024 pixels. All image processing was done with the three-dimensional volumetric rendering program VGStudio Max 2.0.1. All measurements taken from the CT images (indicated throughout the paper) are taken using this same software.

CRANIAL DESCRIPTION

IGM 100/973 consists of a complete skull, pelvic girdle, and hindlimb. This specimen is the only completely prepared *Khaan mckennai* skull, which allows physical examination in three dimensions. This specimen was originally designated *Ingenia yanshini* (Dingus et al., 1995) but was subsequently referred to *Khaan mckennai* in Clark et al. (2001). The skull includes the articulated cranium and mandible, which has been displaced posteriorly giving it the appearance of a severe overbite in lateral view (fig. 3A). Preserved on the skull are the premaxilla, maxilla, partial nasal, lacrimal, jugal, postorbital, frontal, parietal, laterosphenoid, prootic, opisthotic, partial squamosal, supraoccipital, quadratojugal, quadrate, exoccipital, basioccipital, pterygoid, parasphenoid rostrum, and the epibranchials and ceratobranchials of the hyoid. The vomer, orbitosphenoid, epipterygoid, ectopterygoid and parabasisphenoid are not visible on the external surface of the skull, but many of the palatal elements such as the ectopterygoid, vomer, palatine, and part of the parabasisphenoid can be observed in the CT images. The mandible is completely preserved, and CT imagery allows access to the medial surface of this structure that otherwise would be unobservable.

Unlike the rounded crania of the holotype IGM 100/1127 and 100/1002 (fig. 5), which were preserved resting on their lateral sides, the skull of IGM 100/973 is slightly compressed dorsoventrally. This compression is most easily seen on the posterior surface of the skull, especially in the mediolaterally elongate foramen magnum (compare fig. 3F with that of IGM 100/1002, fig. 6). The rostrum accounts for approximately 42% of the skull length, which is 118.8 mm in IGM 100/973 (table 1). This measurement is close to values obtained for the two other specimens, where the preorbital region of the skull accounts for approximately 39% (IGM 100/1127) and 42% (IGM 100/1002) of the total skull length (table 1). At least one poorly preserved cervical vertebra is attached to the skull of IGM 100/973.

The overall shape of the skull is obtained from the holotype and IGM 100/1002 (fig. 5)

Fig. 5. Skull of *Khaan mckennai*. **A,** Right lateral view of holotype (IGM 100/1127), and **B,** right lateral view of IGM 100/1002 (above); **C,** right lateral view of IGM 100/1127 (opposite page). Abbreviations in appendix 2.

due to of the dorsoventral distortion of IGM 100/973. The dorsal cranial surface is rounded and ends in a vertically oriented occiput, unlike the quadrangular skull and posterodorsally facing occipital surface of *Citipati osmolskae* (Clark et al., 2002) and *Conchoraptor gracilis* (personal obs.). The nasal is extensively pneumatized but not dorsally enlarged to form a distinctive crest, differing from the morphologically diverse crests that are present on the skulls of *Citipati osmolskae*, *Oviraptor philoceratops*, *Nemegtomaia*

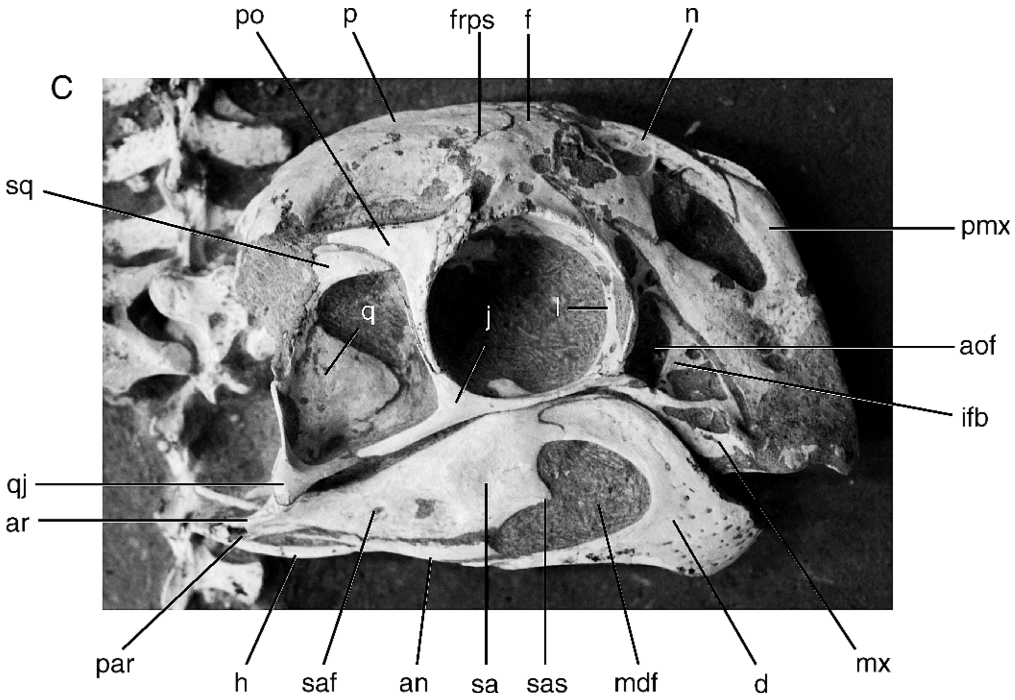


Fig. 5. Continued.

barsboldi, IGM 100/42, and *Rinchenia mongoliensis*. The transitional area between the dorsal and occipital surfaces of the skull lacks the more pronounced nuchal crest seen in taxa such as *Incisivosaurus gauthieri* and *Conchoraptor gracilis* (Balanoff et al., 2009). The orbit is rounded in IGM 100/1002 and 100/1127 as it is in all coelurosaurs except advanced tyrannosaurids. The infratemporal fenestra is subrectangular in shape, closely approximating that of *Citipati osmolskae* (Clark et al., 2002). The quadrates extend below the ventral surface of the cranium (fig. 3C, D), an arrangement present in all oviraptorosaurs. This condition, however, is not as pronounced in *Khaan mckennai* as it is in the basal taxon *Incisivosaurus gauthieri* (Balanoff et al., 2009: fig. 3). Another basal taxon, *Caudipteryx zoui*, does not approach that in *Incisivosaurus gauthieri*. The palatal surface of *Khaan mckennai* for the most part is not visible, and only a small portion of the anterior palate including the premaxilla and maxilla can be observed in IGM 100/973 (fig. 3B). This specimen also preserves a small part of the anterior tips of the vomer and pterygoids; however, little palatal morphology can be determined from physical examination. No part of the palate is visible in any of the other specimens. Similar to all other oviraptorids and caenagnathids, the skull is completely edentulous.

PREMAXILLA

Figures 3, 5, 7

The right and left premaxillae meet along the midline in a straight vertical unfused suture (fig. 3E), unlike the condition in *Citipati osmolskae*, where the premaxillae completely fuse to form a single compound element. The premaxillae also remain unfused in the basal taxa *Incisivosaurus gauthieri* and *Caudipteryx zoui* (IVPP V 12430). The premaxilla contacts the nasal posterodorsally, the maxilla and nasal posterolaterally, and the maxilla along its posterior margin on the palatal surface. The posterodorsal contact with the nasal is not preserved in IGM 100/973 but is visible in IGM 100/1127 and 100/1002 (fig. 5). Together the premaxilla and nasal form the dorsal

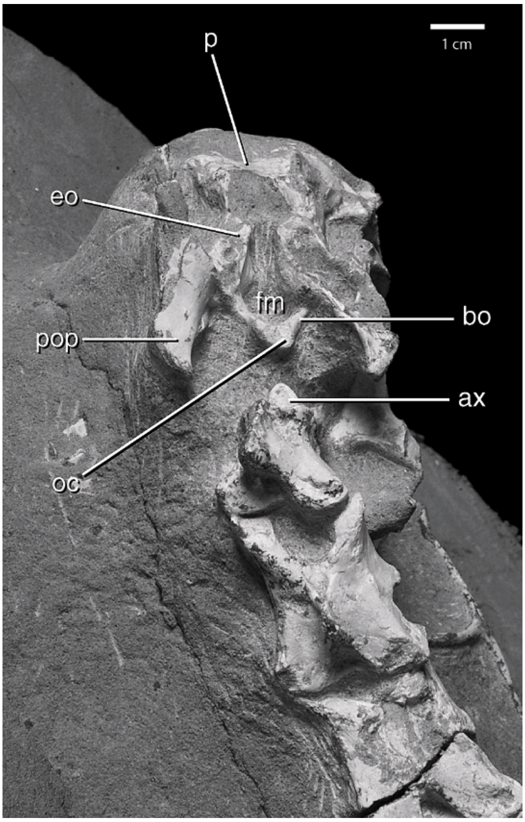


Fig. 6. Occipital surface of skull of *Khaan mckennai* (IGM 100/1002). Abbreviations in appendix 2.

margin of the anteroposteriorly elongate, almost slitlike external naris, which slants posterodorsally. The external naris in the basal taxa *Incisivosaurus gauthieri* and *Caudipteryx zoui* and the oviraptorids *Citipati osmolskae*, *Rinchenia mongoliensis*, *Ingenia yanshini*, and *Conchoraptor gracilis* differs significantly from this morphology, having a more circular appearance (see Balanoff et al., 2009: fig. 3; Clark et al., 2002: fig. 2). Although *Caudipteryx zoui* and *Conchoraptor gracilis* have an elongate shape, the slitlike morphology of the naris appears diagnostic of *Khaan mckennai* and possibly the oviraptorid *Banji long* (Xu and Han, 2010). The nasal process of the premaxilla in *Khaan mckennai* has a straight anterior edge that slants posteroventrally. There is a slight bend near its posterior end where it contacts the nasal. The posterior slant to the nasal process of the premaxilla distinguishes *Khaan mckennai* from most other oviraptorosaurs such as *Citipati osmolskae*, *Rinchenia mongoliensis*, or *Conchoraptor gracilis* where the premaxilla is almost vertically oriented (see Osmólska et al., 2004: fig. 8.1). Again, the oviraptorid *Banji long* also appears to bear a similar morphology to *Khaan mckennai* (Xu and Han, 2010).

The maxillary process of the premaxilla is a posteriorly tapering strap of bone extending posterodorsally and is overlain at its posterior end by a laterally descending process of the nasal (figs. 3C, D, 5). These two elements together overlie the premaxillary process of the maxilla. The premaxilla and nasal form a bar that separates the naris from the antorbital fenestra and completely excludes the maxilla from the narial border (also excluding the maxilla from any contribution to the naris). This character is shared among all oviraptorosaurs (Osmólska et al., 2004), being easily identified in *Caudipteryx zoui*, *Incisivosaurus gauthieri*, and *Citipati osmolskae*. The posterior tip of the maxillary process of the premaxilla also overlies a small portion of the anterior lacrimal. The premaxilla, maxilla, and lacrimal form the anterior and dorsal borders of the triangular antorbital fenestra. The lateral surface of the maxillary process of the premaxilla is scarred by a shallow depression also seen in *Caudipteryx zoui*, *Conchoraptor gracilis*, and *Citipati osmolskae* (see Ji et al., 1998; Clark et al., 2002) but not *Oviraptor philoceratops* or *Incisivosaurus gauthieri* (Clark et al., 2002; Balanoff et al., 2009). The anterior and lateral surfaces of the premaxillary body are marked by numerous randomly distributed foramina (figs. 3C, D, E, 5, 7), which presumably represent nervous colliculi that transported small divisions of the medial branch of the ophthalmic nerve (CN V) to innervate the "beak." This structure probably was overlain by a keratinous sheath, based on modern analogs in turtles and birds (Bubien-Waluszewska, 1981) and at least one ornithomimid (Norell et al., 2001). Such foramina are also present in other oviraptorids but lacking in the basal oviraptorosaur *Incisivosaurus gauthieri* (Xu et al., 2002; Balanoff et al., 2009). Another basal oviraptorosaur *Caudipteryx zoui* and *Erlikosaurus andrewsi*, a

TABLE 1
Selected measurements (in mm) from the cranial skeleton of *Khaan mckennai*

	IGM 100/973	IGM 100/1127	IGM 100/1002
Skull length*	118.8	~127.0	113.8
Preorbital skull length	50.1	48.8	47.7
Orbit length	37.2	35.4	–
Orbit height	27.0	33.4	–
Premaxilla length (palate)	14.6	20.4	20.0
Premaxilla height (below naris)	–	38.8	33.2
Maxilla length (palate)	31.7	–	–
Frontal length	12.0	8.6	–
Parietal length	42.6	44.0	–
Infratemporal width	27.2	26.5	–
Infratemporal height	25.3	31.0	–
Supratemporal fenestra width	15.7	11.6	–
Supratemporal fenestra length	28.7	27.9	–
Mandible length	104.0	108.4	101.6
Mandible height	30.8	32.4	30.0
Mandibular fenestra length	26.7	29.2	26.1
Mandibular fenestra height	18.8	20.7	20.4
Foramen magnum width	14.8	–	–
Foramen magnum height	7.5	–	–

*Measured from the occipital condyle.

member of Therizinosauria the purported outgroup to Oviraptorosauria, also have vascularized premaxillary surfaces.

The palatal surface of the premaxilla possesses a distinct triturating surface as it does in all oviraptorosaurs and therizinosaurs (Clark et al., 1994, 2002) even though more basal oviraptorosaurs such as *Incisivosaurus gauthieri*, *Similicaudipteryx yixianensis,* and *Caudipteryx zoui* retain premaxillary teeth (Ji et al., 1998; Xu et al., 2003; He et al., 2008). The triturating surface of both *Khaan mckennai* and *Citipati osmolskae* and the corresponding surface in *Incisivosaurus gauthieri* and *Caudipteryx zoui* each have a series of denticles. Those of *Khaan mckennai* differ from other taxa in having only two large denticles similar to the morphology of *Rinchenia mongoliensis* (fig. 7). Other oviraptorosaurs have smaller more numerous denticles. *Citipati osmolskae* has five pairs (Clark et al., 2002: fig. 2), *Incisivosaurus gauthieri*, *Caudipteryx zoui*, and *Avimimus portentosus* have at least four pairs (Kurzanov, 1987; Ji et al., 1998; Balanoff et al., 2009). The ventral outline of the triturating surface on the premaxilla forms a U-shape that is characteristic of therizinosaurs and oviraptorosaurs. The posterior margin of this surface slants dorsally, forming a parrotlike beak especially prominent in IGM 100/973 (fig. 3C, D). The premaxilla has a larger exposure on the palate in *Khaan mckennai* than in *Citipati osmolskae* (table 1) and

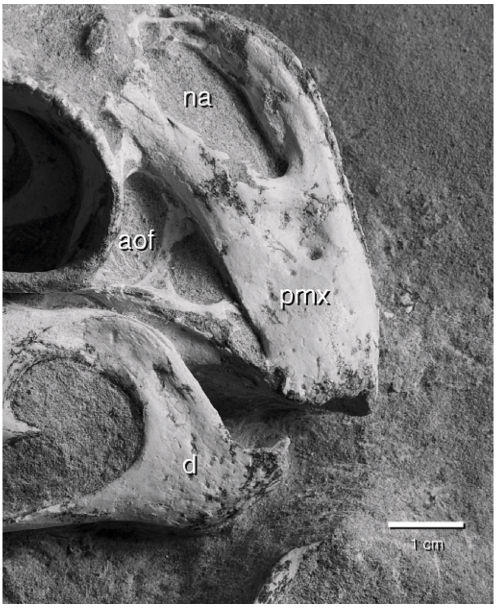


Fig. 7. Detail of premaxilla of IGM 100/1127. Abbreviations in appendix 2.

expands at the palatal contact with the maxilla. The interdigitating suture between these elements has a chevron shape in both *Citipati osmolskae* and *Khaan mckennai*. This suture in *Incisivosaurus gauthieri* is V-shaped. The premaxilla of *Khaan mckennai* is edentulous, but two parasagittal rounded ridges mark the palatal surface of the element and extend to the posterior margin of the maxilla (fig. 3B). Two additional ridges are present lateral to these structures on the maxilla. Such ridges are present in all oviraptorids, *Chirostenotes pergracilis*, and *Avimimus portentosus* (Barsbold, 1981, 1983, 1986; Kurzanov, 1981; Maryańska and Osmólska, 1997; Sues, 1997; Elzanowski, 1999; Clark et al., 2002), but absent in the more basal oviraptorosaur *Incisivosaurus gauthieri* (Balanoff et al., 2009).

MAXILLA

Figures 3, 5

The paired maxillae are edentulous and anteroposteriorly short in lateral view (figs. 3C, D, 5), being more similar to the morphology of *Citipati osmolskae* and *Conchoraptor gracilis* than *Incisivosaurus gauthieri*, *Chirostenotes pergracilis* (Sues, 1997), or *Oviraptor philoceratops* (Clark et al., 2002), all of which have a relatively longer maxilla. On the lateral surface of the skull, the maxilla contacts the premaxilla anterodorsally, the lacrimal dorsally, and the jugal posteriorly. On the palatal surface, the maxillary contact with the premaxilla is the only one visible because the anterior portions of the vomer and palatines are not preserved. The maxilla makes up the ventral margin and floor of the antorbital fossa as well as the interfenestral bar. The interfenestral bar is inset in *Khaan mckennai* as it is in all oviraptorids (figs. 3C, D, 7) and unlike that in *Incisivosaurus gauthieri*, which is confluent with the lateral surface of the rostrum. The interfenestral bar is badly damaged in IGM 100/973; however, this damage exposes many of the pneumatic fossae at the anterior end of the antorbital fossa where it typically is overlain by the premaxilla (figs. 3C, 5C). These pockets presumably were pneumatized by the promaxillary fenestra (Witmer, 1997). The posteriorly located antorbital fenestra is dorsoventrally elongate and occupies approximately one-third of the triangular-shaped antorbital fossa. Based on IGM 100/1127 and 100/1002, there are at least two accessory antorbital fenestrae, one large fenestra at the anterior margin of the fossa and a smaller more posterodorsal fenestra (fig. 7). This arrangement is similar to the condition in the basal taxon *Incisivosaurus gauthieri*, in which two accessory fenestrae are present (Balanoff et al., 2009: fig. 3a), as well as the oviraptorid *Citipati osmolskae* (Clark et al., 2002: fig. 2); therefore, homologies for this region can be followed throughout Oviraptorosauria but are difficult to correlate with other coelurosaurs (Witmer, 1997). The purported sister taxon to Oviraptorosauria, Therizinosauria, possesses no accessory antorbital fenestrae (e.g., *Erlikosaurus andrewsi*; Clark et al., 1994).

The maxilla underlies the jugal along its posterior (jugal) process (figs. 3C, D, 5). The jugal process of the maxilla is thin and rod shaped as in *Citipati osmolskae* (Clark et al., 2002), but not *Incisivosaurus gauthieri* (Balanoff et al., 2009). Approximately midway along the length of the maxilla of *Khaan mckennai*, the maxilla and jugal extend dorsally to contact the preorbital process of the lacrimal to form the preorbital bar separating the antorbital fossa from the orbit.

The palatal surface of the maxilla in *Khaan mckennai* is confluent with that of the premaxilla (fig. 3B), and the aforementioned ridges present on the premaxilla extend along the entire length of the maxilla as well. Two additional ridges are added lateral to these premaxillary ridges and are present exclusively on the maxilla, as they are in *Citipati osmolskae* (Clark et al., 2002). Although present in all observed oviraptorids and caenagnathids, no longitudinal ridges are present on the palatal surface of *Incisivosaurus gauthieri*. A small bony projection is located at the posterior end of the medial maxillary palatal ridges in *Khaan mckennai* (figs. 3B, 5C). This structure is usually formed by both the maxilla and the vomer in oviraptorids (Elzanowski, 1999; Clark et al., 2002), but the contact between these elements is not preserved in IGM 100/973. It, therefore, cannot be determined whether other elements contributed to these toothlike structures. Such palatal protuberances are diagnostic of oviraptorids plus caenagnathids (see maxilla of *Chirostenotes pergracilis*; Sues, 1997). This structure may also be present in *Avimimus portentosus*; however, damage to PIN 3907/1 makes it difficult to discern (Kurzanov, 1981). Additional specimens of *Avimimus portentosus* recently collected in China may shed light on their presence or absences (Currie et al., 2008). The triturating surface of the maxilla of *Khaan mckennai* lacks denticles. These structures are continued from the premaxilla onto the maxilla in other oviraptorids such as *Citipati osmolskae*, *Oviraptor philoceratops*, and the caenagnathid *Chirostenotes pergracilis* (Sues, 1997), but are completely absent in the more basal form, *Incisivosaurus gauthieri*.

NASAL

Figures 3, 5, 8

The nasals are paired and fully fused along the midline (figs. 3A, 8), like most other oviraptorids, but unlike *Incisivosaurus gauthieri*, *Caudipteryx zoui* (IVPP V 12430), therizinosaurs, or other paravians (e.g., Clark et al., 1994; Ji et al., 1998; Norell et al., 2006; Balanoff et al., 2009). Much of the nasal of IGM 100/973 is damaged; therefore, many of structures, particularly on the anterior part of the dorsal surface, are not easily distinguished. Most observations are taken from IGM 100/1127. The nasal contacts the premaxilla anteriorly and laterally, the lacrimal posterolaterally, and the frontals posteriorly. The dorsal surface of the nasal is flared substantially posterior to the posterior edge of the naris (approximately four times the width of the premaxillary process). This morphology is similar to *Citipati osmolskae*, but substantially different from *Incisivosaurus gauthieri* and *Caudipteryx zoui*, where the nasals are subequal throughout their entire length, similar to other theropods (Turner et al., 2007a; Balanoff et al., 2009: fig. 4). The premaxillary process of the nasal in *Khaan mckennai* is thin and extends anteriorly from the midline to meet the premaxilla. The posterior contact with the frontal is not fused and forms an irregular pattern (fig. 3A). The dorsal surface of the nasal in this region is marked by numerous openings that through the use of CT imagery can be seen to extensively pneumatize the element. One large nasal recess dominates this area, and a small ridge along the midline is raised above the highly pneumatic surface (figs. 3A, 8). Numerous small fenestrae are distributed around the large opening and extend onto the premaxillary process as well. A similar morphology is apparent in *Citipati osmolskae*, *Rinchenia mongoliensis*, and *Nemegtomaia barsboldi*—all oviraptorids that are known to possess a large nasal crest (Clark et al., 2002)—but it does not appear to this same extent in other taxa that lack an extensive crest such as *Conchoraptor gracilis* (Barsbold, 1986). *Incisivosaurus gauthieri* also possesses pneumatic foramina in this region of the skull but not to the extent seen in any of the oviraptorids (Balanoff et al., 2009).

The lateral descending process of the nasal slightly overlaps the maxillary process of the premaxilla and dorsal surface of the lacrimal (fig. 5C). This process is abbreviated in comparison to the condition in *Citipati osmolskae* (compare fig. 5C to Clark et al., 2002: fig. 2). The nasal and premaxilla together form the dorsal border of the naris (extends less than half way along the length of the maxillary process of the premaxilla); however, only the descending process of the nasal forms the posterior border of the opening (fig. 5C). The shape of the naris (based on IGM 100/1127) is elongate with a slightly triangular shape (the apex being at the midpoint along the posteroventral margin). The relative size of the external naris is larger than the antorbital fenestra, yet comparable to that of the entire antorbital fossa (fig. 5A, C). This condition also is similar to that present in oviraptorids such as *Citipati osmolskae* and *Conchoraptor gracilis* (Osmólska et al., 2004), but the antorbital fenestra is larger than the external naris in *Incisivosaurus gauthieri* (Balanoff et al., 2009: fig. 3) and *Caudipteryx zoui* (Ji et al., 1998; Zhou et al., 2000). The nasal of *Khaan mckennai* is excluded entirely from the border of the antorbital fossa by the lacrimal and premaxilla like in all other oviraptorosaurs.

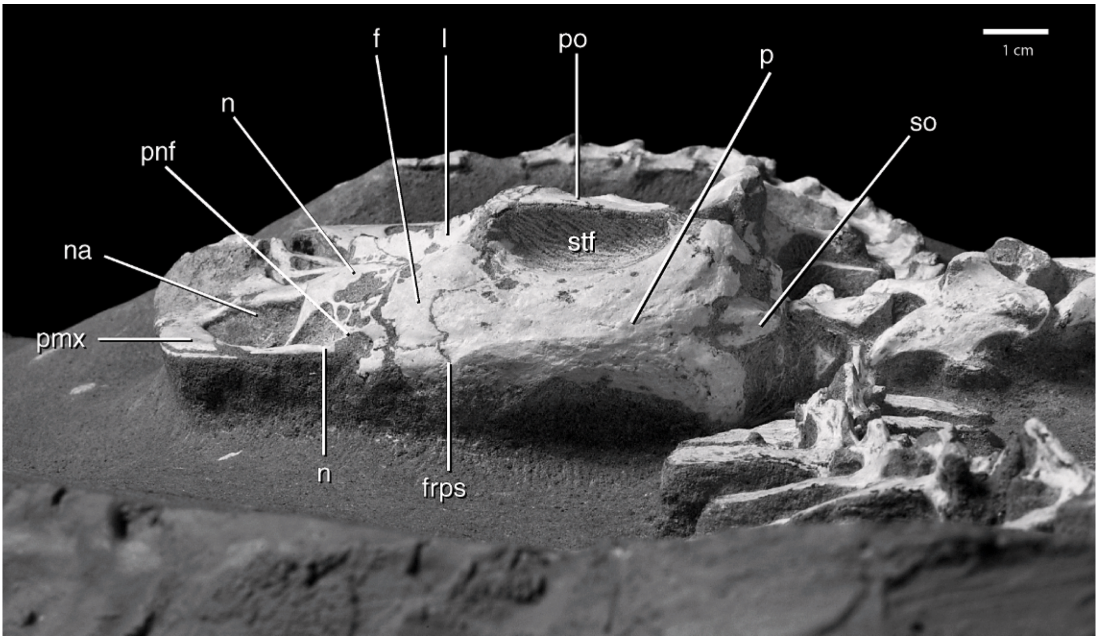


Fig. 8. Dorsal surface of skull of holotype of *Khaan mckennai* (IGM 100/1127). Abbreviations in appendix 2.

FRONTAL

Figures 3, 5, 8

The dorsal surface of the frontal is damaged in IGM 100/973 and not well exposed in IGM 100/1002, so much of the description is based on 100/1127 (fig. 8). The paired frontals are sutured together along their midline, but the interdigitating nature of the suture between the elements is still visible (fig. 8). The anteroposterior length of the frontal is short, about one-quarter of the length of the parietal (table 1), a feature shared with all other oviraptorids (Osmólska et al., 2004). The frontal of the more basal *Incisivosaurus gauthieri*, however, is approximately the same length as the parietal (Balanoff et al., 2009: fig. 4) and longer than the parietal in *Caudipteryx zoui* (Ji et al., 1998; Zhou et al., 2000). The dorsal surface of the frontal is convex in IGM 100/1127 and 100/1002, but more flattened in IGM 100/973. This disparity in shape is likely influenced by dorsoventral compression and deformation of IGM 100/973, although the morphology of this specimen does approach that of *Citipati osmolskae* and *Ingenia yanshini*. The anterior suture of the frontal with the nasal is complexly folded, but it is not fused. This condition is the same as that described for *Citipati osmolskae* (Clark et al., 2002). The posterior contact with the parietal on the dorsal surface is difficult to discern because of damage to IGM 100/973, but appears to be the typical condition with the frontal overlying the parietal. IGM 100/1127 shows that the contact is sinuous (saddle-shaped), similar in shape to *Conchoraptor gracilis* (Balanoff and Norell, in prep.) but differing from the straight, diagonal contact present in *Citipati osmolskae* (Clark et al, 2002). Although the frontal typically forms part of the supratemporal fossa, it is prohibited from contributing to this structure by the frontal ramus of the postorbital (fig. 8). The same arrangement is seen in *Conchoraptor gracilis* and possibly *Caudipteryx zoui* (Balanoff and Norell, in prep.; Zhou et al., 2000: fig. 1), but absent in most other oviraptorosaurs (e.g., *Incisivosaurus gauthieri* and *Citipati osmolskae*). Broken portions of the dorsal surface of IGM 100/973 reveal that the frontal is pneumatized at least along its lateral margin. CT imagery further reveals that this lateral pneumatic pocket is connected to a large midline frontal sinus that begins anteriorly in the frontal and extends posteriorly through to the parietal (fig. 9). This sinus is similar to the frontal sinus described for *Citipati osmolskae* and *Conchoraptor gracilis* (Clark et al., 2002; Kundrát and Janáček, 2007). Unlike the initial description of *Citipati osmolskae* in which a median septum was not discernible in the CT data, the sinus of *Khaan mckennai* has a median septum separating the paired structure, as is also the case in *Conchoraptor gracilis* (Kundrát and Janáček, 2007).

