



Mammalian petrosal from the Lower Cretaceous high paleo-latitude Teete locality (Yakutia, Eastern Russia)

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Abstract

A mammalian petrosal from the Lower Cretaceous Teete locality in Yakutia (Russia) shows a prominent and complex system of venous channels in the bony wall of the pars cochlearis surrounding the straight cochlear canal. This complex venous system is distinctive and more strongly developed than in other mammalian petrosals. A bony ridge is present on the ventral side of the cochlear canal endocast, continuing from between fenestra vestibuli and fenestra cochleae in anterior direction. This ridge corresponds to the position of the scala tympani, and is similar to the secondary bony lamina of crown therians, but lacks the sharp laminar edge. The fenestra cochleae is separate from the canal for the aqueductus cochleae (derived), but the fenestra retains a deep sulcus that resembles the perilymphatic sulcus (plesiomorphic). The fenestra cochleae is oval shaped and deep. The straight cochlear canal with a ridge on the ventral side strongly resembles that of eutriconodontans like *Priacodon fruitaensis* from the Upper Jurassic of North America. However, thick and extensive venous channels in the pars cochlearis are otherwise known from docodontans. In the Teete petrosal the channels are even more developed, and resemble the pattern recently reported from possible haramiyidan petrosals from the Middle Jurassic of western Siberia (Russia). Both eutriconodontan and haramiyidan dental remains are known from the Teete locality beside that of tritylodontids and docodontans.

Keywords

3D reconstruction, anatomy, bony labyrinth, eastern Siberia, endocast, Eutriconodonta, inner ear

Introduction

The Teete locality in Yakutia (Fig. 1) is known since 1960 when the first dinosaur bones were discovered (see historic survey in Averianov et al. 2018). In Teete high-latitude Lower Cretaceous strata (paleo-latitude estimate of 62–66.5° N) are exposed and provide the northernmost sauropod record (Averianov et al. 2020, Skutschas et al. 2021). At the Teete locality occur invertebrates such as freshwater bivalves and gastropods, and floral elements such as mosses, horsetails, lycopods, ferns, and conifers (Kolosov et al. 2009). The non-mammalian vertebrates comprise dinosaurs, turtles, lizards, choristoderes, and salamanders (Skutschas et al. 2018, 2020, 2021; Averianov et al. 2020). Mammalian forms are represented by the tritylodontid *Stereognathus kolosovi*, the euharamiyidan *Cryoharamiya tarda*, the tegotheriid docodontan *Khorotherium yakutense* (corrected here from *K. yakutensis* Averianov et al. 2018 to neuter gender *K. yakutense*), the eutriconodontan *Sangarotherium aquilonium* (Lopatin and Agadjanian 2008; Averianov et al.

2017, 2018, 2019), and a yet undescribed gobiconodontid. Three joint Russian-German field seasons (2017–2019) focused on screen washing of fossiliferous matrix which yielded numerous micro-vertebrate remains including a mammalian petrosal from the Teete locality. Beside teeth and lower jaw bones, the petrosal bone, as the hardest and densest bone in the mammalian body (Frisch et al. 1998), is very resistant to erosion. Petrosals are frequently found isolated from the skull in Mesozoic fluvio-lacustrine sediments (Hughes et al. 2015; Schultz et al. 2021).

Here we describe the first and so far only mammalian petrosal from Teete locality. This record is the northernmost and adds substantial information on early mammalian ear anatomy. We dedicate this study to Professor Dr. Wolfgang Maier (Tübingen), one of the pioneers of the 3D reconstruction and analysis of mammalian internal skull anatomy (e.g., Maier 1987, 1993; Maier and van den Heever 2002), on the occasion of his 80th birthday.

