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Cranial pneumatization and auditory perceptions of the oviraptorid dinosaur *Conchoraptor gracilis* (Theropoda, Maniraptora) from the Late Cretaceous of Mongolia

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Abstract The distribution of air-filled structures in the craniofacial and neurocranial bones of the oviraptorid ZPAL MgD-I/95, discovered at the Hermiin Tsav locality, Mongolia, is restored. Based on the complete obliteration of most of the cranial sutures, the specimen is identified as an adult individual of *Conchoraptor gracilis* Barsbold 1986. Except for the orbitosphenoids and epipterygoids, the preserved bones of the neurocranium are hollow. Three types of tympanic recess are present in *Conchoraptor*, a characteristic shared with troodontids, dromaeosaurids, and avian theropods. The contralateral middle ear cavities are interconnected by the supraencephalic pathway that passes through the dorsal tympanic recesses, the posterodorsal prootic sinuses and the parietal sinus. The spatial arrangements of the middle ear cavity and a derived neurocranial pneumatic system in *Conchoraptor* indicate enhancements of acoustic perception in the lower-frequency registers and of auditory directionality. We further speculate that this improvement of binaural hearing could be explained as an adaptation required for accurate detection of prey and/or predators under conditions of low illumination. The other potentially pneumatic structures of the *Conchoraptor* cranium include (1) recessus-like irregularities on the dorsal surface of the nasal and frontal bones (a putative oviraptorid synapomorphy; pos); (2) a subotic recess; (3) a subcondylar recess; and (4) a posterior condylar recess (pos).

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Introduction

The reconstruction of neurocranial anatomy has a potential for yielding information on the complex evolutionary transition from non-avian to avian theropods. Neurocranial pneumatization is one of the most poorly understood aspects of the non-avian theropod skeleton, despite considerable advances in recent years. Available data are mostly based on descriptions of more or less complete neurocrania of maniraptoran theropods, e.g., the oviraptorid *Citipati* (Clark et al. 2002) and the troodontids *Saurornithoides* (Barsbold 1974), *Troodon* (Currie and Zhao 1993), *Sinovenator* (Xu et al. 2002), and *Byronosaurus* (Makovicky et al. 2003), as well as the dromaeosaurids *Dromaeosaurus* (Currie 1995), *Velociraptor* (Barsbold and Osmólska 1999), and *Tsaagan* (Norell et al. 2006). In most of these taxa, the pneumatization of neurocranial bones has been considered, but no detailed reconstruction of the extension and connection of the pneumatic recesses inside the theropod neurocranium has yet been performed.

The oviraptorid neurocranium studied herein had been described as *Oviraptor* sp. by Osmólska (1976) but is now assigned to *Conchoraptor* Barsbold 1986 (Barsbold 1986).

Here, we describe a CT-based 3D reconstruction of the pneumatization of this animal's neurocranium and draw inferences from this reconstruction concerning the oviraptorid's ability to perceive acoustically.

Materials and methods

The oviraptorid specimen ZPAL MgD-I/95 (Fig. 1) analyzed below comes from the collection of the Institute of Palaeobiology of the Polish Academy of Sciences (ZPAL). It was collected by members of the Polish–Mongolian Palaeontological Expedition in 1971 at the Hermiin Tsav locality (Upper Cretaceous) in the Gobi Desert, Mongolia. The antorbital region is incompletely preserved. The supraoccipital, a posteriormost part of the parietal, and most of the basicranium are missing. The left lateral wall of the braincase is considerably eroded. Otherwise, most of the braincase and premaxillary regions are fairly complete and undistorted.

The snout and the braincase of the specimen were scanned at the CT Facility of the NMR Unit (Pace Plus; General Electric) of the First Faculty of Medicine, Charles University in Prague, Czech Republic. The parameters of this CT scanning were 160 kV, 130 mA, 3 s (time of each single slice scan), 1 mm (slice thickness), 1 mm (inter-slice spacing). The contrast of tonal values between bones and matrix in the CT imagery was enhanced with Adobe Photoshop. Transverse CT images (see supplementary Figs. 1, 2, and 3 in the electronic supplementary material) were used for 3D reconstruction of the bones and their pneumatic sinuses. The contours of the pneumatic sinuses were outlined using the Ellipse program (ViDiTo Systems, Slovakia). A virtual model of the *Conchoraptor* cranial pneumaticity was created by plotting the contours in successive planes of the 3D data set. To enhance the contours of the bones, the images were processed by using the 2D top hat filter. The surfaces were constructed by detection of triangulated iso-surfaces, properly colored, and combined in the VRML model. The images of the models were made by rendering the resulting 3D constructs in VRML View program (Systems in Motion, Norway).

Results

A characteristic feature of the preserved cranial bones of *Conchoraptor*, except for the orbitosphenoid and the epipterygoid, is the presence of enlarged pneumatic sinuses. The description of the pneumatic system of *Conchoraptor* can be organized under two headings: craniofacial (premaxilla, lacrimal, nasal, frontal) and neurocranial (parietal, laterosphenoid, prootic, opisthotic, supraoccipital, exoccipital, basioccipital, parabasisphenoid). In this oviraptorid, the pneumatic sinuses of the craniofacial bones presumably represent extensions of the nasal sinuses, whereas the neurocranial pneumatic sinuses are derived from the pharyngeal cavity through the Eustachian tube and middle ear cavity. Pneumatic sinuses of both sources connect with each other at the frontal/parietal interface in *Conchoraptor*. The quadrate pneumatic sinus is directly connected with the middle ear cavity, and the pterygoid pneumatic sinus may be connected with the tympanic cavity, possibly through the parabasisphenoid pneumatic sinus.