Laterally, the lacrimal contacts the anterior surface of the frontal for a short distance along a distinctive lacrimal process, and these two elements together form part of the supraorbital rim (figs. 3, 5). This contact with the lacrimal extends onto the orbital surface. The supraorbital rim lacks the pronounced everted lip present in *Incisivosaurus gauthieri* (Balanoff et al., 2009), but is more pronounced than the condition of *Citipati osmolskae* where a supraciliary rim essentially is absent. The ventral surface of the supraorbital rim lacks pneumatic pockets like those on the orbital surface in *Citipati osmolskae* (Clark et al., 2002). The orbit is round in IGM 100/1127 and 100/1002 but slightly flattened into an ellipse in IGM 100/973, again due primarily to dorsoventral compression (fig. 3C, D). The posterodorsal and posterior margins of the orbit are formed by the postorbital, which overlaps approximately the posterior one-third of the lateral edge of the frontal. The orbital surface of the frontal is oriented almost horizontally, giving the element a somewhat flattened L-shape in cross section. A distinct fossa is present posteriorly on the orbital surface for the acceptance of the postorbital (capitate) process of the laterosphenoid.

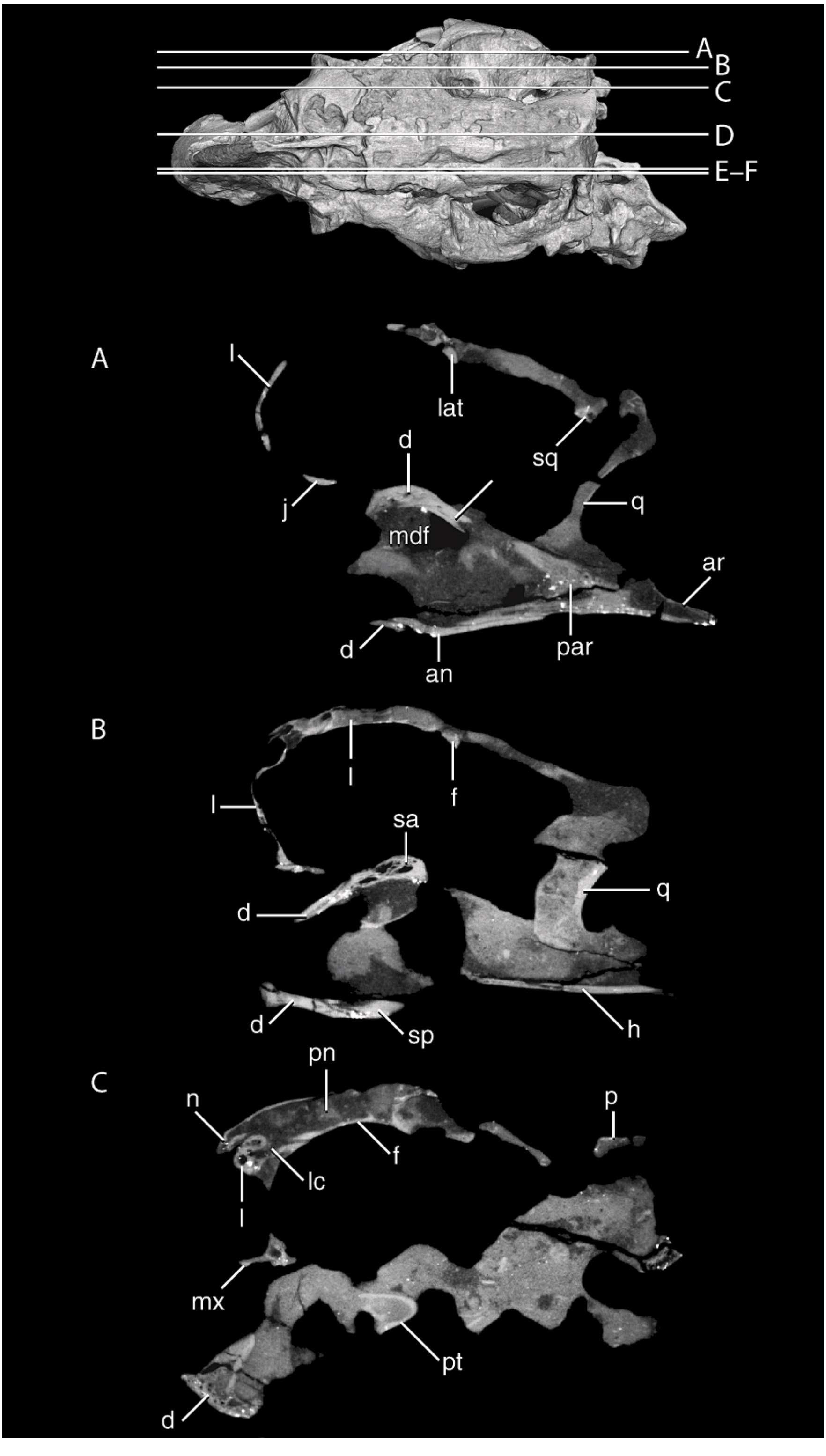
PARIETAL

Figures 3, 5, 8

Like other bones exposed on the dorsal surface of the skull, the parietals of IGM 100/973 and 100/1002 are damaged and incomplete. In IGM 100/1127 this surface is well preserved but only partially exposed (fig. 8). The parietals are completely fused along the midline and no suture is evident like all known oviraptorosaurs (and most coelurosaurs). This composite bone forms the majority of the skull roof, approximately one-third of the total length of the skull (table 1; compare with *Citipati osmolskae*, Clark et al., 2002: fig. 5). The parietals make up a smaller portion of the skull roof in basal oviraptorosaurs like *Incisivosaurus gauthieri* and *Caudipteryx zoui*. The dorsal surface of the parietal in *Khaan mckennai* contacts the frontal anteriorly and the postorbital laterally along its anterior margin. Along the occipital surface the element contacts the supraoccipital ventrally and laterally, and the lateral surface contacts the laterosphenoid anteriorly and the prootic and squamosal posteriorly.

In IGM 100/1127 and 100/1002 the dorsal surface of the parietal, which is confluent with the frontal, is round (fig. 5A). This shape differs from the flattened parietals in the basal *Incisivosaurus gauthieri* and the oviraptorids *Citipati osmolskae, Ingenia yanshini*, and *Conchoraptor gracilis*. Thus, the top of the braincase of *Khaan mckennai* has a dome-shaped profile. The parietal, which contacts the frontal at its widest point, narrows slightly posteriorly. The posterior end of the element again widens and forms a weakly developed nuchal crest. This condition differs from most other maniraptorans (see *Tsaagan mangas*; Norell et al., 2006) as well as more closely related oviraptorids like *Conchoraptor gracilis* (Balanoff and Norell, in prep.), which have a more pronounced nuchal crest. A weak sagittal crest runs along the midline of the element.

The lateral surface of the parietal extends ventrally to form the majority of the medial margin of the supratemporal fossa (fig. 8). This arrangement is the same as that of *Incisivosaurus gauthieri* and *Conchoraptor gracilis* but differs from *Citipati osmolskae*, whose parietal contributes only the posteromedial margin of the fossa, about one-quarter of the length (Clark et al., 2002). The parietal does not form a deep dorsal tympanic recess in *Khaan mckennai* as is obvious in *Citipati osmolskae* (fig. 3C, D; Clark et al., 2002). The occipital surface of the parietal in IGM 100/973 and 100/1002 is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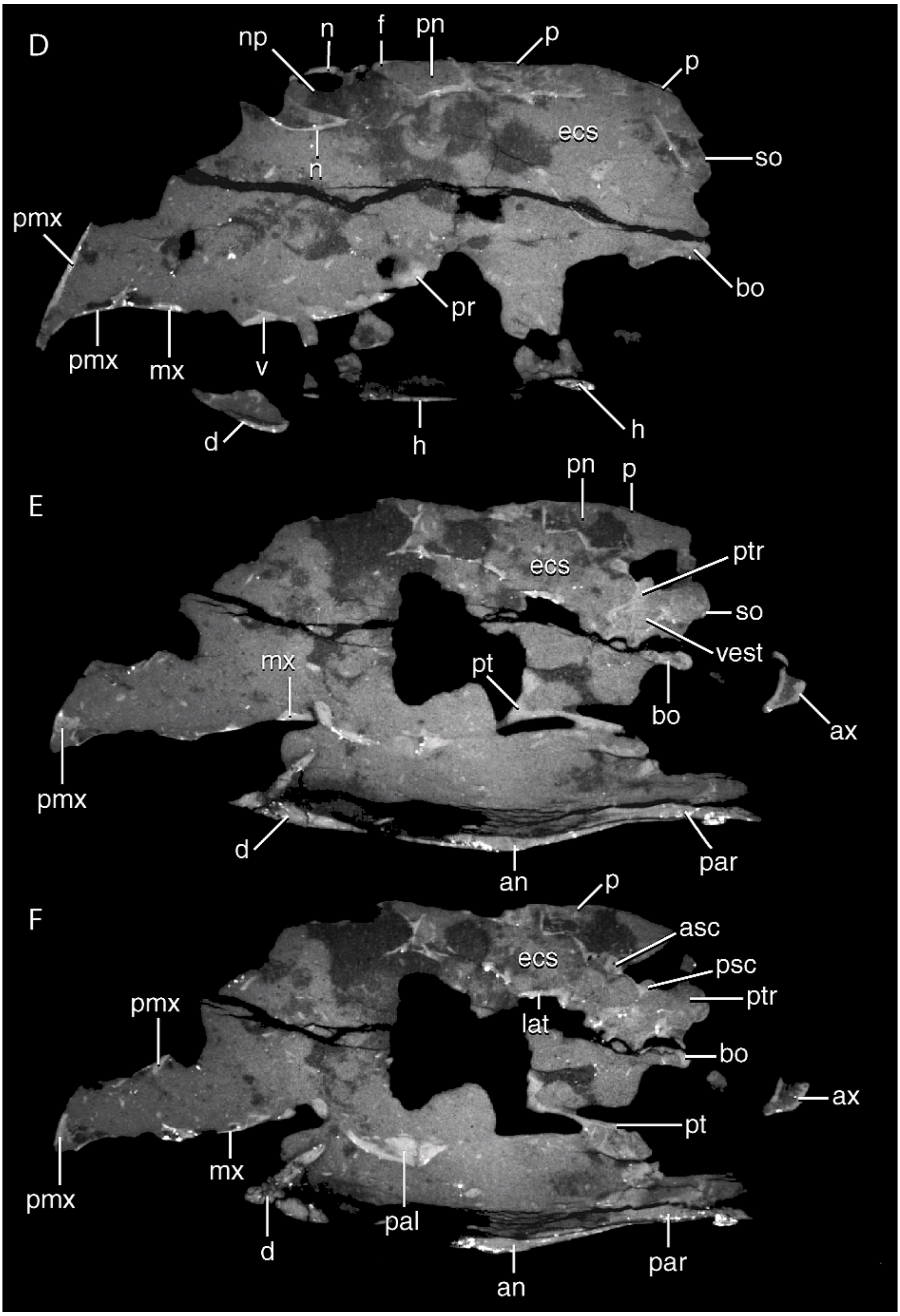

Fig. 9. Continued.

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Fig. 9. CT images showing sagittal slices at various levels through IGM 100/973 (in mm). Abbreviations in appendix 2. **A,** 13.33 mm; **B,** 17.22 mm; and **C,** 22.09 mm (opposite page); **D,** 33.97 mm; **E,** 41.67 mm; and **F,** 42.50 mm (above).

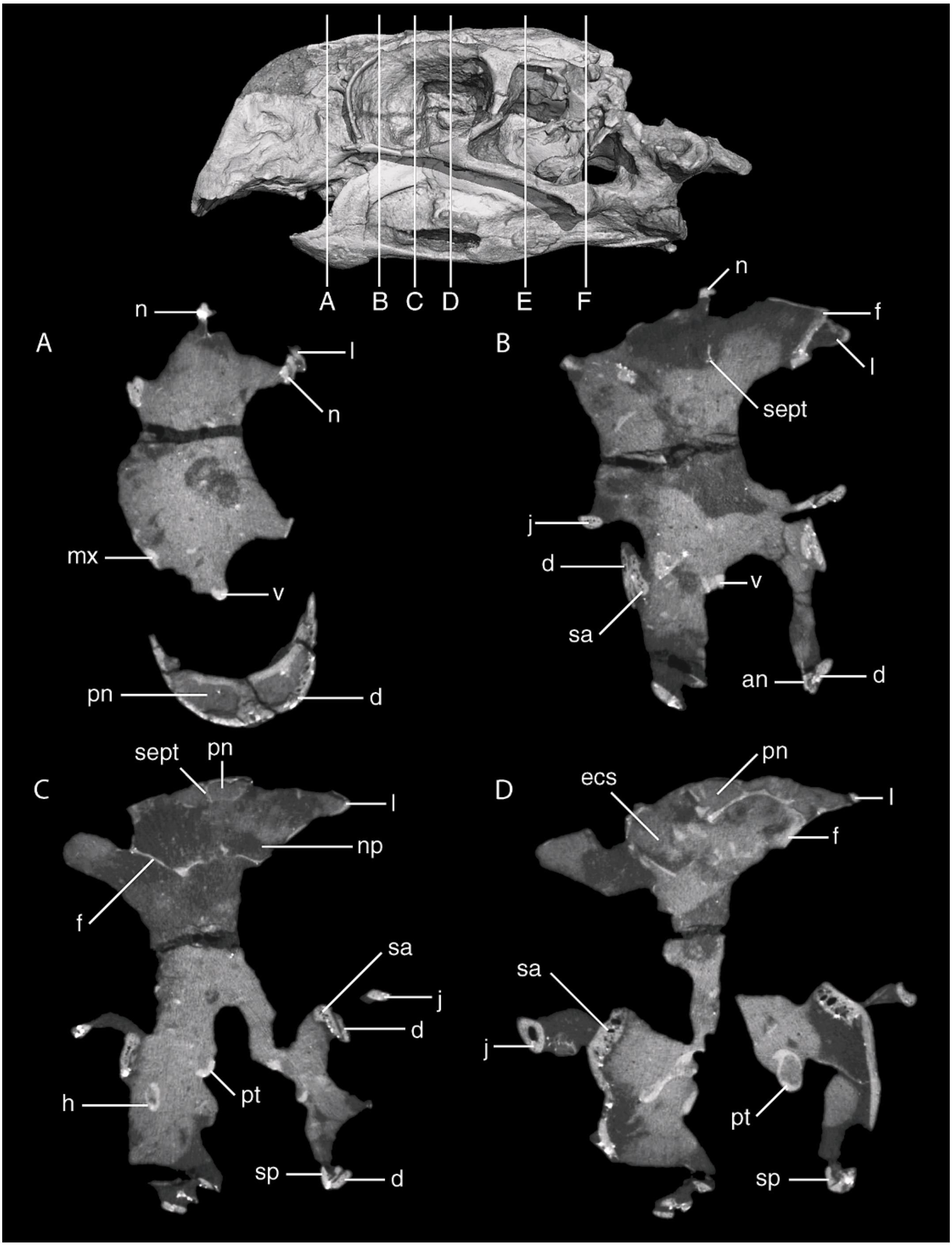


Fig. 10. CT images showing coronal slices at various levels through IGM 100/973 (in mm). Abbreviations in appendix 2. **A,** 37.65 mm; **B,** 50.75 mm; **C,** 61.39 mm; and **D,** 69.57 mm (above); **E,** 89.22 mm; and **F,** 103.95 mm (opposite page).

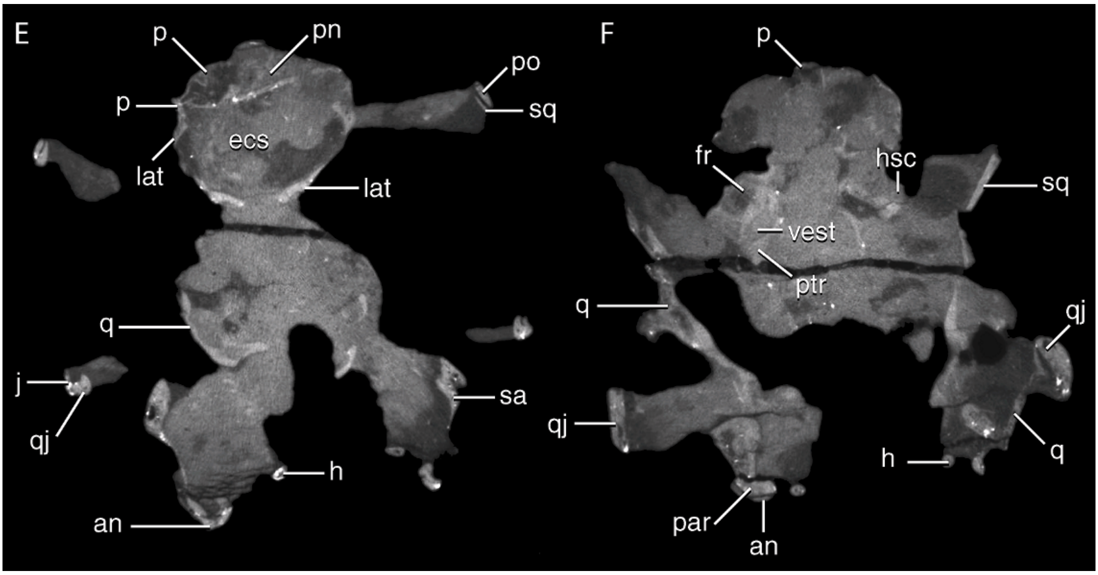


Fig. 10. Continued.

not preserved, and this surface is not exposed in IGM 100/1127.

LACRIMAL

Figures 3, 5, 8

The lacrimal of *Khaan mckennai* is a triradiate element; however, the anterior nasal process is significantly shorter than that seen in deinonychosaurs (see Norell et al., 2006: fig. 3), more closely approximating that of *Incisivosaurus gauthieri* (Xu et al., 2002; Balanoff et al., 2009). *Caudipteryx zoui* diverges from this typical oviraptorosaur morphology in having a true T-shaped lacrimal. In *Khaan mckennai* the lacrimal contacts the premaxilla and nasal anteriorly, the frontal posteriorly, and the jugal and maxilla ventrally along its preorbital process.

The concave posterior surface of the descending process of the lacrimal forms nearly the entire anterior border of the orbit. This surface is marked by a large opening penetrating through the element to the anterior surface and opening into a recess (fig. 10B). This foramen likely transported the nasopharyngeal duct while the recess housed the laterally exposed nasopharyngeal canal (see Clark et al., 2002; Witmer, 1997). Another opening directly anterior to this foramen leads into the nasopharyngeal cavity (fig. 9). The anterior (nasal) process of the lacrimal extends a short distance over the dorsal edge of the antorbital fossa, underlying the maxillary process of the premaxilla and the nasal. This process of the lacrimal is marked by a deep pneumatic recess on its lateral surface directly dorsal to the nasopharyngeal canal (fig. 10B), a feature found in both *Incisivosaurus gauthieri* and *Citipati osmolskae*. CT slices show that the lacrimal is highly pneumatic, as it is in all tetanurans (Witmer, 1995, 1997). These pneumatic spaces are more extensive and join with the larger sagittal and lateral sinuses of the frontal (fig. 10C, D) like in *Incisivosaurus gauthieri* and *Citipati osmolskae*. Kundrát and Janáček (2007), however, were not able to establish this connection in *Conchoraptor gracilis*. The pneumatic spaces are not exposed laterally to form an enlarged lacrimal fossa as in *Caudipteryx zoui* (IVPP V 12430). The jugal process of the lacrimal, with the jugal, forms the preorbital bar separating the antorbital fossa from the orbit. The posterior (frontal) process of the lacrimal is short and extends only the anterior quarter of the length of the orbit. The medial border of the frontal process in *Khaan mckennai* abuts the frontal along a straight contact.

The lacrimal is not significantly exposed on the skull roof along its medial contact with the frontal; instead, only a narrow portion of the element is visible tapering posteriorly (fig. 8).

JUGAL

Figures 3, 5

The jugal is elongate and slender, differing from the straplike morphology of the jugal in the basal oviraptorosaur *Incisivosaurus gauthieri* (compare fig. 5A with Balanoff et al., 2009: fig. 3) and most other coelurosaurs. The rodlike shape of the jugal has been considered diagnostic of all oviraptorids (Turner et al., 2007a); however, this element in *Conchoraptor gracilis* also has a distinctly straplike appearance more closely resembling the morphology in *Incisivosaurus gauthieri*.

The jugal contacts the maxilla anteriorly in a simple overlapping contact, the postorbital dorsally along the dorsal (postorbital) process, and the quadratojugal posteriorly (although this contact is not well preserved in any of the specimens). The maxillary process of the jugal forms the ventral margin of the orbit. Similar to *Citipati osmolskae* and *Conchoraptor gracilis*, this process inflects slightly ventrally anterior to the margin of the orbit to make a small contribution to the posteroventral corner of the antorbital fossa (fig. 5A, C). The jugal in *Incisivosaurus gauthieri* does not contribute to the fossa; however, the process does reach this extent in *Caudipteryx zoui* (Ji et al., 1998; Zhou et al., 2000).

The posterior margin of the orbit is composed of the postorbital and postorbital process of the jugal. The postorbital process of the jugal extends posterodorsally for at least two-thirds of the orbit height, somewhat less than in *Citipati osmolskae* (Clark et al., 2002) and *Conchoraptor gracilis* (Osmólska et al., 2004). The posterior flexion of the postorbital process of the jugal differs in the *Khaan mckennai* specimens observed here (figs. 3C, D, 5). Flexion in IGM 100/973 is much more pronounced than it is in either IGM 100/1127 or 100/1002. Both specimens have a postorbital process that is nearly vertical (similar to *Incisivosaurus gauthieri* and *Citipati osmolskae*). Posteriorly the quadratojugal process lies lateral to the quadratojugal, and these two elements are sutured but unfused. The quadratojugal process of the jugal extends at least two-thirds the length of the infratemporal fenestra, further than in *Citipati osmolskae*. The medial surface of the jugal is not visible.

POSTORBITAL

Figures 3, 5

The triradiate postorbital is best preserved in IGM 100/1127 and on the right side of IGM 100/973 (figs. 3C, 5A, C). The postorbital contacts the frontal anteriorly along the frontal process, the squamosal posteriorly along the posteriorly projecting squamosal process, and the jugal ventrally. The medial surface of the frontal process of the postorbital also has a short contact with the lateral extension of the laterosphenoid. The postorbital and jugal form the postorbital bar that completely separates the orbit from the infratemporal fenestra. The anterior margin of the jugal process of the postorbital is concave and forms the posterior margin of the orbit. The infratemporal fenestra is subrectangular in shape. (Although the squamosal is damaged and its shape cannot be assessed confidently on IGM 100/973, it is better preserved in IGM 100/1127 [fig. 5C]. Almost all other oviraptorosaurs, however, have a subrectangular fenestra.) The dorsal margin of the infratemporal fenestra is shortened by the squamosal in *Khaan mckennai*, similar to the condition in *Citipati osmolskae*. Conversely, *Ingenia yanshini* and *Conchoraptor gracilis* appear to have longer dorsal margins (Osmólska et al., 2004). The infratemporal fenestra is bordered by the postorbital and jugal anteriorly, jugal ventrally, quadratojugal posteroventrally, quadratojugal and squamosal posteriorly, and squamosal and postorbital dorsally. The distal end of the frontal process of the postorbital turns dorsally and expands slightly at the terminus. Although similar to most oviraptorids such as *Citipati osmolskae* and *Conchoraptor gracilis*, this morphology differs substantially from *Incisivosaurus gauthieri*, which has a frontal process that curves slightly ventrally to echo the shape of the orbit (Balanoff et al., 2009: fig. 3). The posterior squamosal process is damaged on the right side of IGM 100/973, but well preserved in IGM 100/1127. This process extends only one-half of the length of the infratemporal fenestra, differing from the elongate processes seen in *Citipati osmolskae* and *Conchoraptor gracilis* that extend almost the entire length of the fenestra (Osmólska et al., 2004). The jugal process of the postorbital extends ventrally approximately two-thirds the length of the infratemporal fenestra (based on IGM 100/1127), unlike the process in *Citipati osmolskae* that extends the entire length of the fenestra (Clark et al., 2002). On the dorsal surface of the skull the postorbital and squamosal form the lateral border of the supratemporal fenestra.

SQUAMOSAL

Figures 3, 5

The squamosal is too severely damaged in all three of the specimens to make any confident statements about its morphology. The quadrate process does overlap the quadrate to form the immobile joint that is present in other oviraptorids (fig. 3C; see Clark et al., 2002). The contact with the postorbital is also visible in IGM 100/1127 and, as described above, the postorbital lies anterior and lateral to the squamosal.

SUPRAOCCIPITAL

Figures 3, 6

The supraoccipital is not exposed in IGM 100/1127 and is severely damaged in IGM 100/1002 (fig. 6). In IGM 100/973 the supraoccipital is wide and triangular but damaged along its dorsal border where it presumably contacted the parietal (fig. 3F). The only other contact that can be discerned is the long diagonal contact with the exoccipital along the ventral edge of the supraoccipital. The majority of the foramen magnum is bordered by the paired exoccipitals; however, the ventral margin of the supraoccipital provides a very small contribution to the dorsal border of this structure (figs. 3F, 6; the supraoccipital may be excluded from foramen magnum in *Citipati osmolskae* and *Conchoraptor gracilis*—see Clark et al., 2002). The supraoccipital makes a broad contribution to the foramen magnum in *Incisivosaurus gauthieri* (Balanoff et al., 2009: fig. 5). A pronounced vertical nuchal prominence is present on the external surface of the supraoccipital in *Khaan mckennai* (fig. 8).

EXOCCIPITAL

Figures 3, 6

The paired exoccipitals are damaged in all of the specimens, yet several aspects of their morphology can still be discerned (figs. 3F, 6). These elements form the lateral and most of the dorsal margins of the foramen magnum. However, as indicated above, the supraoccipital may contribute a small portion to the dorsal midline and the basioccipital forms the ventral border of this structure. The foramen magnum is mediolaterally elongate. This shape may be due to dorsoventral compression in IGM 100/973 (fig. 3F); however, a similar shape is also present in IGM 100/1002 (fig. 6), which (if deformed) is more likely compressed along the mediolateral axis. Dorsally, the exoccipital contacts the supraoccipital (described above). A small opening is present on the border between these elements, but it is difficult to ascertain whether this is real or an artifact of breakage. The opening is bilaterally symmetrical and may represent the foramen for the external occipital vein (fig. 3F), a feature present in most other theropods. The only other contact visible on IGM 100/973 is the ventral contact with the basioccipital. The exoccipital sits on the dorsal surface of the basioccipital and forms part of the neck to the occipital condyle. This element does not appear to contribute to the condyle itself. This same arrangement is present in *Citipati osmolskae*. One small opening is visible on the ventral surface of the exoccipital of IGM 100/973. This foramen likely transported the hypoglossal nerve (CN XII) (fig. 3F). The paroccipital processes are preserved and visible only in IGM 100/1002 (fig. 6). These structures possess the characteristic ventrolaterally curved or pendant shape of all oviraptorosaurs (including the basal form *Incisivosaurus gauthieri*). Although the shape of the paroccipital processes corresponds closely with *Citipati osmolskae*, the dorsoventral depth is much more slender in *Khaan mckennai* (compare fig. 6 with Clark et al., 2002: fig. 6). The neck of the paroccipital processes is slightly pinched toward the proximal end.

