Cranial Osteology of the Theropod Dinosaur
Incisivosaurus gauthieri
(Theropoda: Oviraptorosauria)

AMY M. BALANOFF,[1] XING XU,[2] YOSHITSUGU KOBAYASHI,[3] YUSUKE
MATSUFUNE,[4] AND MARK A. NORELL[5]

ABSTRACT

We provide a description of the holotype skull of the unusual oviraptorosaur *Incisivosaurus gauthieri*. Previous phylogenetic analyses have placed this taxon firmly within Oviraptorosauria near the base of the clade; however, until now only a cursory description of this important specimen was available. The presence of many primitive characteristics (e.g., maxillary and dentary teeth as well as an extended palate and rostrum) indicates that the observed similarities between avians and derived oviraptorids are convergences rather than shared derived characters. In addition, we clarify previous descriptions of several ambiguous anatomical features, most notably of the palate. We also employ computed tomographic (CT) analysis, which allows for a more complete description of the braincase and the reconstruction of an endocranial endocast. CT imagery reveals features that were before unobtainable, such as the presence of a replacement tooth behind the large rodentiform incisor in the premaxilla. This arrangement indicates that although the incisiform teeth of *I. gauthieri* are morphologically distinct they are replaced in typical archosaurian fashion.

[1] Division of Paleontology, American Museum of Natural History, New York, New York (abalanoff@amnh.org); Department of Earth and Environmental Sciences, Columbia University, New York, New York.
[2] Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China (xu.xing@ivpp.ac.cn).
[3] Hokkaido University Museum, Hokkaido, Japan (ykobayashi@museum.hokudai.ac.jp).
[4] Hokkaido University, Hokkaido, Japan (ymatsufune@mail.sci.hokudai.ac.jp).
[5] Division of Paleontology, American Museum of Natural History, New York, New York (norell@amnh.org).

INTRODUCTION

Oviraptorosaurs with their toothless beaks, large eyes, extensive skeletal pneumaticity, and occasional cranial crests are some of the most unusual theropod dinosaurs yet discovered (Barsbold, 1976, 1981, 1983, 1986, 1997; Osmólska et al., 2004). Until recently oviraptorosaurian dinosaurs also were among the rarest and most enigmatic members of Theropoda. Most aspects of their paleobiology, from their relationships to their origins, were unknown and highly controversial. This uncertainty stems from their extremely apomorphic skeletons and the absence of more primitive members of the group. This situation gradually has changed because of the description of several newly discovered taxa from various ontogenetic stages (e.g., Norell et al., 1994; Barsbold, 1997; Ji et al., 1998; Barsbold et al., 2000; Norell et al., 2001; Clark et al., 2001; Lü, 2002, Lü et al., 2004, Osmólska et al., 2004), the recent reassignment of previously known taxa to the group Oviraptorosauria (e.g., *Microvenator celer* [Makovicky and Sues, 1998], *Elmisaurus rarus* [Osmólska, 1981] and *Avimimus portentosus* [Kurzanov, 1987]), as well as the unique "preservation" of behavior in the fossil record (i.e., nesting; Norell et al., 1995; Dong and Currie, 1996; Clark et al., 1999).

Incisivosaurus gauthieri is certainly one of the more bizarre theropods ever to be described (Xu et al., 2002a); therefore, the inclusion of *I. gauthieri* within the bizarre group Oviraptorosauria may not have been completely unexpected. This unusual theropod was discovered in the Early Cretaceous rocks of northeastern China, which have produced many other amazing dinosaur specimens (see Xu and Norell, 2004; Norell and Ellison, 2005; Norell and Xu, 2005). Similar to many of the taxa recovered from the Jehol beds, *I. gauthieri* is known only from a unique specimen (IVPP V 13326), although a synonymy with *Protarchaeopteryx robusta* (Ji and Ji, 1997), another unique specimen, has been suggested (Senter et al., 2004).

Aside from the familiar feathered dinosaurs, the Jehol beds (Zhou et al., 2003; Barrett and Hilton, 2006) also have produced myriad transitional forms. These dinosaurs (e.g., *Liaoceratops* [Xu et al., 2002b], the basal deinonychosaurs *Microraptor* [Xu et al.,
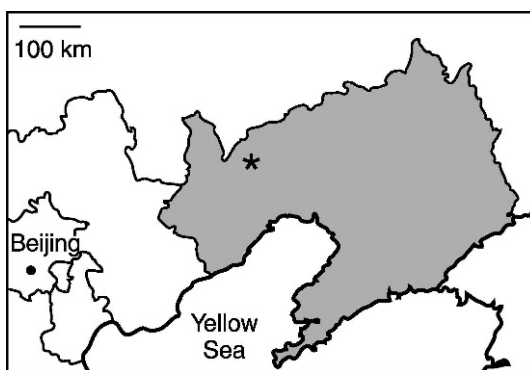

Fig. 1. A map of Liaoning Province (shaded gray). Beipiao City is marked by an asterisk.

2003] and *Sinovenator* [Xu et al., 2002c], the basal oviraptorosaur *Caudipteryx* [Ji et al., 1998], the transitional tyrannosaurid *Dilong* [Xu et al., 2005], the transitional therizinosaur *Beipiaosaurus* [Xu et al., 1999], the basal toothed ornithomimosaur *Shenzhousaurus* [Ji et al., 2003], and the stem hadrosaurid *Jinzhousaurus* [Wang and Xu, 2001]) display many characteristics that place them at the base of established clades and therefore are crucial to the development of accurate phylogenetic trees. This generality holds true for *Incisivosaurus gauthieri*, which continually falls at the base of the oviraptorosaur tree.

A list of abbreviations is given in appendix 1.

MATERIALS AND METHODS

LOCALITY AND GEOLOGICAL SETTING

LOCALITY: Lujiatun, Shangyuan, Beipiao City, Liaoning, China (fig. 1).

GEOLOGICAL OCCURRENCE: The specimen was collected from the lower part of the Yixian Formation. These beds are considered older than 128 million years old (Swisher et al. 1999, 2002).

SCANNING

The use of computed tomography (CT) provides a nondestructive means to view and study the internal structures of braincases (Carlson et al., 2003). In addition, CT allows the creation of digital endocasts of the endocranial cavity and its related structures of fossilized taxa. These casts preserve incredible

detail such as the cranial nerves and vessels through the skull as well as the morphology of the sinus cavities (e.g., Rogers, 1999; Brochu, 2000; Franzosa, 2004; Franzosa and Rowe, 2005; Balanoff et al., in press).

We use CT to assist in both the description of the specimen and the creation of a digital endocast of the endocranial cavity. IVPP V 13326 was scanned at Stony Brook University medical scanning facility. The specimen was scanned along the coronal axis for a total of 404 DICOM images at an image resolution of 512×512 pixels. The z-spacing (i.e., axial spacing) is 0.310 mm, and the x- and y-spacing (i.e., sagittal and horizontal spacing) is 0.188 mm.

The endocranial endocast was reconstructed using the original DICOM imagery in the volumetric rendering program VGStudioMax© 1.2.1. The reconstruction was made by adjusting the contrast in the images until bone and matrix were easily distinguishable. The endocranial cavity was selected using the segmentation tools available in the program, separated into its own volume, and exported as an isosurface. Measurements taken from the endocast were done using VGStudioMax© 1.2.1. Endocast volume measurements were taken by calculating the volume of negative space of the endocranial cavity. For ease of description, features of the endocranial casts are referred to by the names of the soft tissues of the brain that they reflect (e.g., cerebrum rather than cast of cerebrum). It is important to note, however, that what actually is preserved is a cast of the endocranial space, which may reflect structures other than the brain, such as meninges and sinuses. The endocast, however, does help to determine relative size and shape of regions of the brain as well as recognizing the branching points of the cranial nerves (Hopson, 1979). The original slice data and movies showing the endocranial cast are available at the DigiMorph website (www.digimorph.org/specimens/Incisivosaurus_gauthieri).

DESCRIPTION

IVPP V 13326 consists of a skull and anterior mandibles (figs. 2–7). Although Xu et al. (2002a) reported a postdentary bone, it could

not be located in IVPP collections at the time this paper was written. Most of the skull is freed from matrix, yet some of the skull is still enclosed in original sediments, removal of which would seriously endanger the specimen. Distinguishing sutures between some of the bones is difficult due to the degree of fusion between elements as in many other oviraptorosaurs specimens (e.g., Barsbold, 1981; Kurzanov, 1987; Sues, 1997; Clark et al., 2002). The cranium is well preserved and relatively undistorted; however, the left side of the skull is displaced anteriorly relative to the right as is obviously seen in the shape of the braincase and the more forward placement of the left preorbital bar (figs. 3–5). The right side of the skull is more complete than the left, yet overall the skull has seen some lateral compression. Compared to many oviraptorosaurs, the cranium is low in profile (see Osmólska et al., 2004: fig. 8.1) with a distinctly rounded roof. The nares have a dorsal position on the skull and are displaced posteriorly lying dorsal to the antorbital fossa as in other oviraptorosaurs. The orbits are large and circular and the infratemporal fenestra is extensive and triangular (fig. 3). The fragmentary anterior mandibles that are preserved are fused at the dentary symphysis, the condition present in other oviraptorosaurs (figs. 5 and 6).

Rostrum

Figures 2–5, 8

The rostrum is well preserved except for the slight deformations noted above. The short rostrum measured from the preorbital bar accounts for 44% of the total length of the skull. The nares are large and elliptical and, as in most other oviraptorosaurs, displaced posteriorly from the anterior margin of the skull (see Osmólska et al., 2004: fig. 8.1 and compare with fig. 3). The orbits are very large (making up 48% of the total skull length) and nearly circular, the condition found in other oviraptorosaurs. The infratemporal fenestra also is large and triangular with a larger ventral expanse.

Although much of the palate is distorted and many of the bones are tightly fused, which obscures most sutural connections, the majority of the palate is preserved (fig. 4B). In

Fig. 2. Oblique view of the skull of the holotype of *Incisivosaurus gauthieri* (IVPP V 13326).

comparison with other oviraptorosaurs, the most distinctive features of the palate of *Incisivosaurus gauthieri* are the anteroposterior elongation and the lack of tapering of the skull posterior to the premaxillary-maxillary shelf. The slitlike choanae are remarkably different from the rounded choanae found in other oviraptorosaurs (see Clark et al., 2002: fig. 3). The interpretation in this analysis of these slitlike openings as choanae differs from that reported by Xu et al. (2002a), which indicated that the openings may represent confluent choanae and subsidiary palatine fenestrae. A subsidiary palatine fenestra is not known in other oviraptorosaurs (Currie, 1995; Elzanowski, 1999; Clark et al., 2002); therefore, the presence or absence of this structure remains ambiguous. The palatine fenestra is small but is much larger than in more derived oviraptorosaurs. Xu et al. (2002a) also de-

scribes a subsidiary ectopterygoid fenestra as a narrow opening lying in a depression on the right side of the skull between the ectopterygoid and palatine. CT imagery shows this fenestra opening into a pneumatic space within the ectopterygoid; thus, this opening may represent part of the ectopterygoid recess (Witmer, 1997).

PREMAXILLA: The premaxillae remain unfused along the anterodorsal external surface (fig. 5A), unlike other oviraptorosaurs (however, fusion does not occur in *Conchoraptor gracilis*, *Khaan mckennai*, and *Caudipteryx zoui*). In lateral view the premaxilla forms the dorsal, anterior, and ventral boundary of the elliptical naris. The posterior margin is made up of the contact between the maxillary process of the premaxilla and the nasal. The maxillary processes are thick and massive similar to other oviraptorosaurs and have extensive exposure on the lateral surface of the
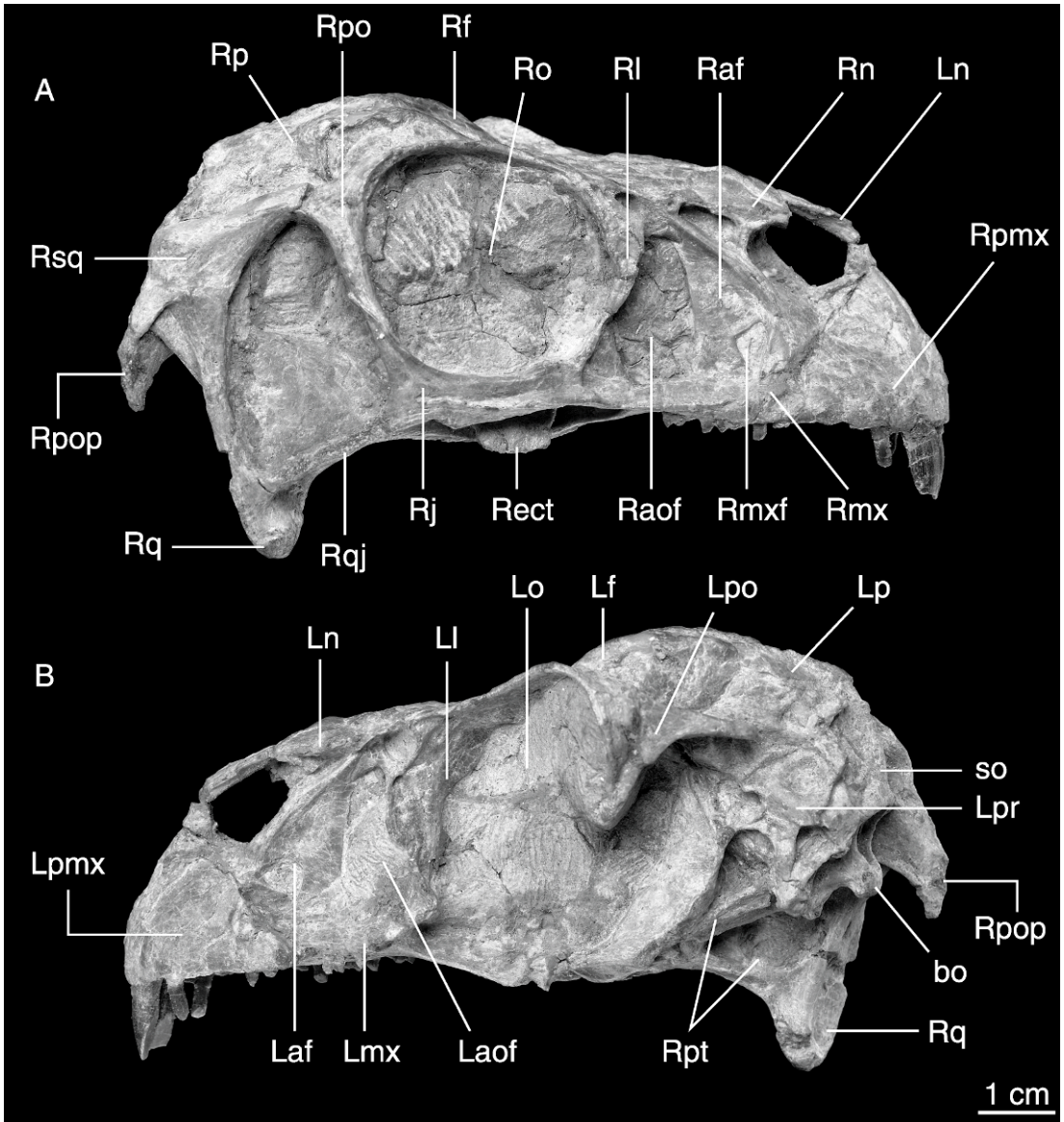
Fig. 3. The skull of the holotype of *Incisivosaurus gauthieri* (IVPP V 13326) in (**A**) right lateral and (**B**) left lateral views. Abbreviations in appendix 1.

skull (fig. 3). In many oviraptorosaurs the maxillary process of the premaxilla extends posteriorly below the premaxillary process of the nasal to contact the lacrimal on the lateral surface of the skull. If this is the case in *Incisivosaurus gauthieri*, this contact is obscured by the overlaying nasal.

