



General palaeontology

3D computational imaging of the petrosal of a new multituberculate mammal from the Late Cretaceous of China and its paleobiologic inferences

Imagerie en trois dimensions d'un os pétreux d'un nouveau mammifère multituberculé du Crétacé supérieur de Chine et ses implications paléobiologiques

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ABSTRACT

The derived middle and inner ears of mammals are the major features distinguishing them from non-mammalian vertebrates. Among them, multituberculate mammals represent an important transitional stage and a groundplan for further therian ear evolution. We present the reconstruction of petrosal features of a new multituberculate from the Late Cretaceous of Inner Mongolia (China) based on high resolution computed tomography and three-dimensional imaging analysis. Besides questioning some aspects of previous interpretations, this study reveals a combination of derived and primitive characters, such as a therian-like vascular and nervous pattern and internal acoustic meatus, and a monotreme-like inner ear, but with a derived semicircular canal planarity. The possible presence of a primary bony lamina for the basilar membrane could demonstrate that the first step in the elaboration of a coiled cochlea was already present in multituberculates. Auditory capabilities can be deduced for this animal, which was certainly terrestrial and possibly fossorial.

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RÉSUMÉ

Les oreilles moyenne et interne dérivées des mammifères représentent une caractéristique majeure qui les distingue des vertébrés non mammaliens. Parmi eux, les mammifères multituberculés constituent une étape transitoire importante et un plan d'organisation pour l'évolution des thériens. Nous présentons la reconstruction d'un os pétreux d'un nouveau multituberculé du Crétacé supérieur de Mongolie intérieure (Chine), fondée sur des tomo-graphies (CT) à haute résolution et des analyses d'imagerie en trois dimensions. Cette étude permet de remettre en question certains points d'interprétations proposées précédemment et de mettre en évidence une combinaison de caractères primitifs et dérivés, tels qu'un *pattern* vasculaire et nerveux et un méat acoustique interne de type thérien, une oreille

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interne de type monotrème, mais dont la planarité des canaux semi-circulaires est dérivée. La présence éventuelle d'une lame osseuse primaire pour la membrane basilaire pourrait attester que le premier pas dans l'élaboration d'une cochlée enroulée était déjà effectué chez les multituberculés. Les capacités auditives peuvent être inférées chez cet animal, qui était terrestre et peut-être fouisseur.

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1. Introduction

The ear region has undergone major changes in the history of mammals, one of the most fundamental being the evolution of the coiled cochlea. While the origin and evolution of the mammalian ear has long been of interest to embryologists and comparative anatomists (e.g., Gaupp, 1913; Goodrich, 1930), significant new perspectives have more recently been advanced by vertebrate palaeontologists. The fossil record provides the only direct evidence concerning the course of evolution of the ear, presenting a rich source of novel characters in a temporal context, and accordingly can contribute to both phylogenetic reconstruction and functional interpretation. Fossils can address specific questions regarding the origin and evolution of the mammalian ear (Luo et al., 2007; Martin and Luo, 2005), such as the evolutionary steps in the coiling of the therian cochlear canal and duct (Ruf et al., 2009). Furthermore, fossils provide new and relevant information about the vascular and nervous pathways on the petrosal bone as dictated by grooves, foramina, or other bony indicators of soft anatomical features (e.g., MacIntyre, 1972; Rougier et al., 1992; Wible and Rougier, 2000).

Multituberculate mammals have played a major role in the understanding of the evolution of the ear structures among Mammalia, and in the possible patterns of transformation in the petrosal and inner ear structures from non-cynodont mammaliaforms to therian mammals. Because they are phylogenetically nested between monotremes and living therians, and because they are part of the paraphyletic stem group to cladotherians, multituberculates represent a ground plan for the evolution of the cladotherian or even therian ear morphology.

Despite several detailed works on the petrosal, however, the anatomy of the multituberculate ear still suffers from limited and sometimes controversial information (see below). Unlike the external morphology of the petrosal bone that has been studied in a wide range of Mesozoic mammals, the inner ear of early mammals is much more difficult to investigate (because of the small number of specimens in collections, its inaccessible location within the petrosal, and because of the delicacy of these internal structures). This is unfortunate because the inner ear is crucial for the study of hearing specializations.

Multituberculates currently known from their petrosal anatomy include the North American ptilodontid *Ptilodus* (Simpson, 1937), neoplagiaulacid *Mesodma* (Wible and Hopson, 1995), taeniolabid *Catopsalis* (Kielan-Jaworowska et al., 1986; Wible and Hopson, 1995), paulchoffatiid (Hahn, 1988; Lillegraven and Hahn, 1993), the Mongolian djadochtatherioids *Kryptobaatar* (Wible and Rougier, 2000), *Chulsanbaatar*, *Nemegtbaatar* (Hurum et al., 1996; Hurum, 1998; Kielan-Jaworowska et al., 1986), taenio-

labidoid *Lambdopsalis* (Miao, 1988), and the sloanbaatarid *Kamptobaatar* (Hurum et al., 1996). However, their petrosal anatomy remains incompletely documented as this bone is rarely isolated from the skull and the cerebellar part is hidden.

Despite the difficulties in accessing the inner ear, soft tissue anatomy of the inner ear of early mammals has been reconstructed based on the internal bony architecture of the petrosal using naturally exposed inner ears, broken petrosals, or internal molds (e.g., Fox and Meng, 1997; Lillegraven and Hahn, 1993; Meng and Wyss, 1995), serial sections of fossils (e.g., Hurum, 1998; Kielan-Jaworowska et al., 1986), and early attempts using medical CT scanning and 3D reconstruction (e.g., Luo and Ketten, 1991). It is only in the last decades that the use of high-resolution CT has allowed a better documentation and knowledge of the detailed inner ear structure and anatomy of mammals (e.g., Ladevèze et al., 2008; Ruf et al., 2009; Schmelzle et al., 2007; Spoor et al., 2002), but this has not yet been applied to multituberculates.

According to various authors, multituberculates have a rod-like and straight or slightly curved cochlea, of a length relative to the skull length about the same as for *Morganucodon* (Luo and Ketten, 1991; Luo et al., 1995; Miao, 1988), and they are said to be characterized by an inflated vestibule, which may represent a synapomorphy of Multituberculata (Luo and Ketten, 1991), or a subclade of some multituberculates but not Multituberculata as a whole (Fox and Meng, 1997). The proposed reconstructions of the ancestral inner ear characters, such as vestibule size, would require further studies of all multituberculates and other theriiiforms.

The use of state-of-the-art micro-CT scanning technology (μ CT) not only improves knowledge of the ear anatomy of multituberculates, but also verifies the accuracy of previous studies, and presents data germane to fundamental issues. The μ CT scanning of the skull of a new multituberculate mammal from the Late Cretaceous of Inner Mongolia (China) reveals not only many characters of the petrosal but also the structure of the bony labyrinth of the inner ear, including the cochlea for hearing and the vestibule and semicircular canals for balance and equilibrium. The study of the tympanic surface of the petrosal reveals a novel pattern of vascular and nervous pathways. The reconstruction of the vessels and nerves on the petrosal bone has been made for only a few multituberculates and conflicting accounts are recorded in the literature (e.g., Fox and Meng, 1997; Hurum, 1998; Kielan-Jaworowska et al., 1986; Wible and Hopson, 1995; Wible and Rougier, 2000). Here we offer a different view of the previously proposed vascular and nervous patterning in multituberculates. Thanks to this new data, the evolution of the auditory apparatus in early mammals is discussed and a view about the life

style of Asian Late Cretaceous multituberculates is proposed.