BASIOCCIPITAL

Figures 3B, F, 6

The basioccipital forms the entire occipital condyle and the ventral margin of the foramen magnum. The occipital and ventral surfaces of the basioccipital are preserved in IGM 100/973. In IGM 100/1002 only the occipital surface is visible, but it lacks the distortion present in IGM 100/973 (compare figs. 3F, 6). The occipital condyle of *Khaan mckennai* does not possess the distinctly elongate neck projecting beyond the occipital surface of the skull present in *Citipati osmolskae* (Clark et al., 2002). The neck of the occipital condyle, rather, is similar to other oviraptorosaurs such as *Conchoraptor gracilis*, *Incisivosaurus gauthieri*, and *Caudipteryx zoui* (Ji et al., 1998; Osmólska et al., 2004; Balanoff et al., 2009) in being short and unconstricted (in contrast, *Chirostenotes pergracilis* possesses a ventrally constricted neck; Sues, 1997). The occipital condyle is rounded with no central depression (differing significantly from the flat morphology with a central depression in *Citipati osmolskae*) and is narrower than the foramen magnum, similar to other oviraptorosaurs including *Chirostenotes pergracilis* (Sues, 1997). This condition cannot be assessed in *Incisivosaurus gauthieri* as the skull is too distorted.

On the ventral surface of the skull the basal tubera are reduced relative to those in *Incisivosaurus gauthieri* (Xu et al., 2002; Balanoff et al., 2009: fig. 4b). The basal tubera of *Khaan mckennai*, however, are relatively larger than those in *Citipati osmolskae*. Despite the differences in size, the basal tubera of *Khaan mckennai* and *Citipati osmolskae* both are separated by a small circular depression along the midline. The basal tubera in IGM 100/973 have an anterior orientation differing drastically from the vertical orientation present in *Conchoraptor gracilis* (Balanoff and Norell, in prep.). No pneumatic openings (subcondylar recesses) are visible opening on the lateral surface of the basal tubera like in *Citipati osmolskae* and *Conchoraptor gracilis* (Clark et al., 2002). The anterior contact of the basioccipital with the parabasisphenoid is not preserved in any of the specimens. CT imagery of IGM 100/973 reveals that this region of the skull is poorly ossified, as it is in all oviraptorosaurs including *Incisivosaurus gauthieri*, and therefore probably not preserved in this specimen.

PARABASISPHENOID

Figure 3

This element is not wholly preserved in any of the specimens, but a small portion of the mediolaterally compressed parasbasisphenoid rostrum is visible through the orbit of IGM 100/973 (fig. 3D). CT data show that the parasphenoid rostrum has a slight anterodorsal slant relative to its base (fig. 9) and lacks pneumatization like that present in troodontids (Norell et al., 2009).

QUADRATOJUGAL

Figures 3, 5

The quadratojugal is an L-shaped element with only a short, rounded posterior process that is abbreviated compared to the same process of *Citipati osmolskae*, *Rinchenia mongoliensis*, or IGM 100/42 (Zamyn Khondt oviraptorid in Osmólska et al. [2004]) (figs. 3C, D, 5; Clark et al., 2002; Osmólska et al., 2004). In IGM 100/1127 and 100/973 the quadratojugal is present but damaged; in IGM 100/1002 the element is not articulated with the skull but preserved in its entirety (fig. 5A). The quadratojugal contacts the jugal anteriorly, the squamosal dorsally, and the quadrate dorsally and ventrally along its medial surface. It forms the posterior and ventral margins of the infratemporal fenestra. The anterior (jugal) ramus of the quadratojugal extends just over half the length of the infratemporal fenestra and contacts the jugal along its lateral surface. An elongate posterior process extends from the posteroventral surface of the quadratojugal. This extension is approximately one-half the length of the jugal process and shorter than that of *Citipati osmolskae*. The cross section of the element where it underlies the infratemporal fenestra is similar to the jugal in that it is extremely gracile and circular—the same morphology present in *Citipati osmolskae* and *Caudipteryx zoui* (Ji et al., 1998; Zhou et al., 2000). The extent of the dorsal (squamosal) process cannot be determined in any of the three specimens; however, the medial contact of this process with the quadrate is preserved in IGM 100/973. A large quadrate foramen (visible in posterior view) is present along this contact between the quadratojugal and quadrate, (fig. 3F; see also Clark et al., 2002).

QUADRATE

Figures 3, 5, 6

The quadrate is difficult to observe due to the presence of overlying bones; however, the overall structure of the element can be pieced together using a composite of all three specimens as well as CT imagery (figs. 3C, D, F, 5). The quadrate is oriented obliquely, the same arrangement seen in other oviraptorosaurs. Visible contacts include the pterygoid anteriorly (IGM 100/1002) and medially (IGM 100/973), the quadratojugal dorsally and ventrally on the lateral surface (IGM 100/973), and the squamosal dorsally on the lateral surface of the optic wing (IGM 100/973 and 100/1002). Although established in other oviraptorosaurs (Maryańska and Osmólska, 1997) such as *Incisivosaurus gauthieri*, *Citipati osmolskae*, and *Conchoraptor gracilis* (Kundrát and Janáček, 2007), the dual contact with the braincase and prootic is not visible externally on any of the specimens of *Khaan mckennai*. CT images also fail to show an extensive contact between the quadrate and exoccipital/opisthotic of *Khaan mckennai* (fig. 10F).

The overall size of the quadrate is large due to an extremely expanded optic wing that forms the medial wall of the infratemporal fenestra and, with the dorsal expansion of the pterygoid, covers much of the lateral wall of the braincase (figs. 3C, 5). This unusual arrangement is present in other oviraptorosaurs including the basalmost form *Incisivosaurus gauthieri*, but in no known theropod taxa outside this group (Xu et al., 2002; Balanoff et al., 2009). The optic wing of the quadrate contacts the pterygoid ventrally, so that this entire structure is made up of at least the quadrate and pterygoid and extends anteriorly to just posterior to the trigeminal foramen. The contact of the optic wing with the pterygoid is best observed in IGM 100/1002 (although also present in IGM 100/973). The distal end of the optic wing is rounded and lateral to the pterygoid wing (fig. 5B), as is the morphology of *Citipati osmolskae*. The quadrate of *Incisivosaurus gauthieri* also has this same basic construction.

The articulation of the quadrate with the squamosal is not visible in IGM 100/973; however, IGM 100/1002 shows the squamosal overlying the optic wing of the quadrate in a nonmoveable joint, as is present in all oviraptorosaurs except *Incisivosaurus gauthieri*. The squamosal is badly damaged in IGM 100/1002, but the articulation remains visible. The posterior surface of the dorsal process of the quadrate as seen in IGM 100/973 is flat with no pneumatic foramen (fig. 3F); however, this absence may be the result of other bones or matrix obscuring the foramen. CT data reveal a hollow, presumably pneumatic quadrate (figs. 9B, 10E). The lateral edge of the dorsal process bears a thin lip likely for the articulation with the quadratojugal. Because the mandible is still articulated with the skull in all three specimens of *Khaan mckennai*, the mandibular surface of the quadrate is not visible, but CT imagery shows a sliding articulation as is present in known oviraptorids (see Barsbold, 1983, 1986; Clark et al., 2002; Osmólska et al., 2004) except *Avimimus portentosus* (Kurzanov, 1981, 1987; Vickers-Rich et al., 2002).

LATEROSPHENOID

Figures 3, 5

The laterosphenoid of IGM 100/973 is well preserved on the right side of the skull (fig. 3C). IGM 100/1002 does not preserve the laterosphenoid, and only the orbital surface is partially preserved in IGM 100/1127. This description, therefore, is based almost entirely on IGM 100/973. The element has a similar morphology to that of other oviraptorids (see Clark et al., 2002) in that it is compressed anteroposteriorly and oriented almost horizontally with a thin, elongate postorbital process (*capitate process* of Clark et al., 2002). The laterosphenoid contacts its opposite medially, the frontal, parietal, and postorbital along the lateral postorbital process, and the prootic posteriorly. A depression on the anterior surface of the element lateral to the optic foramen implies that the epipterygoid also contacted the laterosphenoid in IGM 100/973, as it does in *Citipati osmolskae* (Clark et al., 2002: fig. 2). A small, fused orbitosphenoid can be seen in CT images contacting the laterosphenoid along its medial edge (fig. 11A).

A small vertical ridge runs posterior to the postorbital process of the laterosphenoid dividing the main body of the element into two surfaces, an anterior orbital surface and a posterior lateral surface (fig. 3C). Such an arrangement is also present in *Citipati osmolskae* and *Conchoraptor gracilis*. On the anterior (orbital) surface of the laterosphenoid, a notch is present approximately halfway along the medial margin to form (along with the other laterosphenoid) a single midline opening for the exit of the optic nerve (CN II). All oviraptorids possess a single opening for the optic nerve; however, all specimens of *Khaan mckennai* lack the ventral midline process that underlies this foramen in *Citipati osmolskae*, *Rinchenia mongoliensis*, and *Nemegtomaia barsboldi* (Clark et al., 2002: fig. 2; Lü et al., 2004). The morphology of the anterior surface of the laterosphenoid is not visible (or not preserved) in basal oviraptorosaurs including *Incisivosaurus gauthieri*. The postorbital process of the laterosphenoid of *Khaan mckennai* sits in an impression that spans the posterior orbital surface of the frontal and the anteroventral portion of the postorbital.

The laterosphenoid's lateral surface abuts the prootic posteriorly, and these two elements form the single trigeminal opening (CN V; fig. 3C). The trigeminal foramen is approximately one-half the size of the optic nerve opening. The opening for CN V is small in the oviraptorids *Citipati osmolskae* and *Conchoraptor gracilis* (see prootic description), but relatively large in the basal oviraptorosaur *Incisivosaurus gauthieri* (Xu et al., 2002; Balanoff et al., 2009: fig. 3b) and in *Chirostenotes pergracilis* (Sues, 1997: fig. 3b). The prootic and laterosphenoid are not fused in *Khaan mckennai* or *Conchoraptor gracilis* but are in *Citipati osmolskae* (Balanoff and Norell, in prep.; Clark et al., 2002).

PROOTIC

Figure 3D

The lateral braincase elements are difficult to distinguish in all specimens of *Khaan mckennai* because of the overlying bones (figs. 3D, 5). The only contacts of the prootic that can be differentiated are the dorsal contact with the parietal inside the supratemporal fenestra and the anterior contact with the laterosphenoid. A small arm extends anteriorly beneath the laterosphenoid to contribute to the trigeminal foramen (CN V). A relatively deep impression corresponding to the dorsal tympanic recess lies dorsally on the lateral surface (Norell and Makovicky, 1997, 1999; Witmer, 1997), although no foramina penetrate the recess as is seen in *Conchoraptor gracilis* (Balanoff and Norell, in prep.), *Citipati osmolskae* (Clark et al., 2002), and *Incisivosaurus gauthieri* (Balanoff et al., 2009). As in *Citipati osmolskae*, a distinct horizontal swelling forms the ventrolateral border of the fossa. The foramen for the facial nerve (CN VII) is not visible on the external surface of any *Khaan mckennai* specimens, but can be seen in the CT imagery piercing the prootic directly anterior to the vestibule of the ear (fig. 11). The ear region also is completely obscured on the external surface by the extensive quadrate/pterygoid wing.

INNER EAR

Figure 12

The precise size of the canals of the inner ear is difficult to determine because of mineral deposits within the canals (especially the horizontal canal; fig. 12A–D). The cochlear canal is not discernible in the CT data. These hindrances notwithstanding, the internal ear structure was digitally reconstructed using CT imagery for IGM 100/973 (fig. 12). The overall structure of the inner ear is roughly triangular in lateral view, similar to all other theropods (Witmer and Ridgely, 2009); however, it lacks the elongate morphology of many coelurosaurs. Instead, the overall shape is slightly compressed, which undoubtedly is influenced by the dorsoventral compression of the skull as a whole. The inner ear, otherwise, closely resembles that of the typical coelurosaur. The posterior semicircular canal is bowed dorsally so as to twist at the common crus. The anterior and posterior semicircular canals have a thin appearance; however, the horizontal canal appears more robust than in typical coelurosaur ears, even basal taxa such as tyrannosaurids (Witmer and Ridgely, 2009; Brusatte et al., 2009; Bever et al., 2011).

The anterior semicircular canal expands anteriorly and posterodorsally, and extends only slightly beyond the common crus, not as far as it does in the basal oviraptorosaur *Incisivosaurus gauthieri* (Balanoff et al., 2009) and paravians (Dominguez Alonso et al., 2004). The canal, therefore, lacks the extreme kidney shape that is characteristic of most coelurosaurs (Norell et al., 2006). The horizontal canal has an arc shape. The posterior and horizontal canals join posteriorly (and the posterior canal extends ventrally beyond the level of the horizontal canal), so that they cannot be distinguished from one another at this point. The vestibule resembles other theropods in that it does not extend dorsally above the dorsal margin of the horizontal semicircular canal. The endolymphatic duct is not visible in the reconstruction or the CT slices.

The bony division (crista interfenestralis) between the vestibular portion of the inner ear and the pseudorotundum is not visible externally (covered by the bony quadrate/pterygoid flange) or in the CT imagery. This division likely is present, as it is present in the basal taxon *Incisivosaurus gauthieri* (Balanoff et al., 2009) as well as *Citipati osmolskae* (Clark et al., 2002). Although not visible externally on the skull, the vestibular foramen is discernible in the CT imagery (fig. 12) set into a depression, as it is in all maniraptorans. The stapes is not preserved (even in CT imagery) in any of the specimens.

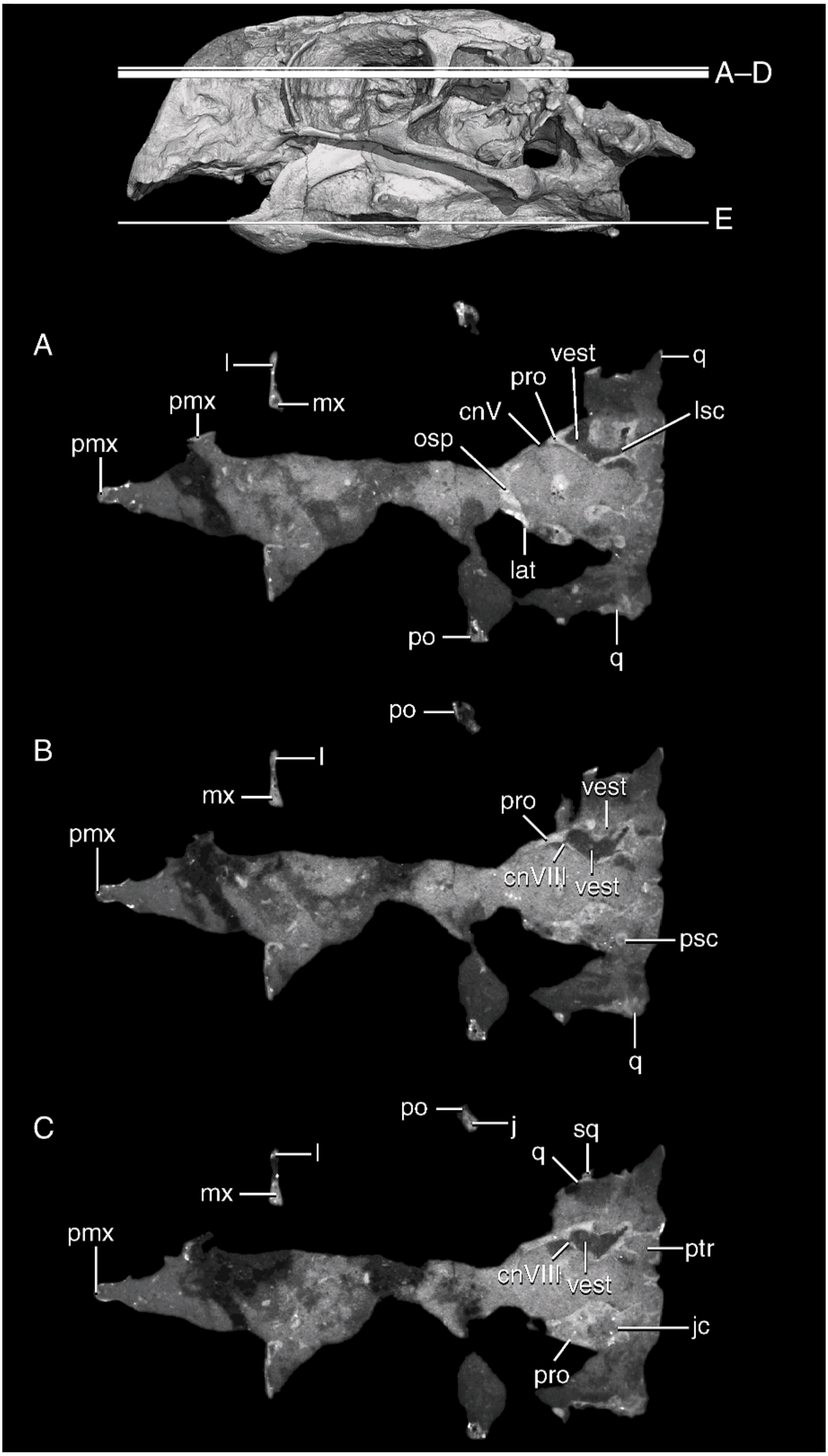
MANDIBLE

The lateral surface of the mandible of *Khaan mckennai* is exceptionally preserved in all three specimens. The best example, however, is IGM 100/1127, and most of the description is based on that specimen. IGM 100/973 exhibits good preservation, and IGM 100/1002 is disarticulated slightly at its posterior end (figs. 3B, C, 5B). The mandible of *Khaan mckennai* preserves the bizarre anteroposterior shortening present in all other oviraptorids, which lack the elongation of other theropods, caenagnathids, and basal oviraptorosaurs such as *Incisivosaurus gauthieri* and *Caudipteryx zoui* (Sternberg, 1940; Barsbold, 1981; Currie et al., 1993; Sues, 1997; Ji et al., 1998; Zhou et al., 2000; Balanoff et al., 2009). Oviraptorids also share a dorsoventrally high coronoid eminence with corresponding surangular spine that extends anteriorly into (but not completely dividing) the enlarged heart-shaped mandibular fenestra. The only oviraptorid taxon in which the morphology of the mandibular fenestra differs slightly is the large-bodied *Gigantoraptor erlianensis*. This taxon has an oval fenestra that lacks the surangular spine, more similar to caenagnathids (Xu et al., 2007). *Khaan mckennai* shares with caenagnathids, *Caudipteryx zoui*, and *Similicaudipteryx* to the exclusion of *Incisivosaurus gauthieri* an edentulous, U-shaped dentary symphysis that is slightly downturned. All oviraptorosaurs including *Incisivosaurus gauthieri* possess an elongate, slender retroarticular process (Xu et al., 2007; Balanoff et al., 2010). The coronoid bone of *Khaan mckennai* likely is either absent or reduced. Although *Citipati osmolskae* (Clark et al., 2002) and *Gigantoraptor erlianensis* (Xu et al., 2007) possess a reduced coronoid, the medial surface of the mandible in *Khaan mckennai* is not visible in external view, and CT images do not suggest its presence.

DENTARY

Figures 3, 5

The dentaries of IGM 100/973 are sutured at the midline but not fully fused, similar to other oviraptorids but differing from *Gigantoraptor erliansensis*, which is completely fused and does not bear any trace of a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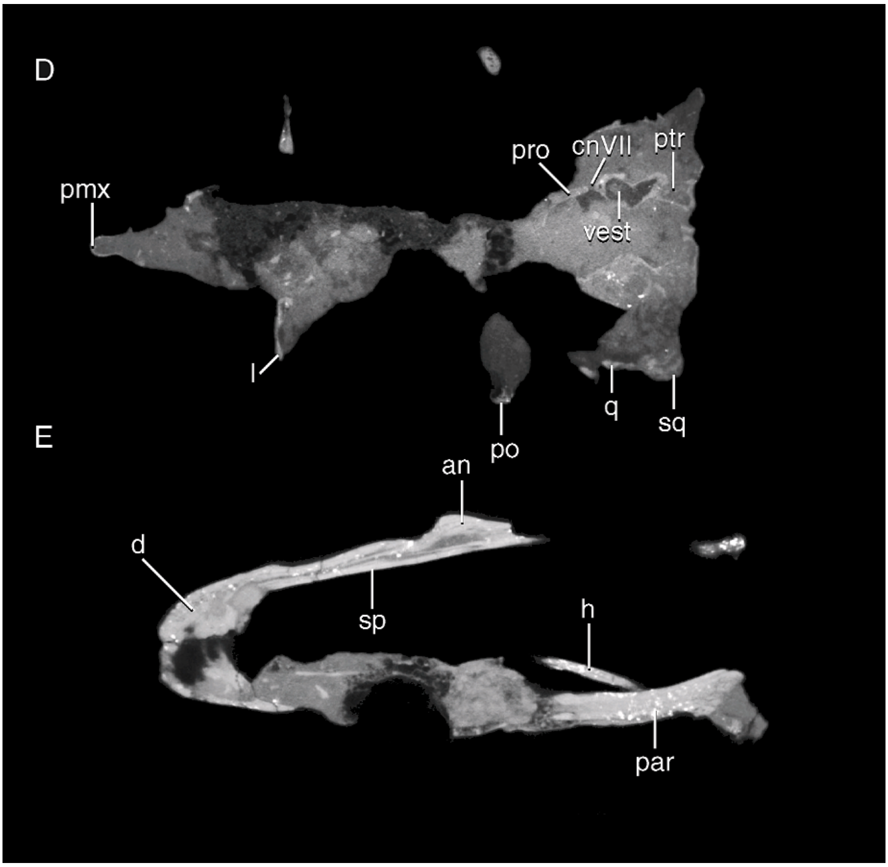

Fig. 11. Continued.

midline suture. The dentaries are U-shaped in dorsal view, as in all oviraptorosaurs and therizinosaurs. CT data also indicate a highly pneumatic internal structure of the dentary (fig. 10A). The overall morphology of the dentary in oviraptorids is very distinctive, and *Khaan mckennai* does not differ substantially from this morphology, which is preserved even in the extremely large-bodied *Gigantoraptor erlianensis* (Xu et al., 2007). The dentary contacts its opposite anteriorly along the medial surface, the surangular posteriorly by way of the dorsal process, and the surangular and angular posteriorly along the ventral process (fig. 5). The dentaries are edentulous, and all oviraptorosaurs have a pronounced downturn at the anteriormost edge to form, with the premaxilla, a parrotlike "beak." If the ventral process of the dentary is held horizontally, the degree of downturn does vary between oviraptorosaur taxa. The basal taxa *Incisivosaurus gauthieri* and *Caudipteryx zoui* are almost completely horizontal. *Microvenator celer* has a pronounced bend anteriorly in its dentary (Makovicky and Sues, 1998), but all of the observed caenagnathids have an almost horizontal dentary (Currie et al., 1993). All

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Fig. 11. CT images showing horizontal slices at various levels through IGM 100/973 (in mm). Abbreviations in appendix 2. **A,** 21.02 mm; **B,** 21.70 mm; and **C,** 22.31 mm (opposite page); **D,** 22.85 mm; and **E,** 57.88 mm (above).

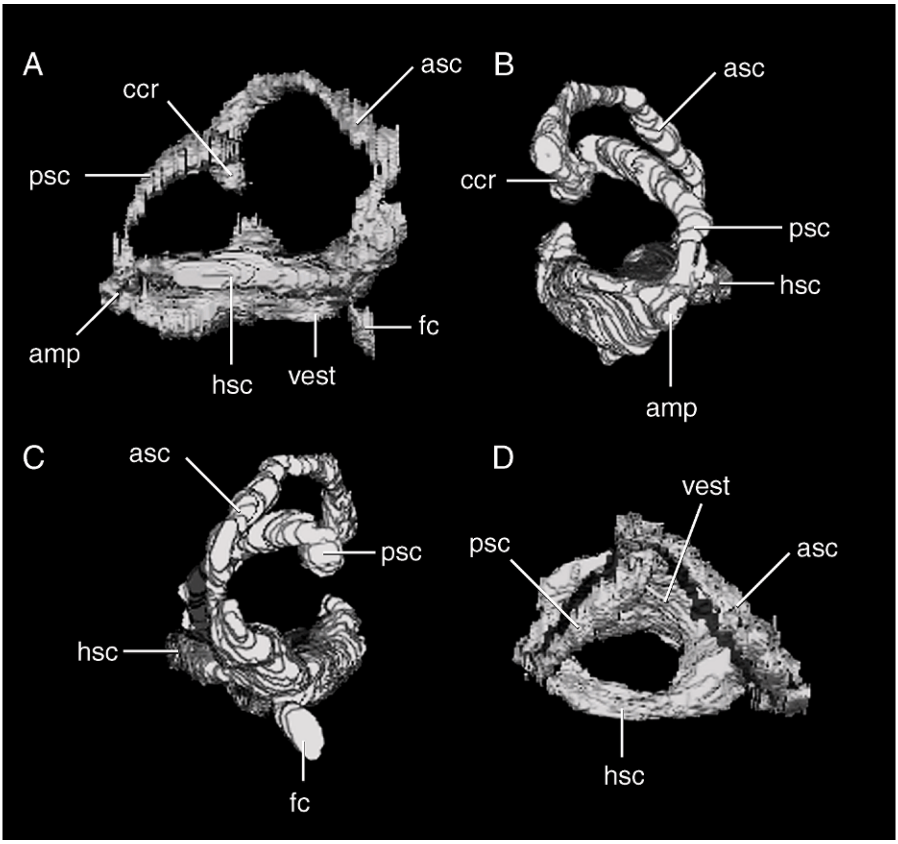


Fig. 12. Reconstruction of the inner ear of IGM 100/973 using CT images. Abbreviations in appendix 2. **A,** lateral view; **B,** posterior view; **C,** anterior view; **D,** dorsal view.

oviraptorids have some degree of downturn at the anterior margin of the dentary. The anterior dentary of *Khaan mckennai* is fairly subdued, forming only about a 20° angle from the horizontal plane. *Citipati osmolskae* (Clark et al., 2002) and *Oviraptor philoceratops* (Osborn, 1924) are more pronounced, angling at least 40° from the horizontal plane. An expanded ventrally sloping shelf is present on the labial surface of the dentary of *Khaan mckennai*, forming a sharp triturating surface dorsally.

The lateral surface of the dentary bifurcates into dorsal and ventral processes posteriorly. These processes enclose a central space forming the enlarged mandibular fenestra. The dorsal process spans approximately two-thirds the length of the entire fenestra and is overlain by the surangular laterally. The dorsal process of *Khaan mckennai* curves dorsally forming a large coronoid prominence like that present in all known oviraptorids (figs. 3C, 5; Osmólska et al., 2004) and possibly *Microvenator celer* (Makovicky and Sues, 1998: fig. 2). Caenagnathids and basal oviraptorosaurs such as *Incisivosaurus gauthieri* and *Caudipteryx zoui* lack a coronoid prominence (Sues, 1997; Ji et al., 1998; Balanoff et al., 2009). The ventral process spans the entire length of the mandibular fenestra but tapers posteriorly and sits underneath the angular at its posterior end. All oviraptorosaurs, including *Incisivosaurus gauthieri*, have elongate dorsal and ventral dentary processes. Although the dorsal process in *Gigantoraptor erlianensis* extends the same length, it begins to taper approximately midway along the length of the mandibular fenestra. The external surface of the dentary in *Khaan mckennai* is pierced by numerous neurovascular foramina, which are concentrated toward the anterior symphyseal region (figs. 3C, E, 5). The presence of these foramina, as in the premaxillae, suggests that the dentary was covered by a keratinous rhamphotheca in life similar to what is seen in modern birds and turtles (Bubien-Waluszewska, 1981). These foramina are present in other oviraptorids and caengnathids as well as the basal forms of *Incisivosaurus gauthieri* and *Caudipteryx zoui* (Currie et al., 1993; Ji et al., 1998; Osmólska et al., 2004; Xu et al., 2003). Such structures cannot be distinguished in *Gigantoraptor erlianensis.* The medial surface of the dentary is not readily visible in any of the three specimens (except a small anterior portion in IGM 100/973, although no morphology can be assessed), however CT imagery shows a medial contact with the straplike splenial along the posteroventral process (fig. 11E). The straplike morphology is also found in caenagnathids and other oviraptorids but not in the basal *Incisivosaurus gauthieri* or *Caudipteryx zoui*, which tend to have a more triangular morphology similar to the splenial in other coelurosaurs.