Fig. 1 Left lateral view of the neurocranium of *Conchoraptor gracilis*, ZPAL MgD-I/95, from the Late Cretaceous of Hermiin Tsav, Gobi, Mongolia
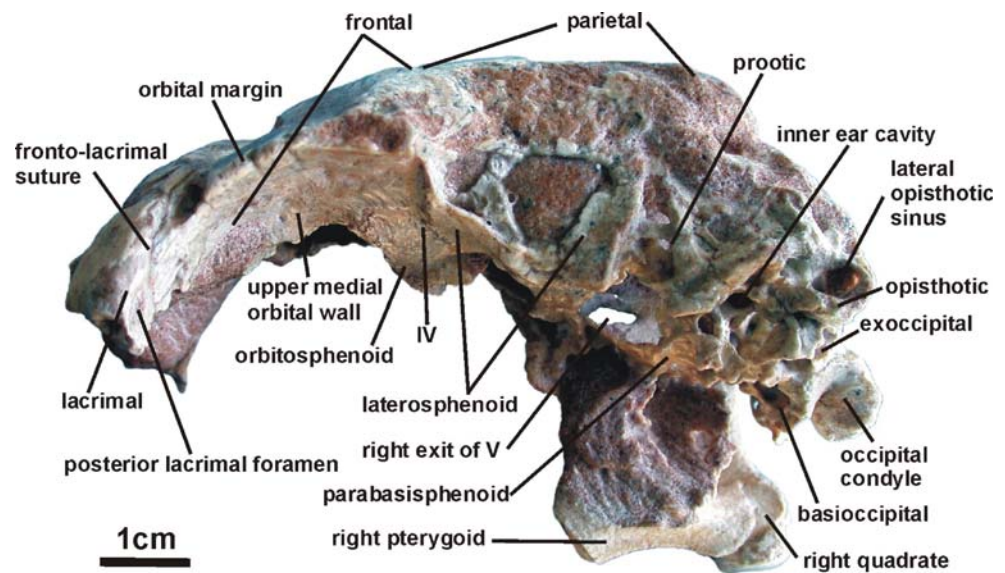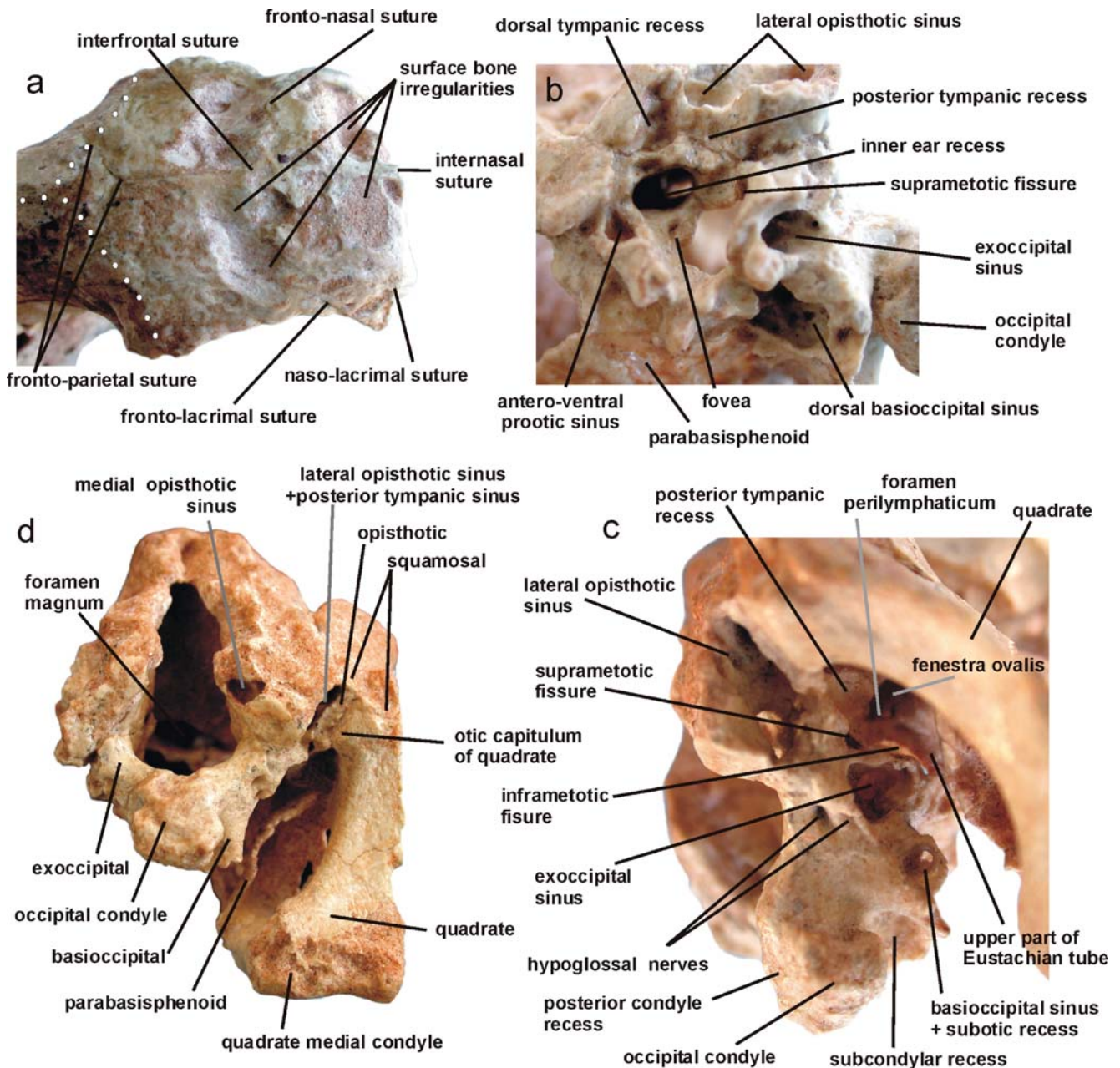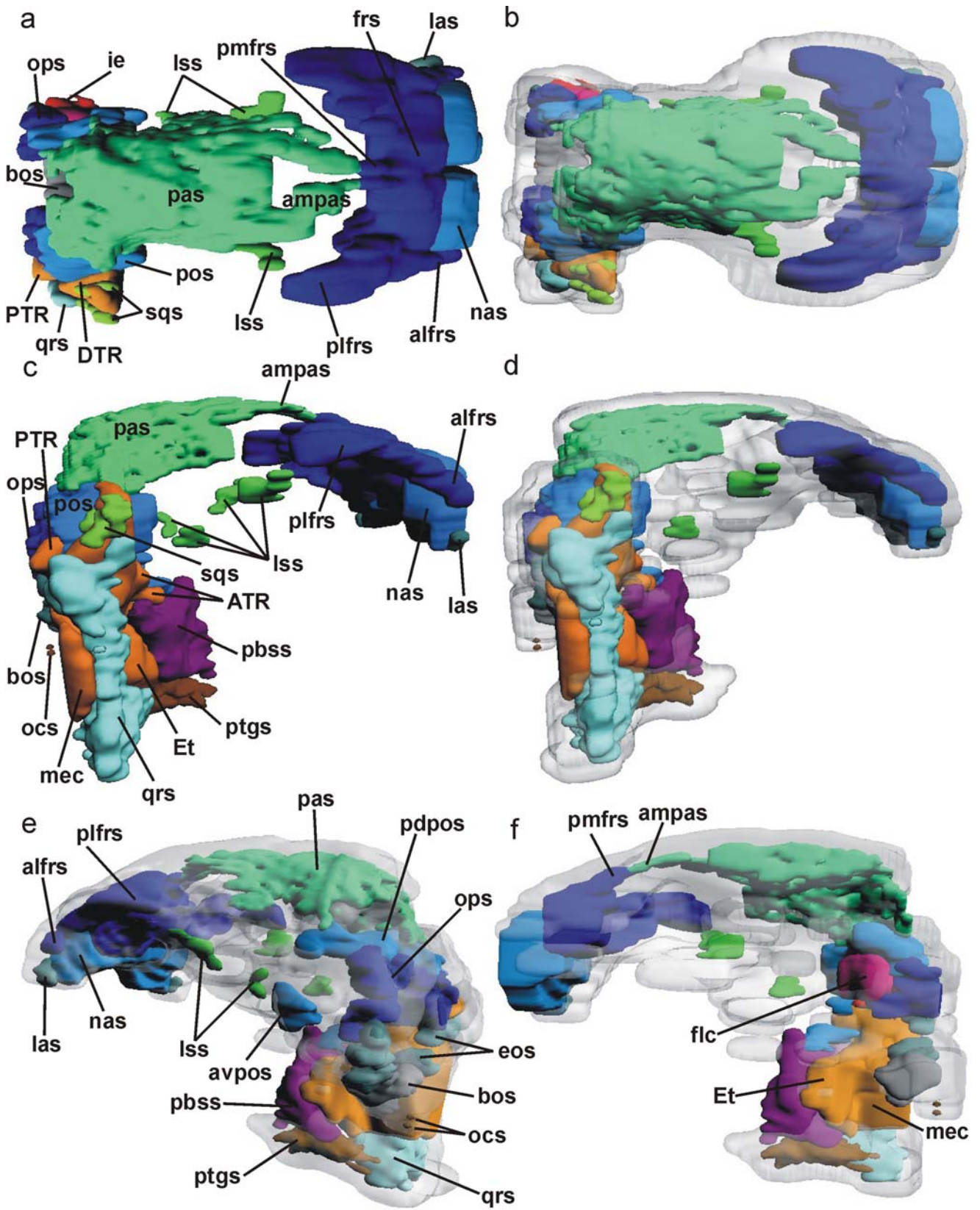
Fig. 2 Cranium of *C. gracilis*, ZPAL MgD-I/95. **a** dorsal view of the fronto-nasal region; **b** latero-ventral view of the left otic region; **c** lateral view of the right otic region; **d** posterior view of the occipital region