2. Material and methods

The skull of the multituberculate mammal (IMM 99BM-IV/4, Fig. 1A) from which the petrosal is here reconstructed and described was discovered in September 1999 during the Sino-Belgian expedition in the southern Gobi desert in Inner Mongolia at Bayan Mandahu, Urad Houqi Banner, Bayan Nor League. The Late Cretaceous Bayan Mandahu locality is situated about 50 km north-west from the city of Urad Houqi in the southern part of the Gobi Basin near the Lang Shan Mountains in China. The Bayan Mandahu redbeds extend there over 12 km length and 2 km width and have yielded a large quantity of vertebrates including dinosaurs, lizards, snakes, turtles and mammals. Among the latter, some multituberculate mammals have been described (Smith et al., 2001). The deposits are generally correlated with the Campanian aged Djadokhta Formation of South-central Mongolia, 350 km to the north-west (Jerzykiewicz et al., 1993). The red sandstone deposits have been interpreted to represent an eolian sedimentary environment but local alluvial and lacustrine component representing a proximal to distal depositional gradient in a semi-arid climate have also been documented (Eberth, 1993).

The specimen is identified as a typical djadoctatheriid multituberculate (crown group Cimolodonta) by the following: large frontals, inserted between the nasals and pointed anteriorly in the middle, U-shaped frontoparietal suture, sharp edge between the lateral and palatal walls of premaxilla (rounded in other multituberculates), and parietal postorbital process (Kielan-Jaworowska and Hurum, 2001). The specimen can further be referred to the family Djadoctatheriidae by the subtrapezoidal snout in dorsal view, with wide anterior margin and lateral margins confluent with zygomatic arches rather than incurved in front of the arches. The snout extends for about 50% of the skull length and shows two pairs of vascular foramina on the nasals. P2 is absent and replaced by a small diastema, a synapomorphy shared with *Catopsbaatar* and *Tombaatar*. The skull is 44 mm long, which is smaller than *T. sabuli* Rougier et al. 1997 and *C. catapsaloides* Kielan-Jaworowska, 1994. Although this new specimen may represent a new genus, the tooth morphology is quite similar to *Tombaatar* and it is thus provisionally referred to cf. *Tombaatar* n. sp. Its description and precise systematic attribution will be addressed in a work in progress by some of the authors.

CT scanning of IMM 99BM-IV/4 was performed at the University of Texas CT facility at Austin. The slice thickness and interslice spacing was 0.04275 mm, and the in-plane interpixel spacing was 0.03906 mm, for a total of 1030 slices along the coronal axis of the skull. The MIMICS software (Materialise 2010, Release 13.1; license UMR 7207 CNRS-MNHN, Paris) was used to complete visualization, segmentation and 3D rendering. MIMICS allows different types of segmentation to be performed. Regions of interest (i.e., petrosal bone and inner ear) can be selected with accuracy using threshold method to create segmentation masks and, when necessary, manual outlining operations.

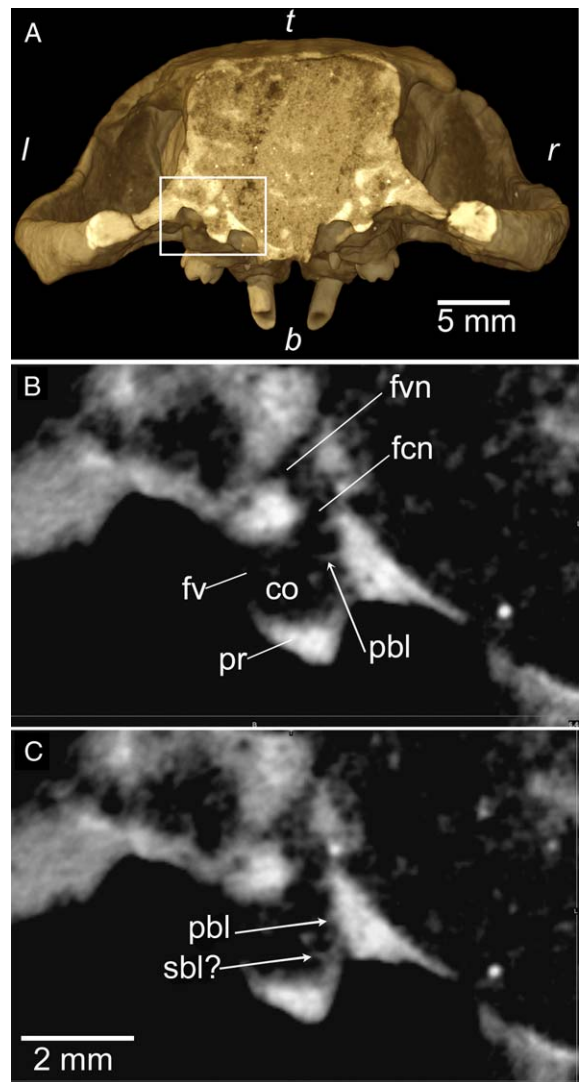


Fig. 1. Skull of cf. *Tombaatar* sp. (IMM 99BM-IV/4) in coronal view, sliced at the level of the auditory region. **A:** 3D reconstruction (VG Studio max) showing the endocranium and the basicranium with the cochlear canals. The background shows the two first incisors, pointing ventrally. **B:** The corresponding slice (+006.46) and **C:** an additional coronal slice (+006.41), with a zoom of the boxed area. A bony lamina (arrow) is visible into the left cochlear canal and is interpreted as primary bony lamina for attachment of the medial part of the basilar membrane.

Fig. 1. Crâne de cf. *Tombaatar* sp. (IMM 99BM-IV/4), en vue coronale, coupé au niveau de la région auditive. **A:** Reconstruction 3D montrant la cavité endocrânienne et la base du crâne avec les canaux cochléaires. L'arrière-plan montre les deux premières incisives qui pointent ventralement. **B:** La coupe correspondante (+006.46) et **C:** une coupe coronale additionnelle (+006.41), avec un agrandissement de la zone encadrée. Une lame osseuse (flèche) est visible dans le canal cochléaire gauche et est interprétée comme la lame osseuse primaire pour l'attachement de la partie médiale de la membrane basilaire.

Abbreviations: **A:** b: bottom; l: left; r: right; t: top; **B:** cochlear canal; fcn: foramen for cochlear nerve; fv: fenestra vestibuli; fvn: foramen for the vestibular nerve; pbl: primary bony lamina; pr: promontorium; sbl?: maybe the secondary bony lamina for the basilar membrane.

Table 1

Measurements of the bony labyrinth dimensions (vestibule, cochlea, semicircular canals) in cf. *Tombaatar* sp. (IMM 99BM-IV/4) and other multituberculates.