SURANGULAR

Figures 3, 5

The surangular makes up the majority of the lateral surface of the posterior body of the mandible, continuing from its anterior articulations with the dentary posteriorly to a point near the mandibular articulation with the cranium. The surangular articulates with the dorsal process of the dentary anterodorsally, angular along its ventral margin, and articular posteriorly. CT imagery shows the medial contact of the surangular with the prearticular (fig. 11E). The surangular sits within a fossa on the prearticular. The anterior end of the surangular and the dentary make up the majority of the mandibular fenestra as in all oviraptorosaurs. As is characteristic of oviraptorids (but not caenagnathids or basal oviraptorosaurs), the enlarged surangular spine projects into the mandibular fenestra. In *Khaan mckennai*, however, the spine extends less than halfway across the length of the opening. This distance is far less than the three-quarters length of the mandibular fenestra that the surangular spine extends in *Citipati osmolskae* and other larger oviraptorids (see IGM 100/42; Osmólska et al., 2004), although the spine is missing completely and does not appear to be broken in the extremely large oviraptorid *Gigantoraptor erlianensis*. The shortened spine in *Khaan mckennai* also does not appear to be a result of breakage (fig. 3C, 5). The posterior end of the surangular tapers along the articulation with the articular, ending just under the mandibular articulation surface with the cranium. The surangular does not contribute to the mandibular articulation and is not fused into a surangular/articular/coronoid complex as in caenagnathids (Currie et al., 1993). The posterior region of the lateral surface of the surangular has a shallow fossa that is longitudinally oriented for the attachment of the adductor muscles. Just posterior to the adductor fossa a small foramen pierces the lateral surface of the surangular (figs. 3C, 5). A similarly small foramen also is present in *Citipati osmolskae* in this same position. Neither of these taxa has the distinct surangular foramen that is seen in *Banji long* (Xu and Han, 2010). CT data show that the dorsal margin of the surangular is narrow along its entire length.

ANGULAR

Figure 9

The angular is difficult to observe in any of the specimens, but can be visualized in the CT images (fig. 9A). The splintlike element extends approximately two-thirds the length of the mandibular fenestra overlying (although ventral to) the dentary and reaches posteriorly to the mandibular articulation. The posterior end tapers but does not reach the level of the retroarticular process as it does in *Citipati osmolskae* and *Gigantoraptor erlianensis*.

PREARTICULAR

Figure 11E

Most of the prearticular is located on the medial (labial surface) of the mandible and is therefore partially obscured by matrix. Externally, the ventral surface of the prearticular is visible adhering to the ventral surface of the articular along this element's midline. CT imagery shows the prearticular articulates with the surangular medially, the angular ventrally, and the articular posteromedially (figs. 9, 10, 11E). The element is shallow along its entire length and extends to the posterior end of the retroarticular process as it does in all oviraptorosaurs.

Articular

Figure 3C

The entire articular is visible only in IGM 100/973 (fig. 3C). The articular makes up all of the dorsal surface of the mandibular articulation with the cranium as well as the dorsal surface of the retroarticular process, which lies immediately posterior to the articulation. The articular contacts the prearticular anteriorly along the midline of its ventral surface and surangular along its lateral surface. CT images show that the articulation surface of the articular is entirely convex (fig. 9A), as in all other oviraptorids and caenagnathids (Currie et al., 1993). *Avimimus portentosus* and therizinosaurs differ from this morphology, instead possessing a cotyle (Kurzanov, 1981, 1987; Clark et al., 1994). *Caudipteryx zoui* also appears to possess a cotyle rather than the sliding articular joint characteristic of oviraptorids and caenagnathids (contra Ji et al., 1998). The dorsal surface of the mandibular articulation of the articular flares laterally beyond the margins of the mandibular ramus. The slender and elongate retroarticular process is a distinctive characteristic of all known oviraptorids (Maryańska et al., 2002; Lü et al., 2004; Lü 2005; Turner et al., 2007b, Xu et al., 2007). This process in *Khaan mckennai* makes up approximately one-fifth the entire length of the mandible (table 1).

Splenial

Figure 3B

The splenial is exposed only in IGM 100/973 along the medioventral surface of the mandible (fig. 3B, D). From what can be gleaned from such limited exposure, the splenial lies along the medial surface of the mandible and extends from the anterior region of the dentary posteriorly to just beyond the mandibular foramen (at about the midpoint of the adductor fossa). This arrangement corresponds with that in *Citipati osmolskae* and *Gigantoraptor erlianensis* but differs from *Incisivosaurus gauthieri*, where the splenial expands dorsally at its anterior end (Xu et al., 2002). CT imagery shows that, similar to the arrangement in most other oviraptorosaurs, except *Incisivosaurus gauthieri* and *Caudipteryx zoui* where it is triangular (consistent with other theropods), the splenial is elongate and straplike (figs. 9B, 11E) (Sternberg, 1940; Maryańska et al., 2002).

Hyoid

Figure 3B

A pair of hyoid elements is preserved in specimen IGM 100/973 of *Khaan mckennai* (fig. 3B). These likely are the ceratohyals and closely resemble those of *Citipati osmolskae* (compare fig. 3B with Clark et al., 2002: fig. 10). The ceratohyals are small and rodlike and approximately one-half the length of the mandible. They do not, however, curve medially as they do in *Citipati osmolskae*; instead, the ceratohyals are almost straight. These elements bend only slightly laterally at their posterior ends. The anterior and posterior extremities are expanded and somewhat compressed mediolaterally as is seen in *Citipati osmolskae*. The hyoid elements were preserved in an orientation parallel to the mandibular rami.

POSTCRANIAL DESCRIPTION

Khaan mckennai provides a unique opportunity to observe both articulated and disarticulated postcranial skeletons. As previously mentioned, the postcranium of IGM 100/973 has been physically disarticulated. It includes the pelvis and hindlimbs. No forelimb for IGM 100/973 is preserved. IGM 100/1127 and IGM 100/1002 remain in articulation with both fore- and hindlimbs (figs. 1, 2). The forelimb description, therefore, comes exclusively from these specimens. The holotype (IGM 100/1127) is the most completely preserved postcranial skeleton, being complete except for a few dispersed dorsal vertebrae. Some elements that appear to be missing are likely preserved lying below the rest of the skeleton. IGM 100/1002 also retains the postcranial skeleton almost in its entirety, except for an incomplete caudal series; only the seven most proximal caudal vertebrae are present in IGM 100/1002, as the distal end of the tail was eroding out of a hill when discovered. Because the descriptions of the forelimbs and vertebral column are based on these two specimens still encased in blocks, not all surfaces can be described.

The postcranial skeleton of *Khaan mckennai* is very gracile when compared to the much larger and more robust skeleton of *Citipati osmolskae*. It possesses a morphology that more closely resembles the small oviraptorid *Conchoraptor gracilis*. *Ingenia yanshini*, though considered a small oviraptorid, is larger than both *Khaan mckennai* and *Conchoraptor gracilis* (but, of course, smaller than *Oviraptor philoceratops*, *Citipati osmolskae,* and *Gigantoraptor erlianensis*). As stated above, a complete vertebral column does not exist for any of the specimens of *Khaan mckennai*; yet, using a composite of the two articulated specimens (IGM 100/1127 and IGM 100/1002) a rough estimate of the total number of vertebrae can be attained at approximately 57. This number is consistent with other oviraptorid taxa (see Barsbold, 1997; Osmólska et al., 2004). Oviraptorosaurs such as *Caudipteryx zoui* and *Nomingia gobiensis* are exceptional in having a reduction in the number of caudal vertebrae relative to other oviraptorosaurs in addition to other theropods (Ji et al., 1998; Barsbold et al., 2000).

CERVICAL VERTEBRAE

Figures 13, 14

The cervical series in oviraptorosaurs typically is composed of 12–13 vertebrae (Osmólska et al., 2004), with *Citipati osmolskae* (IGM 100/978) and *Caudipteryx zoui* each having 12 (Ji et al. [1998] gives the vertebral count as 10, but personal observations revise this number to at least 12—that earlier count did not include the atlas and axis). Both articulated specimens of *Khaan mckennai* have 13 cervical vertebrae including the atlas, axis, and cervicodorsal vertebra. Long necks are characteristic of oviraptorosaurs in general, whereas other theropods typically possess 10 or fewer cervical vertebrae (e.g., Wellnhofer, 1992; Norell and Makovicky, 1997; 1999; Novas, 1997). The atlas is not visible in any of the specimens, and the best example of an axis is seen in IGM 100/1002 (fig. 14). Only the dorsal, lateral, and part of the anterior surfaces of the axis are exposed. The overall morphology of the axis closely approximates that of other oviraptorids such as *Citipati osmolskae*, *Conchoraptor gracilis*, and *Ingenia yanshini* (Barsbold, 1981; Osmólska et al., 2004). This vertebra is not fused with the succeeding vertebra as described for *Heyuannia huangi* (Lü, 2005). A small odontoid process is visible on the anterior articular surface just ventral to the neural canal in *Khaan mckennai*. The dorsal surface of the neural arch bears a subtriangular spine oriented posteriorly similar to other oviraptorid taxa. The spine is minimally taller than the succeeding cervical vertebra. A small oval pleurocoel is present on the axis and a pleurocoel is also present in *Citipati osmolskae* but is much larger (as are pleurocoels in all subsequent cervical vertebrae of that taxon as well). *Conchoraptor gracilis* lacks a pleurocoel on its axial vertebra (Balanoff and Norell, in prep.). In *Citipati osmolskae* the posterior surface of the neural spine on the axis is pneumatized; however, this surface is not exposed in *Khaan mckennai*.

Postaxial cervical vertebrae are best seen in dorsal view in IGM 100/1127. IGM 100/1002 provides a detailed view of the lateral surface of this series (fig. 13B). The anterior (approximately 3–5) postaxial vertebrae are distinctive from the more posterior ones in having a rectangular neural arch in dorsal view, being relatively shorter and fatter than the elongate cervical vertebrae of *Citipati osmolskae*. This rectangular morphology of *Khaan mckennai* is a result of an osseous lamina extending between the zygapophyses and transverse processes as well as the zygapophyses being oriented nearly parallel to each other (fig. 13A). The zygapophyses of the first preserved cervical vertebrae in *Oviraptor philoceratops* (AMNH FARB 6517) also are oriented parallel to each other, so that they closely resemble those of *Khaan*

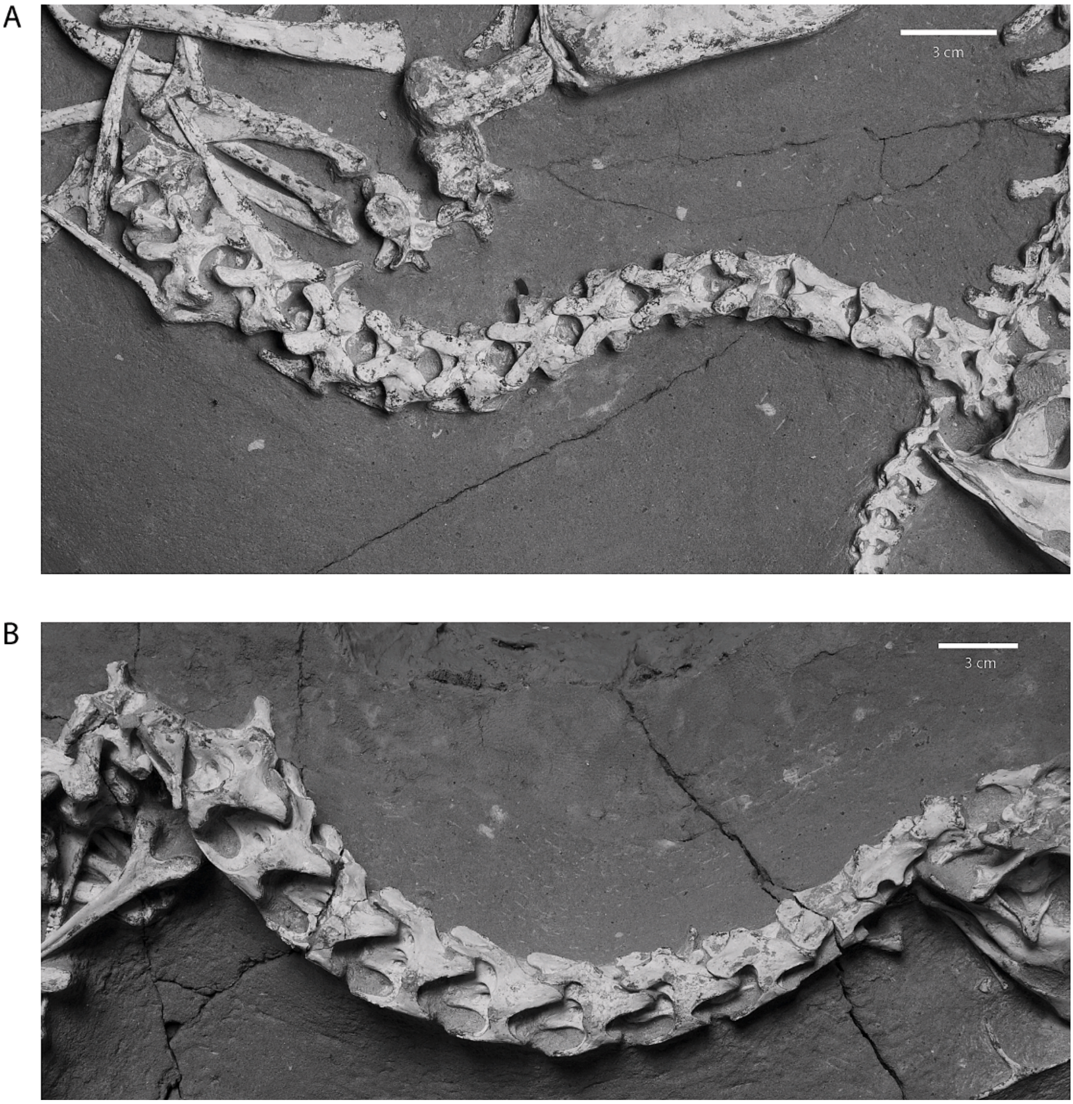


Fig. 13. Cervical vertebrae. **A,** dorsal surface of cervical vertebral series in IGM 100/1127; **B,** lateral surface of cervical vertebral series in IGM 100/1002.

mckennai. The zygapophyses in both *Khaan mckennai* and *Oviraptor philoceratops* begin to spread more laterally proceeding posteriorly along the series. Also, the bony lamina between the transverse processes and postzygapophyses are more excavated toward the posterior end of the cervical column to produce the distinctive X-shape (when viewed dorsally) of oviraptorosaur cervical vertebrae (fig. 13A) (Makovicky and Sues, 1998). The neural spine on all postaxial vertebrae is low, rectangular, and centered on the neural arch (at the intersection of the X). The neural spine becomes longer in more posterior vertebrae (this morphology is shared by *Oviraptor philoceratops*, but appears to be the opposite of the arrangement in *Citipati osmolskae* [IGM 100/978 and 100/1004], where the neural spine becomes shorter and more triangular). The bases of the postzygapophyses, beginning with the third postaxial vertebra, have posterolaterally facing fossae with associated pneumatic foramina. At the base of the anterior and

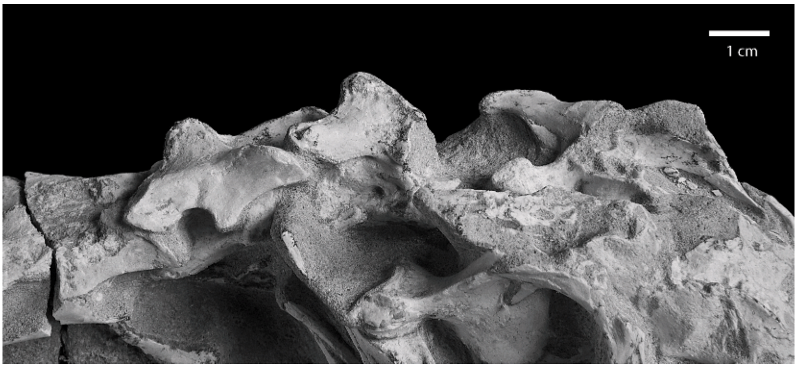


Fig. 14. Lateral view of axial vertebra in IGM 100/1002.

posterior surfaces of the neural spine of all the postaxial cervical vertebrae there are large fossae and pneumatic foramina; therefore, both the centra and neural arches are pneumatized. In *Citipati osmolskae* and *Conchoraptor gracilis* the ventral surface of the base of the transverse processes also possesses a pneumatic fossa with associated foramina. It is likely that this structure also is present in *Khaan mckennai*, but the surface is not exposed.

The centra of the cervical vertebrae are not extensively exposed in either of the specimens; nonetheless, they are best seen in IGM 100/1002. The centra are more easily visible in the posterior cervical vertebrae (fig. 13B). The cross-sectional shape of each centrum appears rectangular (wider than tall), although shape is difficult to determine because of lack of exposure. All cervical vertebrae possess a single pleurocoel on the lateral surface of the centrum, as is the arrangement in all oviraptorosaurs and many theropods in general, except the oviraptorosaur *Microvenator celer*, which has two pleurocoels on each cervical vertebra (Makovicky and Sues, 1998). The pleurocoels in *Khaan mckennai* are placed anteriorly on the anterior centra and gradually migrate toward the center of the lateral face proceeding toward the posterior end of the series. The articular central faces are not visible; the posterior articular faces of the anterior cervical vertebrae (through the fourth cervical) are directed posterodorsally with the succeeding anterior face corresponding to the posterior face (directed anteroventrally). The extreme slant of the articular facets is present in all oviraptorids and possibly caenagnathids (i.e., *Chirostenotes pergracilis*; Sues, 1997), but not present in the more basal forms *Caudipteryx zoui* (Ji et al., 1998) or *Avimimus portentosus* (Kurzanov, 1981, 1987). This condition gradually changes proceeding posteriorly along the cervical series as the articular faces become more vertical in orientation. Most of the cervical ribs are tightly fused to the vertebrae in *Khaan mckennai*; however, the third and fourth cervical ribs are not fused to the vertebral body (fig. 13B). This is also the case in *Citipati osmolskae* (IGM 100/978), whose anterior cervical ribs remain unfused. Fused cervical ribs also are found in *Avimimus portentosus*, *Oviraptor philoceratops*, *Conchoraptor gracilis*, and *Heyuannia huangi* among oviraptorosaurs (Kurzanov, 1981, 1987; Osmólska et al., 2004, Lü, 2005), but not in *Caudipteryx zoui* (Ji et al., 1998; Zhou et al., 2000). In the anterior cervical vertebrae the cervical ribs do not extend past the associated centrum; however, the cervical ribs extend well past the margin of the associated centra in more posterior cervical vertebrae, a condition also found in *Citipati osmolskae*. The cervicodorsal vertebra lies at a transitional point between the cervical and dorsal vertebrae (Osmólska et al., 2004) and is marked by distally expanded transverse processes that are oriented laterally and horizontally (fig. 13B). *Oviraptor philoceratops* shares a similar morphology of flared transverse processes; however, neither possesses a morphology as distinctive as in *Citipati osmolskae*.

DORSAL VERTEBRAE

Figure 15

There are approximately 10 dorsal vertebrae present in *Khaan mckennai*. This number is considerably larger than that of *Citipati osmolskae* (IGM 100/978) and *Caudipteryx zoui*, each of which has only seven (Ji et al., 1998; Zhou et al., 2000). The dorsal vertebral count has been taken from the dorsocervical to the first sacral vertebra, and all vertebrae included in the series possess a parapophysis on the anterior margin of the centrum and a diapophysis on the lateral margin of the transverse process. The dorsal vertebral column of IGM 100/1127 is disarticulated and not all dorsal vertebrae are preserved; therefore, the description of this region is based primarily on IGM 100/1002 (fig. 15), except when features are visible only in disarticulation (i.e., articular surfaces of the centra). Only dorsal and lateral surfaces of the vertebrae are exposed in IGM 100/1002. The dorsal surface of the neural arches in this region, like the cervical vertebrae, has a centrally placed neural spine unlike *Avimimus portentosus*, which has a more posteriorly placed neural spine. The neural spines in the anterior part of the series are rectangular in lateral view and lack an accessory spinal process as in most oviraptorosaurs, including *Avimimus portentosus*, *Oviraptor philoceratops*, *Conchoraptor gracilis*, and *Citipati osmolskae*. *Nomingia gobiensis* differs from these taxa by possessing an accessory process on its neural spine. The neural spines of the dorsal vertebrae of *Khaan mckennai* are short compared with those of the cervical series. This condition changes posteriorly along the dorsal vertebral column, as the spine becomes slightly longer and more robust. In *Oviraptor philoceratops* the neural spine is relatively longer than in the cervical vertebrae. The neural spine of *Citipati osmolskae* is long throughout the entire series but becomes progressively taller proceeding posteriorly. A similar condition is found in other oviraptorosaurs including oviraptorids and the more basal *Caudipteryx zoui*. The pre- and postzygapophysis of *Khaan mckennai* are oriented almost parallel to the midline. The transverse processes of the anterior dorsal vertebrae expand laterally beyond the prezygapophyses and have rounded distal ends that are oriented almost horizontally, similar to the processes present in the anterior dorsal vertebrae of *Conchoraptor gracilis* and *Oviraptor philoceratops*. The transverse processes located toward the posterior end of the dorsal column become shorter with rectangular distal ends. Again, this differs from *Citipati osmolskae*, which has very short transverse processes throughout the entire dorsal series. The excavations of fossae within the neural arch are the same in the dorsal vertebrae as in the cervical vertebrae. These fossae, however, are more extensive than in the cervical series, and a bony strut divides those at the base of the neural arches, a condition shared with *Citipati osmolskae*, but not present in *Nomingia gobiensis* (Barsbold et al., 2000).

The centra of the dorsal series are spool shaped, as they are in most maniraptorans (fig. 15). The circular articular surfaces are flat to minimally concave toward the posterior end of the series; this feature cannot be assessed in *Citipati osmolskae* (IGM 100/978) because of damage to the articular surfaces of the centra caused by postmortem arthropod feeding. All dorsal vertebrae have an anteroposteriorly elongate pleurocoel (much larger than is present in the cervical series) that is centered on the lateral surface of the centrum. The pleurocoel increases in size toward the posterior end of the dorsal column, a feature also occurring in oviraptorids including *Citipati osmolskae* and *Nomingia gobiensis*. The pleurocoels present in *Citipati osmolskae*, however, are significantly larger, relatively and absolutely. Although only the anteriormost dorsal vertebrae can be observed in *Oviraptor philoceratops* (AMNH FARB 6517), the pleurocoels share the same basic morphology as those in *Khaan mckennai*. Among oviraptorosaurs for which dorsal vertebrae are preserved, only *Avimimus portentosus* and *Caudipteryx zoui* lack dorsal pleurocoels (Kurzanov, 1981; Ji et al., 1998; Osmólska et al., 2004). Along the ventral edge of the centrum (in lateral view) on the first three to four dorsal vertebrae is an extremely expanded hypapophysis. The body of this structure is anteriorly placed, but its posterior extension reaches almost to the posterior edge of the centrum. A hypapo-

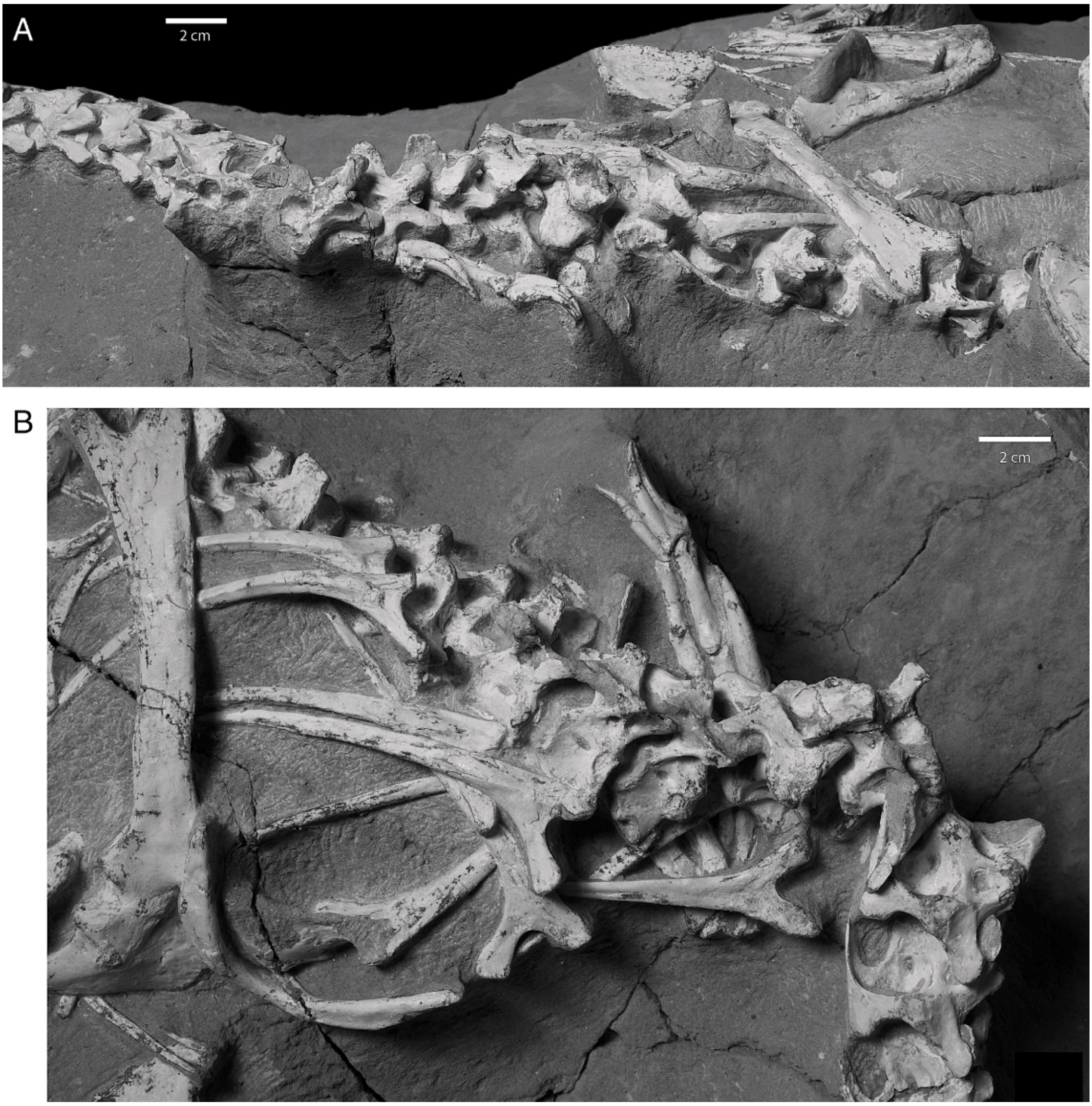


Fig. 15. Dorsal vertebrae in IGM 100/1002. **A,** dorsal surface; **B,** lateral surface.

physis is present in most oviraptorosaurs that preserve this region of the vertebral column, including *Avimimus portentosus*, *Nomingia gobiensis*, *Oviraptor philoceratops*, *Citipati osmolskae* (present only on the first two dorsal vertebrae), and *Chirostenotes pergracilis* (Sues, 1997), although the morphology differs among taxa. In *Khaan mckennai*, the hypapophysis extends the anteroposterior length of each centrum and has a rectangular distal end. The process is relatively short (not being longer than the centrum is tall). The hypapophysis present in *Citipati osmolskae* also extends from the anterior end of the ventral centrum as it does in *Khaan mckennai*; however, the shape is more elongate, curving anteriorly with a rounded distal end. The full extent of the shape of the hypapophyses cannot be assessed in *Oviraptor philoceratops*, but *Avimimus portentosus*, *Heyuannia huangi*, and *Nomingia gobiensis* have rounded, less pronounced processes. Dorsal to the hypapophysis in IGM 100/1002 is a circular parapophysis on the lateral surface of the centrum just ventral to the level of the pleurocoel. The dorsal ribs of *Khaan mckennai* are relatively thin in comparison to *Citipati osmolskae* and *Oviraptor philoceratops*, but otherwise closely resemble those taxa.

SACRAL VERTEBRAE

Figure 16

The sacral vertebrae for the most part are not visible. Two anterior sacral vertebrae (IGM 100/1127) and one posterior sacral vertebra (IGM 100/1002) are the only ones that can be observed (fig. 16). The rest of the sacral vertebrae are obscured by the ilium in all specimens. The visible posterior sacral vertebra is distinguished by its greatly expanded, fused sacral ribs. The ribs extend approximately four times the width of the vertebral centrum and have a large pleurocoel on the dorsal surface at their base. The distal end of each sacral rib expands laterally where it contacts the ilium. The neural spines are not fused together (at least at the posterior end of the series); however, they are knoblike and extend posteriorly. A small fossa is visible on the posterior surface of the neural spine. The postzygapophyses are small and extend posterolaterally.