Craniofacial pneumatic sinuses

Premaxilla In *Conchoraptor*, the premaxillae are fused with each other, although the inter-premaxillary suture is not obliterated. The external surfaces of the most rostral part of the premaxillae display numerous pits, presumably representing vascular foramina. The interior of the premaxillae is almost completely hollow; however, numerous trabeculae, concentrated mostly at the anterior and lateral edges, can be recognized. The trabeculae reinforce the oral architecture of the premaxillary and may increase support for its function in a biting action.

Lacrimal Only the upper portions of both lacrimals of *Conchoraptor* have been preserved (Figs. 1 and 2a). Present inside each is an air-filled cavity (Fig. 2a) that opens into the orbit through the posterior lacrimal foramen (Fig. 1).

Nasal The two nasals meet in the midline to form a septum (Fig. 2a–c) separating left and right nasal pneumatic sinuses (Fig. 3). Dorsally, the nasals are formed by a thin bone that shows surface irregularities (Fig. 2a), possibly of a natural origin. The considerable space between the dorsal and ventral walls of the nasals shows no marks of septa or

◀ **Fig. 3** 3D reconstruction of air-filled structures in the cranium of *C. gracilis*, ZPAL MgD-I/95. **a,b** Dorsal view; **c,d** Right lateral view; **e,f** Left lateral view. *alfrs* Anterolateral frontal sinus; *ampas* anteromedial parietal sinus; *ATR* anterior tympanic recess; *avpos* anteroventral prootic sinus; *bos* basioccipital sinus; *dbos* dorsal basioccipital sinus; *DTR* dorsal tympanic recess; *eos* exoccipital sinus; *Et* Eustachian tube passage; *flc* flocculus cerebelli; *frs* frontal sinus; *ie* inner ear region; *las* lacrimal sinus; *lops* lateral opisthotic sinus; *lss* laterosphenoid sinus; *mec* medial ear cavity; *mops* medial opisthotic sinus; *nas* nasal sinus; *ocs* occipital condyle sinus; *ops* opisthotic sinus; *pas* parietal sinus; *pbss* parabasisphenoid sinus; *pdpos* posterodorsal prootic sinus; *plfrs* posterolateral frontal sinus; *pmfrs* posteromedial frontal sinus; *pos* prootic sinus; *ptgs* pterygoid sinus; *PTR* posterior tympanic recess; *qrs* quadrate sinus; *SEP* supraencephalic pathway; *sqs* squamosal sinus; *vbos* ventral basioccipital sinus

trabeculae within the sediment that fills these sinuses. The whole nasal bone architecture is strengthened by the massive medial septum and firm suturation between the nasals and frontals.

Frontal The pneumatization of the frontals in *Conchoraptor* consists of a main chamber (frontal sinus) and three pairs of extensions: (1) anterolateral projections parallel with the nasal pneumatic sinus (anterolateral frontal sinus; Fig. 3), (2) posterolateral projections inside the orbital rim (posterolateral frontal sinus; Fig. 3), and (3) posteromedial projections connecting to the parietal pneumatic sinus (posteromedial frontal sinus; Fig. 3a). The main chamber of the frontal pneumatization appears as a cavernous system inside the anterior part of the frontals (Fig. 3b). This cavernous system might have been covered by a thin corrugated bone (Fig. 2a). It seems that the frontal sinus was confluent with the nasal pneumatic sinuses (Fig. 3). No connection has been found between the anterolateral frontal and lacrimal pneumatic sinuses.

Neurocranial pneumatic sinuses

Parietal The parietals are fused into an arched, tunnel-like structure covering the posterior part of the cerebral hemispheres and the anterior cerebellum (Kundrát 2007). The parietal pneumatic sinus is a multichambered system with two antero-medial projections (anteromedial parietal sinus; Fig. 3) that surround the epiphysis (Kundrát 2007) and connect the posteromedial frontal sinuses. The position of the anteromedial parietal sinuses is traceable from outside by the presence of bony ridges that converge from the posterior points of the orbital rims to join one another about 1 cm behind the anteriormost parietal point (Fig. 2a) and continue further posteriorly to form a blunt sagittal crest. In cross-section, both parietals in *Conchoraptor* are convex [in *Citipati*, they are sharply pointed, and in *Oviraptor philoceratops*, they bear a tall midline crest (Clark et al.

2002)], and this convexity increases gradually in the posterior direction. No mesokinetic hinge between the frontals and parietals can be confirmed for *Conchoraptor*, as had been suggested for *O. philoceratops* (AMNH 6517) by Smith (1993), because the frontoparietal suture is akinetic in this oviraptorid.

A complicated pneumatic labyrinth is found inside the fused parietals. The parietal pneumatic sinus was very likely confluent with the frontal pneumatic sinuses near the epiphysial fossa. In contrast to *Citipati* (Clark et al. 2002), thin bony trabeculae reinforce the internal structure of the parietals of *Conchoraptor*. These form a labyrinth of pneumatic passages proceeding longitudinally in the anterior part of the labyrinth. At some levels, a more open pneumatic space between clusters of sagittal and parasagittal trabeculae can be observed. The parietal pneumatic system has its greatest maximum dorsoventral diameter between the level of the inter-laterosphenoid suture and the exit for the trigeminal nerve. Due to the incompleteness of the specimen, connection between the parietal and laterosphenoid pneumatic sinuses cannot be confirmed. Posteriorly, the parietal pneumatic sinus is confluent with the dorsal tympanic recess (DTR) through the posterodorsal prootic pneumatic sinus (Fig. 4).