The nasal process of the premaxilla forms the internarial bar (fig. 5A), which is thin and

extends to meet the nasals posteriorly at the posterior margin of the narial aperture. This process is flat and straplike, more typical of nonavian maniraptorans than other oviraptorosaurs (see Barsbold, 1981; Clark et al., 2002), in which the rounded internarial bar is thick (with the exception of *Caudipteryx zoui*; Ji et al., 1998; Zhou et al., 2000) and sometimes forms a crest with the nasals.
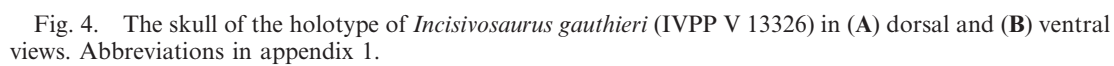
Fig. 4.   The skull of the holotype of *Incisivosaurus gauthieri* (IVPP V 13326) in (**A**) dorsal and (**B**) ventral views. Abbreviations in appendix 1.
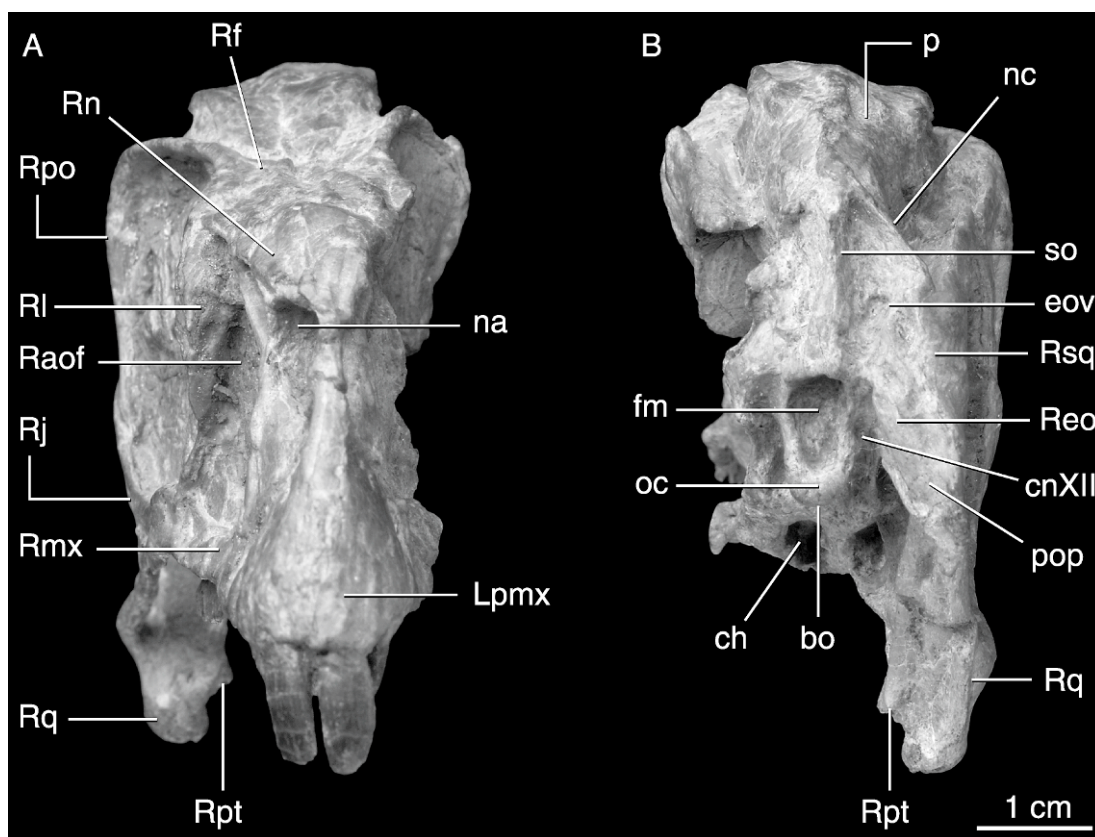
Fig. 5. The skull of the holotype of *Incisivosaurus gauthieri* (IVPP V 13326) in (**A**) anterior and (**B**) posterior views. Abbreviations in appendix 1.

The lateral surface of the premaxilla is medially depressed to form a shallow fossa anteroventral to the naris (fig. 3) as is seen in oviraptorids, *Caudipteryx zoui*, and *Avimimus portentosus* (see Osmólska et al., 2004; Zhou et al., 2000; and Kurzanov, 1987). Several small foramina are scattered on the lateral surface of the bone, and a single larger foramen lies just ventral to the anterior corner of the naris. *Citipati osmolskae* and the unnamed Zamyn Khondt oviraptorosaur also have similar foramina scattered on the lateral surface of the premaxilla (see Clark et al., 2002; Osmólska et al., 2004). The ventral margin of the premaxilla is scalloped corresponding to the undulations of waves of teeth along a typical theropod tooth row. The suture between the premaxilla and the maxilla on the lateral surface of the skull contains a small subnarial foramen in the same position as is found in *Khaan mckennai* (Clark et al., 2001). The premaxilla-maxilla suture sweeps posteriorly below the nares forming a small ridge that defines the anteriormost boundary of the antorbital fossa.

On the ventral surface the premaxillae meet to form an extensive palatal surface typical of oviraptorosaurs (fig. 4); however the palatal surface is smooth, lacking the longitudinal grooves apparent on the palate of oviraptorids. The premaxillae are tightly fused anteriorly as in other oviraptorosaurs to form a well-developed premaxillary shelf. They form a small longitudinal incisive crest at the point where they meet along the palate. The premaxilla meets the palatal shelf of the maxilla along a diagonal suture. Along the midline, the posterior end of the premaxilla overlies the anterior end of the vomer. Although the posteroventral
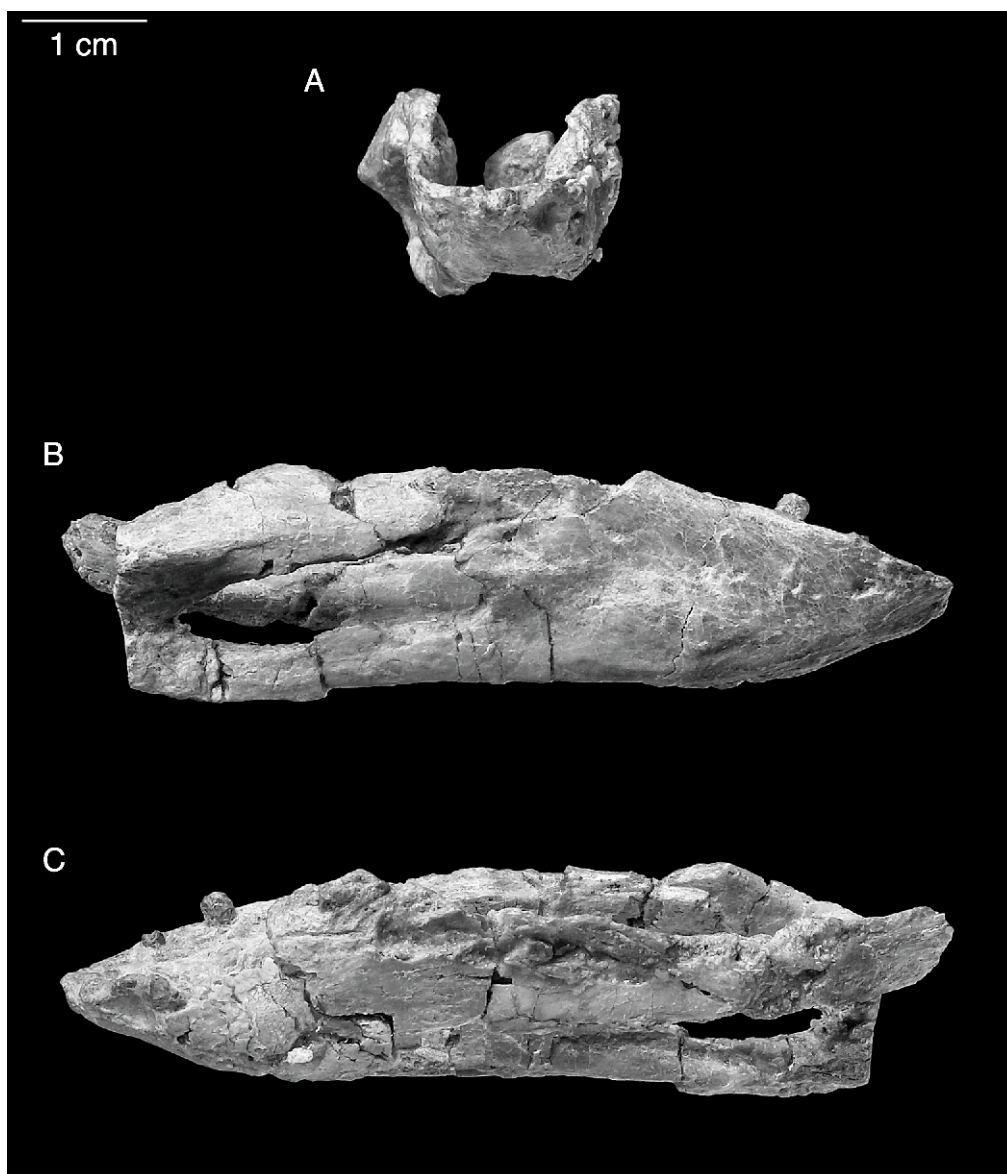
Fig. 6. The mandible of the holotype of *Incisivosaurus gauthieri* (IVPP V 13326) in (**A**) anterior, (**B**) right lateral, and (**C**) left lateral views.

contact of the premaxilla with the maxilla and vomer is indistinct, there seems to be some hint that the vomers display the familiar "fleur de lis"–shaped contact present in other oviraptorosaurs (Elzanowski, 1999; Clark et al., 2002), especially evident at the left vomer-premaxilla contact.

MAXILLA: In contrast to most other maniraptorans, the contribution of the maxilla to the lateral surface of the skull is minimal (fig. 3). The maxilla contacts the jugal and lacrimal just ventral to the preorbital bar. The jugal ramus of the maxilla is thin and progressively overhangs the tooth row posteriorly. The nasal ramus of the maxilla is a small splint of bone that forms a ridge with the premaxilla and the nasal and defines the dorsal and anterior margins of the antorbital fossa.
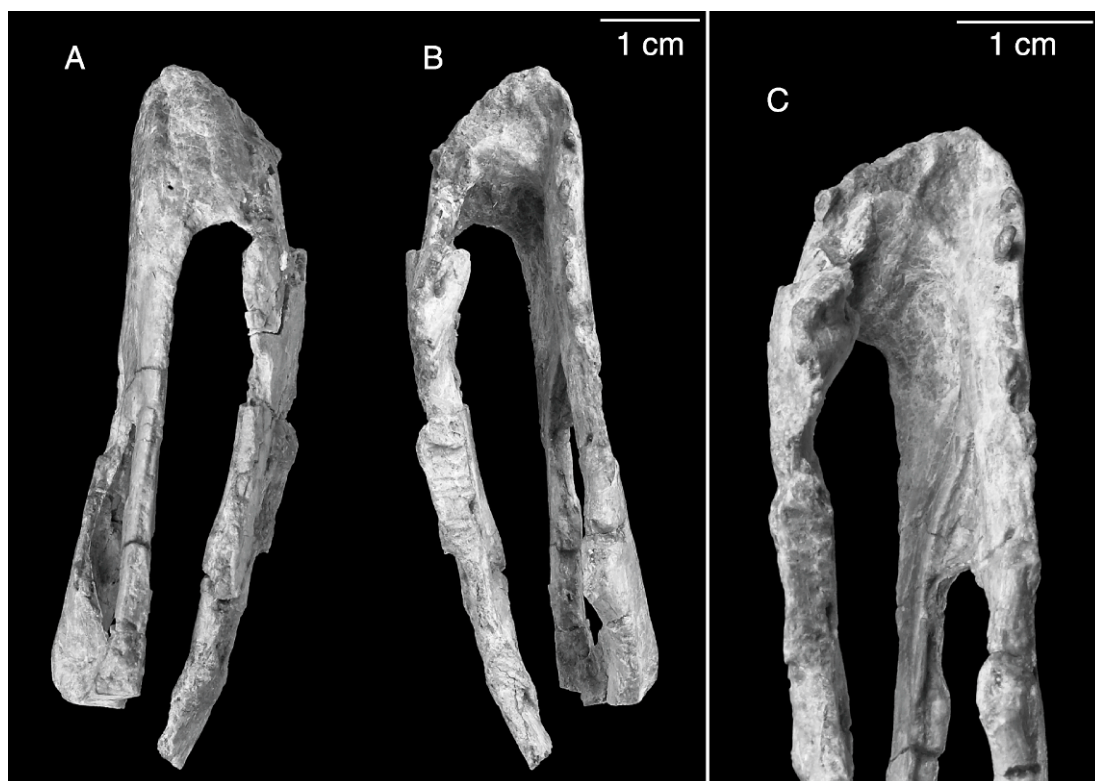
Fig. 7. The mandible of the holotype of *Incisivosaurus gauthieri* (IVPP V 13326) in (**A**) ventral and (**B**) dorsal views. View (**C**) shows magnified dorsal view of dentary teeth.

The maxilla makes up a large part of the osseous floor and interfenestral bar located in the anterior portion of the antorbital fossa. The antorbital fossa is subtriangular and large, with a truncated anterior apex. The antorbital fenestra occupies approximately half of the entire fossa. Anteriorly, the concave margin of the interfenestral bar defines the antorbital fenestra within the fossa. Dorsally, a slightly concave lip of the maxilla overhangs the fossa. One small and one large foramen lie within the interfenestral bar (fig. 3). The smaller of these foramina is positioned posteriorly just dorsal to the anterior extent of the jugal ramus. The larger foramen typically has been interpreted as the maxillary fenestra, a feature common to most theropods, yet it lies at the anterior apex of the fossa, a position usually associated with the promaxillary fenestra. The ventral position of the smaller foramen is extremely unusual if it represents the maxillary fenestra, as this

foramen usually lies topographically more dorsal relative to the promaxillary fenestra.

Although the paired maxillae are not exposed extensively on the palatal surface, they do contact the premaxillae anteriorly and the vomer anteriorly along the midline to form a secondary palate (fig. 4B). In palatal view, the maxillae are separated along the midline by the vomer and taper posteriorly to terminate just posterior to the last tooth. The maxilla has at least five teeth set in a groove but lacks the toothlike projection on the palatal surface that is present medially in more derived oviraptorosaurs (see fig. 3: Clark et al., 2002). The contact with the jugal can be seen along the lateral surface of the maxilla along this tapering edge. The vomerine process of the maxilla does not contact the vomer but, with the remaining medial margin of the palatine, forms most of the lateral border of the choana (figs. 4B and 8). The anteromedial edge of the maxilla comprises
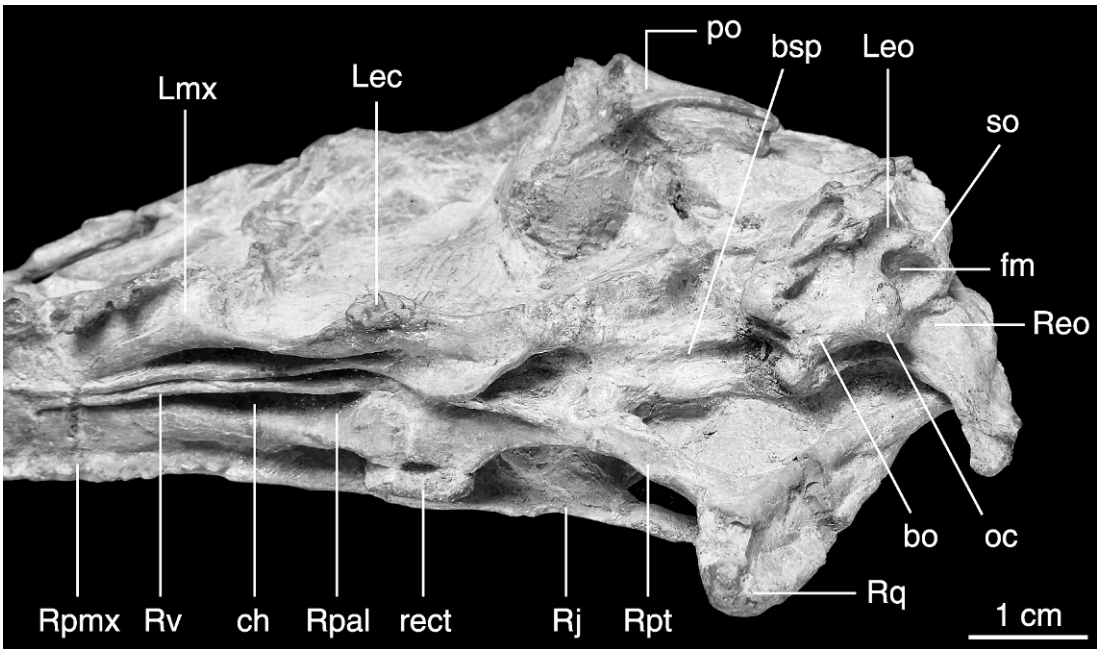
Fig. 8. Ventrolateral view of the skull of the holotype of *Incisivosaurus gauthieri* (IVPP V 13326). Abbreviations in appendix 1.

only the anteriormost lateral edge of the choana.

VOMER: The vomers are two vertically oriented sheets of bone that contact at the midline forming a septum that divides the choanae anteriorly (fig. 4B). CT data reveal that the vomers remain unfused along most of their length and are fused only dorsally at the anterior end of the element (figs. 9E and 10C). This arrangement is in contrast to the typical condition seen in maniraptorans including oviraptorosaurs, which consists of a single stubby "hourglass shaped" vomer that separates the large rounded choanae along their entire length (see Elzanowski, 1999; Clark et al., 2002). The vomer contacts the maxilla anterolaterally, and together these elements form the anterior boundary of the choana. The vomer extends the length of the choana, forming the length of its medial boundary. The stereotypical fleur de lis contact between the vomer(s) and premaxillae may be present, but is not distinct. Instead, the vomers contact the premaxilla anteriorly in a simple contact in which the vomer underlies the premaxilla. Posteriorly the vomer divides to form a notch

that accepts the anterior vomerine process of the pterygoid. These elements form the posterior border of the choana.

PALATINE: The palatines are extensively exposed on the palatal surface (figs. 4B and 8). The element resembles that of other theropod dinosaurs in that it is divided into three distinct rami: an anterior vomerine process, lateral maxillary process, and posterior pterygoid process. It is unclear if the maxilla contacts the vomer along the medial vomerine process as these elements contact on one side of the specimen but not the other; however, the palatine clearly abuts the maxilla along its lateral edge in a long diagonal process that terminates at the maxillary process. The maxillary process is small and contacts the maxilla at a level corresponding to the midpoint of the antorbital fenestra on the lateral surface of the skull. This contact sits dorsal to the ventral margin of the maxilla and defines the anterior boundary of the palatine fenestra (although see Xu et al., 2002a for a conflicting opinion). The medial border of the palatine fenestra is formed exclusively by the palatine (fig. 4B). Posteriorly the palatine underlies the pterygoid just anterior

to the ectopterygoid-pterygoid contact. The pterygoid process of the palatine expands slightly at this articulation.

