Cranial Anatomy of *Citipati osmolskae* (Theropoda, Oviraptorosauria), and a Reinterpretation of the Holotype of *Oviraptor philoceratops*

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ABSTRACT

We describe the skull of the holotype of *Citipati osmolskae*, one of the best preserved oviraptorid skulls known. The skull preserves stapes and epipterygoids, and the mandible preserves a slender coronoid bone, none of which has been reported before in oviraptorids. The braincase is similar to that of other basal coelurosaurs but possesses extensive recesses presumably occupied by pneumatic diverticulae; the circumnarial region is highly pneumatized, and a large recess continues posteriorly from the narial region to invade the frontals and parietals dorsal to the braincase. Circum-otic pneumatic recesses include two dorsal recesses above the otic recess, a posterior recess on the anterior surface of the paroccipital process, and extensive cavities in the basisphenoid beneath the braincase. The more dorsal of the two dorsal tympanic recesses is very deep, and CT scans suggest that it connected medially across the midline dorsal to the otic region and anteriorly with the frontoparietal space. The otic recess is unusually shallow. Comparison of the new skull with the poorly preserved skull of the holotype of *Oviraptor philoceratops* demonstrates that the braincase and palate of the latter are similar to those of other oviraptorids. Its rostrum and dentary are more elongate than in other oviraptorids, however, a more plesiomorphic condition suggesting it may be the most basal oviraptorid. A well-preserved skeleton previously referred to *O. philoceratops*, IGM 100/42, does not belong to this genus or species, and its narial region is very similar to that of *Citipati osmolskae*.

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INTRODUCTION

Among the many specimens collected by American Museum–Mongolian Academy of Sciences expeditions from the Late Cretaceous deposits of Ukhaa Tolgod, Mongolia, are two new species of oviraptorid theropods, *Citipati osmolskae* and *Khaan mckennai* Clark et al., 2001. *Citipati* is represented by an unusually complete and well-preserved skull, which has been CT scanned to expose the internal anatomy of the braincase. In addition to providing information on structures previously unknown in oviraptorids, this exquisite skull provides a basis for reinterpreting the poorly preserved holotypic skull of the first oviraptorid ever discovered, *Oviraptor philoceratops* (Osborn, 1924). This reinterpretation of *O. philoceratops* reveals several differences between it and other oviraptorids, suggesting that it may be the most primitive member of the group and contradicting the previous allocation of other specimens to this genus and species.

Oviraptorids were first discovered in 1923 at Bayn Dzak (''Flaming Cliffs''), Mongolia, during the American Museum's Central Asiatic expeditions (Andrews, 1932). *Oviraptor philoceratops* Osborn, 1924, was initially characterized as an egg eater, due to a misidentification of the eggs over which the holotypic skeleton was preserved. However, the recent discovery at Ukhaa Tolgod of an embryonic oviraptorid in an egg of the same type as beneath the holotypic skeleton corrected this error (Norell et al., 1994, 2001). The interpretation of *O. philoceratops* as an egg eater was engendered in part by its distinctive skull with a short, edentulous beak suggesting feeding habits unusual for a nonavian theropod. This bizarre cranial morphology has led authors to propose various dietary preferences (Barsbold, 1986; Smith, 1990, 1993). Until recently, oviraptorids were among the rarest of nonavian dinosaurs, but happily this is no longer true.

Since the discovery of *Oviraptor philoceratops* four additional genera and five species of oviraptorid have been described (Barsbold et al., 1990; Clark et al., 2001). All are from the Late Cretaceous of Mongolia, and the group is otherwise reported only from correlative deposits in northern China (Dong and Currie, 1996). Oviraptorid relatives, within the Oviraptorosauria, are known from the Early and Late Cretaceous of North America and the Late Cretaceous of Uzbekistan (Sues, 1997; Makovicky and Sues, 1998; Currie et al., 1993). Recent phylogenetic analyses (Sereno, 1999; Holtz, 2001; Norell et al., 2001) of *Caudipteryx* (Ji et al., 1998; Zhou et al., 2000) suggest that this animal is an oviraptorosaur or close relative of Oviraptorosauria. *Caudipteryx* is notable both for its early age and for the preservation of fully formed feathers across the body (Ji et al., 1998)

The Djadokhta Formation at Ukhaa Tolgod in south central Mongolia preserves one of the most abundant, diverse, and well-preserved theropod faunas yet discovered at any Mesozoic locality (Dashzeveg et al., 1995; Norell et al., 1996; Norell, 1997). Surprisingly, among the most common elements of this fauna are oviraptorids. Their remains include skeletons of adults, juveniles, and embryos, and among the adults are three specimens preserved on top of nests of oviraptorid eggs, indicating brooding behavior (Norell et al., 1995; Clark et al., 1999). As with other vertebrate remains from the Djadokhta Formation of Mongolia and China, many of the oviraptorid specimens comprise articulated skeletons, often complete or nearly complete.

METHODS

The holotype skull of *Citipati osmolskae*, IGM 100/978, was CT scanned at the University of Texas High Resolution X-Ray CT Facility in November 1997. The jaws, hyoid, and stapes had been separated from the cranium during initial mechanical preparation, and were not scanned. Interslice spacing was 0.5 mm, with a field of reconstruction of 200 mm and output levels adjusted to 239 grays. The scanning generated 181 original sagittal slices, which were later digitally resliced into 348 coronal and 271 horizontal slices using NIH Image software.

Contrast in the CT imagery between the very thin bones and matrix is weak. Nevertheless a number of sutures can be traced, and the geometries of the endocranial and

several presumably pneumatic cavities in the skull can be traced.

SYSTEMATIC PALEONTOLOGY

THEROPODA MARSH, 1884
COELUROSAURIA VON HUENE, 1914
OVIRAPTOROSAURIA BARSBOLD, 1976

COMPOSITION: The Oviraptorosauria as currently constituted includes three taxa: Caenagnathidae Sternberg, 1940, *Microvenator celer* Ostrom, 1970, and Oviraptoridae Barsbold, 1976 (see Sues, 1997, and Makovicky and Sues, 1998, for discussions of relationships among oviraptorosaurs).

GEOLOGIC DISTRIBUTION: The oldest oviraptorosaurian is *Microvenator celer*, from the Lower Cretaceous Cloverly Formation of Montana (Ostrom, 1970; Makovicky and Sues, 1998). Caenagnathidae are known from the Upper Cretaceous (Upper Turonian) lower part of the Bissetky Formation of Uzbekistan (Currie et al., 1993), the Upper Cretaceous (Campanian) Dinosaur Park Formation and Horseshoe Canyon Formation (Maastrichtian) of Alberta, Canada (Currie et al., 1993; Sues, 1997), and the Late Cretaceous (Maastrichtian correlative) Hell Creek Formation of South Dakota (Triebold et al., 2000). Oviraptoridae currently are known from reliably identified remains only from Late Cretaceous formations of Mongolia and China. Naish et al. (2001) described a possible oviraptorosaur cervical vertebra from the Early Cretaceous of the Isle of Wight; however, we find little evidence to refer this specimen to this group.

Oviraptoridae Barsbold, 1976

TYPE TAXON: *Oviraptor* Osborn, 1924.

COMPOSITION: Oviraptoridae currently includes six genera: *Oviraptor* Osborn, 1924, *Ingenia* Barsbold, 1981, *Conchoraptor* Barsbold, 1986, *Nomingia* Barsbold et al., 2000, *Citipati* Clark et al., 2001, and *Khaan* Clark et al., 2001.

GEOLOGIC DISTRIBUTION: Oviraptorids are known from the Djadokhta, Barun Goyot, and Nemegt formations of Mongolia and China (Barsbold et al., 1990). The Nemegt Formation overlies the Barun Goyot Formation in some areas, but superpositional relations between the Barun Goyot and Dja-

dokhta formations are not known. The vertebrate fauna of the Barun Goyot Formation was considered to indicate a younger age than the Djadokhta Formation (see Jerzykiewicz and Russell, 1991, for a review), but subsequent discoveries have increased the number of taxa shared between the two formations (Dashzeveg et al., 1995; Gao and Norell, 2000). The ages of these three formations are poorly constrained, but the vertebrate faunas suggest that they are within an interval equivalent to the Campanian to Maastrichtian marine stages (Lillegraven and McKenna, 1986; Averianov, 1997; Jerzykiewicz, 2000).

Citipati osmolskae Clark et al., 2001

HOLOTYPE: IGM 100/978, a nearly complete skeleton.

TYPE LOCALITY: Djadokhta Formation at Ankylosaur Flats, Ukhaa Tolgod, Gurvan Tes Somon, Omnogov Aimak, Mongolia. Precise coordinates will be made available to qualified researchers on request.

REFERRED SPECIMENS: IGM 100/979, a partial skeleton overlying a nest, from Ankylosaur Flats, Ukhaa Tolgod; IGM 100/971, an embryonic skeleton within an egg.

DIAGNOSIS: Oviraptorid differing from *Conchoraptor* in having a taller and more highly pneumatized nasal, from *Ingenia* in that metacarpal I is not extremely broad, from *Oviraptor philoceratops* in having a shorter skull and mandible, from *O. mongoliensis* in lacking a convex crest on the frontals and parietals, and from *Khaan mckennai* in the features listed below. Differs from all other oviraptorids where known in the anterodorsally sloping occiput and quadrate, the parietal being much longer along the midline than the frontal and reaching nearly to the level of the anterior end of the orbit, the ascending process of the jugal being perpendicular to the horizontal ramus (rather than extending posterodorsally), the narial opening being more nearly circular and the ascending process of the premaxilla being vertical rather than sloping posterodorsally, and the cervical vertebrae being elongate (approximately twice as long as they are wide).

REMARKS: This specimen was identified preliminarily as *O. philoceratops* (e.g., Web-

ster, 1996), but comparison with the holotype of the latter revealed several significant differences (see below). A postcranial skeleton that is preserved on top of a nest, IGM 100/ 979, is referred to the new species and was described by Clark et al. (1999). IGM 100/ 979 is referred to *C. osmolskae*, pending preparation of the postcranial skeleton of the holotype, primarily on the basis of its large size and its differences from the skeleton of *Khaan mckennai*. An embryonic skeleton referred to this species was given a preliminary description by Norell et al. (1994) and a more detailed description by Norell et al. (2001). This specimen is referred to *Citipati* on the basis of its premaxilla, which is nearly vertical rather than sloping posteriorly as in *Khaan*. An oviraptorid collected from the Djadokhta Formation at Dzamin Khong, IGM 100/42, was previously identified as *O. philoceratops* (Barsbold, 1981; Barsbold et al., 1990, fig. 10.1A and B), but it is more similar to *Citipati* in the shape of its premaxilla and circumnarial region and differs from *O. philoceratops* in the length of the maxilla and dentary (see below). It may represent a second species of *Citipati*.