Laterosphenoid Each laterosphenoid surrounds the fenestra for the optic nerves posteriorly and contributes to the canal transmitting the abducens nerve laterally. Dorsally to the abducens canal, a groove for the ophthalmic branch of the trigeminal nerve (V1) is seen. The laterosphenoid is pneumatized throughout (Fig. 3). Judging from the exposed internal space on the left side, the laterosphenoid space shows no connection to the posterolateral frontal and parietal pneumatic sinuses. It is not clear if the laterosphenoid pneumatic sinus was confluent with the prootic and parabasisphenoid pneumatic sinuses, although there may be some indications of such communication on the exposed posterior part of the right laterosphenoid in the specimen.

Prootic The prootics are preserved on both sides in the specimen. Both are considerably eroded, and an exposed internal relief of their pneumatic labyrinth allows us to reconstruct the extension of pneumaticity inside the prootic. The prootic pneumatic system seems to be divided into two main labyrinths, the anteroventral and posterodorsal sinuses, which were probably confluent at the anterodorsal region of the prootic. The anteroventral pneumatic sinus (Figs. 3e; 4c–e) is derived from the middle ear cavity (Fig. 2b), close to the place where the facial nerve exits the neurocranium. The posterodorsal prootic sinuses (Fig. 4) are much larger and participate in formation of the supraencephalic passage projecting inside the parietal pneumatic system (Fig. 4c–e). The posterodorsal prootic sinus com-
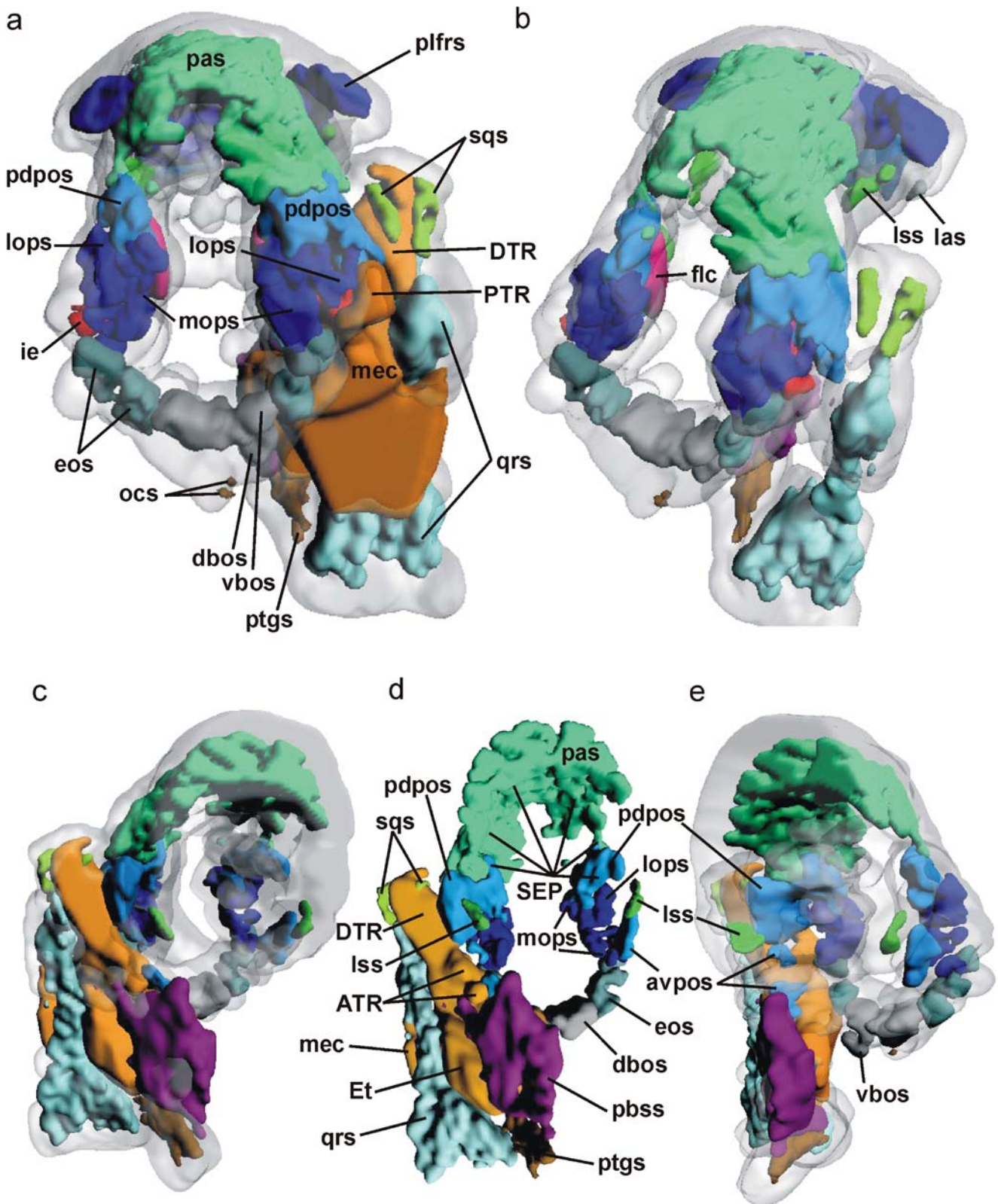
Fig. 4 3D reconstruction of air-filled structures in the posterior neurocranium of *C. gracilis*, ZPAL MgD-I/95. **a** Posterior view; **b** Posterodorsal view; **c**–**e** Posterior part of the cranium in anterior and anterolateral perspectives. Abbreviations as in Fig. 3