PTERYGOID: The pterygoid is a large bone that connects the anterior palatal elements with the braincase and suspensorium (fig. 4B). Anteriorly it contacts the ectopterygoid dorsally and laterally, the palatine anteriorly, and the vomer mediolaterally. The pterygoid forms a small portion of the lateral border of the palatine fenestra. A small depression lies anterolaterally adjacent to the expanded bulbous region of the pterygoid that corresponds with the ectopterygoid articulation (fig. 8). Along the anteromedial edge is a deep trough, which is an arc of flexure adjacent to a large, ventrally projecting process termed the accessory ventral flange by Xu et al. (2002a). These processes on the right and left pterygoids contact each other medially just anterior to the point of contact with the parabasisphenoid (fig. 4B). The pterygoid forms a cuplike structure on its medial surface to accept the basipterygoid process of the basisphenoid. In many theropod dinosaurs this is an area where the pterygoid kinks, changes in elevation (i.e., becomes elevated anteriorly), thins, and diverges strongly laterally. The condition in *Incisivosaurus gauthieri*, in which the pterygoid is nearly equal in mediolateral dimension posteriorly and laterally, has anterior and posterior processes that lie on the same plane, and has no strong kinking or dramatic divergence, is consistent with what is seen in a more extreme state within derived oviraptorosaurs like *Citipati osmolskae* (Clark et al., 2002). The pterygoid contacts an anterior process of the quadrate posteriorly, although this region is indistinct. Nevertheless, it is apparent that the pterygoid, quadrate, and possibly the epipterygoid form an extensive lateral flange that is preserved on the right side of the skull (fig. 3A). This flange exhibits a deep pocket lateral to the braincase and, similar to the condition of more derived oviraptorosaurs, completely covers the lateral wall of the braincase.

ECTOPTERYGOID: As in other theropods, the ectopterygoid is C-shaped and extends between the pterygoid and the jugal defining the posterior boundary of the palatine fenestra (figs. 4B and 8). The jugal ramus of the ectopterygoid forms a concave surface, and has an extensive contact with the jugal just posterior to the preorbital bar. The corresponding inflated surface on the opposite side of the ectopterygoid contacts the pterygoid and palatine and lies within a small depression that is primarily contained on the dorsal surface of the pterygoid.

NASAL: The nasal is a complex element in *Incisivosaurus gauthieri* (figs. 3–5) as it is in all oviraptorosaurs (Ji et al., 1998; Clark et al., 2002; Zhou et al., 2000), but not to the extent seen in derived oviraptorids (Osmólska et al., 2004). The nasals of *I. gauthieri* are paired and not fused, unlike oviraptorids but similar to the other basal oviraptorosaur *Caudipteryx zoui* (see Ji et al., 1998; Zhou et al., 2000). Anteriorly, the nasal process of the premaxilla overlies the paired nasal elements and extends midway through the naris, although the exact architecture of this region is obscured due to poor preservation (figs. 4 and 5). Just posterior to the dorsal apex of the antorbital fenestra, the nasal contacts the lacrimal along a suture that continues onto the dorsal surface of the skull. The contact of the nasals with the frontals appears to be short, transversely oriented, and blunt resulting in a fairly short overall appearance of the nasals (fig. 4A). The blunt frontal-nasal contact differs from all other oviraptorosaurs and most maniraptorans, being more typical of more basally diverging theropods.

The concave anterior margin of the nasal (fig. 3) forms the posterior margin of the narial opening. As in oviraptorids the subnarial process of the nasal is a large flat flange of bone that overlies the premaxilla as it descends, paralleling the anterodorsal border of the antorbital fossa. A slight ridge on the ventrolateral surface of the subnarial process is continuous with the premaxillary nasal ridge and with a corresponding ridge on the maxilla, defining the anterodorsal margin of the antorbital fenestra. Just posterior to the naris is a deep elongate opening, which is enclosed entirely by the nasal. CT data show that this opening communicates with the sinus cavity that extends from the frontals into the anterolateral portion of the frontal. A corresponding feature also is found in *Khaan mckennai*, *Citipati osmolskae*, and possibly *Oviraptor philoceratops*.
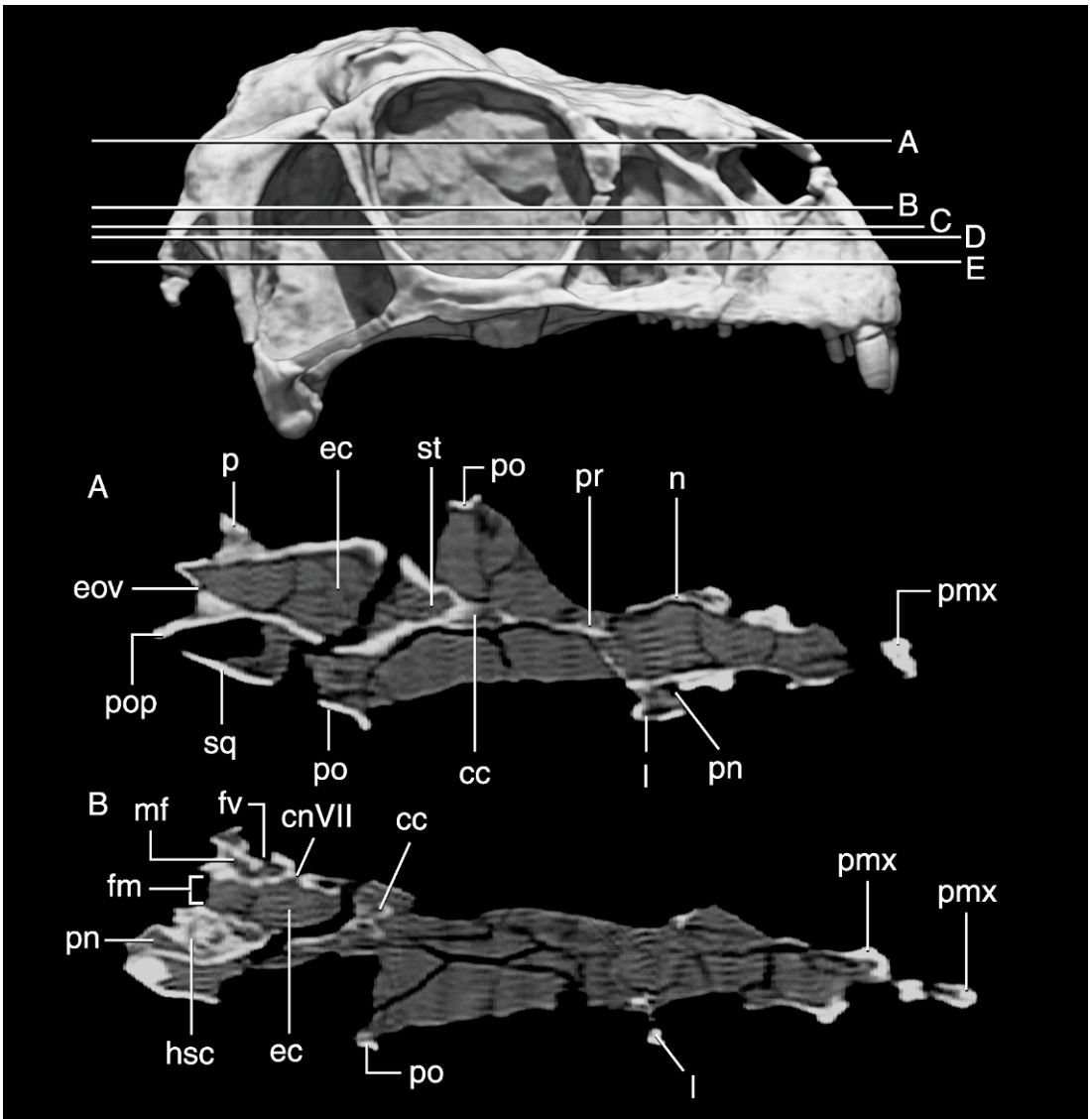
Fig. 9.　Horizontal CT slices through the skull of the holotype of *Incisivosaurus gauthieri* (IVPP V 13326). Abbreviations in appendix 1.

LACRIMAL:　The lacrimal is large and well exposed on the lateral surface of the skull (especially on the right side; fig. 3); however, it is not broadly exposed on the dorsal surface of the skull (fig. 4A). In lateral view the lacrimal is T-shaped (see Xu et al., 2002a) as in other maniraptorans with a large ventral process forming the anterior wall of the orbit (Gauthier, 1986). The anterior process, however, is not nearly as extensive as that seen in paravians (see Norell et al., 2006: fig. 3C, for comparison with the dromaeosaurid condition). The ventrally projecting maxillary process of the lacrimal is posteriorly concave, augmenting the circular shape of the orbit. This condition is similar to that seen in *Caudipteryx zoui* and oviraptorids but differs from the relatively straight preorbital bar apparent in other maniraptorans (see Currie, 1985; Norell et al., 2004, 2006).
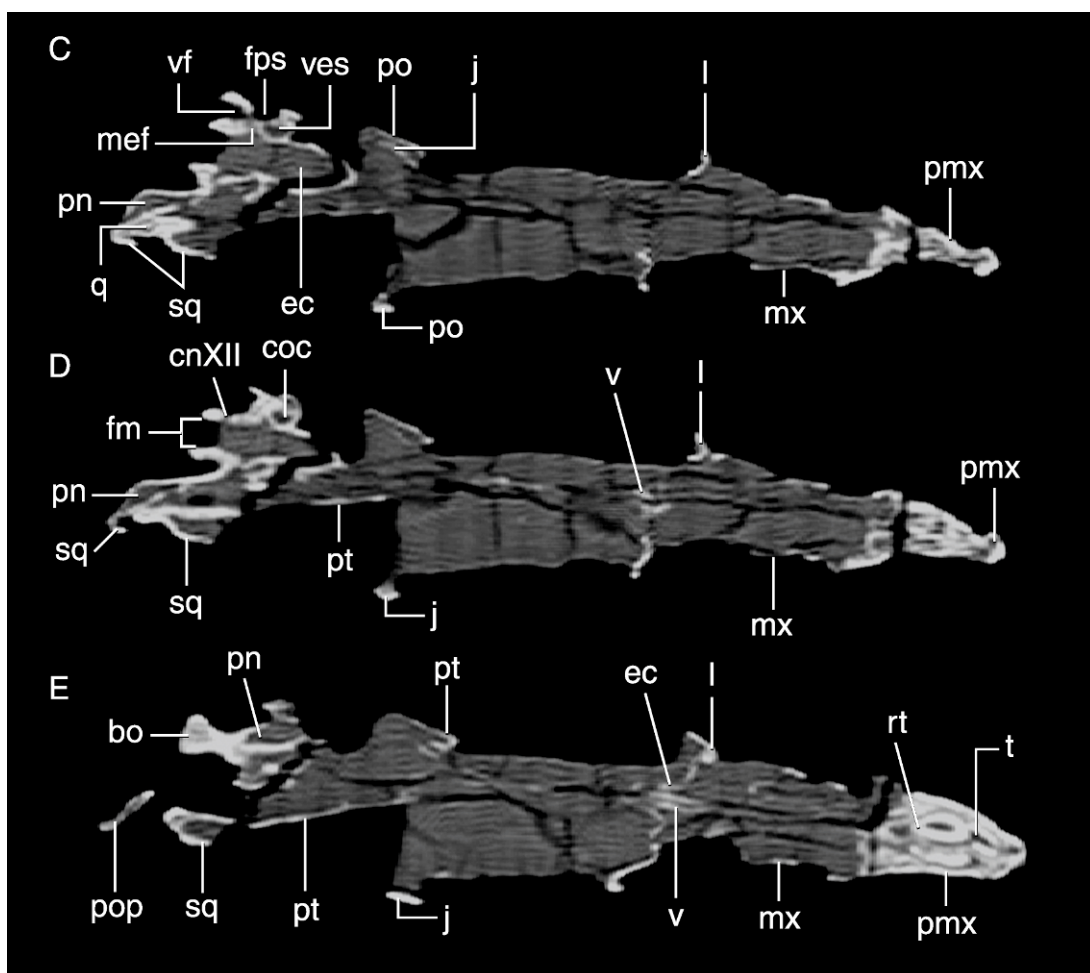
Fig. 9. Continued

Anterodorsally, the lacrimal forms the dorsalmost corner and a portion of the posterior margin of the antorbital fenestra (fig. 3). Just anterior to this corner the lacrimal contacts the ventral surface of the preorbital process of the maxilla and the posteroventral surface of the nasal where it extends onto the skull roof. Although sutures are indistinct on the skull roof, the lacrimal is somewhat exposed between the nasal and the frontal. The medial surface of the lacrimal contacts the frontal on the inside of the orbit along a posteriorly projecting diagonal suture. The posterior wall of the lacrimal is expanded to form a large anterior wall to the orbit. This surface is continuous with the frontal and is slightly concave giving the orbital margin a flared appearance.

The anterior surface of the lacrimal possesses a large lacrimal recess, lying posterodorsal to the antorbital fenestra (fig. 2). This recess is found in most tetanurans (Witmer, 1990, 1997). In *I. gauthieri* the lacrimal recess opens into the lacrimal to pneumatize it and the anterolateral portion of the frontal. This opening also is present in the oviraptorids *Rinchenia mongoliensis* and *Citipati osmolskae*. Unlike *C. osmolskae* (Clark et al., 2002); however, the lacrimal recess appears to be undivided. A large lacrimal foramen perforates the posterior surface of the lacrimal. CT
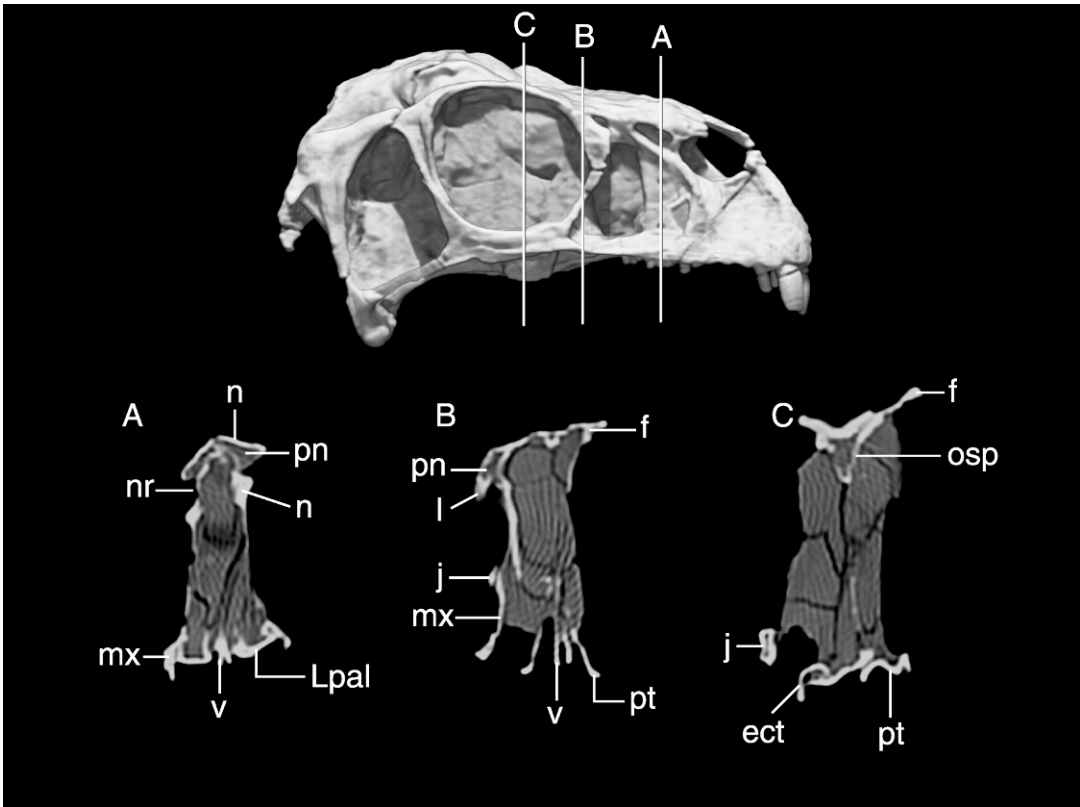
Fig. 10. Axial CT slices through the skull of the holotype of *Incisivosaurus gauthieri* (IVPP V 13326) showing the pneumatic recesses within the facial region. Abbreviations in appendix 1.

scans show that the corresponding canal is completely enclosed in bone and continues anterodorsally to open into the nasal passage (fig. 9). The triangular lateral surface of the preorbital bar, which tapers ventrally, may have housed an additional small pneumatic opening, similar to that seen in *C. osmolskae* (Clark et al., 2002), as is suggested by a small longitudinal depression on the right side (fig. 3). The preorbital bar expands at its ventralmost extent especially anteriorly where it contacts the jugal and the jugal ramus of the maxilla. Anteroventrally it forms a large, recessed buttress in the antorbital fossa.

FRONTAL: The shape of the frontals is slightly distorted on the skull roof; however, the skull roof has a distinctly rounded shape (fig. 3). The frontals are long relative to those of other oviraptorosaurs including *Caudipteryx zoui*, making up approximately 20% of the total skull length (fig. 4A; Xu et al., 2002a). The left

frontal is displaced slightly anteriorly in relation to the left element. The paired frontals contact each other by way of a simple straight suture that is not elevated. The anterior contact with the nasal appears to be fairly blunt, differing from the long tapering nasal process present in other maniraptorans (e.g., Norell et al., 2000, 2006). Laterally, the anterior arm of the postorbital overlies the supraorbital surface of the frontal (fig. 3). The frontal contacts the parietal posteriorly along a straight transverse suture; however, this contact is difficult to distinguish due to the distortion and high degree of fusion. CT slices show a slightly overlapping suture.