DESCRIPTION: The skull of the holotype (figs. 1–10) is complete, including both stapes and the paired elements of the hyoid apparatus. In lateral view (fig. 2), the skull is almost rectangular, with a vertical premaxilla anteriorly. The right and left premaxillae are fused and edentulous. Ventrally (fig. 3), the premaxilla expands transversely to form a curved, U-shaped triturating surface in ventral view that supports a series of parallel ridges and troughs. The oral margin of the premaxilla forms a sharp edge that bears a series of large bony denticles, five on each side. Posterior to these, the palatal surface of the premaxilla supports a pair of robust, longitudinal, parasagittal ridges that extend posteriorly along either side of the midline to the posterior edge of the palate. The palatal surface broadens toward the back of the mouth, where it bears two additional ridges that lie lateral and parallel to the first pair.

The large, elliptical nares are bordered ventrally, anteriorly, and anterodorsally by the premaxilla and posteriorly and posterodorsally by the nasal. Owing to profound foreshortening of the face, the naris lies al-most entirely dorsal to the antorbital fossa, its rear margin lying nearly as far back as the posterior edge of the antorbital fenestra. The posteriorly fused nasals form a complex array of pockets along the posterodorsal edge of the narial opening. The pockets lie dorsal to a horizontal roof to the nares, and another, narrower horizontal roof overlies these pockets anterodorsally. A broad elliptical opening in the horizontal narial roof communicates between the nares and the dorsal nasal pockets. Dorsal to the naris the nasal forms a vertical lamina, and a lip along its dorsal edge was presumably for the attachment of circumnarial soft tissues.

The large premaxilla forms much of the anterodorsal margin of the antorbital fossa. A fossa on the lateral surface of the ascending ramus anterior to the naris (fig. 4) is similar to an accessory opening of IGM 100/42 described by Barsbold et al. (1990). Posterior to the naris, the premaxilla extends dorsal to the maxilla to meet the nasal, separating the maxilla from the narial opening. The antorbital fossa is triangular with a vertical posterior edge and horizontal ventral edge. The tall, oval antorbital fenestra is separated from the large, triangular accessory antorbital fenestra by an hourglass-shaped, inset interfenestral bar formed by the maxilla. Dorsal to the accessory fenestra are several smaller fenestrae near the dorsal margin of the fossa. The anteroventral margin of the fossa is composed of the maxilla, and a small splint of maxilla extends posterodorsally above the anterior edge of the fossa. Posteriorly, ventral to the antorbital fenestra, the fossa is bordered by the slender anterior process of the jugal.

The lacrimal is transversely broad and forms a concave, posteriorly facing surface along the anterior edge of the orbit. It is perforated by a large lacrimal foramen. The lacrimal canal passed through this foramen, traversing a laterally open trough above the internal antorbital fenestra (Witmer, 1997) before penetrating the side of the face to enter the nasopharyngeal cavity just behind the posterodorsal extremity of the naris. The anterior part of the lacrimal dorsal to the antorbital fossa houses a broad pneumatic pocket opening anteriorly, within which lies several recessed pneumatic pockets.

Fig. 1. The holotype skull and mandible of *Citipati osmolskae* (IGM 100/978) in right lateral view before final preparation. The mandible, scleral ossicles, and hyoid elements were later separated from the skull. Abbreviations in appendix 1.

There is no evidence of a prefrontal. The paired frontals contact the nasals in a simple suture (fig. 5). The joint between the frontals is short but highly complex. Posteriorly, the fused parietals divide the frontals for over one-half of their length. The frontal participates in the supratemporal fenestra, but it lacks the mandibular adductor fossa that deeply excavates the dorsal surface of the frontal in many other nonavian theropods. Laterally, it is overlapped by an anteromedial process of the postorbital. The frontals contact one another along the midline to form the dorsal surface of the anterior end of the braincase. The ventral surface of the frontal forming the dorsal edge of the orbit houses several small pockets that may have been pneumatic.

The orbit is bounded ventrally by the jugal and posteriorly by the postorbital, which meets the ascending process of the jugal to form a postorbital bar. The infratemporal fe-
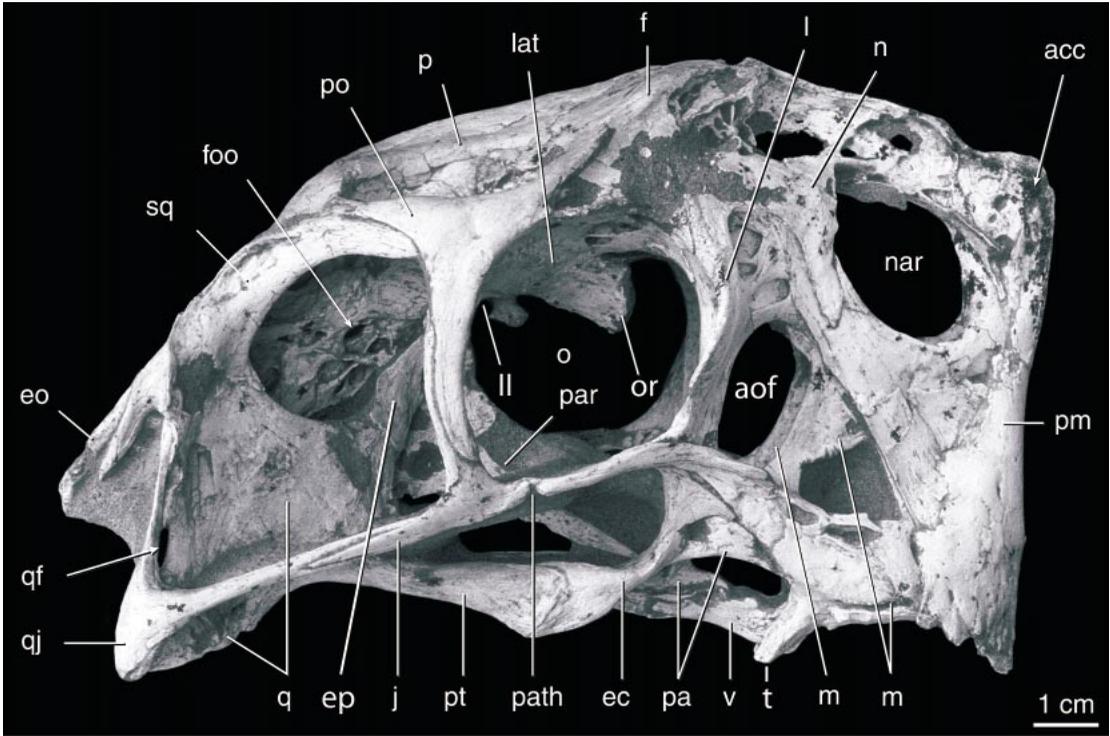
Fig. 2.   Right lateral view of the holotype cranium of *Citipati osmolskae* IGM 100/978. Abbreviations in appendix 1.

nestra is subrectangular, with straight anterior and ventral margins and rounded dorsal and posterior margins. The anterior process of the quadratojugal forms most of the ventral border, and the ascending process forms most of the posterior border of the fenestra. The anterior process is longer than the ascending process. In addition, the quadratojugal possesses a distinct posterior process, as in dromaeosaurids. A large quadrate foramen lies between the quadrate and quadratojugal just dorsal to the posterior angle of the infratemporal fenestra (fig. 6). The quadrate is massive and tightly sutured to the squamosal, quadratojugal, pterygoid, and braincase. The distal articular surface forms two condyles of approximately equal surface and curvature that are separated by a longitudinal groove. The pterygoid flange of the quadrate is tall and extends posterodorsally to meet the short descending process of the squamosal.

The squamosal is a complex bone that forms the entire dorsal margin of the infratemporal fenestra. Medially, it underlies the parietal, extending nearly to the medial edge of the supratemporal fossa. Anteriorly, it lies medial to the postorbital and ventral to its posterior process. The squamosal curves posterolaterally, and its distal end is forked around the external auditory meatus and downturned. A small post-temporal fenestra may be present on the occipital surface between the squamosal and the paroccipital process as seen on the right side, although this may be an artifact. The articulation between the squamosal and the quadrate and quadratojugal is poorly exposed.

The postorbital is a triradiate bone forming most of the postorbital bar. It overlies the frontal anteriorly and the squamosal posteriorly, and it extends lateral to the jugal on the postorbital bar. The laterosphenoid has a short contact with the postorbital at the anterior end of the supratemporal fenestra. The postorbital forms the posterior border of a fossa dorsal to the orbit extending into the pneumatic recesses of the narial region.

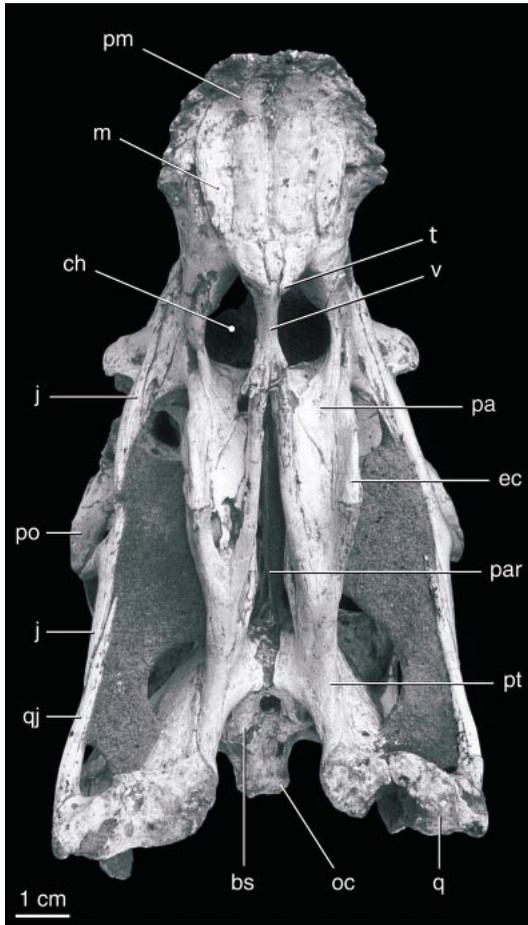The parietals are fused and form the dorsal

Fig. 3.   Palatal view of the holotype cranium of *Citipati osmolskae* IGM 100/978. Abbreviations in appendix 1.