municates with the dorsal and posterior tympanic recesses (PTR; Figs. 2b; 3c,d; 4).

The largely hollow auricular fossa is found posterodorsal to the acoustic fossa in *Conchoraptor* (Fig. 3f). On the outer surface of the neurocranium, the suture between the prootic and the opisthotic runs from the dorsal point of the inframetotic fissure and enters the posteriormost part of the inner ear recess. Further, it appears more anteriorly at a middorsal point of the inner ear region and continues dorsally along the canal-like DTR (Fig. 2c). The lateral margin of the inner ear region (Fig. 2c) suggests that the preserved opening was originally subdivided into the anterior oval opening, the fenestra ovalis, and a posterior ellipsoid opening, the foramen perilymphaticum, with the anterior opening three to four times larger than the posterior one. These openings were separated by a thin interfenestral bony bar, which is not preserved in the ZPAL MgD-I/95 specimen but has left indications on the dorsal and ventral marginal relief of the inner ear recess. Below the ventral margin of the inner ear region, a small fovea is found within the groove running ventrally (Fig. 2b,c). This groove represents the dorso-medial bony wall of the Eustachian tube (Figs. 3c,f; 4d).

Opisthotic The opisthotic on the right side has been used to describe the characteristics of this bone (Fig. 2c,d). The opisthotic pneumatic sinus can be divided into medial and lateral pneumatic sinuses. The medial opisthotic sinus faces towards the supraoccipital region posterodorsally and is adjacent to medioventral portions of the posterodorsal prootic sinus (Fig. 4). The lateral opisthotic sinus occupies that part of the opisthotic communicating with the part of the middle ear cavity abutting the otic capitulum of the quadrate (Fig. 4a). The pneumatic sinus of the quadrate of *Conchoraptor* consists of dorsomedially confluent air-filled chambers separated by more or less thin horizontal bony lamellae (Figs. 3c,d; 4). The quadrate pneumatic sinus becomes multichambered and is divided into lateral and medial parts by the solid bony mass in the area of contact with the articular bone. Both the pterygoid (Figs. 3c–f; 4) and the squamosal (Figs. 3a–d; 4) pneumatic sinuses are quite closely adjacent to the quadrate pneumatic sinuses, the last two probably communicating with each other.

The lateral opisthotic sinus also projects into the paroccipital process and faces onto the exoccipital (Fig. 2b–d). Based on the large cavity in the base of the paroccipital process (Fig. 2b), we speculate that the paroccipital process was highly pneumatized. In addition to the foregoing, the lateral opisthotic sinus opens into the PTR (Fig. 2d) behind a contact between the posterodorsal pneumatic prootic sinus and the DTR (Fig. 4a). However, it seems that the opisthotic and prootic pneumatic sinuses communicated with one another directly, above the DTR,

through an opening between the lateral opisthotic and posterodorsal prootic sinuses. The lateral opisthotic sinus enters the exoccipital sinus ventrally (Fig. 2b). On the right lateral side, the opisthotic shows a shallow concave area, the PTR (Fig. 2b,c).

Supraoccipital The supraoccipital is preserved only as a thin bony sheet inclined between the prootic and opisthotic on the endoneurocranial side. Based on the topography of thin bone fragments of the supraoccipital, it is very likely that this bone was pneumatized and may have had a pneumatic contact with the medial opisthotic sinus. The supraoccipital protected the posterior half of the dorsal surface of the cerebellum.

Exoccipital The exoccipitals converge dorso-medially and give a pyriform appearance to the foramen magnum (Fig. 2d). The exoccipitals are largely pneumatized except for the part transmitting the roots of the hypoglossal nerve. The exoccipital sinus communicates with the lateral opisthotic sinus dorsally (Figs. 3e; 4a,b). It also communicates ventrally with a dorsal subdivision of the basioccipital pneumatic sinus, and it opens externally into the subotic pneumatic recess (sensu Witmer 1997; Fig. 2b,c).

Basioccipital The basioccipital, which is incompletely preserved, has a pneumatic vacuity that consists of a dorsal subdivision (dorsal basioccipital sinus; Figs. 2b; 4a,d) connecting the exoccipital sinus (Fig. 2c), and a ventral subdivision (ventral basioccipital sinus; Fig. 4a,f), occupying most of the basioccipital bone, including the basicranial tubera. The subcondylar recess is seen on the posterior wall of the basioccipital (Fig. 2c). The basioccipital projects behind the dorsal and ventral margin of the foramen magnum (Fig. 2c,d). The dorsal wall of the occipital condyle bends at right angles to the endoneurocranial floor. A shallow recess, the posterior condylar recess (Fig. 2c), occurs on the posterior surface of the occipital condyle. The base of the occipital condyle is pneumatized (Figs. 3c,d; 4a, b). The condyle itself is separated from the basioccipital floor by a laterally constricted condylar base (Fig. 2d).