The dorsal surface of the frontal is elevated slightly above the orbit to form a pronounced supraorbital rim (fig. 3). Posterolaterally, the frontal contacts the postorbital and has a descending process that buttresses the dorsal part of the postorbital bar. The posterior part

of this bar forms the anterior corner of the supratemporal fossa. In comparison with other putatively more derived oviraptorosaurs such as *Citipati osmolskae*, *Oviraptor philoceratops*, and *Rinchenia mongoliensis*, the frontal lacks fenestrae or obvious pneumatic features (although CT imagery shows that the anterolateral portion of the frontal is pneumatized by the lacrimal recess [figs. 9 and 10]).

PARIETAL: The parietals are poorly preserved and few features can be accurately determined (figs. 4A and 5B). Nevertheless, it is apparent that the parietals were fused and contacted the frontal in a transverse suture near, or just posterior to the postorbital bar. CT imagery reveals that this contact is overlapping, with the frontal lying on the dorsal surface of the parietal. Further posteriorly a small sagittal crest develops and is confluent with a nuchal crest that defines the posterior boundaries of the supratemporal fossa (fig. 4A), also present in *Ornitholestes hermanii* (Osborn, 1903) and other coelurosaurs (Turner et al., 2007).

JUGAL: The jugal forms the ventral and posteroventral margin of the orbit and is only preserved on the right side of the skull (fig. 3). The jugal is dorsoventrally broad and straplike along its entire length, in contrast to the rodlike condition of the suborbital jugal seen in all more derived oviraptorosaurs for which material is available, with the exception of *Caudipteryx zoui* (Ji et al., 1998; Zhou et al., 2000).

The lateral surface of the jugal exhibits a longitudinal ridge that emanates from a point at the ventral margin just below the contact with the preorbital bar and terminates posteriorly at the level of the postorbital process in the middle of the element. Anteriorly the jugal receives the maxilla in a cuplike contact where the maxilla inserts into a concave depression on the anterior surface. Just posterior to this contact a small ascending process extends along the posterior margin of the preorbital bar of the lacrimal. The dorsal and ventral edges of the jugal are subparallel, and there is a dorsal expansion midway through the element to form the postorbital process. The postorbital process of the jugal is triangular and reaches only half the height of the orbit; the remainder of the postorbital process is made up of the postorbital, so that each

element contributes equally to the structure (Norell et al., 2006). The posterior surface of the jugal forms the anteroventral border of the infratemporal fenestra. The jugal extends posteriorly from the postorbital bar toward the quadratojugal forming the entire ventral border of the infratemporal fenestra; however, the posterior process and other features of this region have been extensively restored disallowing any accurate description of morphological detail.

POSTORBITAL: The postorbital is a T-shaped bone with posterior and anterior processes of subequal length. This element is preserved best on the right side of the skull (fig. 3). The postorbital comprises most of the posterior margin of the orbit (approximately 2/3 of the entire length). Anteriorly, the postorbital overrides the dorsal surface of the frontal at the posterodorsal corner of the orbit to form an overlapping suture. The posterior process of the postorbital abuts the dorsal surface of the squamosal along an extensive longitudinal suture (fig. 4A).

The anterior process extends anteriorly about 1/3 the length of the orbit to form a small posterior portion of the supraorbital rim. The anterior process is dorsally convex as it is in other maniraptorans (e.g., Currie, 1985, 1995; Norell et al., 2006) and alvarezsaurids (Chiappe et al., 1998). The vertical jugal process tapers to meet the jugal, which it contacts along its posterior surface in an extensive diagonal suture. The postorbital does not extend as far ventrally as in *Citipati osmolskae*, in which it nearly reaches the suborbital bar (Clark et al., 2002: fig. 1). Instead, it is similar to the condition in *Caudipteryx zoui* (Ji et al., 2001) or *Khaan mckennai* (Clark et al., 2001) and with the jugal makes up an equal portion of the postorbital process (fig. 3). The posterior surface of the postorbital bar is straight, causing the anterior margin of the infratemporal fenestra to be rectangular in shape. The long posterior process of the postorbital forms the anterodorsal corner of the triangular infratemporal space. The lateral surface of the postorbital is excavated to form a shallow trough.

SQUAMOSAL: The squamosal is a tetraradiate bone that is exposed on the lateral surface of the skull posterodorsal to the infratemporal

fenestra (fig. 3A). The squamosal is preserved only on the right side of the skull, where it lies in articulation. Anteriorly, the thick postorbital process tapers to meet the postorbital to form a complete division between the supratemporal and infratemporal space. Posteriorly there is an extensive contact with the exoccipital, and a small ventrally directed paroccipital process extends posteriorly (figs. 4A and 5B). This process has some lateral excursion forming a slight roof over the dorsal head of the quadrate. This condition, however, is not as extensive as the large squamosal hood that covers the quadrate head in dromaeosaurs like *Tsaagan maangas* (see Norell et al., 2006) and *Velociraptor mongoliensis* (Norell et al., 2004). A larger posterior process also is present in other oviraptorosaurs such as *Citipati osmolskae* (see Clark et al., 2002: fig. 2). The ventral or quadratojugal process of the squamosal parallels the quadrate shaft, overlying the lateral surface of the quadrate. The quadratojugal process of the squamosal tapers to meet and underlie the ascending process of the quadratojugal at about the midpoint of the quadrate shaft. Thus, the ventral extent of the quadratojugal ramus of the squamosal cannot be determined (fig. 3A).

QUADRATOJUGAL: The quadratojugal is preserved only on the right side (fig. 3A). Unlike most other oviraptorosaurs, the quadratojugal of *Incisivosaurus gauthieri* has three distinct processes. The anterior jugal process is extensively reconstructed, and therefore its anterior extent cannot be determined. The squamosal and quadrate processes are vertical and situated at approximately a 90° angle to the jugal ramus. The squamosal process, described above, underlies the ventral process of the squamosal. The quadrate ramus is large and is fused to the lateral surface of the quadrate so that these two elements together form the articulation with the mandible. The jaw articulation lies well ventral to the level of the infratemporal fenestral bar. Although a ventrally placed mandibular articulation is common in oviraptorids, it is never expressed to the extreme degree that is seen in *I. gauthieri*.

QUADRATE: Only the right quadrate is present, and many features are not well preserved (fig. 3A). Nevertheless, the quadrate is elongate and nearly vertical so that it is visible primarily in lateral view, posterior to the dorsal shaft of the quadratojugal ramus of the squamosal between the posterior process of the squamosal and the paroccipital. This configuration adjacent to the braincase makes it likely that the quadrate articulated both with the braincase and the squamosal as has been reported in other oviraptorosaurs (Maryańska and Osmólska, 1997; Maryańska et al., 2002; Kundrát and Janáček, 2007), alvarezsaurids (Chiappe et al., 1998), troodontids, and derived avialans (Baumel and Witmer, 1993). The posterior surface of the quadrate does not expand significantly ventrally at the mandibular articulation as in *Citipati osmolskae* or *Khaan mckennai*.

The posterior surface is unremarkable except for a small pneumatic foramen present about midway down the shaft. The quadrate contacts the quadratojugal via a dorsoventrally elongate straight suture, observable only in posterior view (fig. 5B). CT imagery reveals that the quadrate is hollow and presumably pneumatic as is the condition in most other maniraptorans (fig. 11; Witmer, 1990, 1995, 1997).

Anteriorly the quadrate with the pterygoid and possibly the epipterygoid forms a large flange, which hides the braincase from lateral view inside the infratemporal fenestra (fig. 3). This feature is present in some other oviraptorosaurs, including oviraptorids but excluding *Caudipteryx zoui* (Ji et al., 1998; Zhou et al., 2000; Osmólska et al., 2004). Although the flange is well preserved on the right side of the skull, sutural boundaries cannot be determined. The flange as a whole is extensive and fills the ventral 2/3 of the visible area on the braincase wall. It is composed of very thin bone and the dorsal boundary forms a convex border increasing in height anteriorly. As can be determined from the right side, this structure terminates on the braincase just anterior to the trigeminal foramen (fig. 3).

LATERAL SURFACE OF THE BRAINCASE

Figures 3 and 12

Little can be determined in the way of sutural boundaries on the braincase wall,
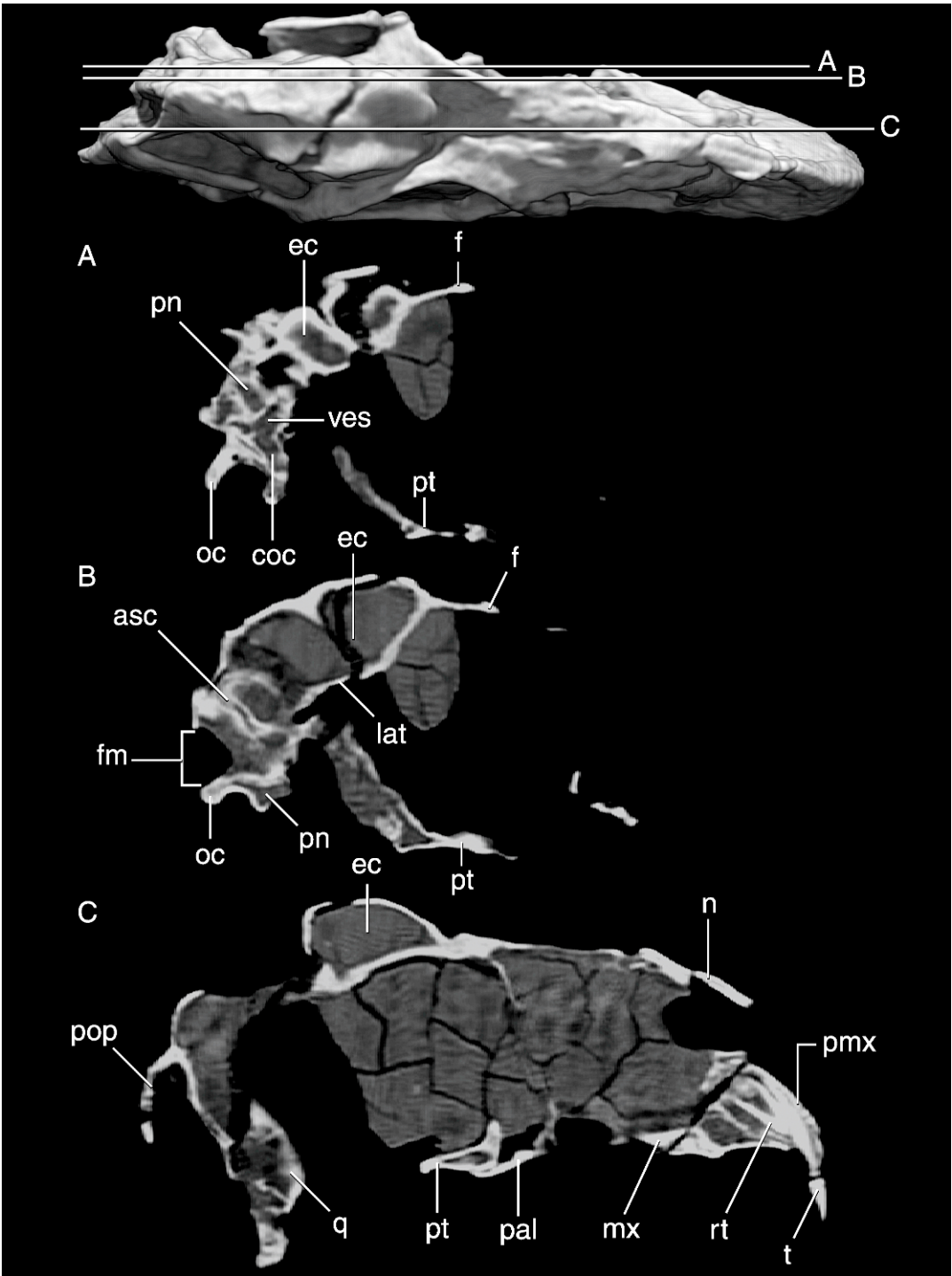
Fig. 11. Sagittal CT slices through the skull of the holotype of *Incisivosaurus gauthieri* (IVPP V 13326). Abbreviations in appendix 1.

therefore features of this area will be discussed in relation to the middle ear opening. The lateral wall of the braincase is obscured on the right side by the large wing made up of the pterygoid, quadrate, and epipterygoid, a feature that is shared by other oviraptorosaurs and therizinosaurs. The left braincase wall on IVPP V 13326 is completely exposed because the quadrate and quadratojugal are not preserved. The paroccipital process also is missing on the left side of the braincase. A large fracture runs obliquely through the middle of this portion of the skull further obscuring features of the braincase (fig. 4 and 13). The exoccipital, opisthotic, prootic, parabasisphenoid, laterosphenoid, orbitosphenoid, and squamosal are all exposed on the lateral surface (figs. 3 and 12). The braincase is divided by a horizontal ridge that extends from the paroccipital process to the inside of the supratemporal fossa just dorsal to the trigeminal foramen (CN V). This ridge divides the braincase into laterally (ventral) and more dorsolaterally (dorsal) directed surfaces. The crista continues ventrally onto the left basal tuber of the basioccipital.

The anteriormost extent of the braincase is formed by the ossified orbitosphenoids and laterosphenoids. The orbitosphenoids are poorly ossified and visible only in CT imagery (fig. 10). These elements contact the frontals dorsally and the laterosphenoids posteriorly. The orbitosphenoids extend anteriorly as thin splints of bone that together form a "V" (most easily seen in coronal cross section) and floor the space for the olfactory tracts (fig. 10). The laterosphenoid, in contrast, is well ossified and best preserved on the left side of the specimen (fig. 3). There is no trace of the pneumatization that is present in the laterosphenoid of oviraptorids (Osmólska et al., 2004). The laterosphenoid contacts the frontal dorsally, parietal posterodorsally, parabasisphenoid ventrally, orbitosphenoid anteriorly, and its posterior margin overlays the prootic. The external surface of the laterosphenoid is flat and relatively structureless. The entire extent of the internal surface is concave for the reception of the optic tectum. The laterosphenoid is notched approximately halfway up its posterior margin to form the anterior portion of the foramen for the trigeminal

nerve (CN V); the remainder of the fenestra is formed by contributions of the prootic and parabasisphenoid (fig. 12). A large unossified space is present along the midline between the two laterosphenoids. This single midline space for the exit of the optic nerve (CN II) opens anteroventrally.

Posterior to the laterosphenoid is the prootic, an irregularly shaped bone that contacts the laterosphenoid anteriorly, parietal dorsally, exoccipital posteriorly, and is overlain by the squamosal laterally (figs. 3B and 12). The lateral surfaces of the prootic and opisthotic form the majority of the middle ear, and this surface is marked by a distinct tympanic cavity. The middle ear opening is an elliptical opening at the base of the aforementioned crista that runs the length of the braincase (fig. 12). The posterodorsal margin of the middle ear is formed by the paroccipital process, of which only the base remains on the left side. The middle ear cavity is divided into the anterior fenestra vestibuli and the posterior fenestra pseudorotundum by a crista interfenestralis, which is deeply recessed and oriented diagonally from anteroventral to posterodorsal. The recessed crista interfenestralis is not described in oviraptorosaurs but similar to the condition found in some dromaeosaurs and troodontids (e.g., Currie, 1985; Norell et al., 2004; Makovicky et al., 2003). In CT imagery the medial aperture of the adult remnant of the metotic fissure, the metotic foramen, is visible through the fenestra pseudorotundum (fig. 9C). The metotic foramen is a small slit on the internal surface of the braincase (fig. 13).