Fig. 4.   Anterior view of the holotype cranium of *Citipati osmolskae* IGM 100/978. Abbreviations in appendix 1.

surface of nearly half of the skull along the midline (fig. 5). The fused parietals narrow anteriorly except where they expand slightly at their anterior end. The occipital portion of the parietal is very broad and is oriented obliquely at an angle of nearly 45° to face posterodorsally. The parietal forms little of the supratemporal fossa except posteriorly, where a descending flange borders the opening of a dorsal extension of the dorsal tympanic recess. This recess extends anteromedially parallel to the occipital margin immediately posterior to it, and lies almost entirely within the parietal. The CT scans of the skull suggest that the recess connects with a large space within the parietal and frontal dorsal to the brain cavity (figs. 7, 8).
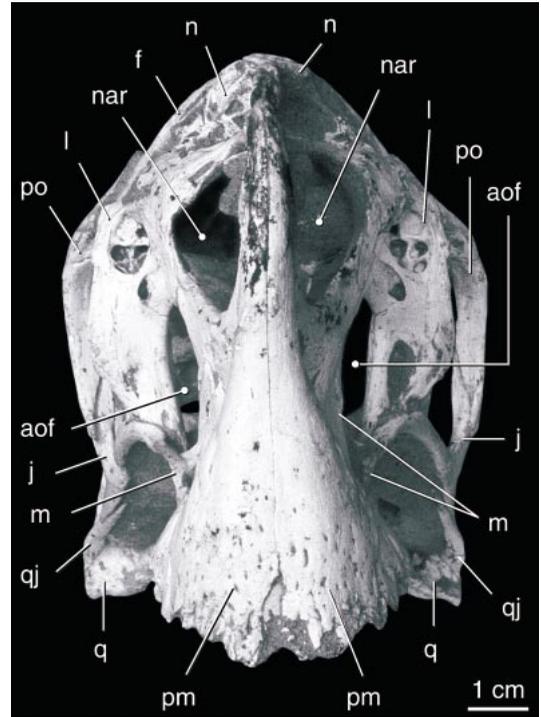
The supraoccipital is poorly preserved, but has a low vertical midline crest and may have been separated from the foramen magnum by the exoccipitals.

Within the parietal and frontals lies an extensive space dorsal to the endocranial cavity, as revealed by CT scans (figs. 7, 8). Indeed, this space is larger in volume than the endocranial cavity itself. It is continuous anteriorly with the circumnarial pneumatic cavities and is largest anteriorly, dorsal to the anterior part of the orbit. There is no apparent partitioning of the space, but in the anterior part of the space radio-opaque areas laterally indicate what may be internal struts. The space attenuates posteriorly and extends nearly to the occiput (fig. 8), and it appears to connect with the dorsal tympanic recess above the otic regions of both sides.

The jugal is extremely slender. Posteriorly, it terminates about halfway along the infratemporal fenestra, where it lies lateral to the more robust quadratojugal. It bends anteroventrally anterior to the orbit and extends
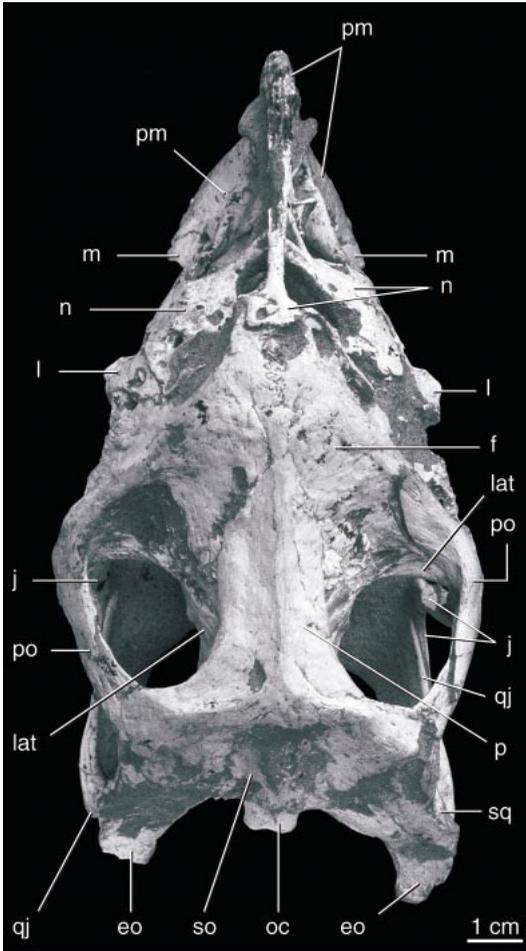
Fig. 5. Dorsal view of the holotype cranium of *Citipati osmolskae* IGM 100/978. Abbreviations in appendix 1.

Fig. 6. Occipital view of the holotype cranium of *Citipati osmolskae* IGM 100/978. Abbreviations in appendix 1.

anteriorly beneath the anterior end of the antorbital fenestra. The right element was damaged beneath the orbit during the life of the animal. The postorbital process of the jugal is robust and forms a broad posterior surface of the orbit. The quadratojugal forms much of the bar beneath the infratemporal fenestra, where it is nearly circular in cross section, and extends anteriorly to beneath the postorbital bar. Dorsally, the quadratojugal extends to meet the squamosal, and it borders the quadrate foramen laterally.

The facial portion of the maxilla is very small and edentulous but includes a single osseous denticle in line with the premaxillary denticl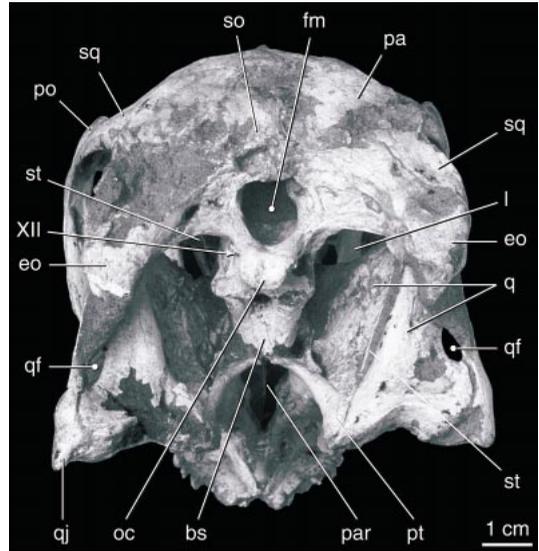es. Posterior to the facial portion, the maxilla forms a narrow shelf ventral to the antorbital fossa. Below this shelf are a variable number of large, anteroposteriorly elongate openings in the ventrolateral surface of the maxilla, two on the right side and one on the left. Posteriorly, the maxilla contacts first the palatine and then the ectopterygoid along its ventral edge. Posterolaterally, the maxilla is overlain by the jugal.

Within the antorbital fossa, the maxilla forms the medial wall. A slender posterodorsal process underlies the premaxilla and forms the dorsal edge of the accessory antorbital fenestra. The nasal overlies the posterodorsal part of the maxilla laterally, and the premaxilla in turn overlies the lacrimal laterally. The interfenestral bar was described above.

The palate (fig. 3) is generally similar to that of an oviraptorid described by Elzanowski (1999). The lateral portion of the palate is oriented ventrolaterally, and medially the palatal portion forms a distinct posteroventrally directed midline process that surrounds the anterior end of the vomer. The maxilla forms most of the palate anterior to this, which bears four stout longitudinal ridges. A deep groove borders the lateral edge of the lateral ridge. The large choanae lie almost
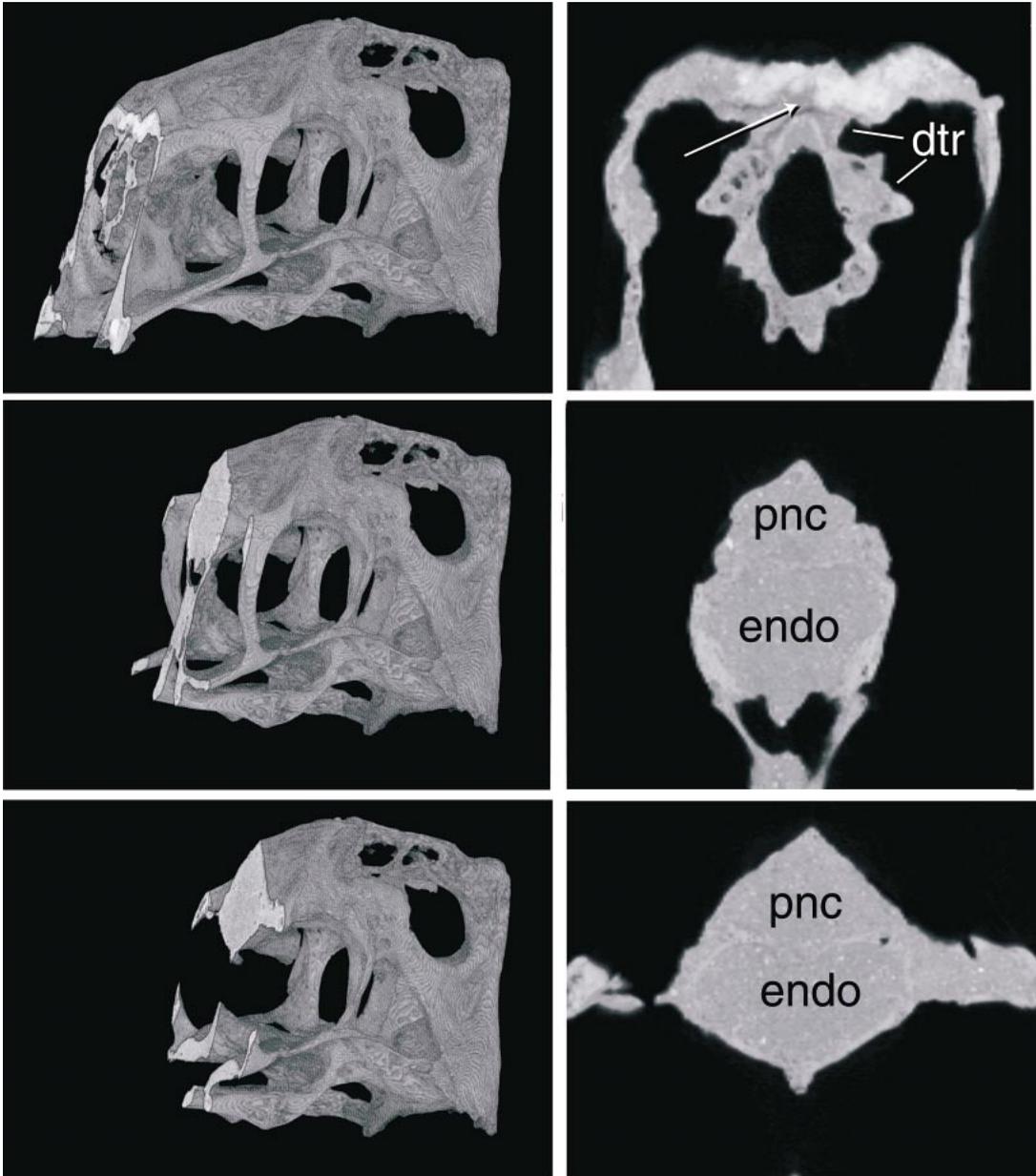
Fig. 7. CT scan transverse sections through the holotype skull of *Citipati osmolskae* IGM 100/978 at three levels showing a large, presumably pneumatized space dorsal to the endocranial cavity and its connection to the dorsal tympanic recess. Arrow indicates apparent connection medially from dorsal tympanic recess to dorsal space. Abbreviations in appendix 1.