Parabasisphenoid The parabasisphenoid is mostly absent in our specimen, but preserved fragments (Fig. 2d) suggest that it was quite deep and pneumatized to a high degree. The parabasisphenoid pneumatic sinus makes contact with the middle ear cavity at the same place as the antero-ventral prootic sinus does (Figs. 2b; 4c–e). The flat longitudinal bony element embedded in the sediment between the medial quadrate wall and lateral braincase wall (Fig. 2d) is partly hidden because it descends into the sediment, where it makes contact with the dorso-medial margin of the pterygoid. This element thus represents the sidewall of the

parabasisphenoid and gives an impression of a latero-ventral extension of this basicranial bone.

Discussion

Tympanic invasion of the neurocranial bones in theropods

The pattern of three tympanic recesses derived from the middle ear (tympanic) cavity, a constant feature of birds (Witmer 1990; reviewed by Starck 1995) including *Archaeopteryx* (Walker 1985) and known also in dromaeosaurids (Norell et al. 2004) and troodontids (Currie and Zhao 1993; Xu et al. 2002; Makovicky et al. 2003), is present in the oviraptorid *Conchoraptor* as well (Figs. 3a,b; 4a,d). The anterior tympanic recess (ATR) and DTR seem to be plesiomorphic characteristics of tetanuran theropods (Rauhut 2004). It has been suggested that the PTR is a primitive characteristic of coelurosaurs (Witmer 1997; Makovicky and Norell 1998). In *Conchoraptor*, the PTR invades the base of the paroccipital process through the lateral opisthotic sinus. A very similar pattern is seen in *Archaeopteryx* (Walker 1985: Fig. 1). The DTR in *Conchoraptor* occupies at first the posteroventral surface of the prootic and then enters the pneumatized interior of the bone as the posterodorsal prootic sinus. This sinus is interconnected with its counterpart through the supraencephalic pathway (SEP), a midline dorsal communication between the contralateral middle ear cavities (Fig. 4c). There is an indication that the DTR might invade a pneumatic labyrinth inside the quadrate of *Conchoraptor* through an opening on the medial side of the otic capitulum. The ATR separately invades the anteroventral prootic and parabasisphenoid sinuses (Figs. 3c; 4d). Because the basicranium is incompletely preserved, it is unclear whether the interaural passage (IAP) was present in *Conchoraptor*, although one other oviraptorid, *Citipati*, seems to possess this passage (Clark et al. 2002: Fig. 8). The other potential pneumatic structures of *Conchoraptor* include (1) recessus-like irregularities on the dorsal surface of the nasal and the frontal bones (a putative oviraptorid synapomorphy); (2) the presence of a subotic recess [as in troodontids (Barsbold 1974; Currie and Zhao 1993; Makovicky et al. 2003) and some ornithomimosaurs (Makovicky and Norell 1998)]; (3) the presence of a sub-condylar recess [unlike those in ornithomimosaurs (Makovicky and Norell 1998)], and (4) a posterior condylar recess (another putative oviraptorid synapomorphy).

Acoustic perceptions of directionality in *Conchoraptor*

Auditory perception plays an important role in many different kinds of avian behavior including individual and species recognition, mate selection, territorial defense, song learning, warning, and prey and predator detection (Dooling and Ryals 1997). The extent of auditory perception is determined by the capacities of the external and middle ear for collecting sound energy and transforming it to provide optimal stimulation of the receptor organ (Kühne and Lewis 1985).

Acoustic abilities in the extinct ancestors of birds can be partly estimated based on the specific characteristics of their middle ear regions. The well-preserved neurocranium of *Conchoraptor* (Fig. 1) is a valuable source of information about the extension of the middle ear cavity-derived tympanic sinuses into neurocranial bones and is, therefore, a basis for our inferences concerning sound propagation through this communicating pneumatic system (Fig. 3). As Kühne and Lewis (1985) pointed out, both the transformer function and the directionality of the ear are affected by the finite physical dimensions of the head, on each side alone or in combination. It is probable that, as in birds, the tympanic membrane in volant and arboreal theropods gradually relocated from the surface of the head to a more protected position inside the acoustic meatus, where it acquired an increased surface area and may have become thinner. This arrangement increases the sensitivity of the tympanic membrane, particularly to higher frequencies (Kühne and Lewis 1985). Reducing the bone mass of the transmitting apparatus by trabeculation or hollowing also improves the high-frequency sensitivity of the middle ear in birds. At the other end of the acoustic spectrum, enlargement of the avian middle ear cavity, derived tympanic recesses, and pneumatic contralateral communication between these structures decrease the impedance of the middle ear at low frequencies and improve transmission of low-frequency sounds to the cochlea (Saunders and Johnstone 1972).