Dorsal to the middle ear and separated from it by a diagonal buttress is a shallow depression that forms the dorsal tympanic depression. Two small foramina pierce the dorsal border of this fossa and lead into the dorsal tympanic recess. These foramina are visible only in the CT imagery (fig. 11). Anterior to the tympanic cavity is a wide pila otica that is pierced by the small opening for the facial nerve (CN VII; fig. 12). The canal for the facial nerve can be traced in the CT images traveling a short distance medially and opening into the internal acoustic fossa on the internal surface of the prootic (fig. 13). Anterior to the facial foramen on the external
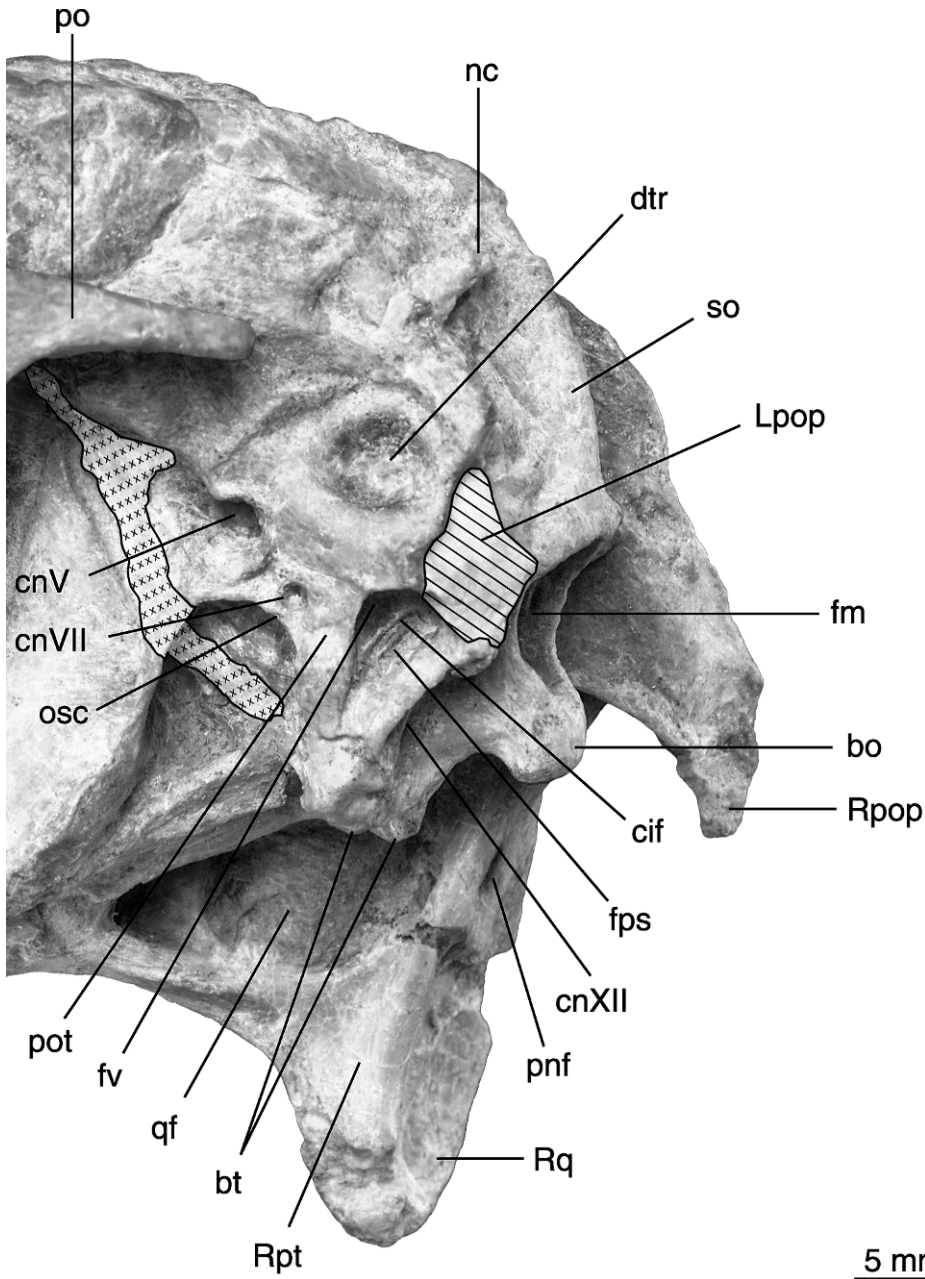
Fig. 12. Ventrolateral view of the left side of the braincase of the holotype of *Incisivosaurus gauthieri* (IVPP V 13326). Abbreviations in appendix 1.

surface is a groove that runs anteroventrally and terminates ventral to the trigeminal fenestra (CN V; figs. 3B and 12). This groove likely transmitted the anterior ramus of the facial nerve. Ventral to this groove, situated between the tympanic cavity and the trigeminal foramen, is the well-developed dorsally convex otosphenoidal crest. The otosphenoidal crest runs from the facial foramen to halfway through the length of the trigeminal
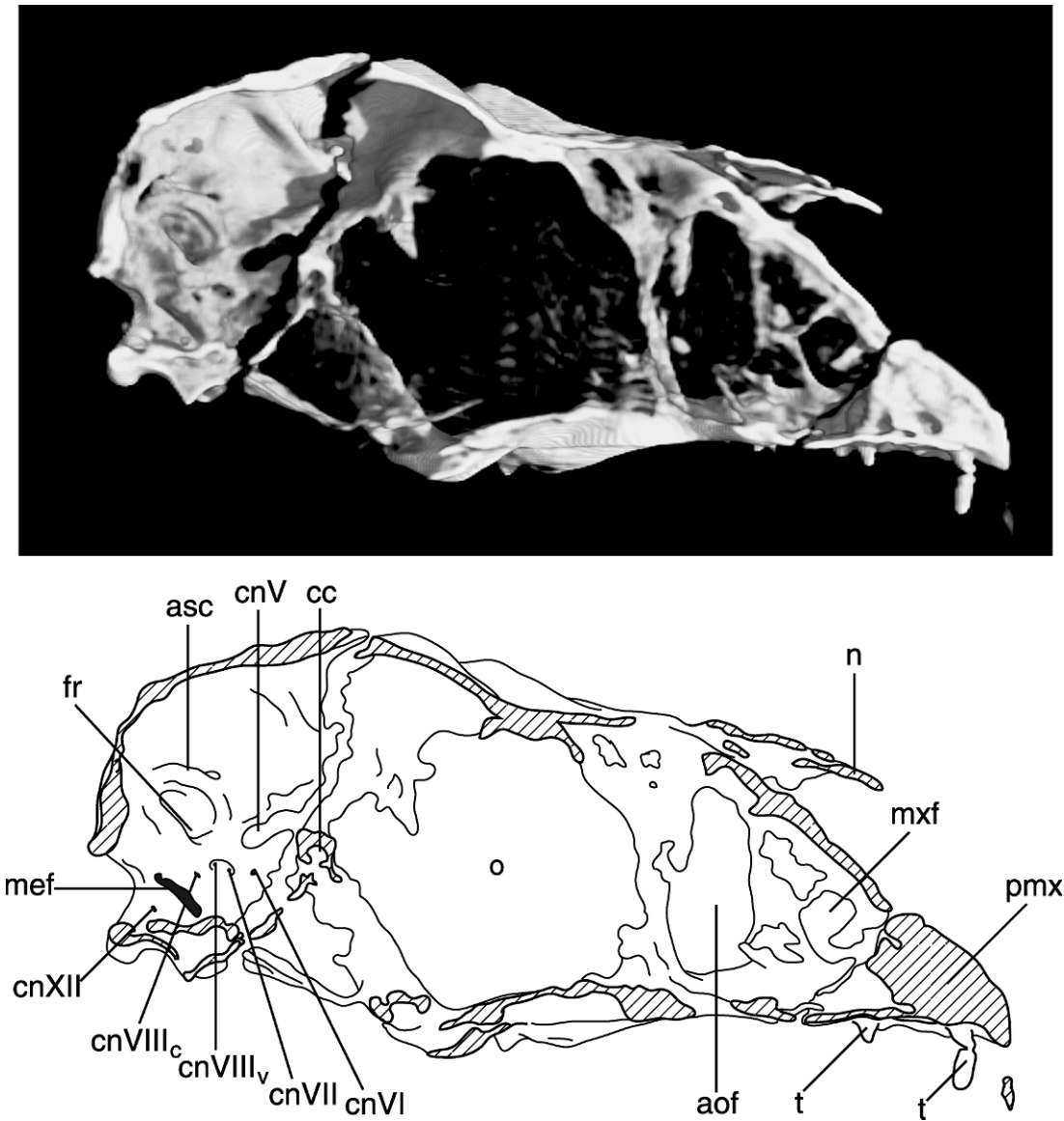
Fig. 13. Sagittal cutaway of a virtual rendering of the skull of the holotype of *Incisivosaurus gauthieri* (IVPP V 13326) with the matrix rendered transparent. Abbreviations in appendix 1.

fenestra. A well-developed otosphenoidal crest is described in *Chirostenotes pergracilis* and troodontids (Sues, 1997; Osmólska et al., 2004; Norell et al., 2006) and marks the anterior extent of the middle ear cavity. Anterior to the facial foramen is the large, "hourglass shaped" trigeminal fenestra. The prootic makes up by far the largest contribution to this partially divided fenestra.

OCCIPITAL SURFACE OF THE BRAINCASE

Figures 5b and 12

Because the skull is distorted many of the features on the posterior region of the skull are difficult to decipher. The skull is broken at the base of the left paroccipital process, which is missing. In general view, the right parocci-pital process drops below the level of the

occipital condyle (fig. 5B). This arrangement is a common feature of oviraptorids (Osmólska et al., 2004), yet how much this condition is influenced by crushing of the specimen is difficult to determine. The occiput is large (at least three times the size of the occipital condyle) and oval, with little of the anterodorsal slope that characterizes some oviraptorid braincases (e.g., *Citipati osmolskae*; Clark et al., 2002). Also because the bones are fused together, individual elements are difficult to discern. The parietals, supraoccipital, exoccipitals, and basioccipital are exposed on the external surface of the posterior braincase (fig. 5B). The nuchal crest is present but only weakly developed. The cerebellar prominence extends dorsoventrally from the nuchal crest ventrally to the foramen magnum. A large oval depression lies on either side of the cerebellar prominence. As in all oviraptorosaurs, the paroccipital processes are oriented ventrally and have a characteristic pendant shape. The foramen magnum is dorsoventrally elongate with a secondary circular depression at the base within the basioccipital, resulting in an opening that has a longer height than width. This shape of the foramen magnum is somewhat novel and differs from most coelurosaurs except some troodontids and dromaeosaurs (Norell et al., 2006). The unusual shape may be due to a minor amount of mediolateral deformation.

The supraoccipital is roughly triangular in shape and forms the majority of the posterior braincase. The contacts of the supraoccipital are difficult to delineate because of the high degree of fusion. Lateral to the central keel are crescentic depressions that may correspond to the epiotic sutures. The element contributes a portion to the dorsal border of the foramen magnum. The entire cerebellar prominence lies within the supraoccipital. The internal surface of the supraoccipital is relatively featureless except for a groove traveling dorsoventrally along its lateral margin that housed the posteriormost extent of the anterior semicircular canal (fig. 11B). The external occipital vein, which served to drain the lateral regions of the cerebellum, exits via a small fenestra between the supraoccipital and parietal at the level of the dorsal margin of the foramen magnum (fig. 5B).

Lateral to the occiput (as preserved on the right side of the skull) is the exoccipital. The exoccipital contacts the supraoccipital dorsomedially, the basioccipital ventrally, the opisthotic anteriorly, and the squamosal laterally (figs. 5B and 12). The exoccipital comprises the majority of the paroccipital processes of *Incisivosaurus gauthieri* with contributions from the opisthotic and squamosal. These processes are highly pneumatic and a foramen can be seen penetrating the distal end through the boundary between the exoccipital and the opisthotic (fig. 9). The paroccipital process extends laterally and ventrally tapering to a ventrally directed tip. The ventral border of the process is convexly rounded as is seen also in *Avimimus portentosus* (Kurzanov, 1987; Hwang et al., 2004; Norell et al., 2006). This condition differs from *Chirostenotes pergracilis* and *Citipati osmolskae*, which possess slender, elongate dorsal and ventral edges (Sues, 1997; Hwang et al., 2004; Norell et al., 2006). A small ridge runs from the occiput onto the surface of the paroccipital process and continues onto the basioccipital (fig. 12). The exoccipital forms the lateral borders of the foramen magnum and extends ventrally onto the stalk of the occipital condyle, but the element does not form any part of the articulating surface.

The ventrolateral region of the occipital surface between the basioccipital and exoccipital is deeply furrowed and a large fenestra is present in the dorsal region of this fossa (between the exoccipital and basioccipital; fig. 5B) through which the jugular vein, glossopharyngeal (CN IX), vagus (CN X), and accessory (CN XI) cranial nerves likely exited, following the basal reptilian pattern (Goodrich, 1930; Romer, 1956). This condition differs from other oviraptorosaurs in which these foramina lie in the same plane as the surface of the exoccipital rather than in a depression (Hwang et al., 2004; Norell et al., 2006). The corresponding canal leads into the adult remnant of the metotic fissure that comprises the space between the occipital bones and the otic capsule (adult otic bones).

The basioccipital is well preserved and forms the floor of the braincase, the ventral border of the occiput and the occipital condyle (figs. 5B and 12). The basioccipital is bordered

by the exoccipitals dorsolaterally, the parabasisphenoid anteriorly, and the prootic and optisthotic dorsolaterally. The basioccipital forms the majority of the occipital condyle (with a small contribution from the exoccipitals), which is mediolaterally elongate and has a kidney shape. The neck of the occipital condyle is short but not constricted, similar to the shape that is present in other coelurosaurs (Norell et al., 2006). Medial to the opening within the fossa at the base of the neck of the occipital condyle are two small foramina for the hypoglossal nerves (CN XII). These canals lie completely within the basioccipital and can be traced in the HRCT imagery traversing the short distance from the posterior surface to the floor of the braincase (figs. 9D and 13). The ventral region of the aforementioned occipital furrow is penetrated by numerous foramina that lead into a pneumatic space within the basioccipital (fig. 9E). The weakly developed basal tubera are located ventral to the occipital furrow and extend ventrolaterally. A shallow saddle separates the basal tubera (figs. 4B, 5B, 12).

VNTRAL SURFACE OF THE BRAINCASE

Figures 4B, 8, 12

The ventral surface of the braincase is obscured by the pterygoids, which extend posteriorly to the anterior border of the basioccipital; however, CT imagery aids in the description of this region of the skull. The ventral surface is well preserved except for some slight deformation on the posterior left side. It is composed of the basioccipital, basisphenoid, and parasphenoid. Unlike other oviraptorosaurs, the basisphenoid and basioccipital are elongate making up approximately 20% of the entire skull length.

A shallow longitudinally oriented basisphenoid depression is the most prominent feature of the ventral braincase (fig. 4B). It is bounded posteriorly by the basal tubera that are hollowed out into two C-shaped structures. A short septum runs along the midline and divides the posterior part of the depression into right and left chambers. Anteriorly, the septum disappears and the depression shallows. It is bounded laterally by low ridges, which also flatten anteriorly grading into the basipterygoid processes. The basipterygoid processes are short, but unlike other oviraptorosaurs they are displaced from the midline and oriented anterolaterally rather than strictly laterally.

Anterior to the basioccipital is the poorly ossified parabasisphenoid. The boundary between these two elements is not well defined due to the high degree of fusion of the braincase as well as a fracture that runs transversely through this region. The parabasisphenoid also contacts the laterosphenoid dorsolaterally and extends dorsally to form the floor of the braincase that houses the sella turcica (fig. 9). The element slopes ventrally anterior to its contact with the laterosphenoid, as it does in all other oviraptorids (Norell et al., 2006). At the anteriormost extent of the element, the pneumatic, platelike parasphenoid rostrum extends anterodorsally roughly two-thirds through the length of the orbit. Although pneumatic, the base of the parasphenoid rostrum is not expanded (as it is in ornithomimosaurs and some troodontids; Turner et al., 2007). At the contact with the laterosphenoid, the parabasisphenoid forms a small portion of the ventral border of the trigeminal fenestra. The entrance of the carotid arteries cannot be determined on the ventral surface of the braincase; however, the canals can be seen in the CT imagery running through the parabasisphenoid and opening at the point of flexure of the parabasisphenoid (fig. 9B). The cranial carotid canals anastomose within the parabasisphenoid and then separate again before exiting into the endocranial cavity. The basipterygoid processes are weakly developed and probably were not fully ossified within *Incisivosaurus gauthieri*, similar to therizinosaurs and other oviraptorosaurs (Norell et al., 2006). Accordingly, the basipterygoid recesses that are present in *Oviraptor philoceratops* and *Rinchenia mongoliensis* are not present in this specimen (IVPP V 13326).

ENDOCRANIAL CAVITY, INNER EAR, AND TYMPANIC RECESSES

Figures 9, 11, 13–14

On the internal surface of the braincase, the floccular recess is easily visible in CT imagery and three-dimensional reconstruc-
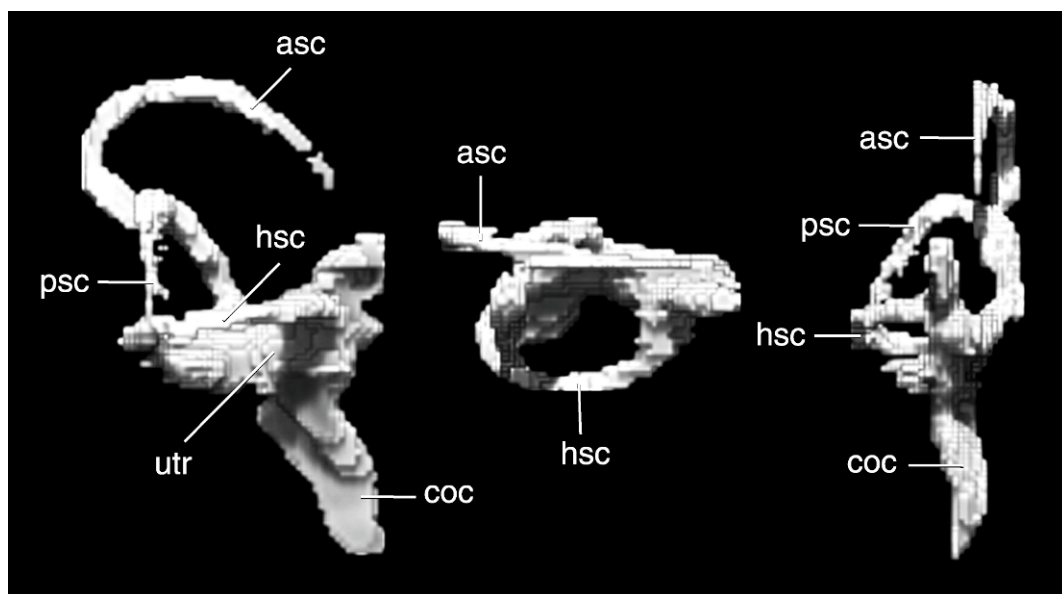
Fig. 14. Lateral, dorsal, and anterior views (respectively) of the endocasts of the inner ear of *Incisivosaurus gauthieri* (IVPP V 13326). Abbreviations in appendix 1.

tions (fig. 13). The large rectangular recess lies posterior to the opening for the trigeminal nerve at approximately the same horizontal level. The floccular recess is located wholly within the prootic/opisthotic (although sutures are not visible on the internal surface of the braincase), oriented posteroventrally, and bounded posteriorly by the horizontal semicircular canal. The entire fossa is outlined in the vertical plane by the inflated anterior semicircular canal (figs. 11B and 14). Inflation of the anterior semicircular canal is found in many paravians (Norell et al., 2004) but is not present in derived oviraptorosaurs like *Citipati osmolskae* (Clark et al., 2002).