directly beneath the naris and antorbital fossa, such that the nasopharyngeal passageway was oriented almost vertically. The choanae are divided by the vomer posterior to the maxillae.

The palatines are anteroposteriorly short and highly modified. They meet on the midline along the posterior edge of the choanae, where their anterior edge curves dorsally to become vertical and transversely oriented.
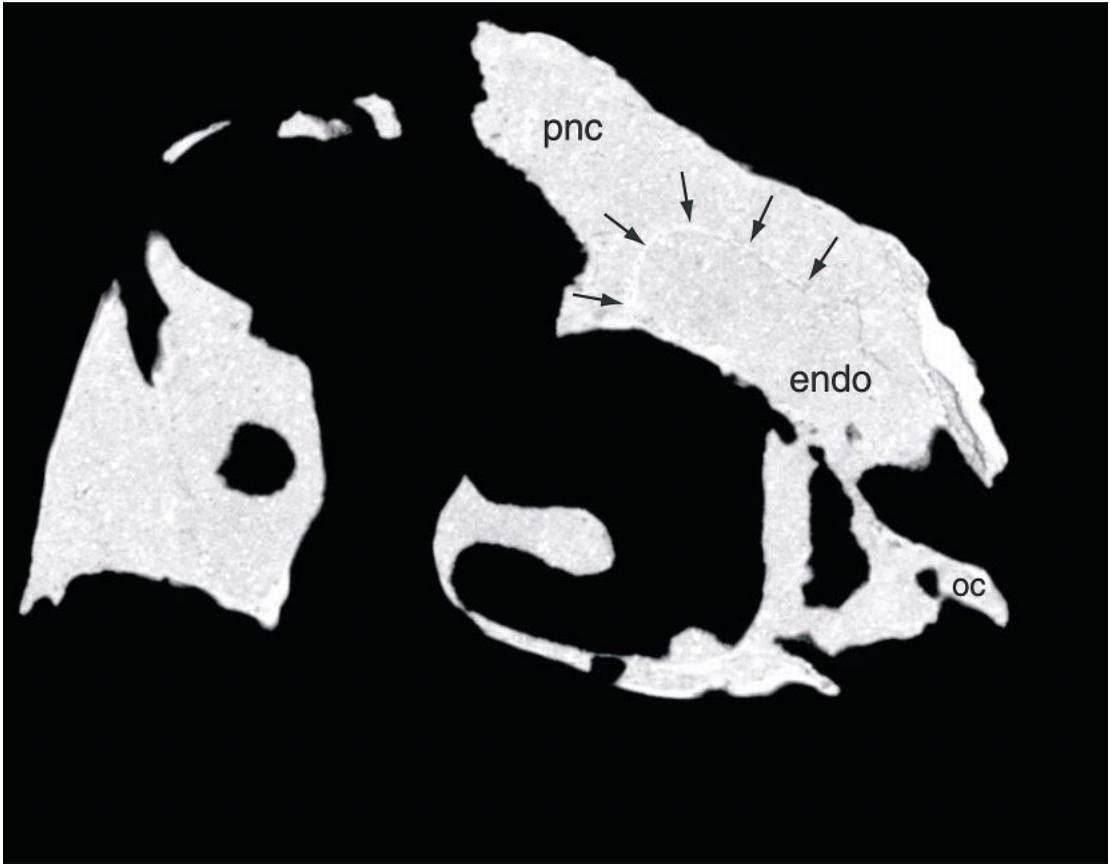
Fig. 8. CT scan parasagittal section through the right side of the holotype cranium of *Citipati osmolskae* IGM 100/978, showing the boundaries of the endocranial cavity and the large, presumably pneumatized space dorsal to it. Abbreviations in appendix 1.

Laterally, the palatine curves dorsally to meet the maxilla and is separated from the anterior margin of the ectopterygoid by a small, circular, nearly laterally facing suborbital fenestra (the "postpalatine fenestra" of Elzanowski, 1999). The ectopterygoid is vertical, meeting the maxilla laterally and the pterygoid medially and abutting the palatine throughout most of its length. The vomers are fused into a single short, solid bone that does not extend posterior beyond its contact with the pterygoid and palatine at the posterior edge of the choana.

The pterygoids have elongate palatal processes that do not appear to meet along the midline until they contact the vomers. The palatal surface of each element has a longitudinal concavity, confluent anteriorly with the choana. The pterygoid flange is greatly reduced compared to theropods with teeth. It is anteroposteriorly elongate, and, in lateral view, it has a linear dorsal edge and a ventrally convex, crescentic ventral edge, the ectopterygoid forming the anterior half. The flange does not extend laterally beyond the body of the pterygoid, indicating that the *M. pterygoideus* was relatively small. There is no evidence for a subsidiary palatal fenestra between the pterygoid and palatine. Posteriorly, the pterygoids converge towards the midline at the basipterygoid joint, but they do not come into contact, suggesting that if a contact was present it was formed by soft tissue. The posteromedial edge of the pterygoid is expanded near the midline, as described by Elzanowski (1999). The quadrate ramus of the pterygoid is anteroposteriorly short but very tall, and with the quadrate

forms the lateral surface of a deep pocket lateral to the braincase that narrows anteriorly. The pterygoid extends posteriorly to end medial to the mandibular articulating surface of the quadrate. A small, dorsomedially opening pocket is formed dorsal to the posterior end at the level of the quadrate foramen. Another pocket on the dorsal surface of the pterygoid lateral to the basipterygoid joint extends anteriorly into the body of the pterygoid.

An isolated oviraptorid quadrate was described by Maryanska and Osmólska (1997), and the quadrate of *Citipati* is generally similar. It is oriented obliquely in lateral view, extending posteroventrally from the squamosal. The quadrate has a mediolaterally biconvex mandibular trochlea. The vertical body of the quadrate narrows dorsally, but its dorsal articulation with the squamosal and, apparently, the paroccipital process is not exposed. The pterygoid ramus of the quadrate is very tall, equal in height to about half that of the occipital region.

An epipterygoid is present on both sides of the skull. It is much broader anteroposteriorly than it is thick. It has a broad articulation ventrally with the pterygoid, where it faces anteromedially, and it twists laterally as it narrows dorsally. Dorsally, it contacts the ventrolateral surface of the co-ossified braincase where a vertical ridge on the laterosphenoid converges with a ridge along the capitate process. On the left side it appears to be fused to the braincase, but not on the right. The dorsal tip twists dorsolaterally and is expanded in the transverse plane, aligned with the vertical ridge on the laterosphenoid above it.

The elements comprising the braincase are co-ossified, although some areas of contact between bones are apparent. The basioccipital is notable for the posterior extension of the occipital condyle well beyond the posterior end of the foramen magnum (fig. 5). Indeed, with the floor of the braincase horizontal most if not all of the basioccipital lies posterior to the dorsal edge of the foramen magnum due to the anterodorsal slope of the occiput. The condyle has a nearly flat posterior surface with a central depression. The basioccipital has a midline depression on its ventral surface. The foramen magnum is

nearly circular except for a ventral midline depression (fig. 6). The lateral surface of the basioccipital is concave, and at least three small openings within the concavity presumably enter a pneumatic recess in the body of the bone. A large opening in this region on the right side is presumably due to the breakage of thin-walled bone covering a cavity.

A large vacuity is present on the ventral midline between the basioccipital and basisphenoid. The foramen lies mainly within the basisphenoid, dividing it in two posteriorly. The basisphenoid and basioccipital expand at their contact, and on the right side they appear to be fused. The ventral surface of the basisphenoid descends anteroventrally from this contact. Basipterygoid processes are absent, although a matrix-filled area between the basisphenoid and pterygoids suggests that poorly ossified processes may have been present. The basisphenoid has several pneumatic openings and cavities on the lateral surface of the braincase ventral to the trigeminal foramen. These are poorly exposed, covered laterally by the epipterygoid and beneath matrix ventrally. Several delicate struts span these openings.

A delicate, tall parasphenoid process extends above the length of the interpterygoid vacuity, terminating slightly posterior to the level of the vomer. It descends and tapers anteroventrally from its tall posterior base. The lateral surface of the base has a shallow depression dorsally that opens anterodorsally, presumably the site of origin of an ocular muscle, perhaps the *M. rectus oculi ventralis*.

The laterosphenoid portion of the braincase forms a ventral floor anteriorly, and a discrete orbitosphenoid ossification is present anterior to it. The large, horizontal orbitosphenoids encircle the anterior part of the endocranial cavity, meeting on the midline dorsally and ventrally. Posterior to the orbitosphenoid the laterosphenoid sends a short, ventrally expanding process ventrally along the midline. This process forms the anterior edge of a large foramen, presumably for cranial nerve (CN) II, that is open ventrally. A posterior descending process forms the posterior edge of this foramen and nearly contacts the top of the parasphenoid rostrum. The capitate process of the laterosphenoid is long and slender and extends laterally along

the ventral surface of the frontal and contacts the postorbital. A small slit separates the process from the frontal anteriorly. A sharp ridge descends posteromedially from the capitate process to the epipterygoid contact. A vertical ridge within the supratemporal fossa presumably separated portions of the *M. adductor mandibulae*. The dorsal contact with the frontal and parietal is apparent but posteriorly the laterosphenoid is fused to the prootic. The posterodorsal contact with the parietal slopes anterodorsally parallel to the occiput. The trigeminal opening (CN V) is relatively small compared with dromaeosaurids (e.g., *Velociraptor*, IGM 100/976) and is smaller than CN II of this specimen. It is slightly longer than tall and exits ventrolaterally from the braincase. The lateral surface of the laterosphenoid is rugose, presumably indicating an origin of adductor muscles.