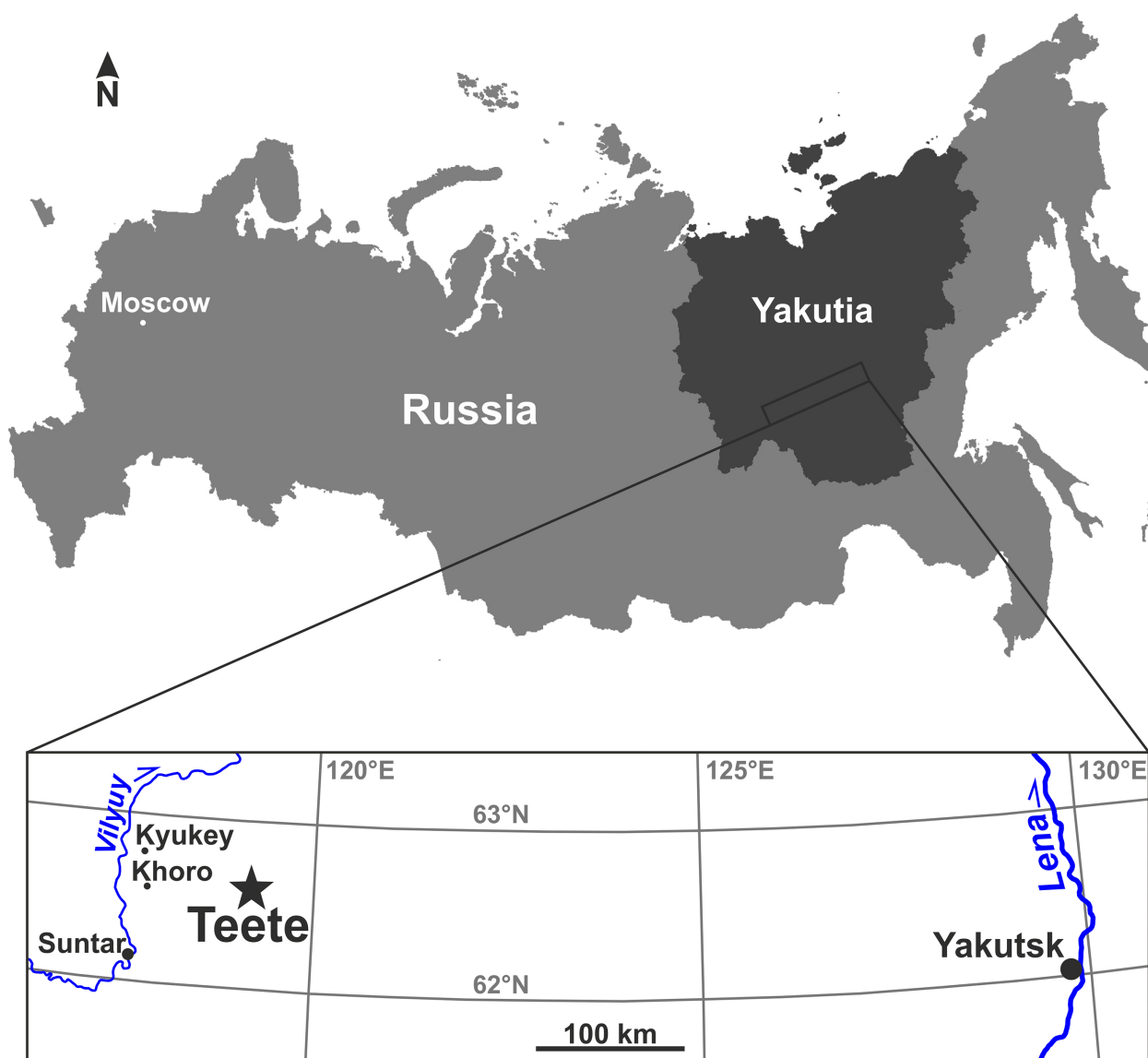


Figure 1. Map of Russia with Teete locality in Yakutia (asterisk).

Materials and Methods

The petrosal (PIN 5614/25) was found during picking the coarse fraction (1–2 mm) of screen-washed fossiliferous matrix at Teete locality in Suntar Ulus, Yakutia, Eastern Siberia, Russia. A detailed description of the Teete section belonging to the Batylykh Formation, Sangar Series (Lower Cretaceous, Berriasian–Barremian) has been provided by Averianov et al. (2018).

JAS scanned the petrosal (PIN 5614/25) using micro-computed tomography (GE phoenix|x-ray v|tome|x 180s; high-power nanofocus) in the Institute of Geosciences, Section Paleontology, Rheinische Friedrich-Wilhelms-Universität Bonn, Germany. Scan parameters were 2.2 μm (voxelsize), 80 kV (voltage), 80 μA (current), and a shutter speed of 1000 ms per capture. The $\mu\text{-CT}$ produced isotropic voxels, and the single image size is 2024×2024 pixels. RS reconstructed the polygonal models using the software Avizo 7.1. Further processing was made using the inspection software PolyWorks 2014 IR13 (InnovMetric Software Inc.).