CAUDAL VERTEBRAE

Figure 17

A nearly complete caudal series is preserved in IGM 100/1127 (fig. 17); only one or two of the distalmost caudal vertebrae are missing. The first seven caudal vertebrae are the only ones preserved in IGM 100/1002. Approximately 28 vertebrae are present in the caudal series, which is less than the 32 vertebrae present in *Citipati osmolskae* (IGM 100/978). Caudal vertebral numbers for oviraptorosaurs in general are reduced compared to other coelurosaur taxa. This reduction is also seen in the putative sister group to Oviraptorosauria, Therizinosauria (27 caudal vertebrae in *Alxasaurus elesitaiensis*; Russell and Dong, 1993). *Caudipteryx zoui* has the most extreme reduction of the tail with only 22 caudal vertebrae. The proximal caudal vertebrae in *Khaan mckennai* are observable in dorsal view in both specimens. They possess slightly curved, narrow but elongate transverse processes that are oriented posterolaterally (fig. 17) and are similar to the morphology of other oviraptorosaurs like *Citipati osmolskae* (IGM 100/978), *Nomingia gobiensis* (Barsbold et al., 2000), *Heyuannia huangi* (Lü, 2005), and *Conchoraptor gracilis* (IGM 100/3006). The distal end of the transverse processes is rounded in more anterior caudal vertebrae but becomes rectangular and progressively expanded at the distal end as one proceeds posteriorly (also in *Citipati osmolskae*). The transverse processes toward the posterior end of the tail become shorter; however, their anteroposterior width remains the same, giving them a short but comparatively robust appearance in the posterior region. Thus, as the size of the vertebrae decreases more abruptly distally, the transverse processes eventually disappear (the exact number cannot be assessed; however, this disappearance occurs in the final four vertebrae of *Citipati osmolskae* [IGM 100/978]). *Nomingia gobiensis* differs slightly from this pattern by the transverse processes becoming gradually diminished in lateral and anteroposterior width proceeding posteriorly. As is the case in all oviraptorosaurs, *Khaan mckennai* lacks a distinct transition point in the tail (Osmólska et al., 2004). A neural spine is present on all the caudal vertebrae that are preserved and has a low and posteriorly inclined morphology along the entire length of the caudal series. This differs somewhat from the morphology of *Gigantoraptor erlianensis* (Xu et al., 2007), which has a tall neural spine in the known proximal caudal vertebrae. In *Khaan mckennai*, the neural spine is located more posteriorly on the neural arch than it is in either the cervical or dorsal vertebrae, also seen in *Gigantoraptor erlianensis* and *Citipati osmolskae*. The anterior and posterior surfaces of the base of the neural spine bear fossae as they do in the rest of the vertebral column. As in *Citipati osmolskae*, the pneumaticity in the neural arches of the caudal vertebrae of *Khaan mckennai* becomes increasingly absent toward the distal end of the tail. Likewise, the distal caudal vertebrae preserved for *Gigan-*

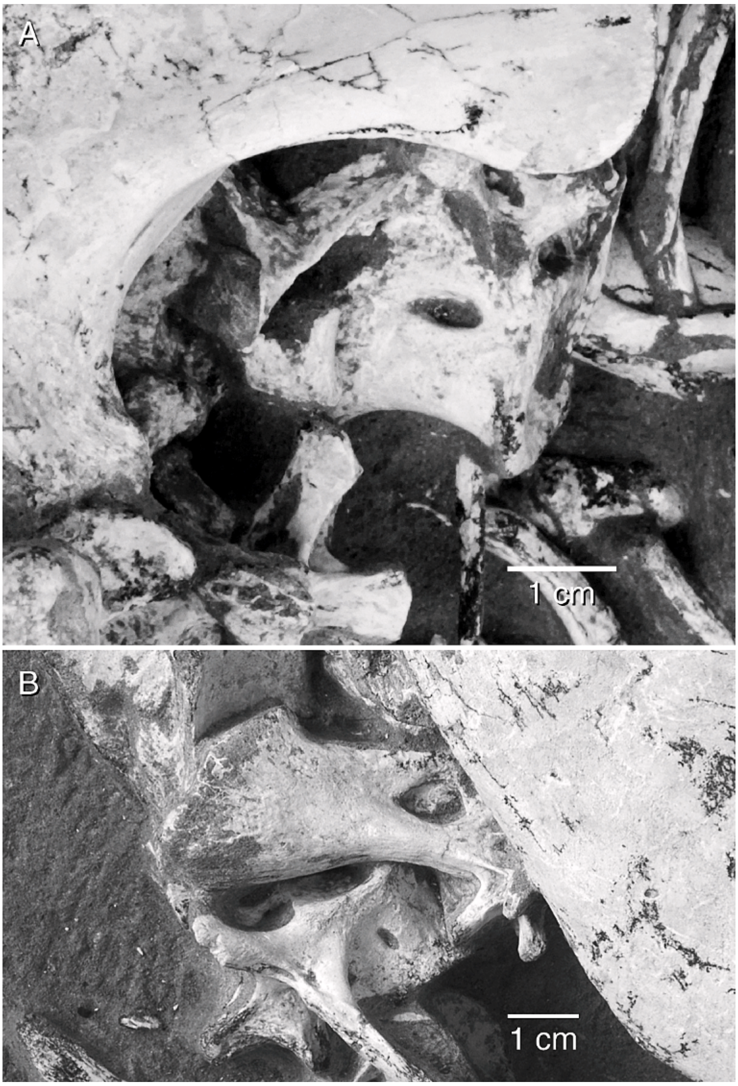


Fig. 16. Sacral vertebrae. **A,** anterior sacral vertebra in IGM 100/1002; **B,** posterior sacral vertebra in IGM 100/1127.

toraptor erlianensis lack pneumatization of the neural arch. The neural arch of *Khaan mckennai*, however, lacks the fossa on the dorsal surface that is observed in *Conchoraptor gracilis* (Lü, 2005). The prezygapophyses are spread wider than the postzygapophyses. Overall, the lengths of the zygapophyses are short (similar to all other observed oviraptorosaurs), extending less than half the length of the preceding vertebra, unlike the distinctive, elongate prezygapophyses in many dromaeosaurids.

The centra of the proximal caudal vertebrae are not observable in any specimens of *Khaan mckennai*. For most of the length of the caudal series only the dorsal surface is exposed, but the tail of IGM 100/1127 twists laterally at its distal end, exposing the lateral surface of the vertebrae in this region (approximately the last five vertebrae). These distal caudal vertebrae lack a pleurocoel on their lateral surface similar to other oviraptorosaurs. It cannot be determined where this absence first occurs in *Khaan mckennai*;

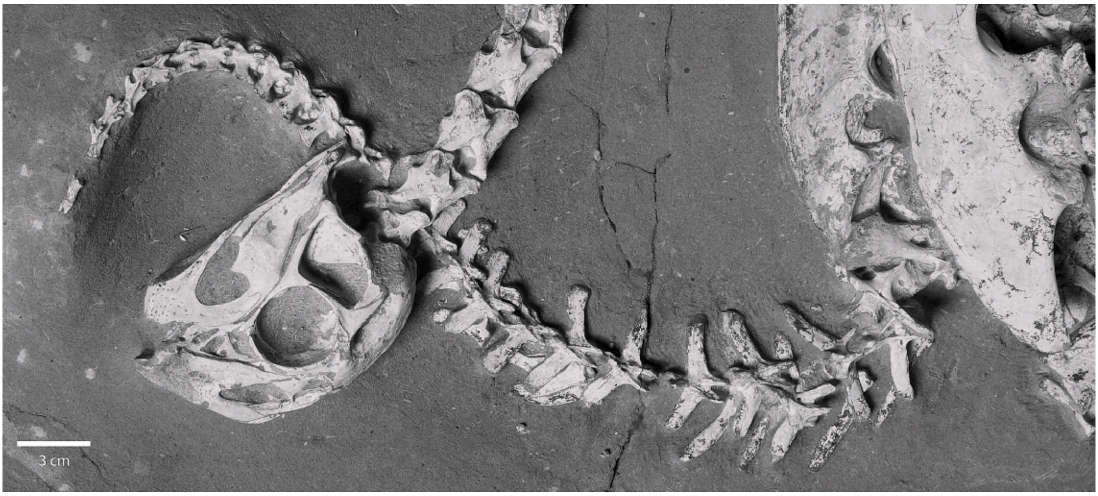


Fig. 17. Caudal vertebrae in IGM 100/1127.

however, in *Citipati osmolskae* the 27th caudal vertebra is the first to completely lack a pleurocoel. The distal caudal vertebrae of *Gigantoraptor erlianensis* also lack pleurocoels. The distal caudal centra of *Khaan mckennai* are concave along their ventral surface in lateral view, like in *Citipati osmolskae* and *Gigantoraptor erlianensis*. The anterior and posterior surfaces of the centra are not visible. There is no evidence of a pygostyle (fused caudal vertebrae) like that described for *Nomingia gobiensis* (Barsbold et al., 2000), *Similicaudipteryx zoui* (He et al., 2008), and *Citipati osmolskae* (Persons et al., 2011) as well as the therizinosaur *Beipiaosaurus* (Xu et al., 2003).

CHEVRONS

Figure 17

Several chevrons are visible articulating with the proximal four vertebrae of the tail in IGM 100/1127 (fig. 17). Although they are not visible along the entire length of the tail, it is likely that chevrons were present as they are in *Citipati osmolskae* (IGM 100/978), *Conchoraptor gracilis* (IGM 100/3006), *Nomingia gobiensis*, and *Caudipteryx zoui* (Ji et al., 1998; Barsbold et al., 2000; Zhou et al., 2000). In *Khaan mckennai*, the chevrons are dorsoventrally elongate and flattened mediolaterally. There is a slight curvature along the shaft such that the posterior border is concave unlike *Nomingia gobiensis* or *Ingenia yanshini* (IGM 100/30). The chevrons are more slender than the same elements in *Nomingia gobiensis* (Barsbold et al., 2000) but have a similar morphology to those from the same region of the tail in *Citipati osmolskae* and *Caudipteryx zoui* (Ji et al., 1998; Zhou et al. 2000). As in other maniraptorans, the chevrons become shallower and more dorsoventrally elongate toward the distal end of the tail.

STERNUM

Figure 18

Paired sterna are preserved in many oviraptorosaurs such as *Caudipteryx zoui* and *Citipati osmolskae*, although these elements are fused into a single sternal element in *Ingenia yanshini* (IGM 100/30). The sternum of IGM 100/1127 is preserved in articulation, but overlying ribs, gastralia, and one of the humeri obscure the ventral surface (fig. 18A). The general shape can be gathered from IGM 100/1002, which is not preserved in articulation but whose dorsal surface is completely exposed (fig. 18B). The paired ossified sterna are thin boney plates lacking obvious articular surfaces for either the coracoid or sternal ribs. This absence does not preclude these articulations from having occurred in life as they are easily seen in *Citipati osmolskae* (IGM 100/978) and reported in *Heyuannia huangi* (Lü, 2005). In

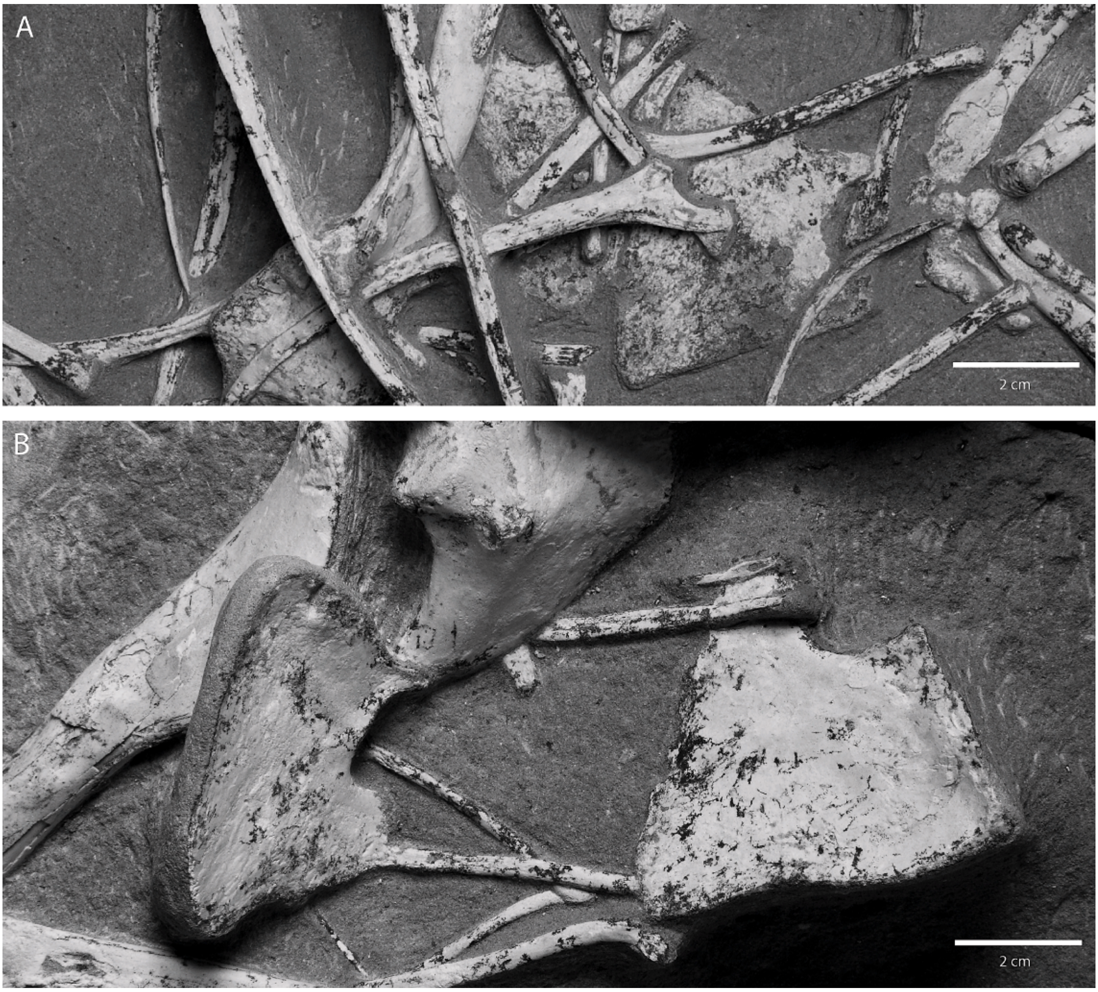


Fig. 18. Sternal plates. **A,** IGM 100/1127; **B,** IGM 100/1002.

Khaan mckennai, the anterior edge of the sternum is straight and slants slightly posterolaterally. It lacks a deep groove for the articulation of the coracoids seen in many other maniraptoran groups (Norell and Makovicky, 2004; Makovicky and Norell, 2004). The medial margin is straight, and the sterna apparently contacted each other along this edge (fig. 18A). The posterior margin of the element slants toward the anterior margin (anterolaterally). The lateral margin is the only part of the sternum that preserves any structures. This border has a deep notch that probably bore articulations with the sternal ribs, as is the case in most other maniraptorans. This notch is bordered by two processes, one anteriorly and one posteriorly. The homologies of these processes are not completely understood; however, it is likely that they correspond to the anterolateral (anterior) and the xiphoid (posterior) processes that are present in other oviraptorosaurs (Clark et al., 1999; Osmólska et al., 2004). The xiphoid processes are found also in paravians including modern avians (Hwang et al., 2002).

SCAPULOCORACOID

Figure 19

The scapula and coracoid of *Khaan mckennai* are fused into a single element with

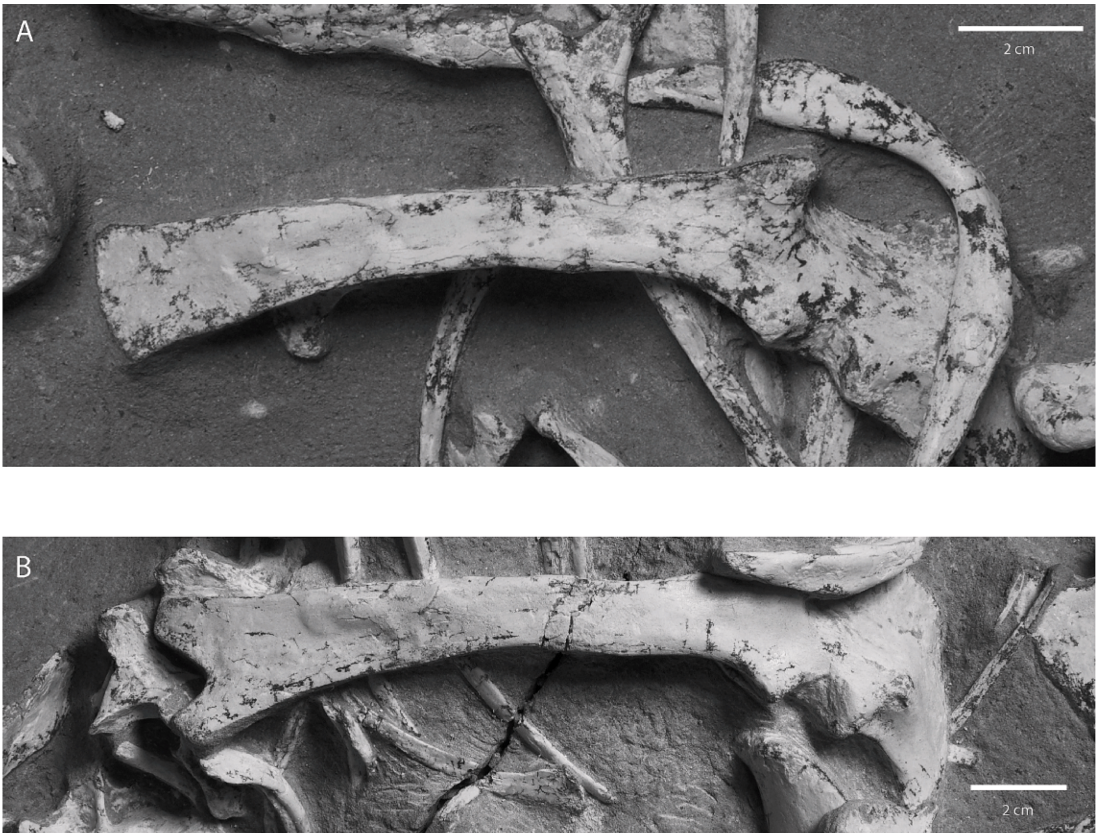


Fig. 19. Scapulocoracoid. **A,** dorsal surface of right scapulocoracoid in IGM 100/1002; **B,** dorsal surface of right scapulocoracoid in IGM 100/1127.

no indication of a suture except a faint trace inside the glenoid fossa (fig. 19). A fused scapulocoracoid is present in most oviraptorids in which these elements are found (e.g., *Citipati osmolskae*, *Oviraptor philoceratops*, and *Ingenia yanshini*), but not the more basal taxa (e.g., *Caudipteryx zoui* and *Microvenator celer*; Ostrom, 1970; Currie and Russell, 1988; Ji et al., 1998; Makovicky and Sues, 1998). An unfused scapulocoracoid, however, is also found in *Conchoraptor gracilis* (IGM 100/3006). The glenoid fossa faces laterally in *Khaan mckennai* as it does in the other oviraptorosaurs *Citipati osmolskae* and *Chirostenotes pergracilis* (Turner et al., 2007b). The scapulocoracoid overall is bowed as in *Oviraptor philoceratops*, with an angle between the two elements being approximately 150°–160° (Osmólska et al., 2004), thus lacking the distinctive L-shape of dromaeosaurs (Norell and Makovicky, 1999) and some basal troodontids (see Hu et al., 2009). The scapular blade is elongate and straplike (making up two-thirds of the entire element, including the coracoid), similar to all oviraptorids. This blade expands slightly distally and has a blunt end like other oviraptorosaurs but differs from the pointed scapular blade present in most paravians (fig. 19) (Wellnhofer, 1974). The scapula possesses a large acromion process along its dorsal edge that is inflected anterolaterally providing a large dorsal surface for articulation of the furcula. This orientation also is observed in other oviraptorids such as *Oviraptor philoceratops*, *Heyuannia huangi*, *Ingenia yanshini*, *Citipati osmolskae*, and *Conchoraptor gracilis* (Osmólska et al., 2004). Most coelurosaurs (excluding paravians) as well as the basal oviraptorosaur *Caudipteryx zoui* possess a more dorsally oriented acromion process (Lü, 2005). The relative size of the acromion process, however, does not approach that of *Ingenia yanshini* (Barsbold, 1981; Osmólska et al., 2004).

The coracoid of *Khaan mckennai* is similar to all oviraptorosaurs in that it is quadrangular in shape and has a large distally tapering caudoventral process that extends just past the glenoid (fig. 19). On the anterolateral surface of the coracoid is an extensive process that corresponds to the coracoid tubercle. This same process was described as the "biceps tubercle" in Osmólska et al. (2004), but see Norell and Makovicky (1999) for discussion. The large tubercle is plesiomorphic for Oviraptorosauria and thus present in all taxa, including basal forms such as *Caudipteryx zoui* and the more derived *Citipati osmolskae*, *Heyuannia huangi*, *Conchoraptor gracilis*, and *Oviraptor philoceratops* (although shape cannot be determined in *Oviraptor philoceratops* because this surface is badly damaged in AMNH FARB 6517). The coracoid foramen is so small as to be hardly noticeable in *Khaan mckennai*, much smaller than the foramen that is present in *Caudipteryx zoui* (Ji et al., 1998; Zhou et al., 2000; Zhou and Wang, 2000) and other oviraptorids such as *Oviraptor philoceratops* (see Osmólska et al., 2004: fig. 8.2G). The small oval-shaped foramen in *Khaan mckennai* is positioned just below the coracoid tubercle on its posterior side. IGM 100/1127 lacks a subglenoid fossa on the posterolateral surface, distinguishing the coracoid from that of paravians (Makovicky and Norell, 2004; Norell and Makovicky, 2004).

FURCULA

Figure 20

The furcula is not unlike that of typical maniraptoran furculae (Nesbitt et al., 2009). It has an interclavicular angle (~90°) that corresponds closely with *Oviraptor philoceratops* and *Heyuannia huangi* (Nesbitt et al., 2009) and overall possesses a dorsoventrally flattened morphology (fig. 20). The suture along the midline symphysis is not visible. The lateral process expands approximately midway along its length and tapers distally after this point. The tapered distal edge, epicleidium, contacts the pectoral girdle (fig. 20). Along the midline of the furcula, a large hypocleidium protrudes ventrally as it does in all oviraptorosaurs except *Caudipteryx zoui* (Nesbitt et al., 2009). The length of the hypocleidium cannot be determined because the ventral portion of this structure is not exposed in either specimen, but it does not appear to be as elongate as the extremely long, ventrally extended hypocleidia of *Oviraptor philoceratops* (AMNH FARB 6517) or *Citipati osmolskae* (IGM 100/1004). The hypocleidium of most theropods (excluding a number of avians) typically extends in the same plane as the furcula (Nesbitt et al., 2009).

HUMERUS

Figure 21

The humeri in both IGM 100/1127 and 100/1002 are preserved. IGM 100/1127 preserves the humerus in medial and anterior views, whereas IGM 100/1002 preserves the humerus in lateral view (fig. 21). The humerus of *Khaan mckennai* is approximately 31% of the entire forelimb length including the manus and 80% of the forearm length without the hand (table 2, measurements taken from the holotype, IGM 100/1127), not unlike the proportions found in other maniraptorans (Ostrom, 1969; Norell and Makovicky, 2004). Overall the shaft is straight with slight torsion at midshaft (Osmólska et al., 2004). The expanded deltopectoral crest stretches over one-third the length of the entire element (table 2) and has an angular apex toward the distal end of the crest. This same morphology is found in other oviraptorids like *Citipati osmolskae* (IGM 100/978), *Heyuannia huangi* (Lü, 2005), *Ingenia yanshini* (IGM 100/30), and *Oviraptor philoceratops* (AMNH FARB 6517), but differs from more basal oviraptorosaurs such as *Avimimus portentosus* (Kurzanov, 1987) and *Microvenator celer* (Makovicky and Sues, 1998) and the large oviraptorid *Gigantoraptor erlianensis* (Xu et al., 2007). Those latter taxa have shallow, rounded deltopectoral crests. Therizinosaurs, however, possess a deltopectoral crest morphology similar to that found in derived oviraptorids (Zanno, 2006). The articular head of the humerus is not well developed in *Khaan mckennai*. A small transversely elongate articular surface is present on the anterior

Fig. 20. Furcula. **A,** dorsal surface of furcula in IGM 100/1002; **B,** dorsal surface of furcula in IGM 100/1127.

surface of the proximal end of the humerus (most easily seen in IGM 100/1127, fig. 21B, C). The distal condyles are not exposed in their entirety in any *Khaan mckennai* specimens. All that can be determined is that they are rounded, and the medial condyle extends further ventrally than the lateral condyle, similar to oviraptorids such as *Conchoraptor gracilis* and *Citipati osmolskae*.

ULNA

Figure 22

The ulna is exposed only in lateral view in both specimens (fig. 22). It is short, approximately 28% of the entire length of the forelimb including the manus (table 2). The relative length of the ulna is approximately the same in *Khaan mckennai* and *Oviraptor philoceratops*, 89% and 88% the length of the humerus, respectively (table 2). The shaft of the element is bowed posteriorly as it is in other maniraptorans (Gauthier, 1986) but differing from the oviraptorids *Ingenia yanshini* and *Rinchenia mongoliensis* where the ulna is straight. (Osmólska et al., 2004). The shaft of the ulna is also relatively straight in *Gigantoraptor erlianensis* (Xu et al., 2007). The ulnar shaft of *Khaan mckennai* tapers distally, and a shallow depression is present on the lateral surface. This structure likely served as an articulation point for the triceps

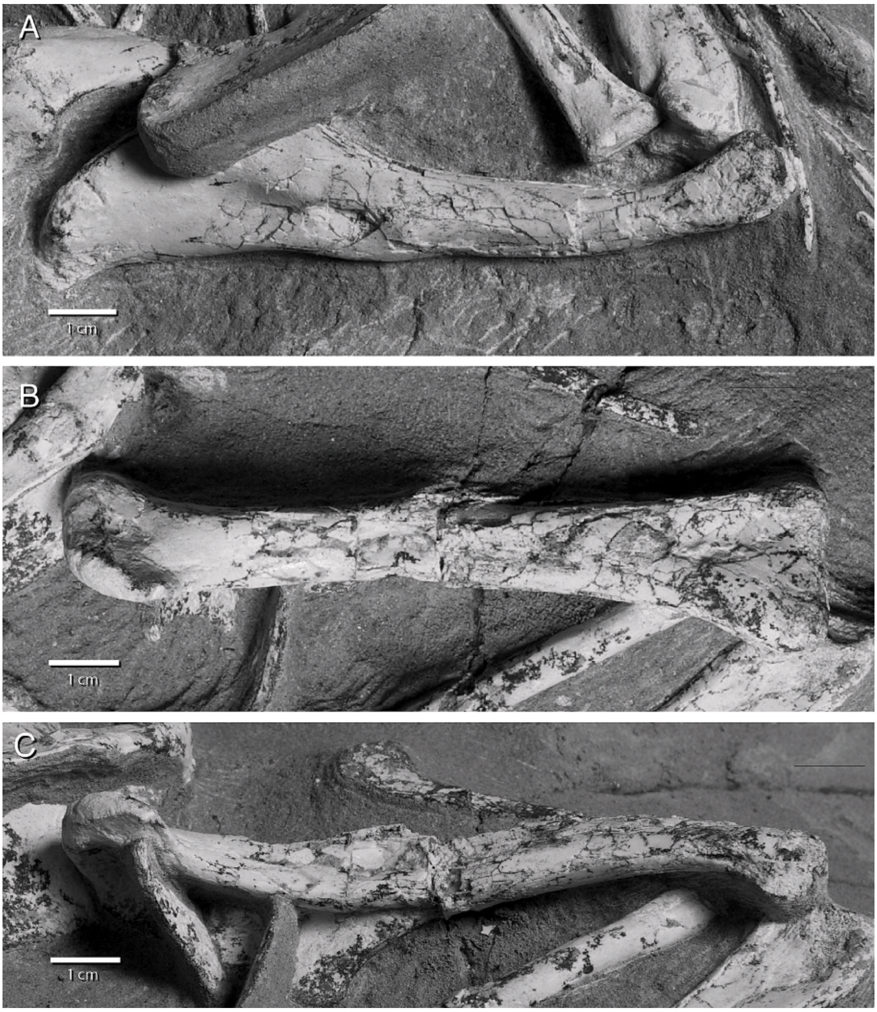


Fig. 21. Humerus. **A,** lateral surface of right humerus in IGM 100/1002; **B,** posterior surface of right humerus in IGM 100/1127; **C,** medial surface of right humerus of IGM 100/1127 showing deltopectoral crest.

tendon. The proximal end of the ulna has a subtriangular articular face that is angled anterodorsally (visible in IGM 100/1002; fig. 22A) for articulation with the humerus and radius. The olecranon process is weakly developed, plesiomorphic for oviraptorosaurs, being present in maniraptorans in general. The distal articular surface is not exposed in either specimen; therefore, it cannot be determined whether this surface expands as it does in *Citipati osmolskae, Heyuannia huangi*, and *Oviraptor philoceratops*. There is no indication of quill knobs on the posterior margin of the ulna as in some maniraptorans (Turner et al., 2007c).