The prootic has a well-developed fossa dorsally, homologous to the dorsal tympanic recess described in dromaeosaurids (Norell and Makovicky, 1997, 1999). A horizontal swelling forms the ventrolateral border of the fossa. Dorsal to this fossa lies a large pneumatic opening extending medially into the braincase, as described above. The prootic apparently surrounds this opening dorsally, separating it from the parietal.

The opening in the prootic for CN VII is well preserved on the right side, but on the left it is apparently within a crushed area just ventral to the horizontal swelling. On the right side a depression with at least two, presumably pneumatic, openings lies dorsal to the foramen for CN VII, but this depression is absent on the left side. The otic recess is poorly preserved on both sides, and the fenestrae ovale and rotundum cannot be identified within it. The recess is larger on the right side than the left, and both are small compared with other coelurosaurs.

The contacts between the opisthotic and the prootic and basioccipital appear to be fused. A posterior tympanic recess is present within the anterior surface of the paroccipital process on the right side, but this region is broken on the left. The recess continues medially into the braincase from within a shallow fossa. The fossa penetrates the posterior surface of the paroccipital process via a narrow, mediolaterally elongate opening. In medial view, the jugular foramen and the exits of two hypoglossal foramina are visible within the braincase. The hypoglossal foramina have a short, simple course ventrolaterally from the foramen magnum, opening into a shallow depression. Two ventrolaterally opening foramina on the ventral edge of the paroccipital process presumably originate within the metotic foramen, and likely conveyed CN IX and X and the associated vasculature. The more ventromedial of the two is larger and may be the foramen vagi. The more lateral foramen is small, similar in size to the hypoglossal foramina, and possibly for CN IX. The paroccipital processes are pendant and curve medioventrally, attenuating distally.

Both stapes are preserved, the left element incompletely and the right disarticulated from the skull. The stapes is elongate, straight, and slender, with a footplate that is approximately three times the diameter of the shaft. As implied by the position of the otic notch in the squamosal, the stapes would have projected posterolaterally from the fenestra ovalis at an angle of about 45° and slightly ventrally.

Five scleral ossicles, from a partial scleral ring, preserved in the right orbit and below it were removed during preparation (fig. 1). They are roughly square in shape with irregular margins and a gently concave medial surface. They are similar to those of other basal coelurosaurs such as troodontids and dromaeosaurids.

The edentulous mandible (fig. 9) is dominated by a high, arching coronoid eminence. The symphysis is short and broad, with a transversely oriented, upturned anterior edge. It is slightly below the level of the mandibular articulation. The dorsal surface of the symphysis is concave dorsally behind the anterior edge, and the posterior edge of the symphysis descends posteroventrally. The coronoid eminence rises abruptly from the posterior part of the symphysis and flattens dorsally. The surangular descends gradually from the eminence and extends posteriorly to the end of the mandible, completely covering the lateral surface of the articular. The large mandibular fenestra is divided by an anterior process of the surangular that reaches approximately three-quarters of the distance
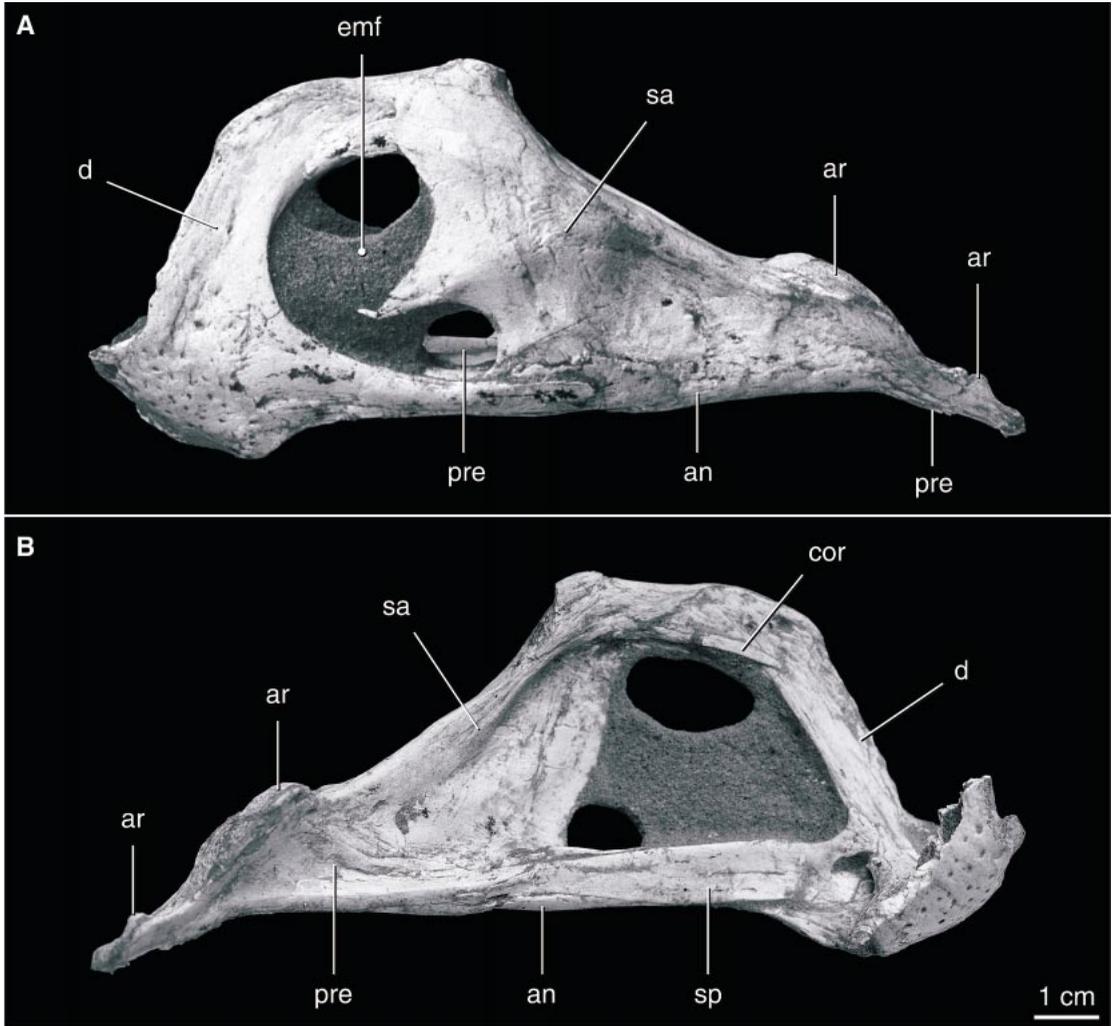
Fig. 9. **(A)** Lateral and **(B)** medial views of the left hemimandible of the holotype of *Citipati osmolskae* IGM 100/978. Abbreviations in appendix 1.

across the fenestra. The lateral surface of the surangular is gently depressed anterior to the mandibular articulation. The adductor fossa on the medial surface of the mandibular ramus is extremely large and bordered ventrally by a slender splenial. The anterior end of the splenial is divided into dorsal and ventral rami in the symphysis. It overlaps the prearticular in the middle of the mandibular ramus, and the prearticular extends posteriorly to the end of the mandible, covering most of the medial surface of the articular.

The mandibular articulation surface is anteroposteriorly elongate and unbounded an-

teriorly or posteriorly, suggesting that the mandible was capable of anteroposterior movement (cf. Osmólska, 1976). The surface bears a longitudinal midline ridge and faces posterodorsally. The retroarticular process descends posteroventrally from the articular surface, with which it is coplanar, and its ventral edge descends slightly below the level of the remainder of the mandible. The mandibular articulation is much wider than the remainder of the mandibular ramus, and it is bordered ventrally by the prearticular medially and the surangular laterally.

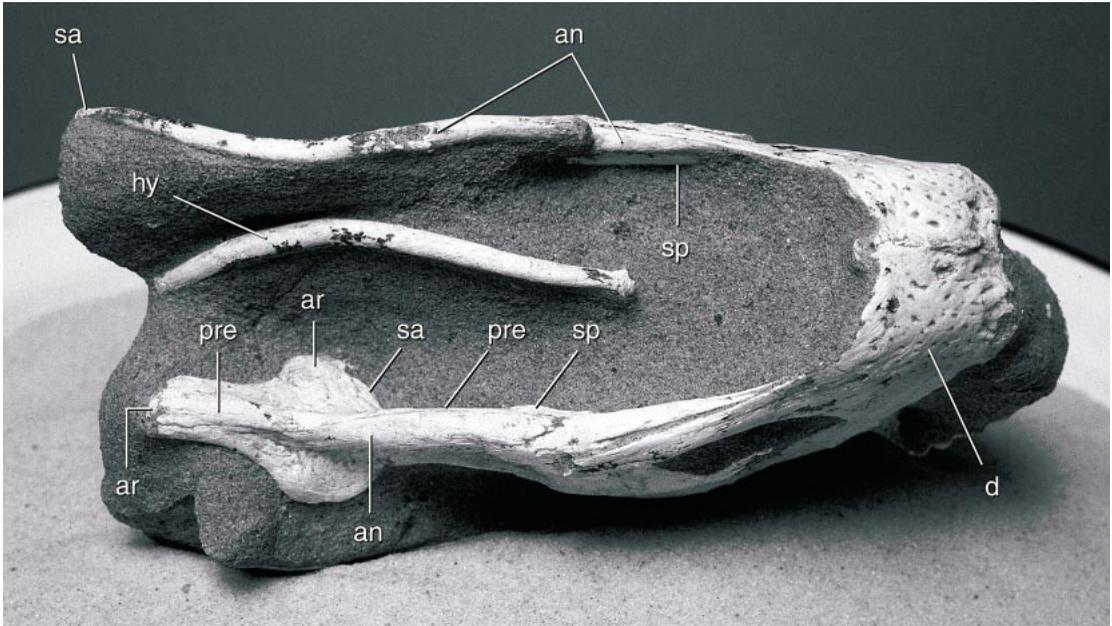A very small coronoid element appears to

Fig. 10.   Ventral view of the holotype cranium of *Citipati osmolskae* IGM 100/978 showing a left hyoid element in natural articulation. Abbreviations in appendix 1.

be present. A splint of bone on the medial surface of the posterodorsal ramus of the dentary on both sides is in the position of a coronoid bone, although this bone is reported as absent in other oviraptorids (Barsbold et al., 1990). A bone as small as this could be easily lost or overlooked in poorly preserved specimens, suggesting that it may also be present in other oviraptorids.