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Description

External morphology of petrosal PIN 5614/25

The petrosal (PIN 5614/25) is broken at the anterior and posterior ends (Fig. 2A, B). The ventral aspect shows a bulbous promontorium with a smooth bone surface. Both the fenestra cochleae and the fenestra vestibuli (broken posterolaterally) are preserved and separated by a thick crista interfenestralis. A thin groove along the inner rim of the circular fenestra vestibuli reflects the position of the footplate of the stapes. In the medial corner of the fenestra cochleae lies a deep open sulcus and a fully separated aqueductus cochleae is preserved dorsally from the fenestra cochleae. The deep fenestra cochleae is oval, antero-posteriorly compressed with a flat medial wall. Anterior to the fenestra vestibuli lies a smaller circular foramen, the prootic canal. This opening connects to a complex venous sinus system inside the petrosal bone. Anterolaterally to the prootic canal lies the wide sulcus for the lateral head vein which leads medially to the broken edges of the pterygoparoccipital foramen. On the anterior aspect of the petrosal, the wide space just posteroventrally to the broken pterygoparoccipital foramen shows a shallow oval shaped depression. This depression is interpreted to have contained the geniculate ganglion (Fig. 2E). From the geniculate ganglion depression a groove turns medially to follow closely along the promontorium. This is interpreted to be the sulcus for the greater petrosal nerve.

On the dorsal side, the petrosal shows an almost complete internal acoustic meatus (IAM) that contains the bony openings for the nervous pathways of the branches of the vestibulocochlear nerve (CN VIII) and the facial nerve (CN VII) (Fig. 2B). The largest opening is the cochlear foramen for the cochlear part of CN VIII, which is oval-shaped. This foramen extends in antero-medial to postero-lateral direction. There are no bony supporting structures visible inside the opening, such as bony lamellae, perforated bony bars or cribriform plates. Anterolaterally from the cochlear foramen are two smaller openings. These openings are separated from the foramen for cochlear nerve by a thick bony transverse crest. The two smaller openings lie in a deep groove; the foramen closer to the transverse crest is identified here to be the utriculo-ampullar branch of CN VIII. Anterolateral to the utriculo-ampullar nerve foramen is the smaller opening of the facial canal for CN VII. Anterior to the large cochlear foramen are the broken edges of the pterygoparoccipital foramen.

Inner ear endocast reconstruction

Due to the damage of the petrosal bone the vestibular region and the apex of the cochlear canal are missing (Fig. 2C, D). Only the middle portion of the cochlear canal with the cochlear nerve is preserved and both spaces that are constituted by the fenestra vestibuli and the fenestra cochleae. The cochlear canal appears straight for the part that is preserved, but might have been slightly curved near the apex which is broken off. The reconstructed endocast shows a distinct ridge with a parallel shallow groove in the position where a therian secondary lamina would be (see discussion below). The ridge and parallel groove are two prominent features on the ventral aspect of the cochlear canal endocast. Both the ridge and the groove extend from between fenestra vestibuli and fenestra cochleae anteriorly until the cochlear canal is broken off (Fig. 2C).

On the dorsal side the endocast shows the typical pattern of nervous pathways of the vestibulocochlear nerve (CN VIII). The entrance of the cochlear part of CN VIII is oval-shaped and the foramen extends in antero-medial to postero-lateral direction. On the posterior side of the inner ear endocast, a sulcus extends from an opening in the internal auditory meatus to the broken vestibule in postero-lateral direction. This sulcus contained the vestibular nerve branch innervating the ampulla of the posterior semicircular canal. There is no sulcus or separate canal on the anterior side of cochlear canal endocast that would lead in antero-medial direction toward a lagenar macula in apical region of the cochlear canal. Lateral to the cochlear branch of CN VIII is the combined entrance of the innervation of the utricular macula and both the ampullae of the lateral and anterior semicircular canals. There is no indication of a separate sulcus or canal for the innervation of the sacculus; the saccular branch probably shared the sulcus with the nerve branch innervating the ampulla of the posterior semicircular canal.