Tableau 1

Mesures des dimensions du labyrinthe osseux (vestibule, cochlée, canaux semi-circulaires) chez cf. *Tombaatar* sp. (IMM 99BM-IV/4) et autres multituberculés.

Reference	cf. <i>Tombaatar</i> This study	<i>Catopsalis</i> Luo and Ketten, 1991	<i>Meniscoessus</i> Luo and Ketten, 1991	<i>Lambdopsalis</i> Miao, 1988	<i>Nemegbaatar</i> Hurum, 1998	<i>Chulsanbaatar</i> Hurum, 1998
Skull length (mm)	44.07	~80	~75		45	21
Length of cochlear canal (mm)	4.2	6.5	5.5		3.0	2.0
Cochlear length/Skull length ratio (%)	9.46	~8.1	~7.3		6.67	9.52
Cochlear canal diameter (mm)	1.21–1.67				0.7–1.2	0.6–0.75
Vestibule volume (mm ³)	19.15	83.83	96.17	> 150	9	
ASC height (mm)	4.0				3.0	
ASC width (mm)	4.0				3.8	
ASC radius (mm)	2.0				1.7	
PSC height (mm)	2.8				2.9	
PSC width (mm)	3.7				2.8	
PSC radius (mm)	1.6				1.4	
LSC height (mm)	2.1				2.8	
LSC width (mm)	2.1				3.3	
LSC radius (mm)	1.1				1.5	

Morphological analysis, based on digital segmentations, is subject to both the preservation quality of the fossilized bones, and also the density contrast between bone and matrix. Uncertainties in both can make minute bony structures difficult or impossible to distinguish from the matrix.

The measurements of the bony labyrinth features follow Luo et al. (1995), Spoor and Zonneveld (1995), and Hurum (1998) and are provided in Table 1.

Anatomical terms used here generally follow terminology summarized by Fox and Meng (1997), Hurum (1998), Kielan-Jaworowska et al. (1986), Rougier and Wible (2006), Wible and Hopson (1995), Wible and Rougier (2000).

The reconstruction of the course of the major cranial nerves and vessels was difficult, given the poor state of preservation of the bones and the difficulty to discriminate bones from matrix using a threshold. However, the foramina, canals, and most sulci present on the petrosal could be reconstructed, mostly thanks to detailed previous studies on the multituberculate petrosal anatomy (cited above).

Discussion of the systematic distribution and pattern of evolution of the observed features is based on phylogenetic relationships according to Kielan-Jaworowska and Hurum (2001), Luo (2007), Luo et al. (2007).

Institutional abbreviations: IMM, Inner Mongolia Museum, Hohhot; BM, Bayan Mandahu.

3. Anatomic description

3.1. Petrosal anatomy

The petrosal is the most complex element of the basicranium; it houses the organs of hearing and balance, and contributes to the braincase wall on the lateral surface, floor, and occiput (Fig. 2, [Electronic Supplementary Data ES1](#)). In living therians, the petrosal is generally conceived as comprising two different regions: the pars cochlearis (housing the saccule and cochlear canal) and the pars canicularis (housing the vestibule and semicircular canals). In multituberculates, in addition to these two regions, an anterior lamina of the petrosal forms part of the

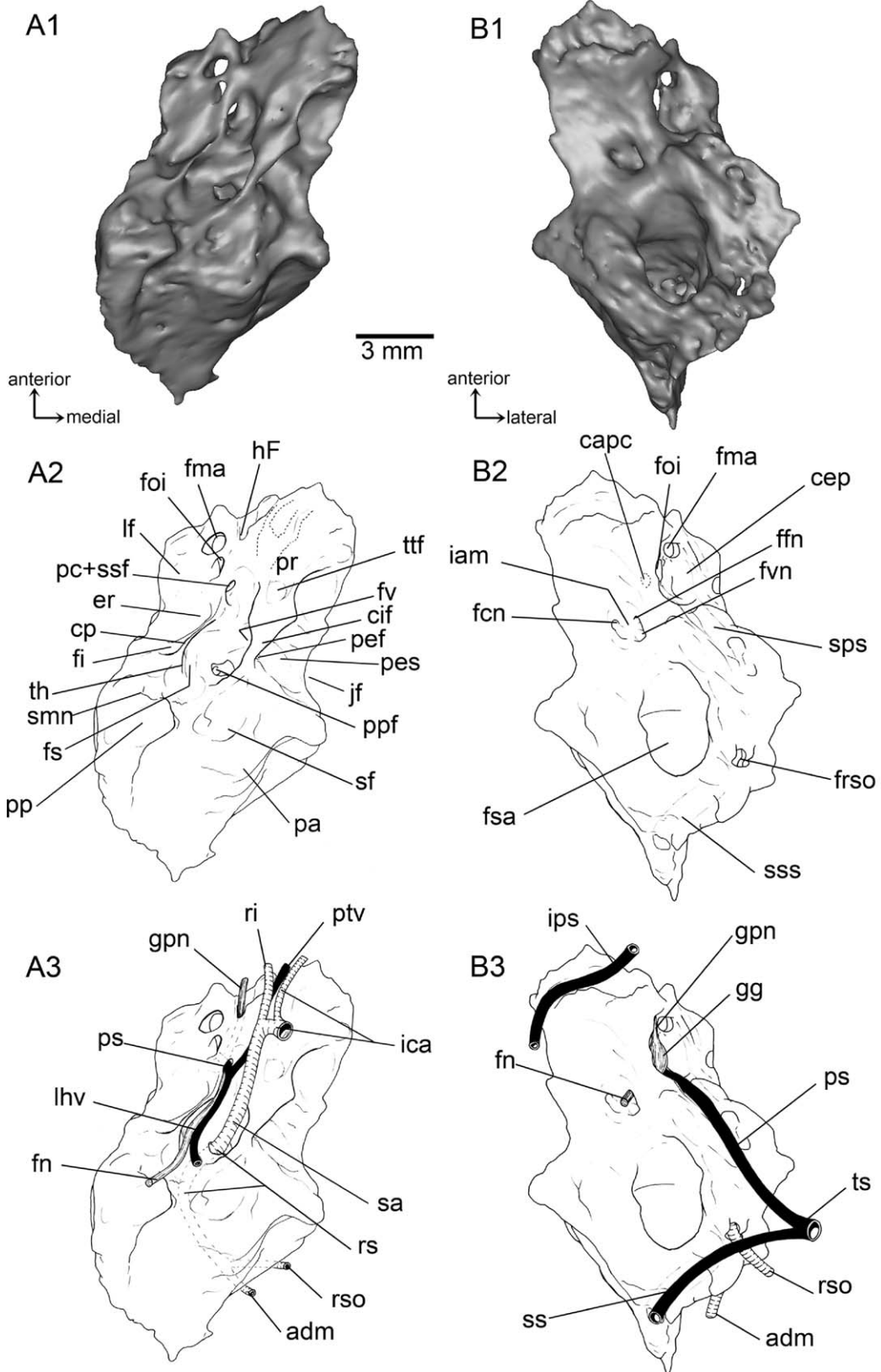
lateral wall of the braincase and an extensive epitympanic recess.