A pair of elements of the hyoid apparatus were preserved beneath the mandible (fig. 10), presumably the ceratohyals (cornua branchiala I). They are simple structures, essentially elongate rods that curve dorsally posteriorly. The anterior and posterior ends are expanded and slightly compressed mediolaterally. They were preserved paralleling the ventral edge of the mandible, possibly their natural position.

Most elements of the postcranial skeleton of *C. osmolskae* were described by Clark et al. (1999) for the referred specimen IGM 100/979. This specimen preserves only a single vertebra, however, and lacks the ilia and most of the scapulae, pubes, and ischia. It differs from *Khaan* in that the first metacarpal of the latter is reduced proximally and

the bone does not expand, whereas that of *Citipati* is unreduced and expanded.

The postcranial skeleton of the holotype of *C. osmolskae* is very well preserved and includes representatives of nearly every element, but it has not yet been fully prepared. The cervical vertebrae are distinctly more elongate than those of *Khaan* and other oviraptorids where known. The cervical ribs are also more elongate, longer than the corresponding centrum in *Citipati* but shorter than in *Khaan*.

A REINTERPRETATION OF THE SKULL OF THE HOLOTYPE OF *OVIRAPTOR PHILOCERATOPS*

Beginning with its brief description by Osborn (1924), the morphology of the holotype of *Oviraptor philoceratops*, AMNH 6517, has been poorly understood. The skull (fig. 11) is crushed and abraded, and initially was incompletely prepared, lying on the original slab adjacent to the skeleton. It was given its most detailed description by Smith (1993), who attempted a reconstruction of the skull and interpreted its functional morphology. Comparison between the new oviraptorid
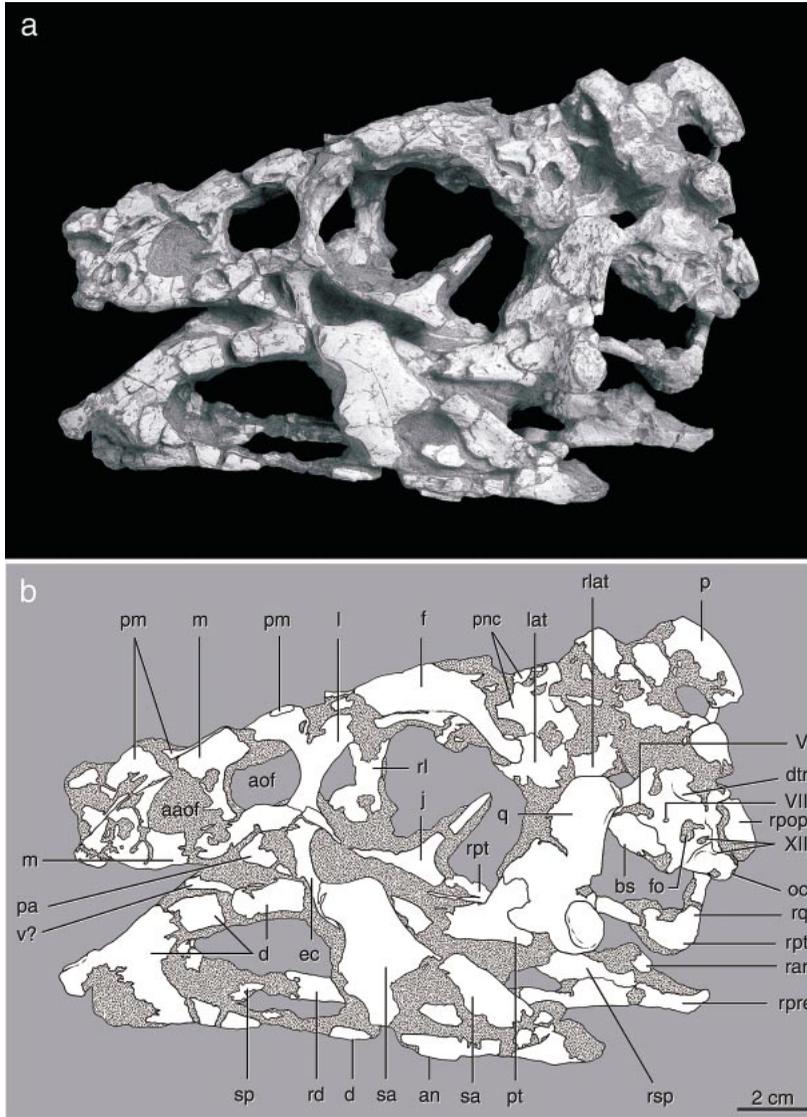
Fig. 11. Left lateral view of the holotype skull of *Oviraptor philoceratops* AMNH 6517. Abbreviations in appendix 1.

material described above and the holotype of *O. philoceratops* elucidates several features that previously were enigmatic.

The skull of AMNH 6517 has been crushed mediolaterally, compressing the temporal region. Thus, its breadth across the occiput is only about half that of the skull of the holotype of *Citipati osmolskae*, which is similar in length. The braincase and right temporal regions have been dislocated as a unit posteriorly. The broken pieces of the individual bones have been separated from one another to varying degrees along a longitudinal axis, to a greater degree on the right side than on the left. This is most evident in the mandible, especially a large gap within the dentary on the right side. The frontals are incomplete dorsally, exposing the roof of the braincase and the interorbital space. The right jugal is missing except for its postor-

bital process and its anterior tip, and the left jugal is missing posterior to the postorbital bar, as is the left quadratojugal.

Smith (1993) did not have the benefit of well-preserved material for comparison, and the Ukhaa Tolgod material suggests that several identifications and interpretations of the distortion of the skull in that paper require modification. The dorsal side of the palatal complex is not "rotated as a unit and exposed on the left side of the skull" (Smith, 1993: 367). Instead, the ectopterygoid and the anterior end of the palatine are in the typical position of oviraptorids in facing laterally rather than ventrally (Osmólska, 1976; Elzanowski, 1999). Thus the dorsal edge of these bones as preserved is comparable to the lateral edge in other theropods, not the medial edge as Smith's interpretation would suggest. Furthermore, a bone identified as the ectopterygoid is actually the quadrate (see below). The occiput has not been "rotated . . . so that the dorsal side faces the left side of the skull" (Smith, 1993: 368). The occiput faces posteriorly in line with the remainder of the skull and is not rotated, although it is slightly compressed mediolaterally.

Smith described the skull as amphikinetic, but it is unclear whether the joints he identified were capable of movement. The "mesokinetic hinge between the frontal and parietal bones" (Smith, 1993: 369) is not apparent, as the contact between frontal and parietal is not preserved and the edges of these two bones are broken. By comparison, this contact on the skull of *Citipati* is oblique on each side, with the parietal extending far forward along the midline, rather than transverse as in taxa with a hinge joint, such as most squamates. Whether or not movement was possible at the jugal-lacrimal or quadrate-squamosal contacts is not readily apparent from the holotype of *O. philoceratops*, because the latter contact (preserved only on the right side) is concealed in matrix and the exoccipital contribution to the joint is not preserved. Furthermore, the force vectors reconstructed for the mandibular adductor muscles do not take into account the posterior displacement of the parietal, and thus should be more vertically oriented.

The left quadrate was identified as the ectopterygoid by Smith, from which he deduced a significant amount of distortion to the palate. (This bone is labeled "ec" in Smith's [1993] figures 2 and 4, but this label is defined as the ectopterygoid in figure 2 and the exoccipital in figure 4 of that paper; in the text [Smith, 1993: 374] it is described as the ectopterygoid of the right side.) The unusually round shape of the skull in occipital view proposed by Smith (1993: fig. 3B), with a ventrolaterally directed quadrate, is apparently due to this misidentification. However, the intact left quadrate is oriented vertically with a broad dorsal ramus, as in other oviraptorids. Furthermore, most of the ventral portions of what is figured as the right squamosal (Smith, 1993: fig. 4H) are instead parts of the quadrate. On the right side, the lateral surface of what was identified as the right quadrate is the quadratojugal.

The mandibular condyles of the quadrate on the left side are well preserved. The quadrate is similar to that of IGM 100/978 in having a well-developed lateral condyle and a smaller medial condyle. The surface generally is oriented transversely and convex ventrally, but the condyles are separated by a groove running slightly posterolaterally. A small process extends laterally from the lateral condyle, on which the quadratojugal would have articulated. Medially, the posterior end of the pterygoid is preserved slightly separated from the medial edge of the quadrate condyle.

The body of the pterygoid is longitudinally oriented and convex dorsally. The two bones diverge gradually posteriorly, although the interpterygoid vacuity is not exposed. There is no evidence for an epipterygoid, as in *Citipati*, although this region has not been fully prepared. The ventral part of the basisphenoid is not preserved, including the region of the basipterygoid joint.

The suborbital process of the jugal is incomplete on both sides, and its contact with the quadratojugal is not preserved, so the length of both these bones is indeterminate. The anterior end of the jugal is apparent on both sides, and does not extend anteriorly beneath the antorbital fenestra as it does in *Citipati*, and is thus similar to *Khaan*. An intact quadrate foramen is preserved on the right side. It lies mainly in the quadrate, and the

quadratojugal is a simple, vertical strap of bone. The foramen is moderately large and about twice as tall as it is wide, similar in size to that of IGM 100/978.

The postorbital is well preserved and similar to that of other oviraptorids. Anterodorsally, it curves medially around the anterior edge of the supratemporal fenestra. A portion of the right frontal adheres to the right postorbital, leading Smith (1993) to mistakenly suggest that the postorbital extended anteriorly over the orbit.