RADIUS

Figure 22

The radius is preserved in both articulated specimens of *Khaan mckennai* and, like the ulna, is exposed only in lateral view (fig. 22). The proximal and distal ends are most clearly visible in IGM 100/1002. The radius is approximately the same length as the ulna (table 2). Overall the element is similar to

TABLE 2
Selected measurements (in mm) from the postcranial skeleton of *Khaan mckennai*

	IGM 100/973	IGM 100/1127	IGM 100/1002
Left humerus length	–	110.5	–
Right scapulocoracoid length	–	154.1	167.0
Right scapula length (from glenoid to distal end)	–	124.7	138.6
Right humerus length	–	108.6	117.5
Right radius length	–	~102.0	95.3
Right ulna length	–	96.5	~101.6
Right metacarpal i length	–	–	24.7
Right metacarpal ii length	–	47.3	50.4
Right metacarpal iii length	–	44.4	47.6
Right digit i length	–	–	99.4
Right digit ii length	–	138.1	135.8
Right digit iii length	–	125.1	122.4
Sternum length	–	58.8	55.1
Sternum width (widest point)	–	43.9	50.7
Left ilium length	193.5	–	–
Left ischium length	133.1	–	–
Left pubis length	156.8	–	–
Left femur length	188.8	–	–
Left tibia length	221.4	–	–
Left fibula length	–	–	–
Left metatarsal i length	26.7	–	23.3
Left metatarsal ii length	82.8	–	91.2
Left metatarsal iii length	97.7	–	–
Left metatarsal iv length	87.3	–	–
Right ilium length	187.5	182.0	186.0
Right femur length	199.0	185.0	196.0
Right tibia length	224.0	212.0	232.0
Right fibula length	–	201.0	214.0
Right metatarsal i length	~23.0	–	–
Right metatarsal ii length	89.9	–	–
Right metatarsal iii length	98.8	–	105.6
Right metatarsal iv length	93.9	~95.0	98.3
Right metatarsal V length	35.8	–	35.9

Oviraptor philoceratops and possesses a straight, mediolaterally compressed shaft. The radial shaft in *Citipati osmolskae* is curved anteriorly; however, the lack of curvature in the radius of *Khaan mckennai* may be a result of its orientation. A small oval divot is present on the lateral surface about one-third the length from the distal end of the element, which was not observed in any other oviraptorosaur taxon. The radial shaft is the same width along its length, somewhat narrower than the ulna, but expands at its extremities. The distal end of the radius extends beyond the distal end of the ulna as it does in *Oviraptor philoceratops* (AMNH FARB 6517). The articular surfaces are not visible.

MANUS

Figure 23

Beautifully and completely preserved hands are present in both articulated specimens of *Khaan mckennai*, including carpals, metacarpals and phalanges (fig. 23). The best example of a complete hand is found in IGM 100/1002. Although little can be discerned about the morphology of the wrist bones, there are at least two separate elements present, the semilunate carpal and radiale (fig. 23). Osmólska et al. (2004) describes the typical maniraptoran condition of three carpals for oviraptorids. The ulnare, however, is not visible in any of the specimens of *Khaan*

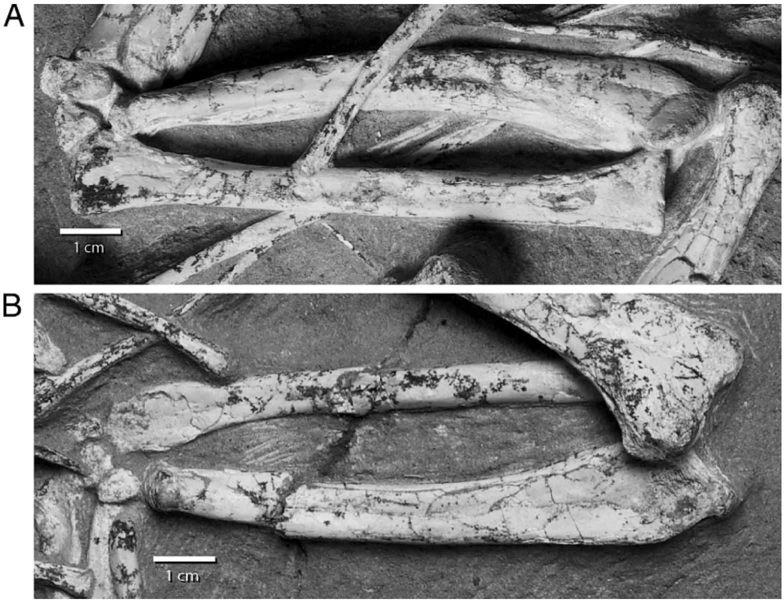


Fig. 22. Radius and ulna. **A,** lateral surface of radius and ulna in IGM 100/1002. **B,** lateral surface of radius and ulna in IGM 100/1127.

mckennai. The absence of this carpal may contribute to the autapomorphic condition of lacking a contact between the carpus and metacarpal III. The semilunate carpal preserves the relationships present in other maniraptorans of having a contact with metacarpals I and II, and the radiale lies proximal to those carpals. *Khaan mckennai* has a typical theropod phalangeal formula of 2-3-4, as do *Citipati osmolskae*, *Ingenia yanshini*, and *Oviraptor philoceratops*. This condition differs from the apomorphic hand of *Avimimus portentosus* and *Caudipteryx zoui* that has a marked reduction in the number of phalanges in digit III (Kurzanov, 1981, 1987; Osmólska et al., 2004). Digit II in *Khaan mckennai* is the longest, followed by digit III and finally digit I. Elongate digits II and III, approximately the same length with only a minor difference, are characteristic of all oviraptorosaur hands, present even in *Gigantoraptor erlianensis* (Osmólska et al., 2004; Xu et al., 2007). Digit I of *Khaan mckennai* and other oviraptorosaurs is approximately half the length of digits II and III (Maryańska et al., 2002). The metacarpals are unfused along their length; *Avimimus portentosus* and *Oviraptor philoceratops* are the only oviraptorosaurs where the metacarpals are proximally fused (Osborn, 1924; Kurzanov, 1987; Osmólska et al., 2004), although this is likely pathological in *Oviraptor philoceratops* (AMNH FARB 6517). The length of the metacarpals in *Khaan mckennai* reflects that of the digits as a whole, with MC II being the longest, followed by MC III, and finally MC I (table 2).

Metacarpal I is robust and the shortest of any of the other metacarpals; about half the length of MC II (table 2). The entire lateral surface of MC I adheres to a flattened area on the posteromedial surface of MC II. The distal articular surface of MC I is strongly concave in dorsal view (fig. 23A), and the proximal surface appears to have a straight contact with the carpals. This straight contact differs from most observed oviraptorids, including *Oviraptor philoceratops*, *Conchoraptor gracilis*, and *Citipati osmolskae*. These taxa have an articular surface of MC I that slants proximally toward MC II in dorsal view. *Caudipteryx zoui*, however, has a morphology similar to that of *Khaan mckennai*. Metacarpal II is approximately twice the length of MC I (table 2), which is similar to all other oviraptorosaurs. This element is

Fig. 23. Manus. **A,** right manus of IGM 100/1002; **B,** right manus of IGM 100/1127.

straight and the proximal articulation surface is ventrolaterally slanted in dorsal view. The proximal articulation surfaces of metacarpals I and II are at the same level. Metacarpal II also has a concave distal articulation surface. Metacarpal III is long and narrower than the other two metacarpals. Its proximal articulation surface lies slightly ventral to that of MC I and II and as previously mentioned did not contact the distal carpals (fig. 23A; Clark et al., 2001), an unusual condition that was used as a diagnostic character of *Khaan mckennai* in its original description (Clark et al., 2001). The distal articulation surface of MC III, however, lies in the same plane as that of MC II and has a convex surface (fig. 23A). The medial and lateral surfaces of the metacarpals are not visible.

Digit I is by far the most robust of the three digits. Phalanx I-1 is long, almost twice the length of MC I, and curves slightly dorsally. This dorsal curvature is much more pronounced than in *Citipati osmolskae* (IGM 100/979, Clark et al., 1999) or *Oviraptor philoceratops* (AMNH FARB 6517), which have straight phalanges I-1. A deep ligament pit is located on the distal trochlea near the dorsal surface. The ungual phalanx associated with digit I is the largest of any on the hand and, like the penultimate phalanx, the most extensively curved. This disparity in curvature is more pronounced in *Khaan mckennai* than in any other observed oviraptorosaurs. Unlike the ungual phalanges of manual digital II and III, there is not a dorsal lip on the articular surface (fig. 23). The dorsal lip also is reduced on the ungual phalanx of digit I in *Citipati osmolskae* (Clark et al., 1999: fig. 5), is present in *Oviraptor philoceratops* (AMNH FARB 6517), and absent on all digits in *Caudipteryx zoui* (IVPP V 12430). The phalanges of digit II in *Khaan mckennai* are more slender than those of digit I. The two proximal phalanges are approximately the same length, which is slightly shorter than phalanx I-1. A distinct ligament pit can be seen on the lateral side of phalanx II-2 in IGM 100/1002. The ungual phalanx

Fig. 24. Ilium. **A,** lateral surface of right ilium in IGM 100/1002; **B,** lateral surface of right ilium in IGM 100/1127.

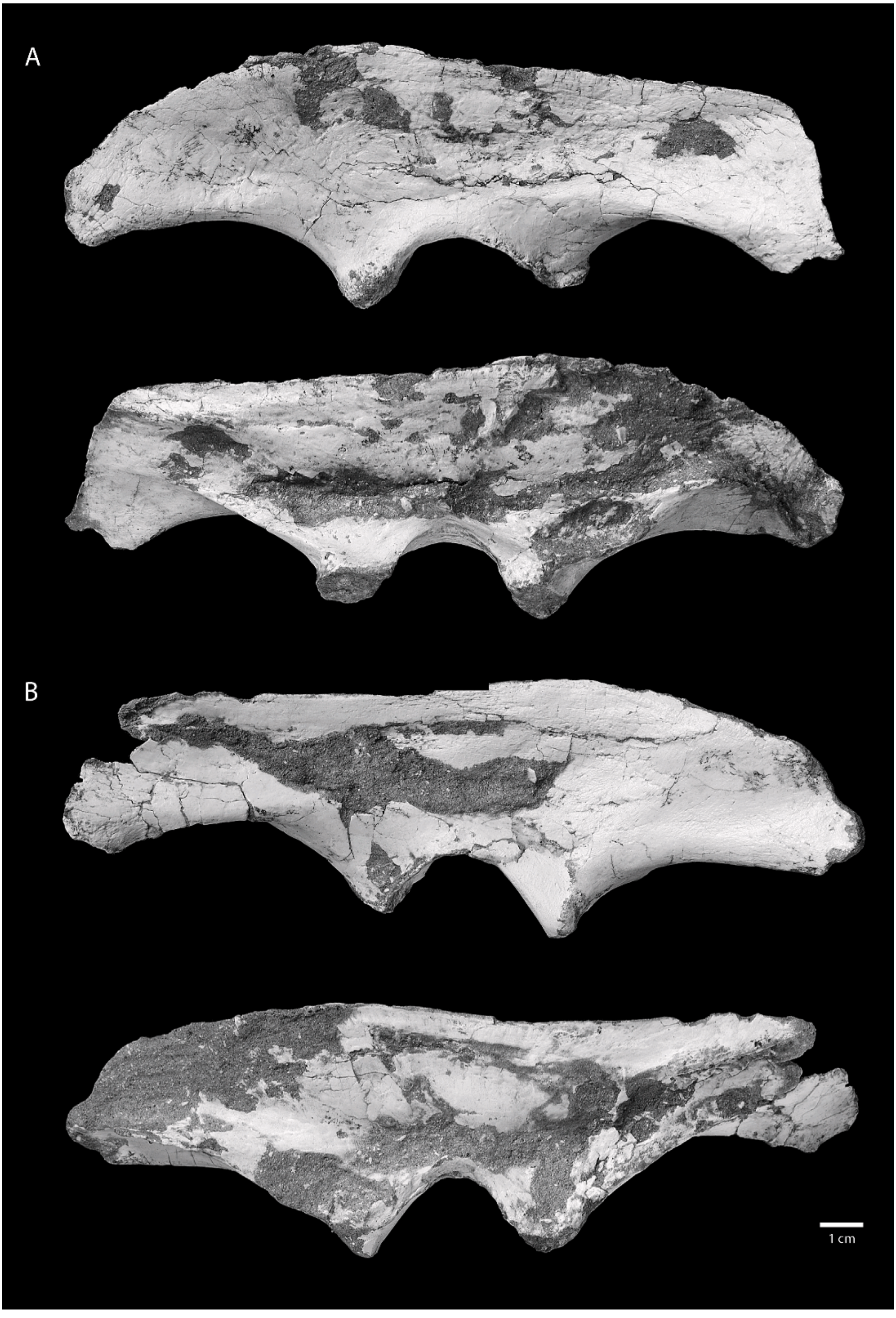
for digit II is approximately the same length as the ungual phalanx in digit I but lacks the extreme curvature, differing from *Oviraptor philoceratops*, whose ungual phalanx I is shorter than that of digit II. The ungual phalanx of digit II in *Khaan mckennai* is also narrower dorsoventrally than the ungual of digit I.

The phalanges of digit III are shorter than those of the other two digits. Phalanges III-1 and III-2 are approximately the same length (table 2), and their cumulative length is longer than that of phalanx III-3, distinguishing oviraptorosaurs from ornithomimids and paravians (Maryańska et al., 2002). Ligament pits are visible on the lateral surfaces of the phalanges of digit III; however, these are much shallower than those present on the phalanges of digits I and II, similar to the depth apparent in both *Citipati osmolskae* and *Oviraptor philoceratops*. The ungual phalanx of digit III in *Khaan mckennai* is shorter than that of digit II and also possesses the dorsal lip above the proximal articular surface.

ILIUM

Figures 24, 25

The ilium, ischium, and pubis are not fused, so each element is described individually. The ilium is well preserved in all three specimens of *Khaan mckennai* (figs. 24, 25). A contact between the ilia is unlikely, as the medial surface of the dorsal edge of each ilium shows no indication of a contact point with its pair. They do, however, diverge from each other posteriorly as suggested by the lateral flexure of the dorsal margin, a feature also present in other maniraptorans (Norell


A
B
1 cm

and Makovicky, 1997). The pre- and postacetabular portions of the ilium are approximately the same length like in most oviraptorids. However, *Rinchenia mongoliensis*, *Nomingia gobiensis*, and the caenagnathid *Chirostenotes pergracilis* have a longer preacetabular ilium, and the preacetabular ilium is shorter than the postacetabular portion in *Avimimus portentosus* (Osmólska et al., 2004). The dorsoventral height of the ilium is approximately the same along the length of the element except for a ventrally expanded preacetabular process, again differing only from those taxa mentioned above. The rounded preacetabular process extends anteroventrally from the anteriormost region of the ilium (as in all oviraptorosaurs except *Avimimus portentosus*; figs. 24, 25), but it does not reach as far ventrally as in *Caudipteryx zoui*, in which the process extends beyond the ventral margin of the pubic peduncle (Ji et al., 1998). The preacetabular process borders a weakly developed cuppedicus fossa anterolaterally (preacetabular fossa of Hutchinson, 2001) on the ventral edge of the element. The cuppedicus fossa is a flat shelf on the ventral surface of the preacetabular process similar to the morphology of other oviraptorosaurs except *Caudipteryx zoui*, which has a well-developed fossa (Ji et al., 1998; Zhou et al., 2000; Osmólska et al., 2004). The dorsal margin of the ilium has a flat profile from the anterior end to the level of the ischiadic peduncle. The flat dorsal margin is similar to most oviraptorosaurs but differs from the apomorphic, curved ilium seen in *Rinchenia mongoliensis* (Barsbold, 1986; Osmólska et al., 2004), *Nomingia gobiensis* (Barsbold et al., 2000), and *Caudipteryx zoui* (Ji et al., 1998; Zhou and Wang, 2000; Zhou et al., 2000). Posterior to the acetabulum, the dorsal edge is slightly rounded as it tapers to a blunt posterior margin (figs. 24, 25). Lü (2005) described a pointed end to the postacetabular ilium in *Heyuannia huangi*. There is some variation in the shape of the posterior margin the three specimens of *Khaan mckennai*, but this shape in IGM 100/1127 appears to be the result of weathering. The supraacetabular rim is not well developed, so there is little overhang over the femoral head. An antitrochantor is present but not pronounced, almost confluent with the supraacetabular rim. This condition is present in almost all oviraptorosaurs except *Avimimus portentosus*, which has a strongly pronounced antitrochantor (PIN 3907; Kurzanov, 1981, 1987). On the medial surface of the ilium an expanded crista curves from the posterior end of the ilium anteriorly to about halfway along the length of the postacetabular process. The ridge then turns and extends anteroventrally to the ischiadic peduncle. The space between the crista and the ventral surface of the ilium forms the small ventromedially facing brevis fossa. This fossa is not developed to the extent that it is in *Caudipteryx zoui* (Zhou et al., 2000). The pubic and ischiadic peduncles are roughly the same dorsoventral length, but the pubic peduncle barely exceeds the anteroposterior length of the ischiadic peduncle. The ischiadic peduncle extends straight ventrally, and the pubic one is inflected medially.

PUBIS

Figure 26

The distal end of the pubis is not visible in either IGM 100/1127 or 100/1002; therefore, most of the description of this element is based on the disarticulated specimen IGM 100/973 (fig. 26). Only the left pubis is preserved in IGM 100/973. Hence, it can be assumed that the pubic elements were not fused distally to form a symphysis as they are in almost all known oviraptorosaurs and even nonavian dinosaurs. The lack of fusion may be due to a relatively younger maturation of IGM 100/973. The pubis of the large-bodied *Gigantoraptor erlianensis* is preserved only on one side, but this element has a large symphyseal region that can be interpreted as

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Fig. 25. Ilium of IGM 100/973. **A,** lateral view of right ilium (top) and medial view of right ilium (bottom); **B,** lateral view of left ilium (top) and medial view of left ilium (bottom).

Fig. 26. Lateral view of pubis in IGM 100/973.

contacting its opposite (Xu et al., 2007). The pubis of *Khaan mckennai* is extremely delicate, as are all the pelvic elements (especially true in IGM 100/973). The shaft of the element is strongly concave anteriorly, a character tying together all oviraptorosaurs (except *Avimimus portentosus*, which has an almost straight morphology; Kurzanov, 1987). The pubic boot is expanded and projects both anteriorly and posteriorly, with the anterior process being much more developed than the posterior process. A pubic boot is present in all oviraptorosaur taxa; however, the extent to which the pubic boot projects both anteriorly and posteriorly varies among taxa (Osmólska et al., 2004). Although the morphology is probably correctly reflected, the distal end of the shaft is damaged in IGM 100/973. The shaft is mediolaterally compressed distally and becomes more rounded toward the proximal end. A pubic apron extends medially from the proximal end of the shaft to about halfway along its length. The pubic apron of *Citipati osmolskae* is located more distally on the shaft. The proximal end of the pubic apron in *Khaan mckennai* is located along the anterior edge of the shaft, but it ends (distally) along the midline of the shaft.

ISCHIUM

Figure 27

Ischia are present in all specimens of *Khaan mckennai*, but there is considerable variation among them (fig. 27). The overlapping morphology in all specimens is typical of oviraptorosaurs in general in that the ischium is short and laterally concave (although *Chirostenotes pergracilis* has a more flattened lateral surface; Sues, 1997). The shaft is mediolaterally compressed. The differences in ischial morphology among specimens is best seen in the morphology of the obturator process and its associated distal edge. In IGM 100/973 the obturator process is located approximately midway along the shaft and is rounded. In IGM 100/1002 the obturator process has the same placement but is much more pronounced, tapering to almost a point with a rounded distal end (fig. 27A). The distal surface of the ischium from the obturator process to the distal end in this specimen is concave while it is straight in IGM 100/973, *Citipati osmolskae* (IGM 100/979), *Ingenia yanshini* (IGM 100/30), *Nomingia gobiensis* (Barsbold et al., 2000), and *Caudipteryx zoui* (Ji et al., 1998) (fig. 27B; although see IGM 100/978). The distal surface of the ischium is smooth in IGM 100/1002 but roughened in IGM 100/973. IGM 100/973 may represent an ontogenetically immature specimen. It cannot be assessed whether the ischia contacted or even approached each other medially as they do in *Avimimus portentosus* (Kurzanov, 1981), *Conchoraptor gracilis* (IGM 100/1203), *Chirostenotes gracilis* (Currie and Russell, 1988), *Ingenia yanshini* (IGM 100/30), and *Citipati osmolskae* (Barsbold et al., 1990; Osmólska et al., 2004).

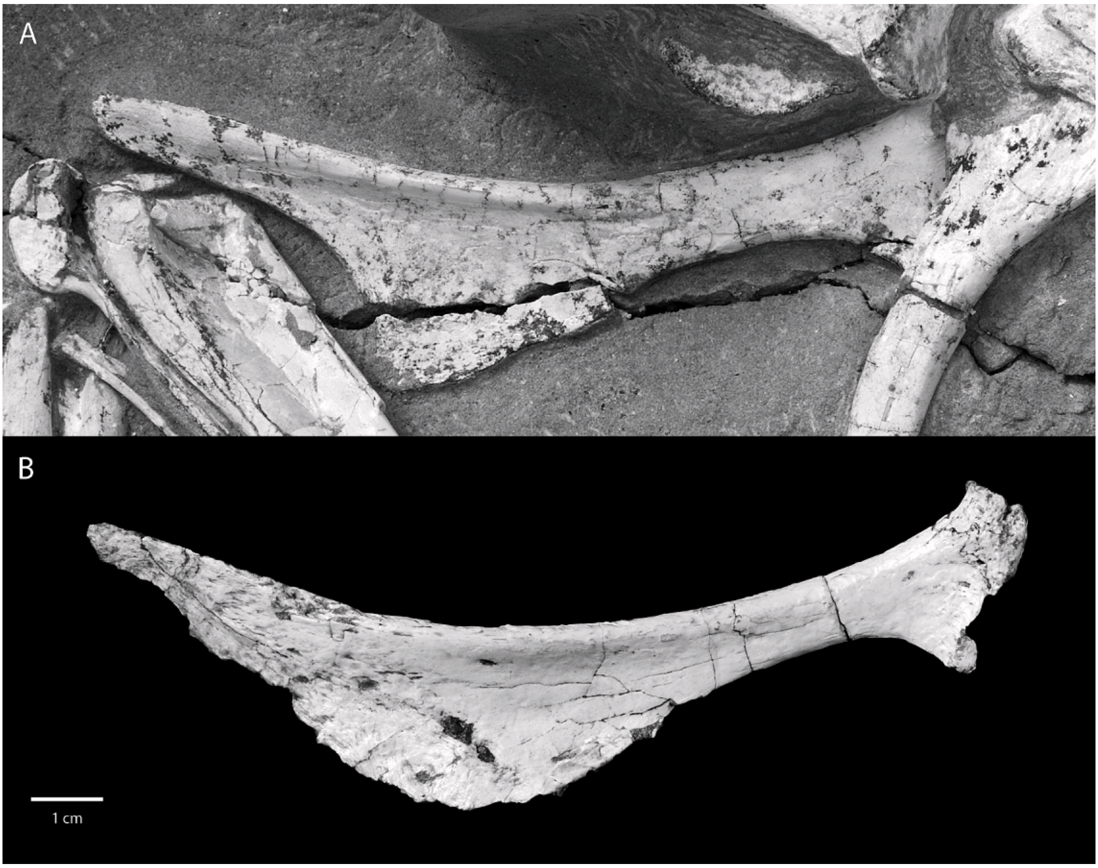

Fig. 27. Ischium. **A,** lateral view of right ischium in IGM 100/1002; **B,** lateral view of right ischium in IGM 100/973.

FEMUR

Figures 28, 29

The femur of *Khaan mckennai* is relatively gracile. IGM 100/973 preserves both femora, and parts of this element also are exposed in the articulated specimens (figs. 28, 29). Neither femur of IGM 100/973 preserves a complete trochanteric crest. The matrix has been prepared to reflect the shape of a crest, yet this shape should not be taken as a real feature (fig. 28). The trochanteric crest is preserved in IGM 100/1002, but only the posterolateral surface is exposed. It does show, however, that the femur has a relatively low greater trochanteric crest similar to the condition in other oviraptorids (fig. 29B), but the lesser trochanter is not exposed in this specimen. The entire lateral surface of the trochanteric crest is visible in IGM 100/1127 and displays morphology similar to what has been described for other oviraptorosaurs including more basal taxa such as *Caudipteryx zoui* (fig. 29A) (Osmólska et al., 2004). The distinct greater trochanteric crest is broad. The lesser trochanteric crest is at the same level as the greater trochanter and not displaced ventrally in relationship to it as in dromaeosaurs (Ostrom, 1970; Norell and Makovicky, 2004). The trochanteric crests are separated from each other by a deep groove, but are still pressed firmly together, similar to the condition seen in *Conchoraptor gracilis* (IGM 100/1203 and 100/3006) (fig. 29A). This differs from the single crest (fused greater and lesser trochanters) that is present in *Citipati osmolskae* (IGM 100/978 and IGM 100/1004; Turner et al., 2007a) and *Gigantoraptor erlianensis* or the deep notch in *Microvenator celer* (Ostrom, 1970; Makovicky and


A
B
C
D
E
F
2 cm

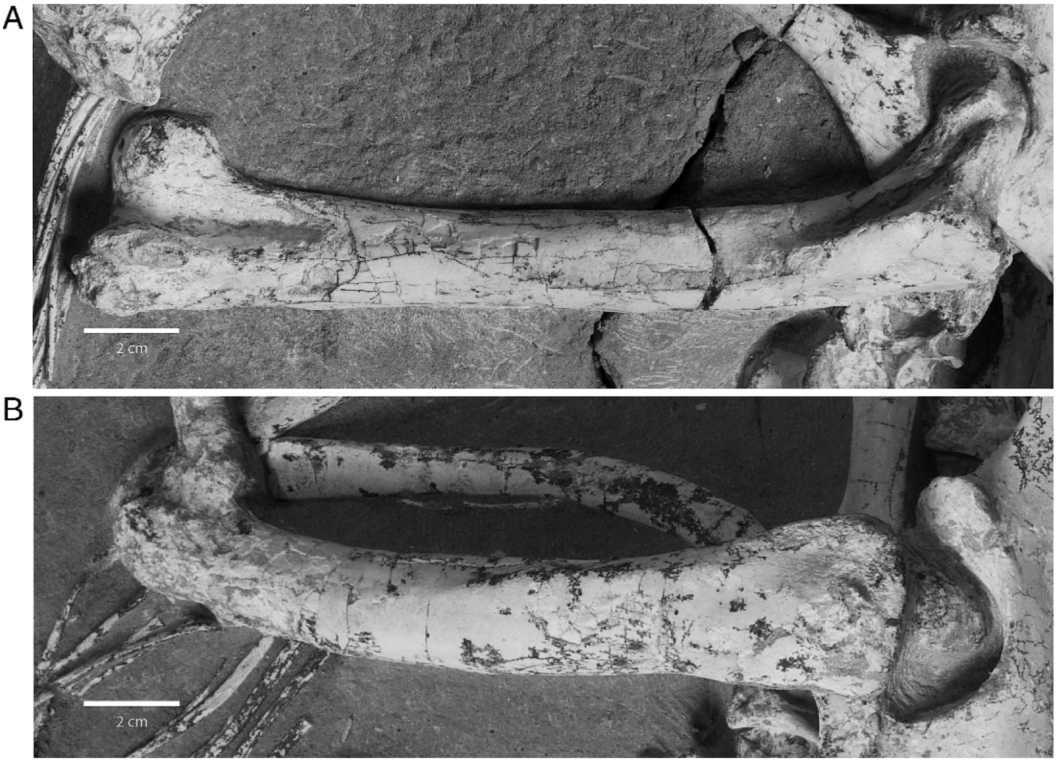

Fig. 29. Femur. **A,** posterior view of left femur in IGM 100/1127; **B,** lateral view of right femur in IGM 100/1002.