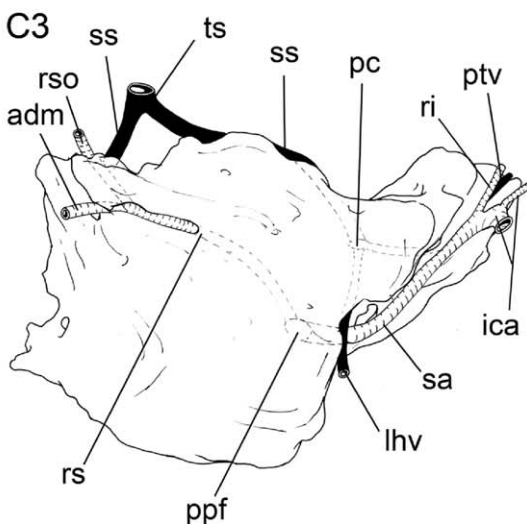
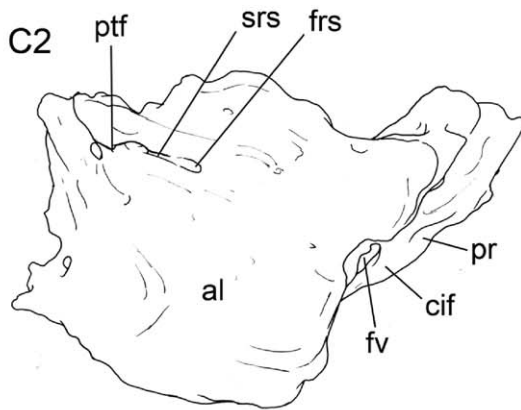
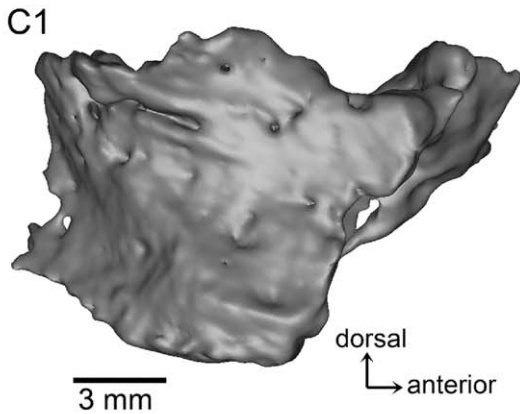
The ventral or tympanic aspect of the pars cochlearis is naturally exposed but its features are covered by matrix. The endocranial aspect of the pars cochlearis and pars canicularis, is hidden in the skull and covered by the original matrix. However, these aspects appear clearly visible in the cutting plane of the three dimensional virtual cast of bone, reconstructed from the CT scan.

The ventral surface of the pars cochlearis forms an elongated and anteromedially directed promontorium (Fig. 2A). The ventral surface of the promontorium is marked on its anterior apex by shallow grooves showing a Y-shaped pattern, presumably for the internal carotid and stapedia arteries, and it bears flange along its medial aspect. At the posterior end of the promontorium there are two apertures, the fenestra vestibuli and the perilymphatic foramen, separated by a narrow bridge of bone, the crista interfenestralis. The fenestra vestibuli forms a large and rounded opening, which is likely to have accommodated a correspondingly large and rounded stapedia footplate [stapedia ratio—i.e., ratio of fenestra vestibuli length to width Segall (1970)—of 1.13]. The perilymphatic foramen, which transmits the perilymphatic duct in life, lies at the base of the promontorium and faces in the opposite direction to that of the fenestra vestibuli. The perilymphatic foramen is posteromedially directed and although its ventral margin is well delimited, its roof lacks a definitive edge and is formed by the petrosal's contribution to the very conspicuous jugular fossa (the large depression around the jugular foramen). A sulcus for the cochlear aqueduct is present as in some other multituberculates (Fox and Meng, 1997; Rougier et al., 1996b), but is lacking in *Kryptobaatar* (Wible and Rougier, 2000).

Immediately behind the perilymphatic foramen is the prominent ventral bulge housing the posterior ampullae of the posterior and lateral semicircular canals (LSC).

Just anterior to the fenestra vestibuli is a deeply excavated pocket, the fossa for the tensor tympani muscle (fossa muscularis major of Kielan-Jaworowska et al. (1986)).





The crista interfenestralis extends posteriorly and contacts the paroccipital process of the petrosal, which is a long, prominent and slanted process. Posterior to the crista interfenestralis and medial to the paroccipital process is a broad depression in the tympanic roof, the fossa for the stapedius muscle. This fossa is conspicuous and its size is at least twice the surface area of the fenestra vestibuli.

The paroccipital process probably represented the site of attachment for the long muscle of the neck, the sternomastoid muscle.

The lateral flange of the petrosal is a sharp and ventrally projecting crest lateral to the promontorium. It contains a fossa, the epitympanic recess following [Kielan-Jaworowska et al. \(1986\)](#), which is a deeply excavated, elongated, ellipsoidal fossa, located above the dorsal margin of the tympanic membrane. The epitympanic recess accommodated the body of the malleus and incus and housed the crus breve of the incus (fossa incudis). The fossa incudis is separated from the fenestra vestibuli by the barrier formed by the crista parotica, which therefore constrained the likely positions of the stapes and incus.

At the posterior end of the lateral flange and slightly posterolateral to the level of the fenestra vestibuli, the crista parotica shows the attachment of the tympanohyal, which has a triangular outline in ventral view.

Anterior to the epitympanic recess, two foramina are interpreted for branches of the mandibular nerve (foramen ovale inferium and foramen masticatorium). As in all known multituberculates, the petrosal of IMM 99BM-IV/4 has multiple apertures for this division of the trigeminal nerve.

Fig. 2. Left petrosal bone of cf. *Tombaatar* sp. (IMM 99BM-IV/4) in **A**: tympanic, **B**: cerebellar, and **C**: lateral views, with **1** the 3D model, **2** a schematic drawing, and **3** the vascular and nervous reconstruction. The Y-shape sulci on the tympanic surface of the petrosal is drawn in dotted lines.

Fig. 2. Os pétreux gauche de cf. *Tombaatar* sp. (IMM 99BM-IV/4) en vues **A**: tympanique, **B**: cérébellaire, et **C**: latérale, avec **1** le modèle 3D, **2** un dessin schématique, et **3** la reconstruction vasculaire et nerveuse. Les sillons en forme de Y sur la face tympanique du périotique sont dessinés en pointillés.