The triangular internal acoustic fossa is located just ventral to the floccular recess and in life houses the geniculate ganglion. The anteroposteriorly wide fossa contains three foramina (fig. 13). The dorsalmost foramen transmitted the facial nerve (CN VII). The corresponding canal exits directly laterally onto the lateral surface of the braincase (fig. 9B; described above). The anteroventral foramen is visible only with CT imagery (fig. 13), opens into the inner ear (vestibular space), and transmitted the anterior ramus of the vestibulocochlear nerve (CN VIII). The

posteriormost foramen within this fossa pierces the internal wall of the braincase. This foramen leads into the inner ear (cochlear canal) and transmitted the posterior ramus of the vestibulocochlear nerve (CN VIII). Posterior to the floccular recess is the metotic foramen, a small slitlike opening that leads into the adult remnant of the metotic fissure. The opening is oriented posterodorsally and transmitted the glossopharyngeal (CN IX), vagus (CN X), and accessory nerves (CN XI). On the floor of the braincase, anterior and lateral to the foramen magnum are two small foramina for the hypoglossal nerves (CN XII).

The structure of the ear region of *Incisivosaurus gauthieri* is similar to the condition found in avians and some paravians (Makovicky et al., 2003; Norell et al., 2004, 2006). The osseous portion of the anterior semicircular canal is kidney shaped, and the long axis is rotated somewhat posteriorly (figs. 11 and 14). The posteriormost extent of the anterior semicircular canal also is exposed on the occipital surface of the braincase. The osseous portion of the horizontal semicircular canal is circular in shape (figs. 9B and 14). A small foramen branches off the posterior ramus of the posterior semicircular canal and

travels posteriorly to exit on the supraoccipital on the occipital surface of the braincase. The three semicircular canals meet at the large utriculus (fig. 14). The cochlea also is similar to the typical avian type and curves ventro-medially (figs. 9D, 11A, and 14).

MANDIBLE

Figures 6, 7

Although only the anterior parts are well preserved, the dentary rami are closer to parallel than they are in other oviraptorosaurs including *Caudipteryx zoui* (Ji et al., 1998; Zhou et al., 2000). It lacks the high coronoid eminence of Oviraptoridae, the concave margin along the dorsal dentary border in Caenagnathidae, and the ventrally concave margin and depressed anterior end of Caudipterygidae (Ji et al., 1998; Zhou et al., 2000). The mandibular fenestra is large and anteroposteriorly elongate (see fig. 11; Barsbold, 1981; Sues, 1997) with no surangular spine entering the fenestra as in caenagnathids and oviraptorids (fig. 6).

DENTARY: The dentary has an unusual morphology and is best preserved on the right (fig. 6). This element is deep and, although distorted anteriorly, the borders converge at the symphysis giving it an anteriorly pointed appearance in lateral view. A row of small foramina on the lateral surface parallels the dorsal margin of the dentary for approximately 1/3 the length of the mandible. The anteriormost foramen is the largest, at about twice the diameter of the subsequent foramina. This area likely was covered with a keratinous beak during life.

Anteriorly the dentaries curve toward the midline to form the U-shaped symphysis as in other oviraptorosaurs, some troodontids, and some ornithomimosaurs. The symphysis is complex and somewhat distorted (fig. 6A). In ventral view there is a large troughlike symphyseal shelf where the upper ''rodentiform'' teeth occluded (fig. 7C). Posterior and ventral to this is a secondary symphyseal shelf that may have served to strengthen the symphysis.

SPLENIAL: The right splenial, a large flat plate on the medial surface of the dentary, is well preserved (fig. 7). It extends anteriorly to the level of the fourth tooth where it forms the dorsal, ventral, and posterior margins of the mandibular fenestra. It does not approach the symphysis as in oviraptorosaurs such as *Khaan mckennai* (Clark et al., 2001) and the unnamed Zamyn Khondt form (Barsbold, 1997). Posteriorly the splenial is straplike and overlies the dentary and the angular nearly to the level of the posterior terminus of the mandibular fenestra.

ANGULAR AND PREARTICULAR: The angular cannot be distinctly differentiated from the dentary on the lateral surface of the mandible (fig. 6). Presumably it articulates with the prearticular to form the bar that forms the ventral border of the mandibular fenestra and the ventral surface of the mandible.

SURANGULAR: The surangular is much thicker than the angular and contacts the dentary at the anterior margin of the mandibular fenestra (fig. 6). Just posterior to this contact is a small but distinct coronoid eminence. The surangular broadens transversely posterior to the coronoid eminence and dorsal to the mandibular fenestra.

DENTITION

Figures 2–7

PREMAXILLARY TEETH: Four teeth are present in each premaxilla (figs. 3–5). Undoubtedly the strangest thing about *Incisivosaurus gauthieri* is the anteriormost pair of large incisorlike premaxillary teeth. Teeth with this morphology are unknown in any other theropod dinosaur. In cross section they are subcircular at their bases. The posterior surface becomes flatter distally, and the anterior and posterior surfaces are delimited by carinae. More distally the posterior or interior surface of the tooth is modified by flat wear surfaces that are extensive and span nearly half the length of the tooth. These wear facets expose the dentine on the interior of the tooth (fig. 4B). Although the tips of the teeth are broken, they apparently were convex and crescent shaped in anterior view, a morphology that corresponds with the edentulous mandibular symphyseal shelf to which they occluded.

One of the more vexing questions concerning *Incisivosaurus gauthieri* is the nature of the large incisorlike premaxillary teeth. Xu et al. (2002a) compared these teeth to the incisors found in rodent mammals, which display a similar morphology. Unlike mammals, however, these teeth in *I. gauthieri* are not ever growing. Our CT analysis offers definitive

evidence showing the presence of a large replacement tooth just behind the exposed tooth (fig. 11C). Interestingly, this tooth is chisel shaped into the same occlusal angle as the erupted tooth.

Posterior to the incisorlike tooth in the premaxilla is a thin tooth with a very tall (7 mm) crown. In cross section these teeth are oval and have labiolingual surfaces defined by very small carinae (fig. 4B). These teeth end in a blunt chisel point formed by the convergence of the labial and lingual surfaces. Posteriorly there appear to have been another pair of similarly shaped teeth, which are represented only by their roots.

MAXILLARY TEETH: There are nine maxillary teeth in each maxilla (figs. 3 and 4B). The maxillary teeth are separated from the premaxillary teeth by a short symphysis and lack serrations or denticles (Xu et al., 2002a). The teeth are smaller than the posterior premaxillary teeth. The tooth crowns are slightly expanded above the bases and display extensive wear facets on their lingual surfaces.

DENTARY TEETH: The dentary has positions for approximately nine small teeth (figs. 6 and 7). Anteriorly, the teeth lie in distinct alveoli, while posteriorly they appear to lie in a common groove. The anteriormost right dentary tooth is just erupting and is labiolingually compressed. The lingual surface is slightly concave, and strong carinae separate the labial from lingual tooth surfaces. It is slightly procumbent. There is no indication of serrations along the carinae at the base of the tooth. The next preserved tooth is in position 3. It is the best-preserved tooth on either dentary. It is much more bulbous than the first tooth and, although it is not well preserved, the labial and lingual surfaces are roughly symmetric and are separated by a faint carina. The more posterior teeth are visible only in cross section at their bases because of breakage during preparation. These teeth resemble the third tooth, perhaps being slightly more labiolingually compressed.

CAST OF ENDOCRANIAL CAVITY

Figures 15–17

The braincase of *Incisivosaurus gauthieri* is complete (fig. 3), and therefore we were able to reconstruct a complete endocast of the endocranial volume along with endocasts of the overlying pneumatic cavities and inner ear structures (figs. 14–17). The volume of the cranial cavity is 5.69 cm^3. Overall, the endocranial cast is mediolaterally compressed. This shape is reflected most prominently in the hindbrain (figs. 16 and 17). The cerebral and pontine flexures are well developed (fig. 15). The apex of the cerebral flexure is at the optic tectum and that of the pontine flexure is at the cerebellum (as defined by Hopson, 1979). The endocast has an unusual orientation within the braincase of *I. gauthieri*, with the cerebral hemispheres sitting entirely dorsal to the orbits and not extending posteriorly. The widest portion of the endocast is approximately halfway along the anteroposterior length of the cerebral hemispheres. A fracture runs transversely across the braincase. This taphonomic structure is reflected on the endocranial cast.

The forebrain includes the olfactory bulbs and tracts, the cerebral hemispheres, the pituitary body, and the optic nerve (CN II). The olfactory tracts of *Incisivosaurus gauthieri* lie within the frontals and orbitosphenoid and are anteroposteriorly reduced, so that they do not extend anteriorly as far as in other theropods rather only to the anterior extent of the orbit (figs. 15 and 16). The reduction of the olfactory tracts may be a result of an anterior rotation of the cranial cavity within the braincase or the reduction of the rostrum relative to the skull as a whole. The parabasisphenoid is not well ossified in the region of the hypophyseal fossa; therefore, the pituitary body is not well defined (figs. 15 and 17). The only characteristic that reasonably can be determined about this structure is that it is relatively small compared with the rest of the endocranial volume. The carotid arteries can be seen anastomosing within the basisphenoid and separating again before entering the sella turcica; however, this feature is not reflected on the endocast (fig. 9B). The optic nerve exits through a large single opening formed by the junction of the laterosphenoids (fig. 17). The cerebral hemispheres are the most prominent structure of the forebrain and have a volume of approximately 2.56 cm^3. These structures are oblong and anteroposteriorly elongate. The cerebral hemispheres extend from the posterior margin of the
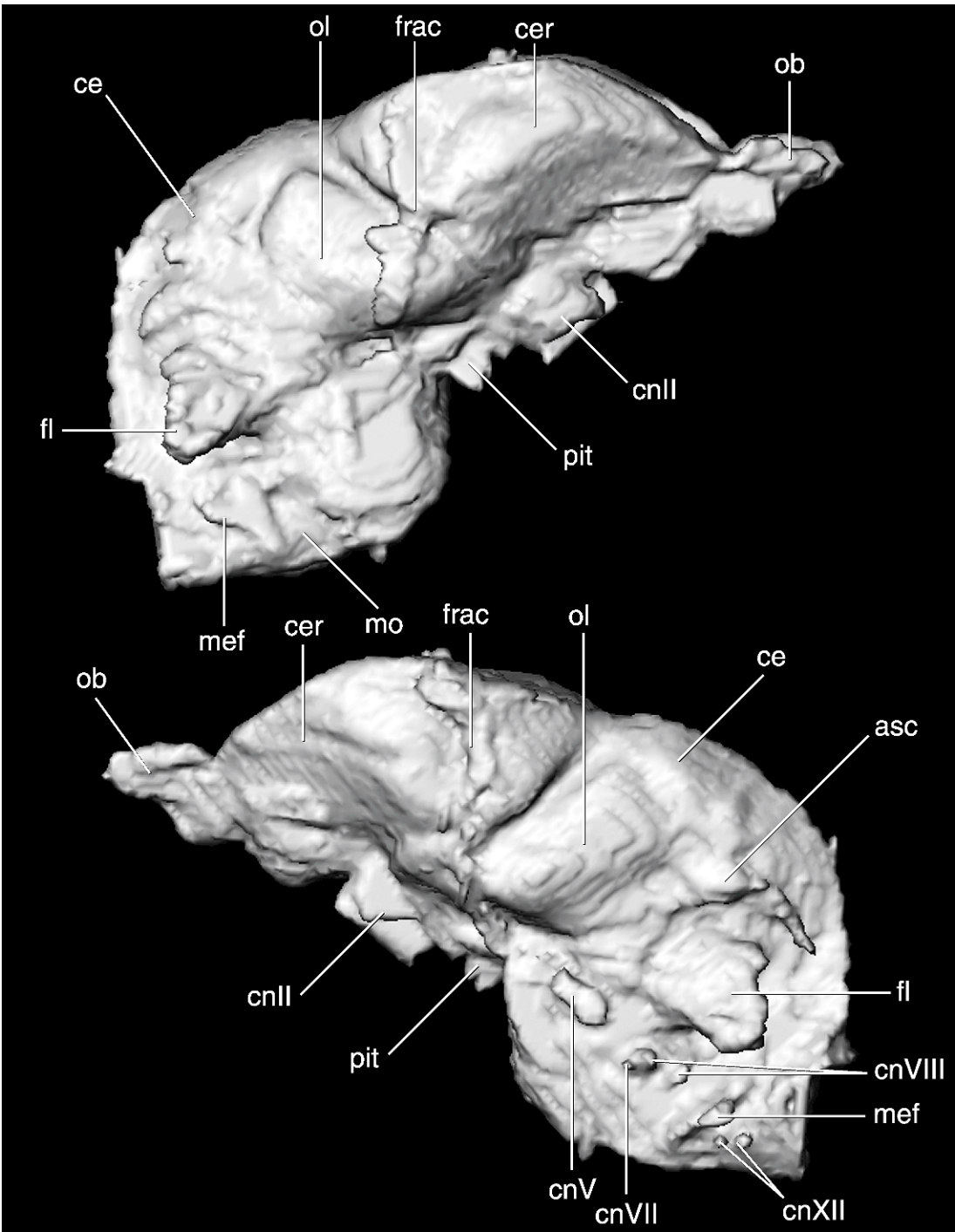
Fig. 15.   Lateral views of the endocranial cast of the holotype of *Incisivosaurus gauthieri* (IVPP V 13326). Abbreviations in appendix 1.
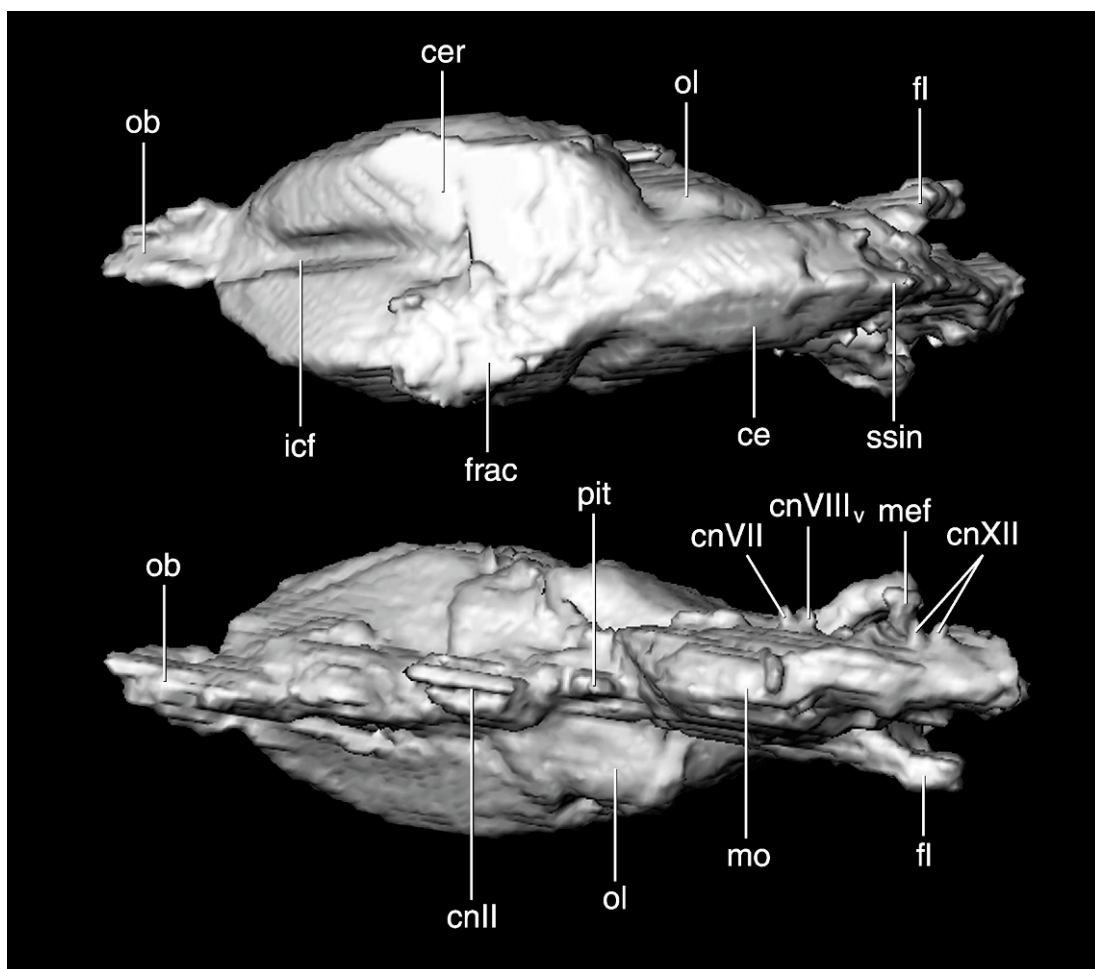
Fig. 16. Dorsal and ventral views of the endocranial cast of the holotype of *Incisivosaurus gauthieri* (IVPP V 13326). Abbreviations in appendix 1.

orbit anteriorly to approximately 2/3 the anteroposterior length of the orbit. A large interhemisphere fissure is present along the midline of the dorsal surface of the endocast (fig. 16). There is little lateral expansion of the cerebral hemispheres. Although they represent the widest region of the endocast, they are only 27% wider than the optic tectum (the next widest region). The anterior extent of the cerebral hemispheres (as mentioned earlier) is unique among theropods. Most other theropods do not have cerebral hemispheres that extend as far anteriorly. Again, this may represent an anterior extension of the forebrain or simply the anterior rotation of the cranial cavity within the skull.