Sues, 1998). A large foramen (likely a nutrient foramen) is found on the medial surface of the trochanteric crest in *Khaan mckennai* and is also present in *Citipati osmolskae*. The greater and lesser trochanters in *Khaan mckennai* are separated from the spherical femoral head by a slightly constricted femoral neck similar to *Conchoraptor gracilis* and differing substantially from *Citipati osmolskae* and *Gigantoraptor erlianensis,* where no or little constriction is present, instead possessing an almost confluent surface from the trochanter to the femoral head. No fourth trochanter could be distinguished on any of the specimens of *Khaan mckennai*; this structure also is lacking in other oviraptorosaurs (Osmólska et al., 2004), troodontids (Currie and Dong, 2001), and most dromaeosaurids (Norell and Makovicky, 1999) A fourth trochanter is present in therizinosaurs (Clark et al., 2004). In *Khaan mckennai*, a muscular scar is present along the shaft in the region where a fourth trochanter would be expected to reside (fig. 28). This roughened surface is also present in *Citipati osmolskae*. No ventral vascular foramen could be found in this area on *Khaan mckennai* although one is present in other theropods including *Citipati osmolskae* (Norell and Makovicky, 1999). *Khaan mckennai* also lacks an accessory crest like that present in more basal taxa such as *Caudipteryx zoui*, *Microvenator celer*, and *Nomingia gobiensis*.

The femoral shaft at midlength is subtriangular in cross section caused by a

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Fig. 28. Right femur of IGM 100/973. **A,** anterior view; **B,** posterior view; **C,** lateral view; **D,** medial view; **E,** distal view; **F,** proximal view.

rounded ridge running on the anterior surface from the lesser trochanter across to the medial condyle. This same crest, although not as pronounced, is also present in *Citipati osmolskae*, but it does not influence the shape of the shaft. The ridge is absent in *Gigantoraptor erlianensis*. The distal region of the femur is poorly preserved on both sides of IGM 100/973, but IGM 100/1002 provides a good example of the posterior surface of this area in *Khaan mckennai* (fig. 29B). The distal condyles are separated from each other, and as in all other observed oviraptorosaurs (including the large-bodied *Gigantoraptor erlianensis*), the lateral (fibular) condyle extends further distally than the medial condyle (Osmólska et al., 2004). The tibiofibular crest is distinct in oviraptorids, and this taxon also possesses an extensive crest that projects posteriorly beyond the level of the medial condyle (fig. 29B). The extent of the tibiofibular crest is much more pronounced in *Khaan mckennai* than in either *Citipati osmolskae* or *Gigantoraptor erlianensis* but is comparable to forms such as *Conchoraptor gracilis* (IGM 100/1203) and *Ingenia yanshini* (IGM 100/30). A distinct but relatively shallow popliteal fossa is present between the two distal condyles. There also is a small ectepicondyle, a feature not present in *Citipati osmolskae*; however, other small-bodied oviraptorids such as *Ingenia yanshini* and *Conchoraptor gracilis* also possess this feature.

Tibia

Figures 30, 31

The right tibia of IGM 100/973 is extremely well preserved in three dimensions. The tibia is elongate (approximately 113% of the length of the femur; table 2) with a pronounced cnemial crest that is inflected only slightly laterally (fig. 30; Osmólska et al., 2004). The cnemial crest of *Khaan mckennai* is more gracile, does not project as far, and lacks the distinct boss that is present on the distal end of the crest in *Citipati osmolskae*, *Gigantoraptor erlianensis*, and *Nomingia gobiensis*. The extension of the cnemial crest onto the tibial shaft in IGM 100/973 is limited to approximately the proximal one-fifth of the element; it ends at the proximal extent of the fibular crest. The fibular crest is preserved on the lateral surface of the tibia in a proximal position and is more pronounced than the crest in *Citipati osmolskae* or *Gigantoraptor erlianensis*. In IGM 100/973 directly posterior to the fibular crest is a small foramen, likely a nutrient foramen, with a short dorsal groove associated with it. This foramen and groove are not present on the tibiae in IGM 100/1002 or IGM 100/1127, nor are they present in other oviraptorids. Their presence and/or absence appears to be intraspecifically variable. The tibia becomes more anteroposteriorly flattened distally. The astragalus (described below) is preserved in articulation, so that the anterior surface of the distal end of the tibia is not visible. The posterior surface of the distal tibia bears a shallow fossa between the condyles of the astragalus, and a distinct tubercle for the attachment of a branch of the fibularis muscle is present on the lateral surface of the distal end.

Fibula

Figures 30, 31

The fibula is preserved in all three specimens and extends from the proximal head of the tibia to contact the distal lateral condyle of the calcaneum (figs. 30, 31). The proximal head of the fibula is expanded anteroposteriorly as in *Citipati osmolskae*, but lacks the mediolateral flattening present in that taxon and *Gigantoraptor erlianensis*. The proximal shaft of the fibula of *Khaan mckennai* is, instead, triangular in cross section. Approximately one-third down the length of the shaft is a rounded, anteriorly projected iliofibularis tubercle. The shaft then tapers as it continues distally to contact the calcaneum.

Astragalus and Calcaneum

Figures 30

The right astragalus and calcaneum of IGM 100/973 are well preserved and still articulated with the tibia (fig. 30). Neither of these elements is fused to each other or to the tibia. The astragalus spans the width of the distal end of the tibia. The two condyles on the articular surface are separated by a wide, shallow depression more closely resembling

Fig. 30. Tibiae and fibulae of IGM 100/973. **A,** anterior surface of left tibia and fibula; **B,** posterior surface of right tibia; **C,** anterior surface of right tibia; **D,** left lateral surface of right tibia; **E,** right lateral surface of right tibia; **F,** detail of anterior surface of proximal end of right tibia showing the astragalus and calcaneum; **G,** distal surface of right tibia.

the indistinct morphology of *Gigantoraptor erlianensis* and *Ingenia yanshini* (IGM 100/30) than *Citipati osmolskae* (IGM 100/978), which has more pronounced condyles. The ascending process of the astragalus spans the entire width at the distal condyles but proximally tapers on the anterodistal surface of the tibia. The height of the ascending process is greater than the width across the widest point of the astragalus, as it is in all oviraptorosaurs (table 2). This morphology differs from that of therizinosaurs, where

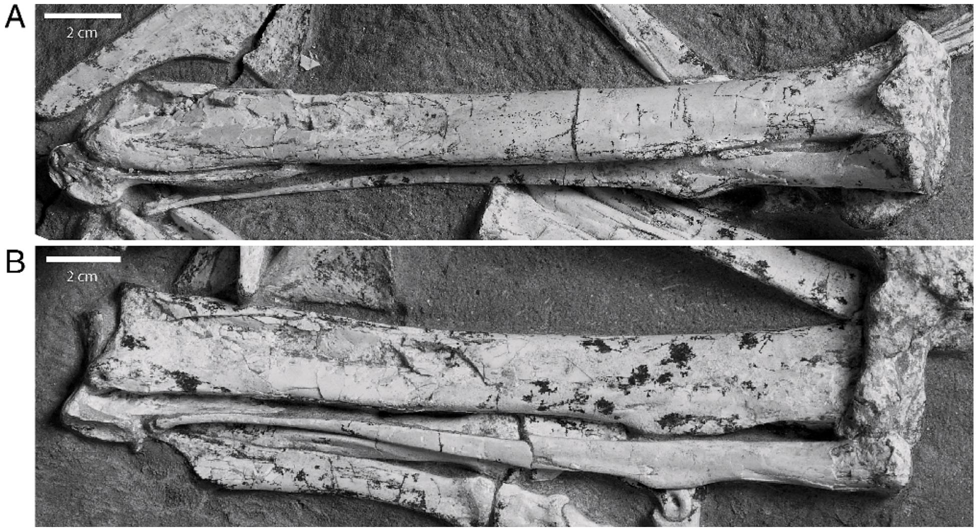


Fig. 31. Tibia and fibula. **A,** posterior surface of right tibia and fibula in IGM 100/1002; **B,** posterior surface of right tibia and fibula in IGM 100/1127.

these lengths are approximately equal. The lateral condyle is more fully developed than the medial, although the medial condyle extends further anteriorly (also present in *Citipati osmolskae*, *Ingenia yanshini*, and *Gigantoraptor erlianensis*). The lateral condyle has a distinct lateral depression in which the calcaneum sits. The calcaneum is preserved in articulation on this same specimen. As would be expected, the calcaneum is similar to other maniraptorans morphologically and is preserved only as a small tab of bone (fig. 30).

PES

Figures 32, 33

The distal tarsals are not easily visible in any of the three specimens of *Khaan mckennai*, but they do not appear to be fused with the metatarsals as in the therizinosaur *Elmisaurus rarus* (Currie and Russell, 1988), the basal oviraptorosaur *Avimimus portentosus* (Kurzanov, 1987), and many maniraptorans. The tarsals of *Citipati osmolskae* (IGM 100/978) also are partially fused to the metatarsus; therefore, this character may vary among oviraptorosaurs or may be ontogenetically correlated. Interestingly, the giant oviraptorid *Gigantoraptor erlianensis* lacks any trace of distal tarsal fusion with the metatarsals. In *Khaan mckennai*, only one indistinct central tarsal is present on the left foot of IGM 100/973 (fig. 33). A small sliver of bone that is most likely a distal tarsal can be seen on the proximal end of MT IV on the right foot of IGM 100/1002 (fig. 32). The distal tarsals, therefore, are interpreted as not fused to the metatarsals in this specimen as well.

Khaan mckennai preserves extraordinary examples of articulated feet in all three specimens (figs. 32, 33). The foot as a whole occupies approximately 32% of the entire length of the hindlimb (table 2). Digits I–V are present in all three specimens of this taxon. The metatarsals are not fused along their shaft as they are in *Elmisaurus rarus* and *Avimimus portentosus* (Currie and Russell, 1988; Kurzanov, 1981; 1987); the third metatarsal, although narrowing somewhat toward the proximal end, is exposed along its entire length. This condition is found in most oviraptorids. MT III is much more tightly constricted in *Caudipteryx zoui* and even *Citipati osmolskae* (Ji et al., 1998, and Clark et al., 1999, respectively). *Avimimus portentosus* and *Chirostenotes pergracilis* are the only oviraptorosaurs to have a true arctometatarsalian condition in which the proximal end of MT III is not exposed in anterior view (Kurzanov, 1981, 1987; Currie and Russell, 1988). None of the proximal

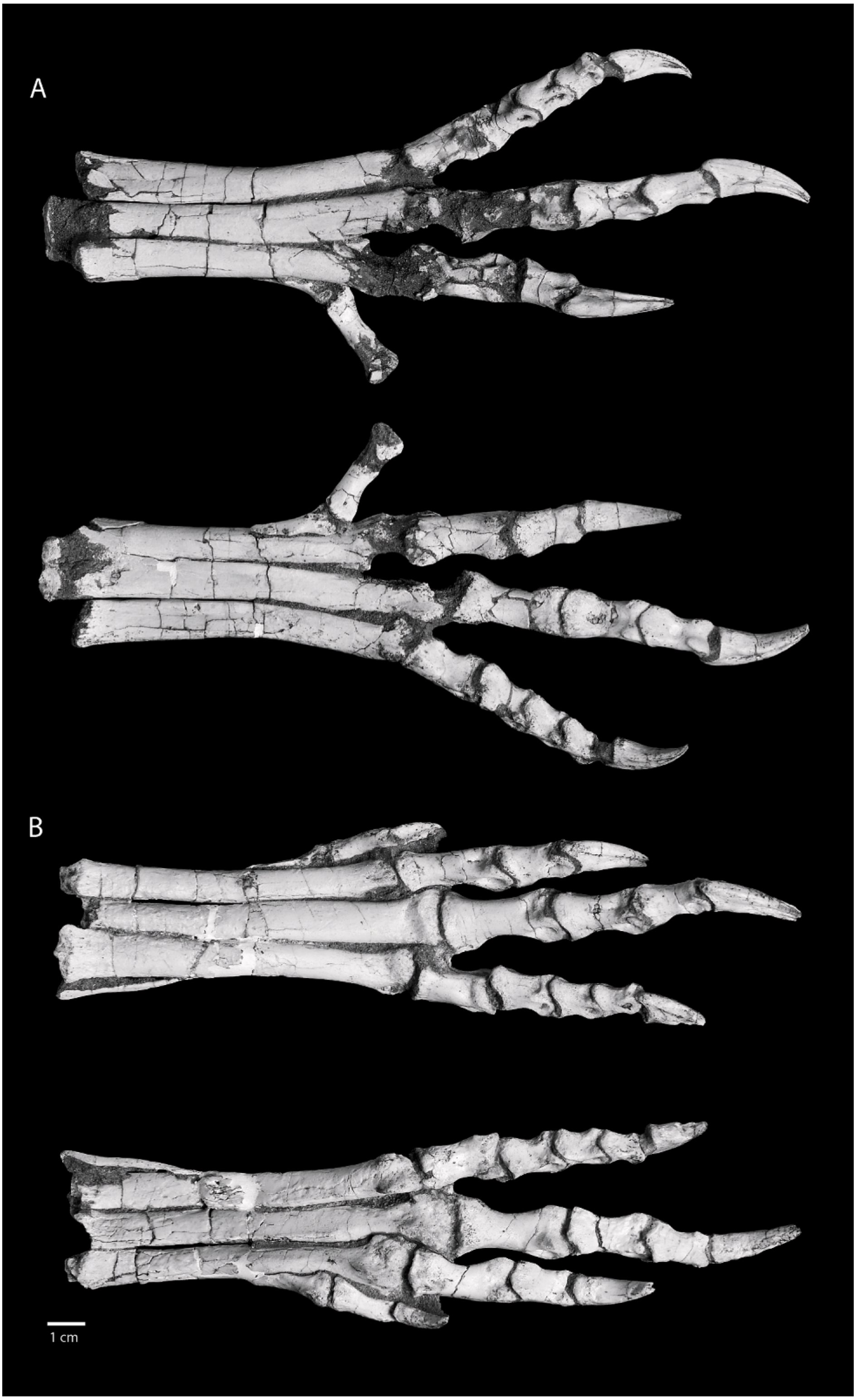
Fig. 32. Feet of IGM 100/1002.

articular surfaces of any of the metatarsals of *Khaan mckennai* are preserved. MT I is highly reduced and represented by a small splint of bone on the distal end of the medial surface of MT II. MT I closely resembles the same element in other maniraptoran taxa (see Norell and Makovicky, 1997). It is crescent shaped and possesses a subtle ligament pit (fig. 33). The distal end of this metatarsal has a rounded articular surface that is medially visible. Digit V is reduced to a small splint along the proximal end of the lateral surface of MT IV and extends a little over a third of the length of the metatarsus. MT III is the longest metatarsal; metatarsals II and IV are approximately the same length. Distal articular surfaces are not visible on the metatarsals. The medial and lateral surfaces appear to possess deep ligament foveae.

Khaan mckennai has the typical theropod phalangeal formula of 2-3-4-5. There is no indication of an enlarged or specialized digit II as in deinonychosaurs. Digit III extends the furthest distally. The articular surfaces again are not visible, but all phalanges possess a deep ligament fovea on the lateral and medial surfaces. These pits are approximately circular in shape. A shallow pit is present on the dorsal surface of the phalanges for insertion of the flexor muscles of the foot. These are pronounced in the proximal phalanges and gradually fade in the more distal ones. The phalangeal joints are symmetrical and ginglymoid. The ungual phalanges are slightly curved (distinct from the purported oviraptorosaur sister-taxon therizinosaurs; see Turner et al., 2007b), with a shallow groove running along the medial and lateral surfaces that becomes deeper as it approaches the distal end of the phalanges.

DISCUSSION

The primary goal of this study is to put forth a relatively comprehensive osteological description for the oviraptorid coelurosaur *Khaan mckennai*. To fully understand the transformations of these morphological observations they must be studied within an explicit evolutionary context. We, therefore,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proceed to place several specific features that are characteristic for the Oviraptorosauria within a phylogenetic framework based on the hypothesized relationships of taxa within this lineage, namely that of Norell et al. (2006), in order to establish preliminary hypotheses of evolutionary transformations. The optimization of characters within oviraptorosaurs subsequently will also help elucidate the larger pattern observed within Maniraptora. This is only the beginning of a much more synoptic treatment of oviraptorosaur phylogeny currently under way (Balanoff and Norell, in prep.).

PNEUMATICITY OF THE NARIAL REGION

Figures 3, 5, 34

One of the most obvious distinctions among oviraptorosaur taxa is the development of a bony crest on the dorsal surface of the skull, which may be either extensively (e.g., *Citipati osmolskae*) or poorly (e.g., *Khaan mckennai*) developed. Because it is such a distinctive feature, it is reasonable to hypothesize that the development of a crest might also be correlated with a series of other frontonasal characters such as degree of pneumatization and the presence or absence of a dorsal sinus. The growth of a highly complex pneumatic frontonasal region is present in both *Khaan mckennai* and *Citipati osmolskae* (fig. 3) and has been used to distinguish between oviraptorosaurs in general (Osmólska et al., 2004; Witmer, 1997; Turner et al., 2007b). The frontonasal pneumatic structures in *Citipati osmolskae* display a degree of density not seen in *Khaan mckennai* (fig. 34), and there also is a large difference in the size of these dorsal openings. The shape and spatial positions of pneumatic recesses on the dorsal surface of the nasal, however, are closely correlated between these two oviraptorid taxa. The overlapping morphology consists of a single large opening (nasal recess) that lies directly dorsal to the antorbital fenestra almost in the center of the main body of the nasal with several smaller accessory foramina scattered around the central opening. The large recess is raised dorsal to (above) the level of the naris in *Citipati osmolskae* but lies on the same horizontal plane in *Khaan mckennai*. A bony strut running along the midline of the nasal separates the paired pneumatic structures in both taxa. Although these taxa share the presence of accessory frontonasal recesses, the pattern of surrounding openings exhibits a fair amount of variation. The openings on the dorsal surface of the frontal, unlike the nasal, are limited to small circular foramina at the anteriormost margin of the element in both taxa.

The invasion of the nasal by pneumatic recesses also occurs in taxa lying phylogenetically outside of Oviraptoridae, namely in the basal oviraptorosaur taxon *Incisivosaurus gauthieri* (Balanoff et al., 2009). Although such pneumaticity is not as extensive in *Incisivosaurus gauthieri* as it is in *Khaan mckennai* or *Citipati osmolskae*, and especially the crested *Rinchenia mongoliensis*, the mere presence of the feature in this basal taxon indicates that it is diagnostic of the entire oviraptorosaur lineage (absent in other maniraptorans; Turner et al., 2007b). Based on a tree of Oviraptorosauria (fig. 4), one would predict that frontonasal pneumatic recesses also are present in caenagnathids; however, published caenagnathid specimens do not include this region of the skull (Triebold and Russell, 1995; Sues, 1997; Triebold et al., 2000).

Overlapping morphology in the frontonasal region of *Khaan mckennai*, *Citipati osmolskae*, and *Incisivosaurus gauthieri* includes the presence of a pair of pneumatic recesses (may be covered by extremely thin bone in *Incisivosaurus gauthieri*; Balanoff et al., 2009) on the dorsal surface of the nasal (fig. 3A). The accessory foramina that appear in this region in both *Khaan mckennai* and

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Fig. 33. Feet of IGM 100/973. **A,** left foot (upper, dorsal surface; lower, palmer surface); **B,** right foot (upper, dorsal surface; lower, palmer surface).

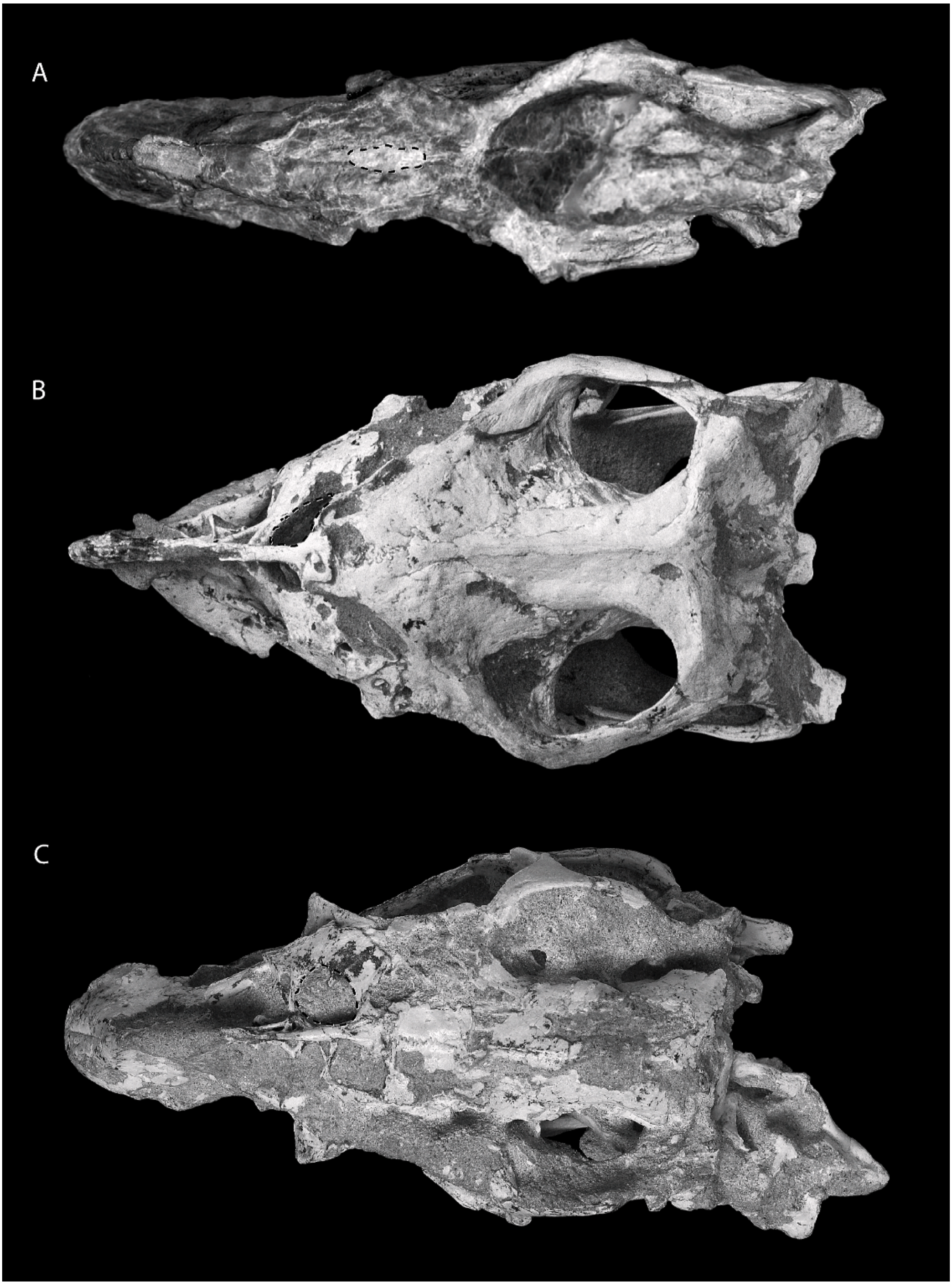


Fig. 34. Pneumatic openings in the dorsal surface of the skull of **A,** *Incisivosaurus gauthieri* (IVPP V 13326); **B,** *Citipati osmolskae* (IGM 100/978); **C,** *Khaan mckennai* (IGM 100/973). The large central nasal recess is outlined in each specimen. Specimens are scaled to the same size.

Citipati osmolskae (figs. 3C, 8) are not observable in *Incisivosaurus gauthieri*. The absence of these structures indicates that, although pneumaticity is present at the base of the lineage, it becomes much more extensive in oviraptorids (possibly Oviraptoridae + Caenagnathidae), resulting in the extreme morphology that is seen in taxa possessing a well-developed premaxillary/nasal crest like *Citipati osmolskae* (Clark et al., 2002), *Rinchenia mongoliensis* (Barsbold, 1986), and *Oviraptor philoceratops* (Osborn, 1924; Smith, 1993; Clark et al., 2002). The presence of pneumatic recesses in both *Incisivosaurus gauthieri* and *Khaan mckennai*, however, shows that although *degree* of pneumaticity may vary with the development of a crest, the presence or absence of frontonasal pneumatic recesses does not.

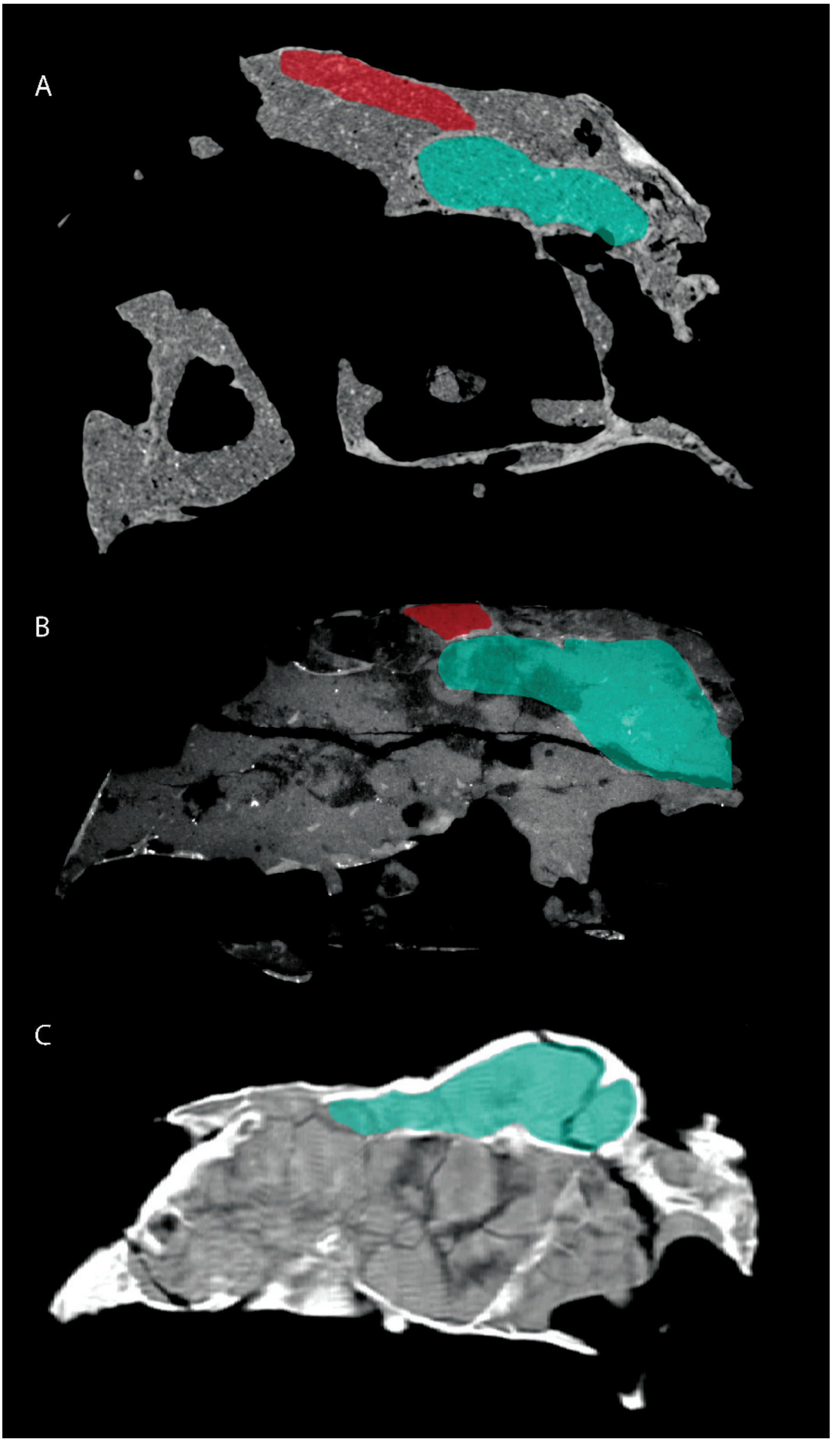
Dorsal Frontal Sinus

Figures 10, 35

Computed tomographic imagery reveals that both *Khaan mckennai* (IGM 100/973) and *Citipati osmolskae* (IGM 100/978) have a dorsal frontal sinus that extends posteriorly from the aforementioned pneumatic openings in the nasal and frontal to invade the parietal and possibly join the tympanic sinuses (fig. 10; Clark et al., 2002: fig. 7). The presence of a frontal sinus is unique among theropods; additionally, it extends almost the entire length of the skull and lies completely dorsal to the endocranial cavity. This feature, first described in an oviraptorid by Clark et al. (2002) in *Citipati osmolskae* and later by Kundrát and Janáček (2007) in *Conchoraptor gracilis*, does not appear outside of oviraptorids nor does it correlate with the presence or absence of an osseous crest (as the sinus is present in *Khaan mckennai* and *Conchoraptor gracilis* [lacking a distinctive crest] and *Citipati osmolskae* [well-developed crest]). The original description of *Citipati osmolskae* was not able to determine with certainty whether bony struts were present subdividing this dorsal cavity (Clark et al., 2002). CT scans for *Khaan mckennai* (this study) and *Conchoraptor gracilis* (Kundrát and Janáček, 2007), however, clearly show a medial partition within the cavity indicating a paired structure (fig. 10B, C). Until several more oviraptorid taxa receive detailed descriptive treatments bolstered by CT data, based only on these two specimens, the optimization of this division within Oviraptoridae cannot be clearly determined.