Abbreviations: adm: arteria diploëtica magna (and accompanying vein); al: anterior lamina; capc: cranial aperture of prootic canal; cep: cavum epiptericum; cif: crista interfenestralis; cp: crista parotica; er: epitympanic recess; fc: foramen for cochlear nerve; fn: foramen for facial nerve; fi: fossa incudis; fma: foramen masticatorium; fn: facial nerve; foi: foramen ovale inferium; frs: foramen for ramus superior; frso: foramen for ramus supraorbitalis; fs: facial sulcus; fs: asubarculate fossa; fv: fenestra vestibuli; fvn: foramen for vestibular nerve; gg: geniculate ganglion; gpn: greater petrosal nerve; hF: hiatus Fallopii; iam: internal acoustic meatus; ica: internal carotid artery; ips: inferior petrosal sinus; jf: jugular fossa; lf: lateral flange; lhv: lateral head vein; pa: subjacent posterior ampulla; pc: prootic canal; pc+ssf: confluent prootic canal and secondary facial foramen; pef: perilymphatic foramen; pes: perilymphatic sulcus (for cochlear aqueduct); pp: paroccipital process; ppf: pterygoparoccipital foramen; pr: promontorium; psprootic sinus; ptf: posttemporal foramen; pvt: post-trigeminal vein; ri: ramus inferior of the stapedial artery; rs: ramus superior of the stapedial artery; rso: ramus supraorbitalis; sa: stapedial artery; sf: stapedius fossa; smn: stylomastoid notch; sps: sulcus for prootic sinus; srs: sulcus for superior ramus of the stapedial artery; ss: sigmoid sinus; sss: sulcus for sigmoid sinus; th: tympanohyal; ts: transverse sinus; ttf: tensor tympani fossa.

A rounded foramen lies just posterior to the foramen ovale inferium and is separated from it by a crest. This foramen is interpreted as the prootic canal for the small vein of the prootic sinus supplying the lateral head vein. Through this aperture also passed the hyomandibular branch of the facial nerve, which took the facial sulcus, medial and parallel to the medial crested border of the lateral flange, and left the middle ear via a stylomastoid notch immediately posterior to the tympanohyal. Anteriorly to the large foramen for the prootic vein and the hyomandibular branch of the facial nerve is a smaller hiatus Fallopii, opened anteriorly onto a distinct sulcus for the greater petrosal nerve, the palatine branch of the facial nerve.

Just posterior to the fenestra vestibuli and medial to the tympanohyal is a recessed area that contains one large foramen leading into a canal within the petrosal. This foramen opens into a posterolaterally directed channel and likely transmitted one of the two end branches of the stapedial artery, the ramus superior, into the ventral ascending canal, here into the pterygoparoccipital foramen.

Two dominant features are evident on the dorsal or cerebellar view of the petrosal of IMM 99BM-IV/4 (Fig. 2B). Anteromedially, the internal acoustic meatus forms a subcircular depression and lies on the roof of the pars cochlearis. At the posteromedial edge of the meatus is an anteroventrally directed foramen for the cochlear nerve (part of cranial nerve VIII). In the deeper part of the meatus is a broad fossa containing two foramina: one posteroventrally directed aperture for the vestibular nerve (part of cranial nerve VIII) and one anteroventrally directed for the facial nerve (cranial nerve VII). The canal for the facial nerve is directed anteromedially and its anterior opening, the primary facial foramen, opens directly into the back of the cavum epiptericum where the geniculate ganglion would have been located. A separate cavum supracochleare for the facial ganglion is thus lacking in IMM 99BM-IV/4, as in *Kryptobaatar* (Wible and Rougier, 2000). The secondary exit of the facial nerve from the cavum epiptericum is in the posterior part of the cavum's floor and opens anteroventrally into the hiatus Fallopii, the conduit for the anterior branch of the facial nerve, the greater petrosal nerve. Lateral to the internal acoustic meatus is the cavum epiptericum, the very deep fossa that lodged the trigeminal (or semilunar) ganglion of cranial nerve V.

At the anterior apex of the petrosal and anterior to the internal acoustic meatus is a large groove, which probably has received the inferior petrosal sinus.

Posterodorsally, the subarcuate fossa, which accommodated the paraflocculus of the cerebellum, is a large, deep, subspherical depression that opens into the braincase through an elliptical aperture. This fossa is bounded by the three semicircular canals, with the anterior bounding the entrance of the subarcuate fossa. On the posterior-most margin of the subarcuate fossa is a broad sulcus, probably for the sigmoid sinus. Anterolateral to the subarcuate fossa in the anterior lamina is the deep, broad, and anteroventrally directed sulcus for the prootic sinus.

In lateral view (Fig. 2C), the petrosal is mostly formed by the anterior lamina, which is ventrally continuous with the tympanic surface of the petrosal through the lateral flange, but posteriorly overlapped by the squamosal. The

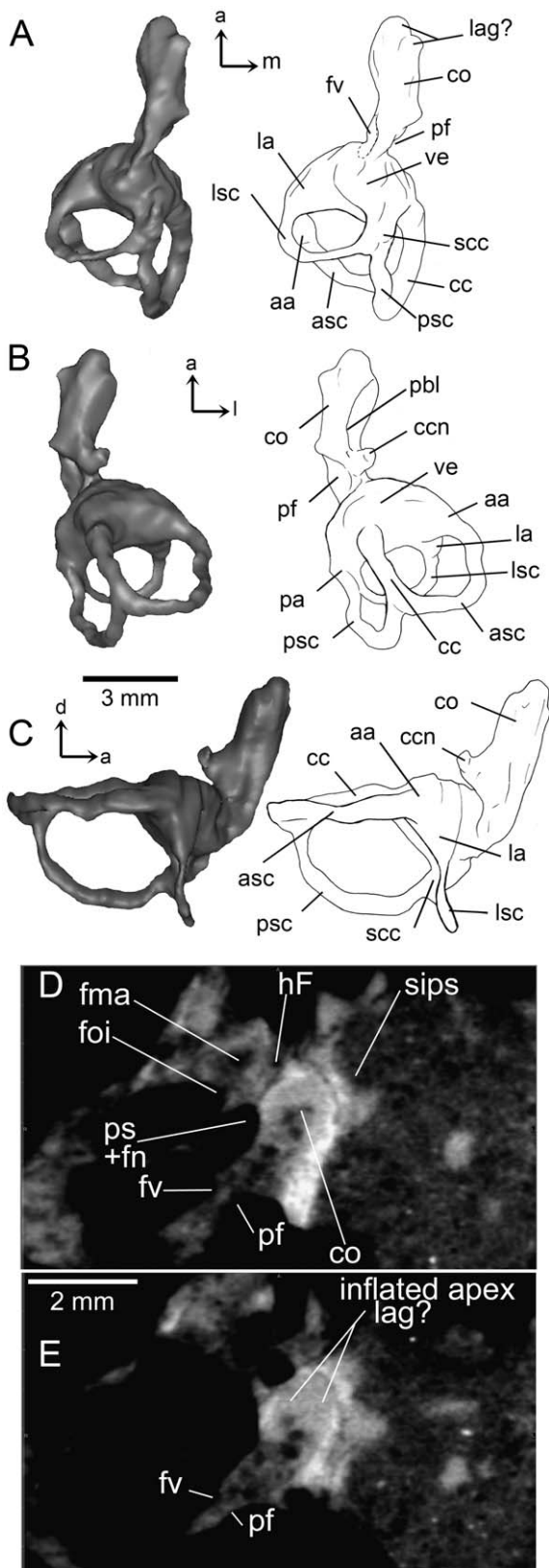
anterior lamina wholly or partially formed a number of passageways for nerves and vessels leaving the braincase for the orbitotemporal fossa, and also provided a major area of attachment for several muscles of mastication. The dorsal part of the anterior lamina is pierced by a foramen which opens caudally into a deep sulcus. This foramen is for the exit of the superior ramus of the stapedial artery, which divided into two branches. The posterior branch ran into the rounded posttemporal foramen and transmitted the diploëtic vessels (arteria diploëtica magna and accompanying vein). The dorsoposterior branch ran into a dorsal foramen and transmitted the ramus supraorbitalis.