Most of the basioccipital is preserved in natural position, and the foramen magnum is intact dorsal to it. The foramen is narrower than in other oviraptorids, probably due to mediolateral compression postmortem. The bones figured and described by Smith (1993) as the exoccipital and supraoccipital correspond to this region of the skull if they are rotated 90° out of position. Thus, one of the "knob-like paroccipital processes" (Smith, 1993: 374) corresponds to the occipital condyle. Most of the occiput dorsal to the foramen magnum is missing, but the position of the parietal suggests that this part of the occiput was vertical, as in *Khaan*, rather than facing posterodorsally as in *C. osmolskae*.

The paroccipital process is well preserved on the right side, but is not preserved on the left. It extends posterolaterally from the foramen magnum and appears to have been deflected slightly posteriorly, perhaps due to mediolateral compression. It is slightly pendant, but its distal end is missing so the extent of its descent cannot be ascertained.

The shape of the narial opening is difficult to determine, because much of this region is not preserved. However, as pointed out by Smith (1993), the ventral edge of the narial opening is preserved where it is bordered by the premaxilla, and it is positioned above the anterior part of the antorbital fossa far from the anterior end of the skull. However, it is unclear that the maxilla bordered the naris because the posterior part of the nasal, which separates the maxilla from the naris in better preserved material, is absent. A slender splint of bone described and figured by Smith (1993), but since lost, probably represents the only part of the nasals preserved, but it does not appear to have been very informative. The premaxillae preserve an ascending process at the anterior end of the skull, but it is unclear how far it rose dorsally. The circumnarial region is quite variable between species of oviraptorids, so it is not possible to reconstruct most of this region in the holotype of *O. philoceratops*. The presence of a bony "tooth" formed by the maxilla and vomer, as in other oviraptorids, cannot be determined as this area has not been exposed.

The dorsal surface of both frontals is missing along the midline, and the missing portion may have been extensive. The fused parietals bear a tall midline crest, and the dorsomedial inclination of the dorsal surface of each frontal suggests that the crest may have continued anteriorly to above the orbits. This inclination is not due to mediolateral compression, as the ventral surface of the frontals is horizontal. Only the posterior part of the frontals is preserved along the midline, from the ventral part of the bone in the anterior part of the braincase. These fragments suggest that the posterior part of the frontals was filled by a large, presumably pneumatic cavity as in *Citipati*.

The crest on the parietal lies only along the midline, unlike the domed crest of *O. mongoliensis* (Barsbold, 1986), which occludes the supratemporal fenestrae. The height of the crest may have been accentuated by mediolateral crushing ventrally, but dorsally it appears to be solid and bears no indication of crushing. In lateral view, it forms a gentle arc interrupted by a missing portion anterodorsally. The anterior edge of the crest is preserved descending to the skull roof, but this area may have underlain the frontal and any crest that it bore.

The oval antorbital fenestra is unlike that of other oviraptorids in being elongate longitudinally rather than vertically. A large accessory antorbital fenestra is present in the anterior part of the antorbital fossa (contra Smith, 1993). The entire border is preserved on the left side but is broken on the right. It is similar in size to that on the right side of IGM 100/978. A small opening anterior to the accessory opening on the left side near the premaxillary suture is not duplicated on the right side, but a broader excavation on the left side is in the same position as a small fossa on the right side; most likely this area has been eroded on both sides.

Below the antorbital fossa the suborbital fenestra is exposed between the vertical ectopterygoid and palatine. The fenestra is larger than in IGM 100/978 and other oviraptorids preserving this region. Much of the posterior part of the left ectopterygoid is visible medial to the mandibular ramus, indicating that this bone is similar to that of other oviraptorids. Thus the pterygoid flange broadens vertically rather than horizontally.

The lateral surface of the braincase is well preserved on the left side but has not been fully prepared. A shallow fossa is evident on the prootic dorsal to the fenestra ovale, in a position corresponding to the dorsal tympanic recess. The foramen ovale is exposed anteriorly on the braincase wall and is longer than high. The right laterosphenoid is preserved with the rest of the braincase, whereas the left adheres to the bottom of the left frontal.

The individual bones of the mandible are difficult to differentiate. The surangular is extensive, but almost certainly does not form the ventral edge of the posterior part of the mandibular ramus (cf. figs. 2 and 3 of Smith, 1993) or extend anteriorly beneath the mandibular fenestra. The articular probably does not extend anteriorly beyond the quadrate articulation on the lateral surface (the bone labeled by Smith as articular in this region is part of the surangular). The second mandibular foramen, in the posterior part of the ramus, may be an artifact, as this feature corresponds to an area of thin bone in the surangular of IGM 100/978. The spine on the surangular that extends anteriorly into the mandibular fenestra is horizontal rather than extending anteroventrally as in IGM 100/978.

The symphysis is poorly preserved and incompletely prepared. Mediolateral compression has dislocated the symphysial portion on the left side from the remainder of the dentary.

Smith (1993: 374) describes ''a sliding articular surface on the quadrate, at its articulation with the articular, permitting an anterior/posterior shearing movement of the mandible.'' However, in archosaurs, the quadrate condyle is convex and articulates with a concave surface on the articular, so a ''sliding'' joint can only be implied by an elongate sur-

face on the articular (as it indeed is in the better preserved oviraptorid material; Osmólska, 1976). The articular is preserved well only on the right side, and it has not been prepared sufficiently to discern the length of the articulation surface, but a dorsal concavity evident in medial view suggests that the surface is not as elongate as in *Citipati*.

The rostrum and lower jaw of *O. philoceratops* were more elongate than in other oviraptorids, although the extent of this difference is difficult to determine in its poor state of preservation. Compared with other oviraptorids, the premaxilla appears to be incomplete anteriorly, and would have extended one or two centimeters farther than its preserved length. The region anterior to the antorbital fenestra is longer than in other oviraptorids even when the gaps between dislocated pieces of the rostrum are taken into account. This is evident from the greater length of the accessory antorbital fenestra in comparison with other oviraptorids (fig. 12). If mandibular length is reconstructed by allowing for the large gap between pieces of the right dentary (fig. 13), then the portion of the dentary anterior to the coronoid process is longer than this region in *Citipati*, which is typical of other oviraptorids. Furthermore, the descent of the dorsal edge of the dentary anterior to the mandibular fenestra is less pronounced than in other oviraptorids.

DISCUSSION

The skull of *C. osmolskae* demonstrates the presence in oviraptorids of epipterygoid and coronoid ossifications and an extensive pneumatic cavity in the dorsal part of the braincase. An epipterygoid is known to be present in several groups of theropods and other fossil archosaurs (Clark et al., 1993) even though it is absent in both groups of extant archosaurs (crocodylians and birds; De Beer, 1937; Gauthier et al., 1988). However, its uneven distribution among theropods suggests that it may ossify only in some, perhaps older, individuals (cf. Madsen, 1976). Among tetanuran theropods, thus far an epipterygoid is known only in allosaurids (Madsen, 1976), ornithomimids (Barsbold,
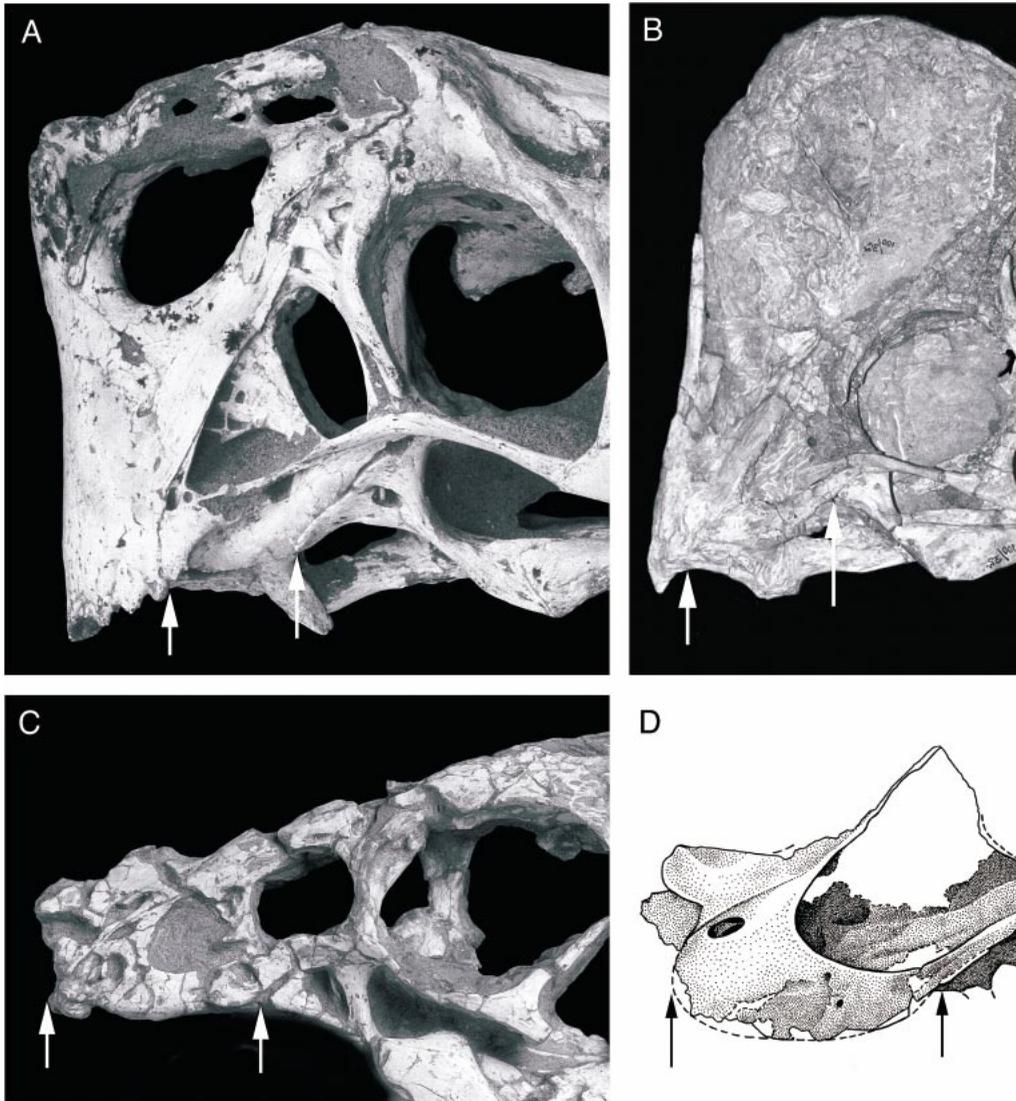
Fig. 12. Rostral regions (not to scale) of **(A)** the holotype of *Citipati osmolskae* IGM 100/978, **(B)** the holotype of ''*Oviraptor*'' *mongoliensis* (IGM 100/32) (reversed), **(C)** the holotype of *Oviraptor philoceratops* AMNH 6517, and **(D)** a referred specimen of the caenagnathid *Chirostenotes pergracilis* (ROM 43250) (from Sues, 1997). The maxilla of *O. philoceratops* is relatively longer than in the oviraptorids (B and C) but shorter than in the caenagnathid (D), which represents the plesiomorphic condition for oviraptorosaurians. Arrows indicate premaxilla-maxilla contact anteriorly and palatine-maxilla contact posteriorly. Abbreviations in appendix 1.