Although pneumatic sinuses also are present in this region of the skull of the basal oviraptorosaur *Incisivosaurus gauthieri* (see Balanoff et al., 2009), these structures are not as extensive nor do they extend as far posteriorly over the endocranial cavity as those in oviraptorids. They instead look similar to the basal theropod condition for frontal sinuses (Sampson and Witmer, 2007; Witmer and Ridgely, 2008). The sinuses in *Incisivosaurus gauthieri* extend posteriorly only into the anteriormost region of the frontal. Absence of frontal sinuses in taxa outside Oviraptorosauria (e.g., *Zanabazar junior* [Norell et al., 2009] and *Tsaagan mangas* [Norell et al., 2006]) suggests that they optimize as a unique feature in this group; however, it should be noted that frontal sinuses are present in crown birds (see Baumel and Witmer, 1993; Witmer and Ridgely, 2009) but are not developed in more basal avialans such as *Archaeopteryx lithographica* (Dominguez Alonso et al., 2004; www.digimorph.org/specimens/Archaeopteryx_lithographica). Some basal theropods like *Majungasaurus crenatissimus* also have a frontal sinus, but the homology of these spaces is tenuous because this space is absent in tyrannosauroids (Sampson and Witmer, 2007; Witmer and Ridgely, 2008; Bever et al., 2011) and ornithomimids (Tahara and Larsson, 2011).

The evolutionary history of the frontal sinus in oviraptorosaurs appears to be an invasion of the frontal by a paired sinus at the base of the clade. Following this initial excavation, the dorsal narial sinus progresses posteriorly and may join the dorsal tympanic recess (fig. 10). The bony division of the cavity might be lost or not preserved in *Citipati osmolskae* (Clark et al., 2002) or might not be apparent in the CT imagery. The addition of high-resolution CT data from caenagnathid taxa would be useful in documenting the posterior progression of the sinuses within this lineage.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ACCESSORY ANTORBITAL FENESTRAE

Figures 3, 5, 36

The accessory antorbital fenestrae in the interfenestral bar of the maxilla are problematic in oviraptorosaurs, and few authors have attempted to work out their homologies relative to those of other coelurosaurs (see Witmer, 1997; Balanoff et al., 2009). The typical coelurosaurian condition includes the presence of at least one large accessory foramen (maxillary foramen) anterior to the antorbital fenestra and a smaller promaxillary fenestra that pneumatizes the maxilla and premaxilla anterior to the maxillary foramen (Witmer, 1997). The pattern present in oviraptorids (e.g., *Khaan mckennai, Citipati osmolskae,* and *Oviraptor philoceratops*) departs from this model and surprisingly appears to correspond most closely to that described for the allosauroid *Sinraptor dongi* (fig. 5) (Currie and Zhao, 1993b; Witmer, 1997). This seemingly derived arrangement includes a large (possibly promaxillary) foramen anterior to the antorbital fenestra and a smaller (possibly maxillary) fenestra immediately posterior and somewhat dorsal to the anterior accessory foramen (figs. 5, 36). Although this may seem an unusual morphology to be found within Coelurosauria, the identification is the simplest based merely on their spatial distribution (although see contradictory labels on *Conchoraptor gracilis* in Osmólska et al., 2004: fig. 8.1G). An additional accessory foramen is also present in the antorbital fossa of both *Khaan mckennai* and *Citipati osmolskae* in the portion of the maxilla that forms the floor of the fossa. The foramen is anteroposteriorly elongate and extends ventrally to the "promaxillary fenestra." This foramen may also be present in *Oviraptor philoceratops*; however, the mediolateral compression of the skull makes determination of the position of the foramen difficult (see Clark et al., 2002). *Citipati osmolskae* exhibits individual variation, with two foramina present on the right side of the skull and only one on the left. In *Khaan mckennai*, at least two smaller foramina are positioned posterior to the "promaxillary fenestra" in a ventral location (fig. 5). This ventral opening does not correspond to any other observed coelurosaurs and appears to be an oviraptorosaur apomorphy.

The accessory antorbital fenestrae within *Incisivosaurus gauthieri* also display a unique spatial arrangement relative to the condition in other coelurosaurs. Similar to *Khaan mckennai* and *Citipati osmolskae*, it shares a large anterior accessory fenestra and a small posterodorsally placed fossa (fig. 36). It also has a small, circular foramen located immediately posteroventral to the margin of the anterior accessory foramen. *Incisivosaurus gauthieri*, however, does not possess a ventral fenestra extending beneath the anterior accessory foramen. All three taxa examined, accordingly, have the overlapping pattern of one large anteriorly placed foramen and at least one smaller foramen between this anterior foramen and the antorbital fenestra. This pattern suggests that the unique arrangement of antorbital accessory fenestrae appears somewhere along the lineage leading to oviraptorosaurs. Unfortunately, the typically recovered sister taxon to Oviraptorosauria, Therizinosauria (however, see Zanno et al., 2009; Xu et al., 2010), does not possess accessory antorbital fenestrae (e.g., *Erlikosaurus andrewsi*; Clark et al., 1994) making optimization of this transformation impossible. Optimization of the ventral accessory fenestra located within the floor of antorbital fossa suggests a first appearance in oviraptorids, as this structure is not present in *Incisivosaurus gauthieri* and there are no accessory antorbital fenestrae in known caenagnathids (i.e., *Chirostenotes pergracilis*; Sues, 1997).

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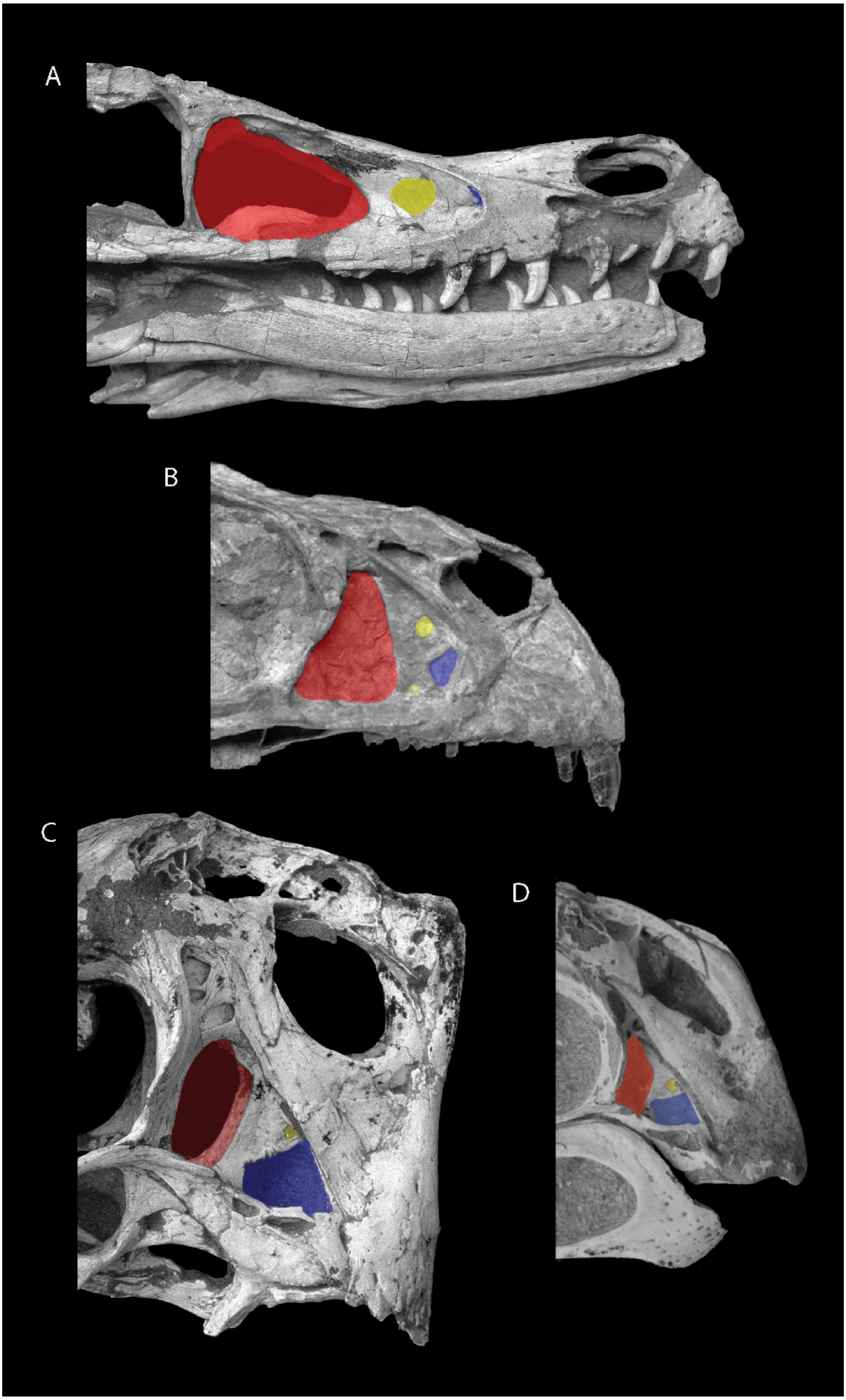
Fig. 35. Sagittal CT section through the skulls of **A,** *Citipati osmolskae* (IGM 100/978); **B,** *Khaan mckennai* (IGM 100/973); **C,** *Incisivosaurus gauthieri* (IVPP V 13326). The frontal sinus in each taxon is highlighted in red and the cranial cavity is highlighted in blue.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TRIGEMINAL FORAMEN

Figure 3

The trigeminal (CN V) foramen in the oviraptorid taxa *Khaan mckennai* and *Citipati osmolskae* is a single opening positioned at the juncture of the prootic and laterosphenoid (compare fig. 3 with Clark et al., 2002: fig. 2 [mislabeled foramen ovalis, "foo"]). This undivided foramen differs from the condition in Therizinosauria (Clark et al., 1994) and tyrannosauroids (Witmer and Ridgely, 2009; Brusatte et al., 2009, Bever et al., 2011), where there are two distinct openings for the separate branches (ophthalmic and maxillomandibular) of the trigeminal nerve. A divided trigeminal foramen is also found in crown birds (Baumel and Witmer, 1993), but deinonychosaurs and basal avialans possess only a single opening (Walker, 1985; Currie and Zhao, 1993a; Currie, 1997; Dominguez Alonso et al., 2004; Makovicky and Norell, 2004; Norell and Makovicky, 2004). A single foramen is typically thought to correlate with a branching of the gasserian ganglion outside of the braincase, and two foramina with a branching of the ganglion within the braincase with separate exits for each branch of the nerve (Goodrich, 1930).

The single opening in these oviraptorids suggests that this group had an external branching point of the trigeminal nerve. The morphology of *Incisivosaurus gauthieri*, however, indicates that another interpretation is also plausible. *Incisivosaurus gauthieri* possesses a single trigeminal foramen that is severely pinched at its midpoint (Balanoff et al., 2009: fig. 12). An alternative interpretation is that *Incisivosaurus gauthieri* and closely related nonoviraptorosaurs (e.g., *Erlikosaurus andrewsi*; Clark et al., 1994) had a gasserian ganglion lying within the braincase that branched internally, but whose dividing strut between the two openings did not fully ossify. *Chirostenotes pergracilis* also possesses a similar morphology to *Incisivosaurus gauthieri* with a pinched trigeminal foramen but additionally has a fossa located directly behind the opening, suggesting that the gasserian ganglion sat in this fossa (Sues, 1997). If this is correct, an internal branching pattern would be an equally parsimonious reconstruction for *Khaan mckennai* and *Citipati osmolskae*. Perhaps a secondary loss of the ossified strut between the foramina occurred early in oviraptorosaur history, making this morphology plesiomorphic for oviraptorids. *Chirostenotes pergracilis* has a morphological pattern very similar to that of *Incisivosaurus gauthieri* (Sues, 1997), indicating that a single, large trigeminal foramen is an oviraptorid characteristic.

MAXILLARY LENGTH

Figures 3, 5

Clark et al. (2002) were the first to note significant differences among oviraptorid taxa in the anterior-posterior length of the maxilla. The length of the maxilla intuitively seems to correlate with the shortening of the facial region as a whole. *Khaan mckennai* and *Citipati osmolskae* both possess shortened maxillae in lateral view relative to the overall length of the preorbital region (~54% and 68% of rostral length, respectively) compared to maniraptoran taxa outside of Oviraptorosauria (e.g., 88% for *Velociraptor mongoliensis* [AMNH FARB 6515]); however, the presence of a "long" maxilla in both *Oviraptor philoceratops* (AMNH FARB 6517) and *Chirostenotes pergracilis* (Sues, 1997) suggests that the shortening of the maxilla is not completely tied to the shortening of the facial region (Clark et al., 2004). Not surprisingly, *Incisivosaurus gauthieri* possesses

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Fig. 36. Right lateral view of the rostrum of **A,** *Velociraptor mongoliensis* (AMNH FARB 6515); **B,** *Incisivosaurus gauthieri* (IVPP V 13326); **C,** *Khaan mckennai* (IGM 100/973); **D,** *Citipati osmolskae* (IGM 100/978). Fenestrae of the antorbital region are highlighted: antorbital fenestra (red) and promaxillary fenestra (blue). What may be considered the maxillary fenestra is indicated by yellow. This designation, however, is tenuous. In *Incisivosaurus gauthieri*, both a fossa (dorsal) and fenestra (ventral) are shown in yellow. The homology of these intermediate structures is uncertain.

a more elongate maxilla than any of the oviraptorids discussed above; however, because the facial region is not shortened in *Incisivosaurus gauthieri* the elongate maxillary morphology is not reflected in the given ratio (~78%; Balanoff et al., 2009: fig. 3). These data suggest that a "short" maxilla evolved within Oviraptoridae and may be diagnostic of a subclade containing both *Khaan mckennai* and *Citipati osmolskae*.

POSTCRANIUM

Figures 1, 2

Similar to other regions of the postcranial skeleton, the vertebral column of members of Oviraptoridae is heavily pneumatized. Both *Khaan mckennai* and *Citipati osmolskae* possess pleurocoels throughout the entire column with only the exception of the distalmost tail vertebrae (figs. 1, 2). Variation within the vertebral column appears to occur not in the presence or absence of pneumatization, but rather primarily in its extent in the cervical vertebrae. The most anterior cervicals of *Citipati osmolskae* (IGM 100/978) have pleurocoels that are large fossae piercing the entire centra so that one can see through to the opposite side. *Khaan mckennai,* however, lacks this feature, and instead possesses a typical theropod vertebral morphology of foramenlike pleurocoels (fig. 13). This appears to be the typical oviraptorid condition, also being present in *Ingenia yanshini* and *Conchoraptor gracilis*. More basal oviraptorosaurs, such as *Caudipteryx zoui,* also possess a nearly completely pneumatized vertebral column, with cervical pleurocoels that are similar to the typical theropod, foramenlike morphology (Ji et al., 1998). The extreme pneumatization, therefore, evolved at some point within the group Oviraptoridae and is possibly an autapomorphy of *Citipati osmolskae*.

The pneumatic features of the axial vertebra display a similar pattern in *Khaan mckennai* and *Citipati osmolskae* to that observed in the remainder of the cervical series. Each axial vertebra of *Khaan mckennai* has a small foramen in the anterior/middle region of the lateral surface of the centrum (fig. 14). Each vertebra of *Citipati osmolskae* possesses a large fossa that pierces the element. To complicate the pattern, *Conchoraptor gracilis* differs from both of these by not having any trace of a pleurocoel on the axial centrum. As it is not apparent whether *Caudipteryx zoui* possesses a pleurocoel in its axis or not, polarization of this character within Oviraptorosauria is not possible at this time.

A shortened tail has long been cited as characteristic of oviraptorosaurs for which relatively complete postcranial material is available (Osmólska et al., 2004). This characterization holds true for all oviraptorids that we evaluated; *Khaan mckennai* has approximately 28 caudal vertebrae and *Citipati osmolskae* has 32 vertebrae. The typical caudal vertebral count for maniraptoran taxa is around 44 or fewer caudal vertebrae (Farlow et al., 2000); therefore, a reduced number is apomorphic for Oviraptorosauria. *Caudipteryx zoui* and *Nomingia gobiensis* take this reduction to a more extreme degree, having no more than 20 and 22 caudal vertebrae, respectively (Ji et al., 1998; Barsbold et al., 2000). The propensity and potential (see Bever and Norell, 2009) for a reduction in the number of tail vertebrae took place early in the history of Oviraptorosauria and is apomorphic for the group.

The relatively low number of caudal vertebrae has been cited as a potential synapomorphy of an avialan and oviraptorosaur clade (e.g., Maryańska et al., 2002; Osmólska et al, 2004). Although this feature does appear to be diagnostic of both clades, it is a convergent feature as there is no reduction in this region in deinonychosaurs, nor is there an indication of a pygostyle in deinonychosaurs, basal paravians, basal oviraptorosaurs, or even basal avialans.

In the pectoral girdle, the overall morphology of the coracoid of *Khaan mckennai* is similar to other coelurosaurs except in the relatively small size of the coracoid foramen (fig. 19). *Citipati osmolskae* also possesses a small coracoid foramen (see Clark et al., 1999). The coracoid foramen in *Caudipteryx zoui* is relatively and absolutely larger than in either of the observed oviraptorids and bears a morphology similar to that of the purported sister taxon of Oviraptorosauria, Therizinosauria (see *Falcarius utahensis*; Zanno, 2006), as well as other maniraptorans (Currie and Dong, 2001). The presence of a large coracoid foramen in *Caudipteryx zoui* (Ji et al., 1998; Zhou et al., 2000) and *Chirostenotes pergracilis* (Currie and Russell, 1988) suggests that the reduction in the size of this structure occurred somewhere near the base of Oviraptoridae.

Oviraptorids also display variation in the shape of the trochanteric crest of the femur (fig. 17). This crest in *Khaan mckennai* is not unlike what has been previously described for oviraptorids (Osmólska et al., 2004) in that it is made up of a lesser and greater trochanteric crest, which are appressed tightly against each other, reaching approximately the same level proximally. This arrangement differs significantly from the trochanteric crest of *Citipati osmolskae* where these processes are fused, forming a single arching trochanteric crest. The morphology of *Caudipteryx zoui* more closely resembles that of *Khaan mckennai* in that it also possesses a groove separating these two processes, which are at approximately the same level (Ji et al., 1998). The distribution of this character indicates that the morphology observed in *Citipati osmolskae* is derived for a more exclusive group within Oviraptoridae. The large-bodied *Gigantoraptor erlianensis* also exhibits this single crest morphology (Xu et al., 2007).

The degree of exposure of metatarsal III along the length of the metatarsus has been used extensively in coelurosaur systematics (see Holtz, 1996, 1998, 2001), and there indeed is some variation in this feature within Oviraptorosauria. *Khaan mckennai* has a MT III that remains visible along the length of the element with only a slight constriction near the proximal end (fig. 33). *Citipati osmolskae* has a MT III that looks much the same as that of *Khaan mckennai* but is slightly more constricted proximally (Clark et al., 1999: fig. 6). *Caudipteryx zoui*, in contrast, has the most extreme constriction of the three taxa, maintaining visibility throughout most of the length but almost completely disappearing near its proximal end (Ji et al., 1998). Only a few other oviraptorosaurs also have this extremely pinched morphology (e.g., the proximal end of MT III in *Avimimus portentosus* is not retained [Kurzanov, 1987]; compare with *Chirostenotes pergracilis* [Currie and Russell, 1988; Sues, 1997]). The apparent transformation of this feature includes the presence of an ''arctometatarsalian'' condition in the basalmost taxa, followed by a loss of the condition within Oviraptoridae.

Although perhaps not useful as a phylogenetic character because it most likely encompasses changes of many features, the evolution of body size in Oviraptorosauria demonstrates an interesting evolutionary pattern. The taxa hypothesized to fall at the base of the oviraptorosaur tree are all relatively small in size (e.g., *Caudipteryx zoui* [Ji et al., 1998; Zhou and Wang, 2000; Zhou et al., 2000], *Avimimus portentosus* [Kurzanov, 1987], *Incisivosaurus gauthieri* [Xu et al., 2002], *Microvenator celer* [Ostrom, 1970; Makovicky and Sues, 1998]), and the more derived caenagnathids and oviraptorids have larger body sizes, apparently culminating in the extraordinarily large *Gigantoraptor erlianensis* (Xu et al., 2007) among known oviraptorids. This pattern corresponds to ''Cope's Rule'' as well as the pattern observed by Turner et al. (2007b) in deinonychosaurs, in which taxa at the base of maniraptoran clades have small body sizes that increase within their individual clades. Overall, small body size at the base of these clades suggests that ''miniaturization'' occurred early along the avian stem (Turner et al., 2007b). The presence of small body size at the base of Oviraptorosauria may help push this transformation even further down the maniraptoran tree.

SUMMARY

Khaan mckennai is a small-bodied oviraptorid from the Late Cretaceous of Central Asia, and similar to other specimens from this region it is known from a number of pristinely preserved specimens. This study presents the most comprehensive description and illustration of an oviraptorid to date, using three specimens both disarticulated and articulated. Few accessible descriptive studies of oviraptorosaurs are available; therefore, we provide an important piece to understanding the morphological transformations within this bizarre group of dinosaurs. By making comparisons with large-bodied, crested oviraptorids (i.e., *Citipati osmolskae*) and more basal oviraptorosaurs (i.e., *Incisivosaurus gauthieri* and *Caudipteryx zoui*) we provide a framework for setting up hypotheses that subsequently can be tested in a more comprehensive phylogenetic analysis. Illustrated descriptions are instrumental in presenting new data to researchers. These analyses can ideally be used to help elucidate the acquisition of characters along the oviraptorosaurian lineage. Working out the transformations within Oviraptorosauria not only clarifies the evolutionary changes within this group, but also within the broader spectrum of Coelurosauria.

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APPENDIX 1

LIST OF TAXA USED FOR COMPARISON IN ANALYSIS

Abbreviations: **AMNH**, American Museum of Natural History, New York, NY; **CMN**, Canadian Museum of Nature, Ottawa, Canada; **IGM**, Geological Institute, Mongolian Academy of Sciences, Ulaan Baatar, Mongolia; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthrolopogy, Beijing, China; **LH**, Long Hao Institute of Geology and Paleontology, Hohhot, Inner Mongolia, China; **NGMC**, Geological Museum of China, Beijing, China; **PIN**, Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; **ROM**, Royal Ontario Museum, Ontario, Canada; **RTMP**, Royal Tyrrell Museum of Palaeontology, Drumheller, Canada; **UMNH**, Utah Museum of Natural History, Salt Lake City, Utah; **ZPAL**, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

- Oviraptorosauria
  - *Incisivosaurus gauthieri* Xu et al., 2002
    - IVPP V 13326
  - *Caudipteryx zoui* Ji et al., 1998
    - NGMC 97-4-A
    - NGMC 97-9-A
    - IVPP V 12430
    - IVPP V 12344
  - *Similicaudipteryx* He et al., 2008
    - IVPP V 12556
  - *Avimimus portentosus* Kurzanov, 1981
    - PIN 3907/1
  - *Chirostenotes pergracilis* Gilmore, 1924
    - CMN 2367
    - CMN 8538
    - CMN 8776
    - RTMP 79.20.1
    - ROM 43250
  - *Microvenator celer* Ostrom 1970
    - AMNH 3041
  - *Elmisaurus rarus* Osmólska 1981
    - ZPAL MgD-I/98
  - *Nomingia gobiensis* Barsbold et al., 2000
    - IGM 1/119

- Oviraptoridae
  - *Nemegtomaia barsboldi* Lü et al., 2004
    - IGM 100/2112
  - *Oviraptor philoceratops* Osborn, 1924
    - AMNH 6517
    - IGM 100/791
  - *Rinchenia mongoliensis* Barsbold, 1986
    - IGM 100/32
  - *Citipati osmolskae* Clark et al., 2001
    - IGM 100/978
    - IGM 100/979
    - IGM 100/1004
  - *Heyuannia huangi* Lü, 2002
    - HYMV1
  - *Ingenia yanshini* Barsbold, 1981
    - IGM 100/30
    - IGM 100/31
    - IGM 100/33
  - *Conchoraptor gracilis* Barsbold, 1986
    - IGM 100/20
    - IGM 100/19
    - IGM 100/1203
    - IGM 100/3006
    - ZPAL MgD-I/95
  - *Khaan mckennai* Clark et al., 2001
    - IGM 100/1127
    - IGM 100/1002
    - IGM 100/973
  - *Gigantoraptor erlianensis* Xu et al., 2007
    - LH V 0011
    - IGM 100/42

APPENDIX 2

ANATOMICAL ABBREVIATIONS

amp	ampulla
an	angular
aof	antorbital fenestra
ar	articular
asc	anterior semicircular canal
ax	axial vertebra
bo	basioccipital
ccr	common crus
cnV	cranial nerve V (trigeminal)
cnVII	cranial nerve VII (facial)
cnVIII	cranial nerve VIII (vestibulocochlear)

d	dentary
ecs	endocranial space
eo	exoccipital
f	frontal
fc	cochlear fenestra
fm	foramen magnum
fr	floccular recess
frps	frontoparietal suture
h	hyoid
hsc	horizontal semicircular canal
ifb	interfenestral bar
inf	infratemporal fenestra
j	jugal
jc	jugular canal
l	lacrimal
lat	laterosphenoid
lc	lacrimal canal
mdf	mandibular fenestra
mt	maxillary “tooth”
mx	maxilla
n	nasal
na	naris
np	nasal passage
o	orbit
oc	occipital condyle
osp	orbitosphenoid
p	parietal
pal	palatine
par	prearticular
pmx	premaxilla
pn	pneumatic space
pnf	pneumatic foramen
po	postorbital
pop	paroccipital process
pr	parasphenoid rostrum
pro	prootic
psc	posterior semicircular canal
pt	pterygoid
ptr	posterior tympanic recess
q	quadrate
qj	quadratojugal
sa	surangular
saf	surangular fenestra
sas	surangular spine
sept	septum
so	supraoccipital
sp	splenial
sq	squamosal
stf	supratemporal fenestra
v	vomer
vest	vestibule