3.2. Bony labyrinth anatomy

The cochlear canal is elongated (9.46% of the skull length, see Table 1 for additional measurements of the inner ear features) and slightly curved laterally with a somewhat inflated apex (Fig. 3, Electronic Supplementary Data ES2). Just posteromedial to the perilymphatic foramen is the canal for the cochlear nerve. Within the cochlear canal are traces of a thin osseous lamina, which can be interpreted as the primary bony lamina for attachment of the medial part of the basilar membrane in the area of the internal auditory meatus (B–C, Fig. 3B) because of its relationship with the medial wall of the cochlear canal. Another structure resembling an osseous lamina is observed and remains unidentified, but it might be the secondary bony lamina for the basilar membrane (Fig. 1C). The connection between the cochlea and vestibule is at the posteromedial aspect of the pars cochlearis. The vestibule communicates with the cochlea anteriorly and the semicircular canals posteriorly. It is an irregular, oval, central space which is connected distally by the ampullae of the three semicircular canals. The vestibule forms a small space, and is different from the derived taeniolabidoid multituberculates (Fox and Meng, 1997; Luo and Ketten, 1991), but similar to other djadochtatherioids (Hurum, 1998) (see Table 1) and the phylogenetically more basal paucholfatiids (Lillegraven and Hahn, 1993).

The spaces for the saccule and utricle are not clearly differentiated from one another, but the approximate dimensions of the two cavities can be inferred. As in most mammals, the semicircular canals join the utricle through five openings: one for the crus commune, the others for the medial entrance to the LSC and the three ampullae (anterior, lateral, posterior). Thus, the distance between the junctions of the semicircular canals with the vestibule delimits the utricle. The saccule is located at the anteroventral side of the utricle and is more inflated than the utricle.

Each semicircular canal curves in a plane approximately orthogonal to the planes of the two other canals. The anterior semicircular canal (ASC) joins with the upper part of the posterior semicircular canal (PSC) to form the crus commune, which is dorsomedial and forms a long and narrow tube. The posterior arm of the LSC and the inferior arm of the PSC build a bony second crus commune, a variable structure among mammals. The ASC is the longest (Table 1) and forms an almost complete half-circle before it ends in the anterior ampullar recess (Fig. 3). The LSC is distinctly



smaller than the other two (Table 1) and arches almost perfectly horizontally (Fig. 3C).

4. Discussion

4.1. The middle and inner ears of djadochtatheriid multituberculates and the evolution of the auditory apparatus in early mammals

4.1.1. Vascular pattern: internal carotid artery, lateral head vein and inferior petrosal sinus

In IMM 99BM-IV/4, as in *Kryptobaatar*, the groove on the anterior half of the promontorium housed the **internal carotid artery**, vein, and nerve. This Y-shaped pattern (anterior and medial arm for the internal carotid artery and posterolateral arm for the internal carotid's main extracranial branch, the stapedia artery) is extremely rostrally positioned on the promontorium, which is unusual among living mammals (Wible, 1987) but which is also present in some other multituberculates (e.g., *Kamptobaatar*, Wible and Rougier, 2000). This anterior position of the sulcus for the internal carotid artery differs from the more posterior condition of the promontorial sulci described for other multituberculates such as cf. "*Catopsalis*" *joyneri* or cf. *Mesodma thompsoni* (Wible and Hopson, 1995); *Lambdopsalis*, which exhibits a peculiar pathway (Miao, 1988), cladotherians (*Henkelotherium*, (Ruf et al., 2009)), *Vincelestes*, (Rougier et al., 1992) and most basal eutherians (Ekdale et al., 2004; McKenna et al., 2000; Rougier et al., 1992; Wible et al., 2001; Wible et al., 2009). A promontorial sulcus for the internal carotid artery is also absent in eutriconodonts, *Zhangheotherium* and adult metatherians (e.g., Horovitz et al., 2008; Hu et al., 1997; Ladevèze and de Muizon, 2007; Ladevèze and de Muizon, in press; Rougier et al., 1996a; Wible, 1990).

The major egress for the dural sinuses in IMM 99BM-IV/4 was via the sigmoid sinus, the inferior petrosal sinus and the lateral head vein. As in monotremes and some marsupials (e.g., Ladevèze and de Muizon, 2007; Ladevèze and de Muizon, in press; Wible, 1990; Wible and Hopson, 1995) the prootic sinus (middle cerebral vein) in IMM 99BM-IV/4 drained into the **lateral head vein** in the middle ear cavity through the prootic canal. The intratympanic course of the lateral head vein was posteromedial and dorsal to the facial nerve. The vein then continued ventrally into the neck as

Fig. 3. Left inner ear bony labyrinth of cf. *Tombaatar* sp. (IMM 99BM-IV/4) in A: tympanic, B: cerebellar, and C: lateral views. D and E: CT coronal slices (+0024.88 and +0024.45) showing the cochlear canal and its inflated apex, interpreted as the lagena.

Fig. 3. Oreille interne gauche de cf. *Tombaatar* sp. (IMM 99BM-IV/4) en vues A: tympanique, B: cérébelleire, et C: latérale. D et E: coupes coronales (+0024,88 et +0024,45) montrant le canal cochléaire et son apex renflé, interprété comme la lagena.

Abbreviations: aa: anterior ampulla; asc: anterior semicircular canal; cc: crus commune; ccn: canal for the cochlear nerve; co: cochlear canal; fma: foramen masticatorium; foi: foramen ovale; fv: fenestra vestibuli; hF: hiatus Fallopii; la: lateral ampulla; lag?: possible lagena; lsc: lateral semicircular canal; pa: posterior ampulla; psc: posterior semicircular canal; pbl: primary bony lamina for the basilar membrane; pf: perilymphatic foramen; ps+fn: foramen for the prootic sinus and facial nerve; scc: second crus commune; sips: sulcus for the inferior petrosal sinus; ve: vestibule.

the internal jugular vein. The lateral head vein most probably did not leave the tympanic cavity with the facial nerve through the stylomastoid notch but via a more medial exit (Wible and Hopson, 1995; Wible and Rougier, 2000; *contra* Kielan-Jaworowska et al., 1986; Miao, 1988). A **posttrigeminal vein** (the other major tributary of the lateral head vein) has been reconstructed accompanying the ramus inferior, as in the other multituberculates described by Wible and Hopson (1995) and Wible and Rougier (2000). However, the presence of the posttrigeminal vein in IMM 99BM-IV/4 and other multituberculates remains equivocal, without specific osteological evidence.