The only structure of the midbrain visible on the endocast of *Incisivosaurus gauthieri* is the optic tectum (fig. 15). The paths of cranial nerves III (oculomotor) and IV (trochlear) cannot be determined from the endocranial cast. The optic tectum is housed almost entirely within the laterosphenoid with a small contribution from the frontal/parietal. The irregularly shaped structure covers a large area on the lateral surface, extending from the posterior limit of the cerebral hemispheres to approximately 1/3 the length of the cerebellum. The optic tectum is located posteroventral to the cerebral hemisphere (comparable to the placement in troodontids—appressed to the anterior region of the cerebellum;
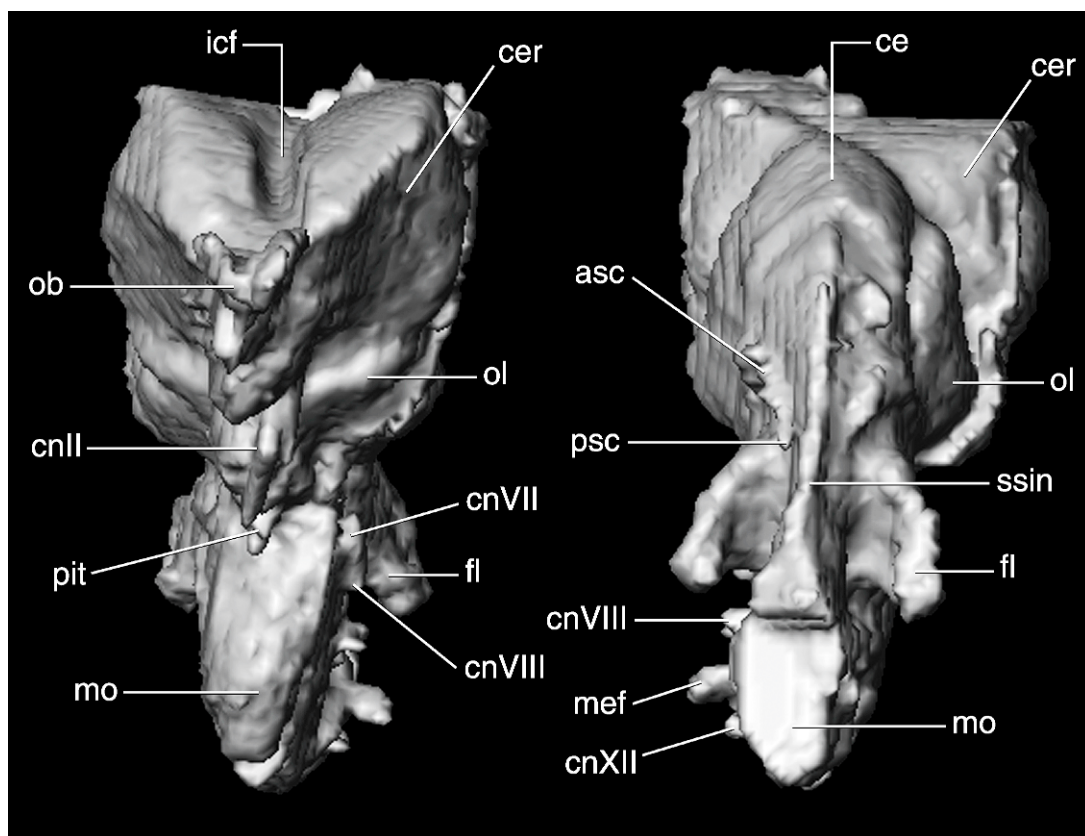
Fig. 17.   Anterior and posterior views of the endocranial cast of the holotype of *Incisivosaurus gauthieri* (IVPP V 13326). Abbreviations in appendix 1.

Franzosa, 2004). Although the optic tectum covers a large amount of surface area, the lateral protrusion is restricted.

The regions of the hindbrain (rhomben-cephalon) that are visible on the endocranial cast include the cerebellum, trigeminal (V), abducens (VI), and facial (VII) nerves (met-encephalon) as well as the medulla oblongata, glossopharyngeal (IX), vagus (X), and hypo-glossal (XII) nerves (myencephalon). The cerebellum is a pronounced structure that is extremely mediolaterally compressed (figs. 16 and 17), and runs about half of the length of the endocast. A distinct ridge runs along the midline of the cerebellum, likely correlating to the sagittal sinus. Running transversely along the cerebellum are a series of indentions that may correspond to cerebellar fissures, which suggest that the cerebellum was folded (see

Kundrát, 2007). At least four distinct impressions (fissures) are present on the cerebellum.

The floccular recess lies within the prootic, opisthotic, and exoccipital. The corresponding cast of the floccular recess projects postero-ventrally. The flocculus is mediolaterally compressed but fills the space between the semicircular canals. The facial (VII) nerve and both branches of the acoustic (VIII) nerve are present on the endocast anteroventral to the flocculus (fig. 15). The cochlear branch of the acoustic nerve extends ventrolaterally towards the cochlear duct. The vestibular branch reaches posteriorly to enter the inner ear. The facial nerve extends laterally to pierce the lateral surface of the prootic. The cast of the metotic foramen is located posterior to these nerves. The structure is elongate anteroventral to posterodorsal and lies directly posterior to

the cochlear duct. The glossopharyngeal, vagus, accessory and possibly the jugular vein traversed this space. Two small nerves that pierce the basioccipital are present posterior to the cast of the metotic foramen. These are interpreted as a pair of hypoglossal nerves (XII). The medulla oblongata is anteroposteriorly short in *Incisivosaurus gauthieri*. The mediolateral width of the medulla oblongata is compressed, but this structure is not out of proportion with the remainder of the hindbrain, which overall is mediolaterally compressed (figs. 16 and 17).

DISCUSSION AND CONCLUSIONS

This paper presents a detailed description of the only known specimen of an extremely unusual and important specimen (IVPP V 13326), *Incisivosaurus gauthieri*, from the Early Cretaceous Jehol beds of northeastern China. This study expands on previous descriptions (i.e., Xu et al., 2002a; Osmólska et al., 2004) by providing further details and reinterpretations of previously described cranial material as well as describing previously unknown regions of the skull such as the internal morphology attained through the use of computed tomography.

Although the phylogenetic position of oviraptorosaurs at the base of the maniraptoran family tree has remained fairly stable (e.g., Gauthier, 1986; Holtz, 1998; Lü, 2005; Turner et al., 2007; Senter, 2007), the interrelationships within the clade have received only cursory attention (e.g., Maryańska et al., 2002; Lü et al., 2004; Lü, 2005). Not surprisingly, these interrelationships appear to have a large effect on the overall position of Oviraptorosauria within Maniraptora, including topologies in which it falls within Avialae based on a series of derived characters (Maryańska et al., 2002; Osmólska et al., 2004; Lü et al., 2004). Studies that include Oviraptorosauria within Avialae, however, suffer from taxon sampling issues (e.g., excluding the primitive oviraptorosaur *Incisivosaurus gauthieri* as well as the paravian group Troodontidae; Maryańska et al., 2002; Osmólska et al., 2004). While it is not our intent here to reanalyze the interrelationships of Oviraptorosauria, the inclusion of *I. gauthieri* is able to break up the long branch leading to caenagnathids and oviraptorids and consequently to stabilize the overall position of this group within Maniraptora.

Not surprisingly, based on its phylogenetic position, *Incisivosaurus gauthieri* presents a mosaic of derived oviraptorosaurian characters and morphologies typical of nonavian theropods that fall outside of Oviraptorosauria. Characters such as the ventrally displaced mandibular articulation and ''pendant shaped'' ventrally curving paroccipital processes unambiguously support the placement of this specimen within Oviraptorosauria. IVPP V 13326 also shares derived features of the mandible with other oviraptorosaurs. For instance, an elongate retroarticular process and reduced splintlike coronoid help diagnose this specimen to Oviraptorosauria (Turner et al., 2007).

Incisivosaurus gauthieri, however, consistently falls at the base of this clade in phylogenetic analyses, lacking many of the more derived characteristics that diagnose oviraptorids and caenagnathids (Xu et al., 2002a; Lü, 2005; Norell et al., 2006; Turner et al., 2007). A rodlike jugal, crenulated palatal surface, toothlike projections on the palatal surface of the maxilla, straight lateral border of the quadrate shaft, constricted ventral fossa on the ectopterygoid, and a large coronoid eminence on the mandible are present in caenagnathids and oviraptorids but missing in *I. gauthieri* (figs. 3–6).

Incisivosaurus gauthieri also preserves many plesiomorphic characters that are not present in other oviraptorosaurs, most noticeable of which is the retention of teeth in the premaxilla, maxilla, and dentary (see Xu et al., 2002a), although premaxillary teeth are found also in *Caudipteryx zoui* (Ji et al., 1998; Zhou et al., 2000). We also offer an alternative interpretation to the original description of the palate (fig. 4B) that is consistent with the condition found in nonavian theropods outside of Oviraptorosauria. The confluent choana and subsidiary palatine fenestra of Xu et al. (2002a) is alternatively identified as solely the choana. Although the choana differs from the rounded shape present in other oviraptorosaurs (Osmólska et al., 2004), its elongate morphology closely resembles that of most theropods outside of this clade (see Clark et al., 1994: fig. 4, for comparison with fig. 4B).

A subsidiary palatine fenestra is not present in other oviraptorosaurs; however, a fully isolated fenestra is present in closely related theropods (Clark et al., 1994). The morphology of the cranial pneumatic spaces as well as that of the endocranium is discussed in further detail below.

CRANIAL PNEUMATICITY

There is little comparative material available to examine for cranial pneumaticity within oviraptorosaurs. No study has looked in depth at the pneumatic spaces within caenagnathids; however, several descriptions are available for comparison within Oviraptoridae (e.g., *Conchoraptor gracilis*, Kundrát and Janáček [2007]; *Citipati osmolskae* [Clark et al., 2002]) and theropods outside of Oviraptorosauria (e.g., Currie, 1985; Currie and Zhao, 1993; Witmer, 1997; Norell et al., 2004). The skulls of these derived oviraptorosaurs possess extremely complex pneumatic spaces. The pneumatic system in *Incisivosaurus gauthieri* corresponds more closely in complexity with that of theropods outside of Oviraptorosauria. The paranasal sinuses of *I. gauthieri* (fig. 10) are more typical of nonavian theropods, and are associated with the promaxillary recess penetrating the maxilla, the nasal recess, and the lacrimal recess (figs. 3 and 10) (Witmer, 1990, 1997). The only specimen of *C. gracilis* examined by Kundrát and Janáček (2007) does not preserve the facial region of the skull; therefore, comparisons are based on unpublished data. *Citipati osmolskae* possesses the same sinuses described for *I. gauthieri*, but they are inflated to a more extreme degree (Clark et al., 2002). All oviraptorosaurs including *I. gauthieri* apparently lack a jugal recess (Witmer, 1997).

The anterior extension of the pneumatic cavity within the nasal appears to be present only in oviraptorosaurs, occurring in *Incisivosaurus gauthieri* (fig. 10), *Citipati osmolskae* and *Conchoraptor gracilis* (Clark et al., 2002). The lacrimal recess of *I. gauthieri* extends into the lacrimal and frontal but lacks the division found in *C. osmolskae*, which sends off various diverticulae (figs. 2 and 3). Likewise, *I. gauthieri* lacks the enlarged sinus overlying the endocranial space that extends posteriorly

from the circumnarial cavities to connect with the dorsal tympanic recess (Clark et al., 2002). This feature is present in *C. gracilis* but is considerably less extensive.

The paratympanic recesses of *Incisivosaurus gauthieri* also most closely resemble those of other nonavian theropods rather than derived oviraptorosaurs. All three paratympanic recesses are present in *I. gauthieri* (three recesses occurring in almost all maniraptorans except some troodontids, which lack the posterior tympanic recess [see Xu and Norell, 2004]); however, the diverticulae that extend distally from the external openings lack the complexity observed in *Conchoraptor gracilis* and *Citipati osmolskae* (Kundrát and Janáček, 2007; Clark et al., 2002). The dorsal tympanic recess of *I. gauthieri* extends into the parietal (the condition found in most coelurosaurs [e.g., Witmer, 1990, 1997; Norell et al., 2006]), but lacks the extensive diverticulae present in *C. gracilis* (Kundrát and Janáček, 2007). The posterior tympanic recess of *I. gauthieri* pneumatizes the entire paroccipital process and sends off small diverticulae along its posterior margin (fig. 9C, D), a condition not observed in *C. gracilis* and not widely assessed in other theropods. The pneumatization of the paroccipital process, however, is a common theropod feature. The anterior tympanic recess of *I. gauthieri* is more difficult to study (possibly owing to the only moderate amount of ossification in the parabasisphenoid), but appears to be simple and not diverging.

ENDOCRANIAL MORPHOLOGY

Figures 15–17

Previous studies based on digitally prepared endocasts established that derived oviraptorosaurs (i.e., oviraptorids) possess a strikingly avianlike morphology (Franzosa, 2004; Osmólska, 2004; Kundrát, 2007). These "avianlike" characteristics include expanded cerebral hemispheres, reduced olfactory tracts, ventrolaterally displaced optic bulbs, and a dorsally expanded cerebellum (Alonso et al., 2004; Franzosa, 2004; Kundrát, 2007; Larsson et al., 2000). Although these characters suggest that the oviraptorid endocranial morphology reflects a close phylogenetic relationship with

Aves, it is not clear whether these similarities are diagnostic for a more inclusive group that includes both oviraptorosaurs and birds or if they evolved independently along the two lineages (Franzosa, 2004; Osmólska, 2004; Kundrát, 2007). The preparation of a digital endocast of *Incisivosaurus gauthieri* allows us to better understand the nature of these transformations (figs. 15–17). The basal position occupied by *I. gauthieri* along the oviraptorosaur lineage (Xu et al., 2002a; Norell et al., 2006) potentially could have a large affect on our perception of the evolutionary history of oviraptorosaur endocranial morphology and also broader trends in coelurosaurian brain evolution.

The endocranial morphology of *Incisivosaurus gauthieri* is a mosaic of plesiomorphic nonavian theropod characters and more derived features that are similar to those found in extant avians. *I. gauthieri* shares with birds and derived oviraptorids reduced olfactory tracts and ventrolaterally displaced optic lobes. The ventrolateral displacement of the optic lobes (fig. 15), however, optimizes much earlier in theropod history; this character is first known to appear in ornithomimosaurs. The reduction of the olfactory tracts actually may be a function of the shortening of the rostrum in relation to the skull as a whole, which is apparent in *I. gauthieri* and reaches its full extent in Oviraptoridae (see Clark et al., 2002). The shortening also may be due to the enlarged orbits present in this taxon, as this same structural change occurs in ornithomimosaurs. In addition, the cerebral hemispheres of *I. gauthieri* are not distinctly expanded as in Oviraptoridae (fig. 16)—a feature more similar to the condition found in nonavialan theropods. A meaningful optimization of this character, however, cannot be resolved without further sampling of taxa, especially within Caenagnathidae, Therizinosauria, and basal paravians.

Although it does not account for evolutionary relationships (see Felsenstein, 1985), the encephalization index is still the most widely used metric to discern whether the volume of an endocast is more typical of "avians" or "paraphyletic reptiles" (i.e., Reptilia in the noncladistic sense, lacking Aves) (Jerison, 1969; Hopson, 1977, 1979; Alonso et al., 2004; Kurochkin et al., 2007). The encephali-

zation index of the oviraptorid *Conchoraptor gracilis* falls within the range of avians (Kundrát, 2007); thus, ostensibly showing another avian similarity. In order to rigorously test the validity of this assignment more extinct nonavialan taxa, including paravians, need to be included within the analysis. As it stands, this statistic is not useful because there is not enough information to conclude whether the endocast of *Incisivosaurus gauthieri* is more avian- or "reptile"-like. The encephalization index of *I. gauthieri* is problematic to calculate because the only known specimen lacks a postcranium, and the most commonly used indicators of body mass are derived from the length and/or diameter of the femur.

Overall, the endocranial morphology of avians and oviraptorosaurs do not unequivocally elucidate the relationships between these groups at this time, although morphological evidence as a whole suggests a placement among nonavian maniraptorans (see Norell et al., 2006). The endocranial morphology of *Incisivosaurus gauthieri*, however, at least complicates the evolution of this character system. The simple hypothesis of a shared origin of avianlike characters between birds and oviraptorosaurs at the avialan node is not the only possibility. The endocranial characters shared between oviraptorosaurs and avians can be either plesiomorphic for both clades or their primary homology is questionable (convergence) and must be more intensively studied (Patterson, 1982; de Pinna, 1991). Thus, the optimization of "avian" characters found in *I. gauthieri* cannot be confidently ascertained without further study.