1981), tyrannosaurids (Lambe, 1904; Molnar, 1973), *Dromaeosaurus* (Currie, 1995), and troodontids (Norell et al., in prep.). In other theropods this bone is generally small, mediolaterally flattened, and triangular with a horizontal base. The epipterygoid of *C. osmolskae* is the largest of any known theropod, and its strongly twisted body and dorsal tip with robust muscle scars are unique.

A coronoid ossification has been considered absent in oviraptorids (e.g., Barsbold et al., 1990), but the presence of a slender coronoid in *C. osmolskae* demonstrates it was present, although reduced in size. This sug-
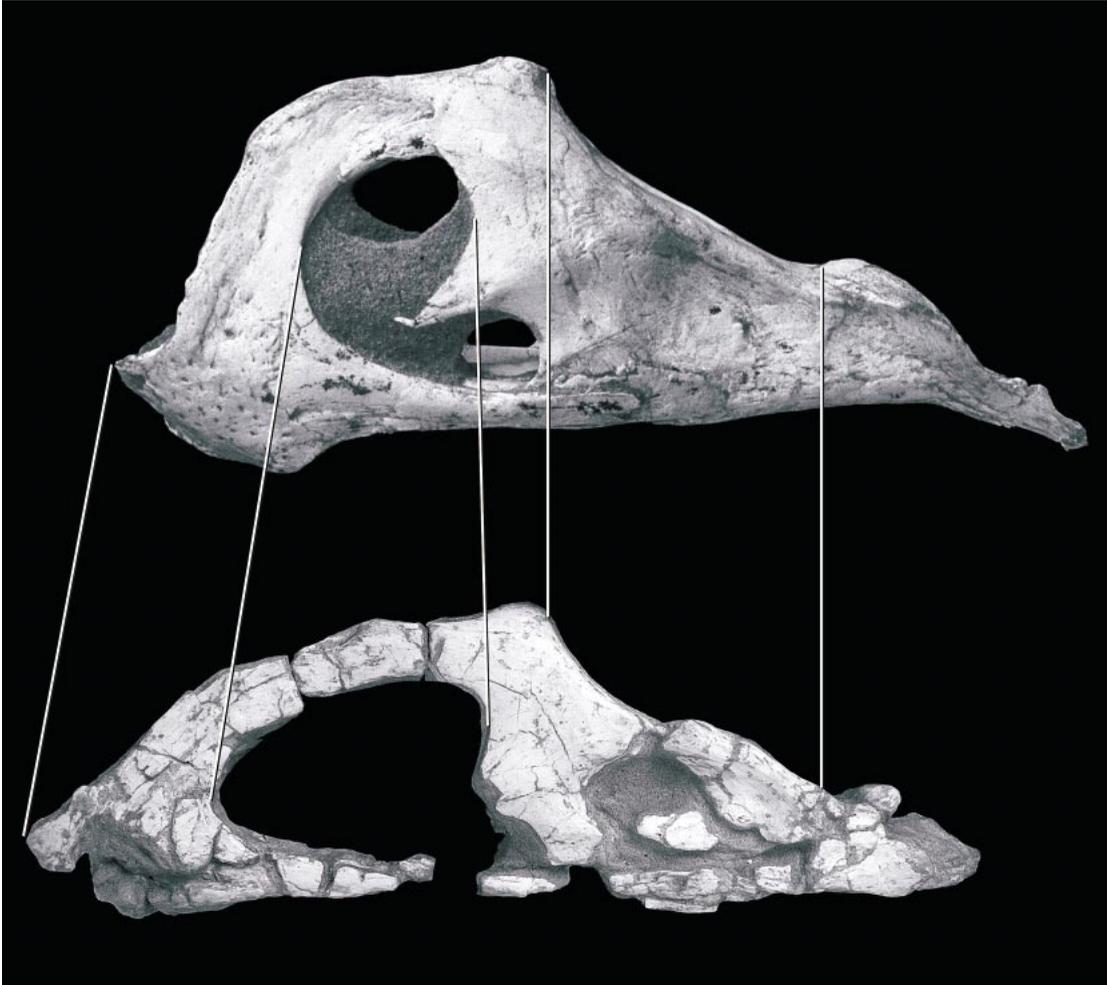
Fig. 13.   The holotype mandibles of *Citipati osmolskae* IGM 100/978 (top) and *Oviraptor philocer-atops* AMNH 6517 (bottom) in left lateral view (not to scale). The *Oviraptor* mandible has been digitally compressed to minimize the separation at two breaks in the dentary. Lines are drawn between topologically comparable points on the two mandibles to illustrate the proportionately greater length of the anterior part of the *O. philoceratops* mandible.

gests that it may be present in other taxa in which it is thought to be absent, such as basal avialans, dromaeosaurids, and troodontids.

The skull of *C. osmolskae* is notable for the extensive pneumaticity of the narial region and the dorsal part of the neurocranium. The unusual pneumatic recesses of oviraptorid skulls have been noted before (e.g., Witmer, 1997: 46), but this is the first time their full internal extent has been revealed with CT scans. The extremely large space dorsal to the area occupied by the brain has not been reported before, and is reminiscent

of the dorsal pneumatic space in the braincase of the pterodactyloid pterosaur *Anhangeura* (Kellner, 1996), although it is obviously not homologous. The apparent intertympanic connection of the dorsal tympanic recess is another feature hitherto unknown in oviraptorids or in any dinosaurs except neornithine birds (Witmer, 1990).

The braincase of *C. osmolskae* does not differ significantly from that of dromaeosaurids (Currie, 1995; Norell et al., in press), differing mainly in the pneumatic features of the dorsal part of the neurocranium, the re-

duced basipterygoid processes, and the autapomorphic anterior shift to the occiput and dorsal part of the skull. The dorsal tympanic recess is deeper than that of velociraptorine dromaeosaurids (Norell et al., submitted) and lies in a slightly more dorsomedial position in *C. osmolskae*. The single, large opening between the basisphenoid and basioccipital ventrally is comparable to that of some velociraptorines, although in others the opening is divided into two or more openings. The struts on the basisphenoid anterior to the trigeminal opening and medial to the epipterygoid are not present in dromaeosaurids, but they are in the same position as similar struts within the ''lateral recess'' of troodontids and in the otic region of therizinosaurids (Clark et al., 1994).

A specimen previously identified as *O. philoceratops* (e.g., Barsbold et al., 1990), IGM 100/42, is more similar to *Citipati osmolskae* than to the former in the shape of its narial region and in the presence of an accessory opening on the lateral surface of the ascending process of the premaxilla. Furthermore, its maxilla and dentary are as short as those of other oviraptorids except *O. philoceratops*. We therefore consider it to belong to *Citipati* rather than *Oviraptor*, although it is unclear whether it represents a species different from *C. osmolskae*. Because it is much better preserved than the holotype of *O. philoceratops* it has often been relied upon for anatomical details of the species, so caution should be used in referring to previous characterizations of this species.

A second species of *Oviraptor* has been described, *O. mongoliensis* Barsbold, 1986, but there is little evidence to place it in this genus. It shares with *O. philoceratops* a parietal crest (albeit much larger), but differs from it in having a maxilla and dentary as short as those of all oviraptorids except *O. philoceratops*. The name ''*Rinchenia*'' was applied to this species by Barsbold (1997), but this name has not been formalized.

Relationships among oviraptorids are poorly understood (see Barsbold et al., 1990, 2000), but our study of the holotypic skull *O. philoceratops* suggests that this species occupies a primitive position in the family. The relatively elongate maxilla and dentary of this specimen (figs. 12, 13) contrast with those of all other oviraptorids, and are more similar to the condition in oviraptorid outgroups such as the oviraptorosaurs *Chirostenotes* (Sues, 1997) and *Microvenator* (Makovicky and Sues, 1998) (i.e., a dentary tentatively identified for the latter). A primitive position for *O. philoceratops* does not necessarily contradict the hypothesis, based on features of the ilium, that *Nomingia gobiensis* may be the most primitive oviraptorid (Barsbold et al., 2000), because the skull of *Nomingia* and the pelvis of *O. philoceratops* are not yet known.

ACKNOWLEDGMENTS

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APPENDIX 1

ANATOMICAL ABBREVIATIONS USED IN FIGURES

aaof	accessory antorbital fenestra
acc	accessory opening
an	angular
aof	antorbital fenestra
ar	articular
bs	basisphenoid
ch	choana
cor	coronoid
d	dentary
dtr	dorsal tympanic recess
ec	ectopterygoid
emf	external mandibular fenestra
endo	endocranial cavity
eo	exoccipital
ep	epipterygoid
f	frontal
fm	foramen magnum
fo	fenestra ovale
foo	foramen ovale
hy	hyoid element
j	jugal
l	lacrimal
lat	laterosphenoid
m	maxilla
n	nasal
nar	narial opening
o	orbit
oc	occipital condyle
or	orbitosphenoid
p	parietal
pa	palatine
par	parasphenoid
path	pathology
pm	premaxilla
pnc	pneumatic cavity
po	postorbital
pre	prearticular
pt	pterygoid
q	quadrate
qf	quadrate foramen
qj	quadratojugal
rar	right articular
rd	right dentary
rl	right lacrimal
rlat	right laterosphenoid
rpop	right paroccipital process
rpre	right prearticular
rpt	right pterygoid
rq	right quadrate
rsp	right splenial
sa	surangular
so	supraoccipital
sp	splenial
sq	squamosal
st	stapes
t	bony "tooth" formed by maxilla and vomer
v	vomer
II, V, VII, XII	openings for cranial nerves II, V, VII, and XII