The **inferior petrosal sinus** ran in a large, superficial groove on the anteromedial region of the petrosal. In extant mammals, this sinus guides the cavernous sinus blood to the internal jugular vein along the petrosal-basioccipital suture (Rougier et al., 1996b). Given the broad size of the jugular foramen in IMM 99BM-IV/4, we believe that this served as the exit for the inferior petrosal sinus from the cranial cavity. This contrasts with *Kryptobaatar* (Wible and Rougier, 2000) in which the inferior petrosal sinus must have left the cranial cavity via the foramen magnum as vertebral veins, as in monotremes (Hochstetter, 1896). This pathway more closely resembles that of marsupials, representing a derived condition relative to the plesiomorphic course of this sinus (via the foramen magnum) as described for other non-therian mammals (*Morganucodon*, triconodontids *Vincelestes*, other multituberculates; see Rougier et al., 1996a, b).

In IMM 99BM-IV/4, the prootic sinus enters the middle ear cavity through the **prootic canal**, which also housed the facial nerve (secondary facial foramen). The cranial aperture of the prootic canal is anterolateral to the internal acoustic meatus and apparently leads the prootic sinus into the cavum epiptericum space. Actually, the preservation of the fossil does not allow us to clearly identify and reconstruct a separate canal for the prootic sinus. However, we believe that, as in other multituberculates, the prootic sinus was enclosed into a canal and separated from the cavum epiptericum space. It is assumed that, in multituberculates, the cranial aperture of the prootic canal is at the anterodorsal margin of the subarcuate fossa, and the tympanic aperture is confluent with the pterygoparoccipital foramen (ventral ascending canal for the superior ramus of the stapedial artery) (Rougier et al., 1996b; Wible and Rougier, 2000). Nonetheless, cf. *Tombaatar* sp. exhibits a different pattern, in which the cranial aperture of the prootic canal is anterolateral to the internal acoustic meatus and the pterygoparoccipital foramen is a separate aperture, much more posterior to the prootic canal, lying lateral and posterodorsal to the fenestra vestibuli. The non-confluence of the pterygoparoccipital foramen and prootic canal is also found in *Chulsanbaatar* (Kielan-Jaworowska et al., 1986), "*Catopsalis*" *joyneri*, and in an isolated petrosal tentatively assigned to *Meniscoessus* (Wible and Hopson, 1995). The condition in paulchoffatiids and *Nemegtbaatar* remains uncertain.

4.1.2. Neural anatomy: facial and trigeminal nerves

The **facial nerve** entered the middle ear through the anterolateral foramen in the deepest part of the internal

acoustic meatus. It differs from *Kryptobaatar* (Wible and Rougier, 2000), in that the facial foramen is separated from the vestibular foramen, and the primary facial foramen opens into the cavum supracochleare, which is not closed by an osseous floor and contained the geniculate ganglion at the back of the cavum epiptericum, as in other described multituberculates.

According to Miao (1993), the **internal acoustic meatus** of multituberculates, even in the most derived forms such as *Lambdopsalis*, is shallow and not as distinct as that of extant mammals, whereas a well-defined and deep internal acoustic meatus is only found in monotremes and therians. However, the internal acoustic meatus of IMM 99BM-IV/4 is conspicuous, with a depression housing two separated areas for nervous circulation. In this aspect, IMM 99BM-IV/4 is more similar to recent mammals than to morganucodontids.

The greater petrosal nerve or palatine ramus of the facial nerve leaves the anterior part of the geniculate ganglion and via the **hiatus Fallopii**, which opens in a tympanic position in IMM 99BM-IV/4. This condition is unusual among multituberculates. In *Kryptobaatar*, the entrance of the greater petrosal nerve is unclear, with no obvious tympanic aperture for the greater petrosal nerve (Wible and Rougier, 2000). The "hiatus Fallopii" (original quotes) described by Kielan-Jaworowska et al. (1986) for *Chulsanbaatar* is more likely to be the posterior aperture of the carotid canal, as suggested by Wible and Rougier (2000).

An interesting character is the position of the foramina for the branches of the **trigeminal nerve** (foramen ovale inferium and foramen masticatorium). Among the Cretaceous multituberculates, the anterior lamina in *Sloanbaatar* has only the foramen ovale inferium, whereas the anterior lamina has both foramina masticatorium and ovale inferium in *Kryptobaatar*, *Kamptobaatar*, *Nemegtbaatar*, *Chulsanbaatar* and *Catopsbaatar* (Wible and Rougier, 2000). The foramina are roughly at the same level in *Kryptobaatar*, *Kamptobaatar* and *Nemegtbaatar*, but the foramen ovale inferium is more posterior in *Sloanbaatar*, *Chulsanbaatar*, and *Catopsbaatar*, as in IMM 99BM-IV/4.

4.1.3. Inner ear morphology

The 3D reconstruction of the inner ear of IMM 99BM-IV/4 and its comparison with other multituberculates provides more accurate distribution of the phylogenetic characters. The first concerns the **vestibule** size. The vestibules described in *Meniscoessus* and *Catopsalis* by Luo and Ketten (1991) and the vestibule of *Lambdopsalis* (known by an endocast of the inner ear; Meng and Wyss, 1995) are extremely large, suggesting that the saccule, utricle, or both were inflated to a much larger extent than in other mammals. This inflated vestibule has thus been regarded as a possible synapomorphy of Multituberculata (Luo and Ketten, 1991) or a uniquely derived feature only for one or more subgroups within the Multituberculata (Fox and Meng, 1997). The vestibules of paulchoffatiids, *Nemegtbaatar* and *Chulsanbaatar*, however, are not more inflated than in most typical mammals (Hurum, 1998; Lillegraven and Hahn, 1993; *contra* Luo and Ketten, 1991). The new 3D restoration of cf. *Tombaatar* sp. (IMM 99BM-IV/4) shows the vestibule is not enlarged, and this is

consistent with the phylogenetically more basal multituberculates who show a typical mammalian vestibule size.

The **cochlear canal** of IMM 99BM-IV/4 is slightly laterally curved. This condition is found in all known multituberculates, in which the cochlea is definitely curved, and the direction of curvature matches that in other mammals (clockwise in the right ear and counterclockwise in the left ear). However, according to Fox and Meng (1997), the degree of curvature in multituberculates differs among different taxa. The μ CT scans reveal two particularly interesting features of the cochlear canal. A thin bony lamina is observed (Fig. 1B–C), connected to the medial wall of the cochlear canal, near the cochlear nerve entry point (B–C, Fig. 3B). This lamina may be interpreted as the **primary bony lamina for support of the basilar membrane**, as described in *Ornithorhynchus* (Pritchard, 1881) and *Chulsanbaatar* (Hurum, 1998). The dimensions of the basilar membrane cannot be estimated because of the possible absence of a secondary bony lamina. The other feature of interest of the cochlear canal is the marked inflation of its apical region (Fig. 3), which suggests the presence of a **lagena** or lagena-like structure, previously known only in monotremes among mammals and one multituberculate specimen (UALVP 26039) (Fox and Meng, 1997). Previous attempts at reconstructing the inner ear of multituberculates from X-ray tomographies (Luo & Ketten, 1991) indicated that the cochlear canal was distally narrow, rather than expanded, in some multituberculates and in monotremes. This supports the assertion of Fox and Meng (1997) in that these 3D reconstructions of the cochlear canal based on serial sections had been too coarse to capture details of its actual shape. The presence of a lagena at the distal end of the cochlear duct is a specialization comparable to that in reptiles and birds (see Fox and Meng, 1997 for more details). Fernández and Schmidt (1963) proposed that the lagena was lost in the common ancestor of marsupials and placentals as a result of the coiling of the cochlea.