The spacious middle ear cavity and derived tympanic recesses, as well as extensive unilateral or contralateral communications between them, are found in birds with excellent acoustic perception abilities, e.g., birds of prey (including owls) (Stellbogen 1930; Freye-Zumpfe 1953; Payne 1971; Norberg 1978). Among non-avian theropods, the most spacious middle ear cavity has been described in troodontids (Barsbold 1974; Currie and Zhao 1993; Makovicky et al. 2003), and a similar extension is reported here for *Conchoraptor* (Figs. 3c,f; 4a,d). Apart from the middle ear cavity, the most extensively pneumatized neurocranial bones among theropods are found in oviraptorids, therizinosauroids, troodontids, and ornithomimosaurs and may indicate enhanced acoustic abilities at the lower-frequency registers. The extension of neurocranial pneumaticity of *Conchoraptor* is comparable to that in palaeognathous birds such as *Struthio*, *Casuarius*, and *Rhea*. Starck (1995) proposed that the large air volumes

in the skulls of these birds result in sensitivity to very low-resonance frequencies, which might correlate with the low frequencies of the calls of most palaeognathous birds. In view of the functional dependence of the hearing ability of birds on the volume capacity of the middle ear space and derived recesses and sinuses invading the neurocranial bones, it seems reasonable to hypothesize that *Conchoraptor* had enhanced acoustic abilities at the lower-frequency registers, presumably employed in intraspecies acoustic communication.

In many birds, the middle ears are connected through an air-filled IAP consisting of an interaural canal and trabeculated bone. Sound transmission through the IAP may improve directional hearing. Experiments with modern birds have demonstrated that the pneumatic sinuses provide a passage (IAP) for the transmission of sounds from one middle ear to the other (Wada 1924; Stellbogen 1930; Schwartzkopff 1952; Payne 1971; Henson 1974; Lewis 1983). Larsen et al. (2006) confirmed that at low frequencies, interaural sound propagation may cause one eardrum to feel the vibrations of a sound considerably earlier or later than the other, thus providing a possible cue for directional hearing. Birds regulate their intracranial air pressure every few minutes to equilibrate with ambient pressure by opening their Eustachian tubes. If the intracranial space is not ventilated, the tympanal transfer function gradually becomes high pass, with increasing air pressure difference reducing both tympanal vibration amplitudes and sound transmission through the IAP (Larsen et al. 1996).

Larsen et al. (2006) revealed an interesting fact that in contemporary birds the feathers enlarge the acoustically effective size of the head compared with the dimensions of the skull. Similarly, the presence of the feathers (e.g., in a basal oviraptorosaur *Caudipteryx*; Ji et al. 1998) and the occurrence of the IAP in non-avian theropods and early birds with a relatively small distance between ipsilateral eardrums might have a considerable acoustic effect and improve directional hearing.

Birds and some troodontids (Currie and Zhao 1993) and oviraptorids (Clark et al. 2002) have been shown to possess an air space connecting their middle ear cavities; however, the considerable incompleteness of a parabasisphenoid precludes any conclusion about the presence of an IAP in the studied specimen of *Conchoraptor*.

The IAP represents a ventral contralateral communication developed between the tympanic spaces and the pharyngotympanic tubes (Hill et al. 1980; Saiff 1988; Starck 1995). The middle ear cavities may be also interconnected through dorsal contralateral passages. The PTRs may fuse in the dorsal midline of the supraoccipital. Furthermore, in *Struthio* and *Casuarius*, the spacious parietal SEP connects the contralateral DTRs, invading the squamosal, the PTRs, and the supraoccipital (Starck

1995). The SEP was suggested to be present in *Troodon* (Currie and Zhao 1993), but until now, the SEP had been documented only in oviraptorids, such as *Citipati* (Clark et al. 2002). Here, we confirm the presence of the SEP in *Conchoraptor* (Fig. 4d).

In *Citipati*, the middle ear spaces are broadly confluent with the DTR and are thus directly interconnected inside the parietal pneumatic cavity (Clark et al. 2002). This morphology implies 1) that the air pressure might have been the same on the interior of the two ear drums, and 2) that sound might propagate from one ear to the other. The timing of sound transmission through the SEP was likely more delayed in *Conchoraptor* than in *Citipati* because the SEP in *Conchoraptor* consists of the trabeculated interior of the posterodorsal prootic sinus and the parietal pneumatic system, whereas there are no bony trabeculae in the parietal pneumatic system of *Citipati* (Clark et al. 2002). Depending on the amount of sound transmission through the SEP, the ears may therefore have been inherently directional. If an IAP was present, the SEP might have further amplified the perceptive capability of binaural hearing in *Conchoraptor*, allowing the animal to pinpoint the source of a sound extremely accurately.

The relatively large size of the orbital space and the eye (Fig. 1) in comparison to the cranium in *Conchoraptor*, as well as its relatively large optic lobes (Kundrát 2007), might suggest an adaptation to a crepuscular or nocturnal life style by this oviraptorid. Animals that are nocturnally active are faced with the task of detecting and interpreting acoustic stimuli correctly. To react in an appropriate manner to acoustic signals, *Conchoraptor* had to be able to recognize the changing locations of sound sources, determining their directions and distances, in the dark. In such a scenario, the enhancement of *Conchoraptor*'s auditory directionality to a high degree could be explained as an adaptation of functional requirements for the accurate detection of prey and/or predators in conditions of low illumination.

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