Incisivosaurus gauthieri represents a significant discovery from a locality that has produced some of the most unique fossils in recent years. Similar to many of the other fossils from the Jehol beds, *I. gauthieri* occupies a basal and thus phylogenetically important position. Within the oviraptorosaur lineage it is the basalmost member (see Norell et al., 2006; Turner et al., 2007); and therefore is able to break up the long branch leading to the extremely derived oviraptorids and caenagnathids. Although there are striking resemblances, primarily within the skull, between oviraptorosaurs and avialans (see Xu et al., 2002a; Osmólska et al., 2004), most phylogenetic analyses of maniraptoran

relationships repeatedly recover a more basal position for this group well outside of Avialae (e.g., Lü, 2005; Norell et al., 2006; Turner et al., 2007; Senter, 2007). This long branch seems to be driving results from those analyses that exclude *I. gauthieri* and posit an avialan affinity for Oviraptorosauria. Therefore, the exclusion of *I. gauthieri* from any study analyzing the interrelationships of Oviraptorosauria or the relationship of this group with respect to other maniraptorans could have significant effects.

ACKNOWLEDGEMENTS

REFERENCES

Alonso, P.D., A.C. Milner, R.A. Ketcham, M.J. Cookson, and T.B. Rowe. 2004. The avian nature of the brain and inner ear of *Archaeopteryx*. Nature 430: 666–669.

Balanoff, A.M., G.S. Bever, and T. Ikejiri. In press. The braincase of *Apatosaurus* (Dinosauria: Sauropoda) based on computed tomography of a new specimen with comments on variation and evolution in sauropod neuroanatomy. American Museum Novitates.

Barrett, P.M., and J.M. Hilton. 2006. The Jehol biota (Lower Cretaceous, China): new discoveries and future prospects. Integrative Zoology 1: 15–17.

Barsbold, R. 1976. On a new Late Cretaceous family of small theropods (Oviraptoridae fam. n.) of Mongolia. Doklady Akademia Nauk SSSR 226: 685–688. [in Russian]

Barsbold, R. 1981. Toothless dinosaurs of Mongolia. Joint Soviet-Mongolian Paleontological Expedition Transactions 15: 28–39. [in Russian]

Barsbold, R. 1983. Carnivorous dinosaur from the Cretaceous of Mongolia. Sovmestnaa Sovetsko-Mongol'skaa Palaeontologiceskaa Ekspedicia Trudy 19: 1–19.

Barsbold, R. 1986. Raubdinosaurier Oviraptoren. *In*: E.I. Vorobyeva (editor), Herpetologische Untersuchungen in der Mongolischen Volksrepublik. Akademia Nauk SSSR Institut Evolyucionnoi Morfologii i Ekologii Zhivotnikh: 210–223. Moskva: A.M. Severtsova. [in Russian, German summary]

Barsbold, R. 1997. Oviraptorosauria. *In*: P.J. Currie and K. Padian (editors), Encyclopedia of dinosaurs: 505–509. New York: Academic Press.

Barsbold, R., H. Osmólska, M. Watabe, P.J. Currie, and K. Tsogtbaatar. 2000. A new oviraptorosaur (Dinosauria: Theropoda) from Mongolia: the first dinosaur with a pygostyle. Acta Palaeontologica Polonica 45: 97–106.

Baumel, J.J., and L.M. Witmer. 1993. Osteologia. *In*: J.J. Baumel, A.S. King, J.E. Breazile, H.E. Evans and J.C. Vanden Berge (editors), Handbook of avian anatomy: nomina anatomica avium. 2nd ed. Publications of the Nuttall Ornithological Club 23: 45–113.

Brochu, C.A. 2000. Digitally-rendered endocast for *Tyrannosaurus rex*. Journal of Vertebrate Paleontology 20: 1–6.

Carlson, W.D., T. Rowe, R.A. Ketcham, and M.W. Colbert. 2003. Geological applications of high-resolution x-ray computed tomography in petrology, meteoritics and paleontology. *In*: F. Mees, R. Swennen, M. Van Geet and P. Jacobs (editors), Applications of x-ray computed tomography in the geosciences 215: 7–22. London: Geological Society.

Chiappe, L., M.A. Norell, and J.M. Clark. 1998. The skull of the stem-group bird *Mononykus*. Nature 392: 275–278.

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

Clark, J.M., M.A. Norell, and R. Barsbold. 2001. Two new oviraptorids (Theropoda: Oviraptorosauria), Upper Cretaceous Djadokhta Formation, Ukhaa Tolgod, Mongolia. Journal of Vertebrate Paleontology 21: 209–213.

Clark, J.M., M.A. Norell, and T. Rowe. 2002. Cranial anatomy of *Citipati osmolskae* (Theropoda, Oviraptorosauria), and a reinterpretation of the holotype of *Oviraptor philoceratops*. American Museum Novitates 3364: 1–24.

Clark, J.M., M. Norell, and L. Chiappe. 1999. An oviraptorid skeleton from the Late Cretaceous of Ukhaa Tolgod, Mongolia, preserved in an avian-like brooding position over an oviraptorid nest. American Museum Novitates 3265: 1–36.

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

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

Currie, P.J., and X.-J. Zhao. 1993. A new troodontid (Dinosauria, Theropoda) braincase from the Dinosaur Park Formation (Campanian) of Alberta. Canadian Journal of Earth Sciences 30: 2231–2247.

de Pinna, M.C.C. 1991. Concepts and tests of homology in the cladistic paradigm. Cladistics 7: 367–394.

Dong, Z.-M., and P.J. Currie. 1996. On the discovery of an oviraptorid skeleton on a nest of eggs at Bayan Mandahu, Inner Mongolia, People's Republic of China. Canadian Journal of Earth Sciences 33: 631–636.

Elzanowski, A. 1999. A comparison of the jaw skeleton in theropods and birds, with a description of the palate in the Oviraptoridae. Smithsonian Contributions to Paleobiology 89: 311–323.

Felsenstein, J. 1985. Phylogenies and the comparative method. American Naturalist 125: 1–15.

Franzosa, J. 2004. Evolution of the brain in Theropoda (Dinosauria). Ph.D. dissertation, University of Texas at Austin, 357 pp.

Franzosa, J., and T. Rowe. 2005. Cranial endocast of the Cretaceous theropod dinosaur *Acrocanthosaurus atokensis*. Journal of Vertebrate Paleontology 25: 859–864.

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

Goodrich, E.S. 1930 [1986 reprint]. Studies on the structure and development of vertebrates. Chicago: University of Chicago Press, 837 pp.

Holtz, T.R. 1998. A new phylogeny of the carnivorous dinosaurs. Gaia 15: 5–61.

Hopson, J.A. 1977. Relative brain size and behavior in archosaurian reptiles. Annual Review of Ecology and Systematics 8: 429–448.

Hopson, J.A. 1979. Paleoneurology. *In*: C. Gans, R.G. Northcutt and P. Ulinski (editors), Biology of the Reptilia. Vol. 9: 39–146. London: Academic Press.

Hwang, S.H., M.A. Norell, Q. Ji, and K. Gao. 2004. A large compsognathid from the Early Cretaceous Yixian Formation of China. Journal of Systematic Palaeontology 2: 13–30.

Jerison, H.J. 1969. Brain evolution and dinosaur brains. American Naturalist 103: 575–588.

Ji, Q., P.J. Currie, M.A. Norell, and S.-A. Ji. 1998. Two feathered dinosaurs from northeastern China. Nature 393: 753–761.

Ji, Q., and S.A. Ji. 1997. Protarchaeopterygid bird (*Protarchaeopteryx* gen. nov.)—fossil remains of archaeopterygids from China. Chinese Geology 238: 38–41.

Ji, Q., M.A. Norell, K.-Q. Gao, S.-A. Ji, and D. Ren. 2001. The distribution of integumentary structures in a feathered dinosaur. Nature 410: 1084–1088.

Ji, Q., M.A. Norell, P.J. Makovicky, K.-Q. Gao, S. Ji, and C. Yuan. 2003. An early ostrich dinosaur and implications for ornithomimosaur phylogeny. American Museum Novitates 3420: 1–19.

Kundrát, M. 2007. Avian-like attributes of a virtual brain model of the oviraptorid theropod *Conchoraptor gracilis*. Naturwissenschaften 94: 499–504.

Kundrát, M., and J. Janáček. 2007. Cranial pneumatization and auditory perceptions of the oviraptorid dinosaur *Conchoraptor gracilis* (Theropoda, Maniraptora) from the Late Cretaceous of Mongolia. Naturwissenschaften 94: 769–778.

Kurochkin, E.N., G.J. Dyke, S.V. Saveliev, E.M. Pevushov, and E.V. Popov. 2007. A fossil brain from the Cretaceous of European Russia and avian sensory evolution. Biology Letters 3: 309–313.

Kurzanov, S.M. 1987. Avimimidae and the problem of the origin of birds. Transactions of the Soviet-Mongolian Paleontological Expedition 31: 1–92. [in Russian]

Larsson, H.C.E., P.C. Sereno, and J.A. Wilson. 2000. Forebrain enlargement among nonavian theropod dinosaurs. Journal of Vertebrate Paleontology 20: 615–618.

Lü, J. 2002. A new oviraptorosaurid (Theropoda: Oviraptorosauria) from the Late Cretaceous of southern China. Journal of Vertebrate Paleontology 22: 871–875.

Lü, J. 2005. Oviraptorid dinosaurs from southern China. Beijing: Geological Publishing House, 200 pp.

Lü, J., Y. Tomida, Y. Azuma, Z. Dong, and Y.-N. Lee. 2004. New oviraptorid dinosaur (Dinosauria: Oviraptorosauria) from the Nemegt Formation of southwestern Mongolia. Bulletin of the National Science Museum (Tokyo) Series C (Geology and Paleontology) 30: 95–130.

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

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

Maryańska, T., and H. Osmólska. 1997. The quadrate of oviraptorid dinosaurs. Acta Palaeontologia Polonica 42: 377–387.

Maryańska, T., H. Osmólska, and M. Wolson. 2002. Avialan status for Oviraptorosauria. Acta Palaeontologica Polonica 47: 97–116.

Norell, M.A., J.M. Clark, and L.M. Chiappe. 2001. An embryo of an oviraptorid (Dinosauria: Theropoda) from the Late Cretaceous of Ukhaa Tolgod, Mongolia. American Museum Novitates 3315: 1–17.

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

Norell, M.A., J.M. Clark, D. Dashzeveg, R. Barsbold, L.M. Chiappe, A.R. Davidson, M.C. McKenna, and M.J. Novacek. 1994. A theropod dinosaur embryo, and the affinities of the Flaming Cliffs dinosaur eggs. Science 266: 779–782.

Norell, M.A., J.M. Clark, A.H. Turner, P.J. Makovicky, R. Barsbold, and T. Rowe. 2006. A new dromaeosaurid theropod from Ukhaa Tolgod (Ömnögov, Mongolia). American Museum Novitates 3545: 1–51.

Norell, M.A., and M. Ellison. 2005. Unearthing the dragon: the great dinosaur discovery. New York: Pi Press, 254 pp.

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

Norell, M.A., P.J. Makovicky, and J.M. Clark. 2004. The braincase of Velociraptor. In: P.J. Currie, E.B. Koppelhus, M.A. Shugar and J.L. Wright (editors), Feathered dragons: studies on the transition from dinosaurs to birds: 133–143. Bloomington: Indiana University Press.

Norell, M.A., and X. Xu. 2005. Feathered dinosaurs. Annual Review of Earth and Planetary Sciences 33: 277–299.

Osborn, H.F. 1903. Ornitholestes hermanni, a new compsognathid dinosaur from the upper Jurassic. Bulletin of the American Museum of Natural History 19(12): 459–464.

Osmólska, H. 1981. Coosified tarsometatarsi in theropod dinosaurs and their bearing on the problem of bird origins. In: Z. Kielen-Jaworowski (editor), Results of the Polish-Mongolian Palaeontological Expeditions. Pt. 9. Palaeontologia Polonica 42: 79–95.

Osmólska, H. 2004. Evidence on relation of brain to endocranial cavity in oviraptorid dinosaurs. Acta Palaeontologica Polonica 49: 321–324.

Osmólska, H., P.J. Currie, and R. Barsbold. 2004. Oviraptorosauria. In: D.B. Weishampel, P. Dodson and H. Osmólska (editors), The Dinosauria. 2nd ed: 165–184. Berkeley: University of California Press.

Patterson, C. 1982. Morphological characters and homology. In: K.A. Joysey and A.E. Friday (editors), Problems of phylogenetic reconstruction: 21–74. London: Academic Press.

Rogers, S.W. 1999. Allosaurus, crocodiles, and birds: evolutionary clues from spiral computed tomography of an endocast. Anatomical Record 257: 162–173.

Romer, A.S. 1956. Osteology of the reptiles. Chicago: University of Chicago Press, 772 pp.

Senter, P. 2007. A new look at the phylogeny of Coelurosauria (Dinosauria: Theropoda). Journal of Systematic Palaeontology 5: 429–463.

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

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

Swisher, C.C., III, Y.-Q. Wang, X.-L. Wang, X. Xu, and Y. Wang. 1999. Cretaceous age for the feathered dinosaurs of Liaoning, China. Nature 400: 58–61.

Swisher, C.C., III, X.-L. Wang, Z.-H. Zhou, Y.-Q. Wang, F. Jin, J.-Y. Zhang, X. Xu, and Y. Wang. 2002. Further support for a Cretaceous age for the feathered dinosaur beds of Liaoning, China: new $^{40}Ar/^{39}Ar$ dating of the Yixian and Tuchengzi formations. Chinese Science Bulletin 47: 135–138.

Turner, A.H., D. Pol, J.A. Clarke, G.M. Erickson, and M.A. Norell. 2007. A basal dromaeosaurid and size evolution preceding avian flight. Science 317: 1378–1381.

Wang, X., and X. Xu. 2001. A new iguanodontid (Jinzhousaurus yangi gen. et sp. nov.) from the Yixian Formation of western Liaoning, China. Chinese Science Bulletin 46: 1669–1672.

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

Witmer, L.M. 1995. The extant phylogenetic bracket and the importance of reconstructing soft tissues in fossils. In: J.J. Thomason (editor), Functional morphology in vertebrate paleontology: 19–33. Cambridge: Cambridge University Press.

Witmer, L.M. 1997. The evolution of the antorbital cavity in archosaurs: a study in soft-tissue reconstruction in the fossil record with an analysis of the function of pneumaticity. Journal of Vertebrate Paleontology Memoir 3: 1–73.

Xu, X., Y.N. Chieng, X.-L. Wang, and C.-H. Chang. 2002a. An unusual oviraptorosaurian dinosaur from China. Nature 419: 291–293.

Xu, X., J.M. Clark, C.A. Forster, M.A. Norell, G.M. Erickson, D.A. Eberth, C. Jia, and Q. Zhao. 2005. A basal tyrannosaurid dinosaur from the Late Jurassic of China. Nature 439: 715–718.

Xu, X., P.J. Makovicky, X.-L. Wang, M.A. Norell, and H.-L. You. 2002b. A ceratopsian dinosaur from China and the early evolution of Ceratopsia. Nature 416: 314–317.

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

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

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

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

Zhou, Z., P.M. Barrett, and J. Hilton. 2003. An exceptionally preserved lower Cretaceous ecosystem. Nature 421: 807–814.

Zhou, Z.-H., X.-L. Wang, F.-C. Zhang, and X. Xu. 2000. Important features of *Caudipteryx*—evidence from two nearly complete new specimens. Vertebrate Palasiatica 38: 243–254.

APPENDIX 1

Anatomical abbreviations. Capital "L" or "R" in front of abbreviation indicates left or right side, respectively.

af	antorbital fossa
aof	antorbital fenestra
asc	anterior semicircular canal
bo	basioccipital
bsp	parabasisphenoid
bt	basal tubera
cc	cranial carotid canal
ce	cerebellum
cer	cerebrum
ch	choana
cif	crista interfenestralis
cnII	cranial nerve II (optic)
cnV	cranial nerve V (trigeminal)
cnVI	cranial nerve VI (abducens)
cnVII	cranial nerve VII (facial)
cnVIII$_c$	cranial nerve VIII (cochlear branch)
cnVIII$_v$	cranial nerve VIII (vestibular branch)
cnXII	cranial nerve XII (hypoglossal)
coc	cochlear canal
dtr	dorsal tympanic recess
ec	endocranial cavity
ect	ectopterygoid
eo	exoccipital
eov	external occipital vein
f	frontal
fl	flocculus
fm	foramen magnum
fps	fenestra pseudorotundum
fr	floccular recess
frac	fracture
fv	foramen vestibuli
hsc	horizontal semicircular canal
icf	intercerebral fissure
j	jugal
l	lacrimal
lat	laterosphenoid
mef	metotic foramen
mf	metotic fissure
mo	medulla oblongata
mx	maxilla
mxf	maxillary fenestra
n	nasal
na	naris
nc	nuchal crest
nr	nasal recess
o	orbit
ob	olfactory bulb
oc	occipital condyle
ol	optic lobe
op	opisthotic
osc	otosphenoidal crest
osp	orbitosphenoid
p	parietal
pal	palatine
pf	palatine fenestra
pit	pituitary
pmx	premaxilla
pn	pneumatic space
pnf	pneumatic foramen
po	postorbital
pop	paroccipital process
pot	pila otica
pr	parasphenoid rostrum
psc	posterior semicircular canal
pt	pterygoid
q	quadrate
qf	quadrate fossa
qj	quadratojugal
rt	replacement tooth
sq	squamosal
so	supraoccipital
ssin	sagittal sinus
st	sella turcica
t	tooth
utr	utriculus
v	vomer
ves	vestibule
vf	vagus foramen