The conformation of the **semicircular canals** of IMM 99BM-IV/4 approaches that of therian mammals in that they are more planar (= they follow the arc of a true circle more accurately) than are monotremes. This is also the case in two other multituberculates, *Nemegtbaatar* and *Chulsanbaatar* (Hurum, 1998).

4.1.4. Phylogenetic implications

At first sight, the overall ear morphology of the djadochtatheriid cf. *Tombaatar* sp. (IMM 99BM-IV/4) is not strikingly similar to that of any other multituberculates. The promontorium shape only resembles to that of other djadochtatheriid multituberculates. The vascular and nervous patterns are quite different from the previously described patterns of arterial, venous and nervous circulation in other multituberculates, and particularly the djadochtatheriid *Kryptobaatar*, suggesting that some previous interpretations and reconstructions (Kielan-Jaworowska et al., 1986; Wible and Hopson, 1995; Wible and Rougier, 2000) may have been biased by the fossil preservation and by the difficulty in accessing these cryptic morphologies without intrusive technology, such

as the μ CT scanning. However, the study of the relative positions of the foramina for the branches of the trigeminal nerve indicates a morphological affinity with *Catopsbaatar*, the other djadochtatheriid. The inner ear morphology of cf. *Tombaatar* sp. (IMM 99BM-IV/4) is typical for multituberculate mammals and we here highlight a new appraisal of the vestibule size and shape and confirm the previously suspected retention of a lagena in multituberculates.

The μ CT technology allows reevaluation of the ear morphology for multituberculates, with the djadochtatheriid cf. *Tombaatar* sp. (IMM 99BM-IV/4) showing a mosaic of plesiomorphic and derived characters, with a vascular and nervous pattern more cladotherian-like than multituberculate-like, a therian-like internal acoustic meatus, and a monotreme-like (or even sauropsid-like) inner ear (slightly coiled cochlear canal, lagena, small vestibule, long and thin crus commune), but with a derived and therian-like semicircular canal planarity.

4.2. Functional implications: auditory capabilities and behaviour

The semicircular canal system of vertebrates helps coordinate body movements, including stabilization of gaze during locomotion, and can be used as a proxy for inferring locomotion habits in vertebrates (e.g., Spoor et al., 2007; Walsh et al., 2009). The 3D reconstruction of the semicircular canals of IMM 99BM-IV/4 shows hitherto unknown condition for multituberculates. The LSC is indeed very short and thin with almost perfectly vertical arches, whereas the ASC is large and arched in a round half circle. A small LSC can be regarded as consistent with less agile behavior (Silcox et al., 2009; Spoor et al., 2007). Moreover it has been concluded that the reduction and verticality of the LSC in humans was related to their upright posture (Spoor et al., 1994). Another analogy can be made with some cimolestean mammals (*Aphronorus* and *Eoryctes*), in which the LSC is also the shortest semicircular canal, and which were likely to have been terrestrial or fossorial animals (Boyer and Georgi, 2007).

Another relevant inner ear feature that potentially can be used to infer hearing capability relates to the cochlear anatomy. The length of the basilar membrane is related to the upper and lower frequency limits of therian hearing (West, 1985). The cochlear canal of cf. *Tombaatar* sp. has a primary bony lamina but apparently lacks a secondary bony lamina in support of the basilar membrane, which was thus probably less efficient in responding to high-frequency airborne vibrations (see Fox and Meng 1997). However this structure is extremely variable among mammals (Fleischer, 1973; Ruf et al., 2009). The cochlea of cf. *Tombaatar* sp. is likely to have supported the basilar membrane and contained at its end a lagena macula, as in monotremes. Because of its coma-shaped and apically expanded cochlea, cf. *Tombaatar* sp. was likely to have been more sensitive to low-frequency sounds (Manoussaki et al., 2008). As a matter of fact, the mammalian cochlea performs analysis of the frequency spectrum of auditory signals by processing different frequencies at different locations along the cochlear duct, the low-frequency sounds lead-

ing to maximum vibrations at the apical end of the cochlea (tonotopy principle, Békésy, 1960).

The study of the middle ear anatomy provides other information as to the auditory capability of cf. *Tombaatar* sp. The stapedial footplate (estimated from the size of the fenestra vestibuli) was very large, suggesting cf. *Tombaatar* sp. might have been fossorial, as stapedial footplates may be significantly larger with respect to body size in fossorial (and low-frequency hearing) species compared to non-fossorial species (Burda et al., 1992). However, in contrast to other fossorial species (e.g., most fossorial placentals), which have large stapedial footplates and degenerated middle ear muscles (Burda et al., 1992), the stapedius muscle is not reduced in cf. *Tombaatar* sp. This differs somewhat from the presumed fossorial *Lambdopsalis bulla*, which is reported to have a large fenestra vestibuli, strongly developed middle ear ossicles, but a reduced fossa for the stapedius muscle (Miao, 1988). Furthermore, while the fossa for the stapedius muscle is broad in cf. *Tombaatar* sp., the fossa for the tensor tympani muscle is small and narrow, as compared to other multituberculates in which the tensor tympani muscle occupied a deep recess (Fox and Meng, 1997; Wible and Rougier, 2000). A similar condition is present in the fossorial marsupials *Necrolestes* and *Notoryctes* (Ladevèze et al., 2008), in which the cochlea is little-coiled (1.1 and 1.6, respectively) and the stapedius muscle is strongly developed. These observations suggest that cf. *Tombaatar* sp. and the marsupial moles might have developed an alternative specialization to a fossorial way of life from the one reported in placental forms (i.e., strong reduction of the middle ear muscles, see Ladevèze et al., 2008).

Most Asian multituberculates, whose lifestyles have been reconstructed based primarily on postcranial anatomy have been interpreted as terrestrial. However, it has been suggested that some multituberculates may have been fossorial, while some later multituberculates might have been arboreal (Kielan-Jaworowska and Gambaryan, 1994; Kielan-Jaworowska et al., 2004). Specializations to a fossorial lifestyle have been suggested for two Asian multituberculates: a possible djadochtatherioid from the Djadokhta Formation (Kielan-Jaworowska, 1989; Kielan-Jaworowska et al., 2004) and *Lambdopsalis* from the Eocene of China (Kielan-Jaworowska et al., 2004).

The semicircular canal system of the new specimen (cf. *Tombaatar* sp.) described here is consistent with a low level of agility, and, as expected for a Late Cretaceous multituberculate from Mongolia (see Kielan-Jaworowska and Gambaryan, 1994), it is likely that it was terrestrial. Moreover, the anatomy of both the petrosal and bony labyrinth of cf. *Tombaatar* sp. is compatible with fossorial habits. These preliminary conclusions nonetheless need to be further tested by improved and combined statistical analyses of the degree of correlation of metric parameters from the semicircular canal system with locomotion habits (David et al., 2010, this issue) to infer with more confidence a locomotor pattern for multituberculates.

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Appendix A. Supplementary data

Electronic Supplementary Data associated with this article can be found, in the online version, at doi:10.1016/j.crpv.2010.07.008.

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