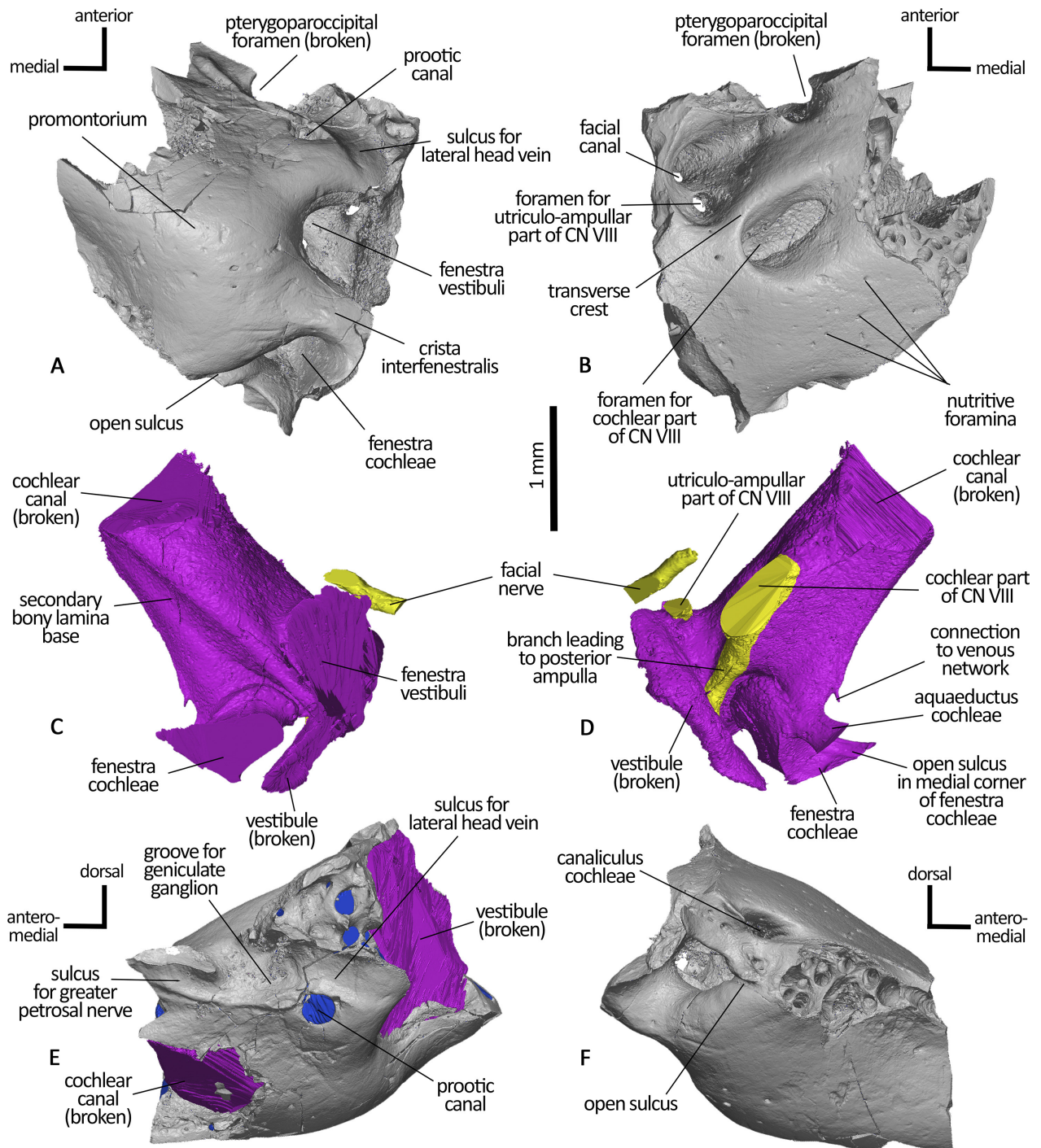


Figure 2. The petrosal from the Lower Cretaceous Teete locality in Yakutia. **A)** Ventral view and **B)** dorsal (endocranial) view of the petrosal. **C)** Ventral view and **D)** dorsal view of the virtually reconstructed cochlear endocast (pink) and innervation areas (yellow). **E)** Anterolateral view of the petrosal with reconstructed soft tissue parts of the cochlear endocast (pink) and venous pathways (blue). **F)** Posteromedial view of the petrosal.

The complex venous system surrounding the cochlear canal consists of an elaborate network of larger channels crossing the cochlear canal dorsally and ventrally. On the dorsal (endocranial) side the venous channels are termed transcochlear (or epicochlear) sinuses (following Panciroli et al. 2019 or Harper and Rougier 2019) (Fig. 3). On the ventral (tympanic) side of the cochlear canal the venous channels are known as the circumpromontorial plexus (following Kermack et al. 1981 and Panciroli et al. 2019). On the medial side of the cochlear canal, the transcochle-

ar sinus channels fuse to form larger canals to connect to the inferior petrosal sinus. On the lateral side, several larger channels of the circumpromontorial plexus connect medially to the inferior petrosal sinus, and laterally to the prootic sinus. On the dorsal side, two larger connections between the vessels on the lateral and the vessels of the medial side lie anterior and posterior to the entrance of the cochlear part of CN VIII. These connections are the anterior and posterior transcochlear (or epicochlear sensu Harper and Rougier 2019) sinuses (Fig. 3C, E).

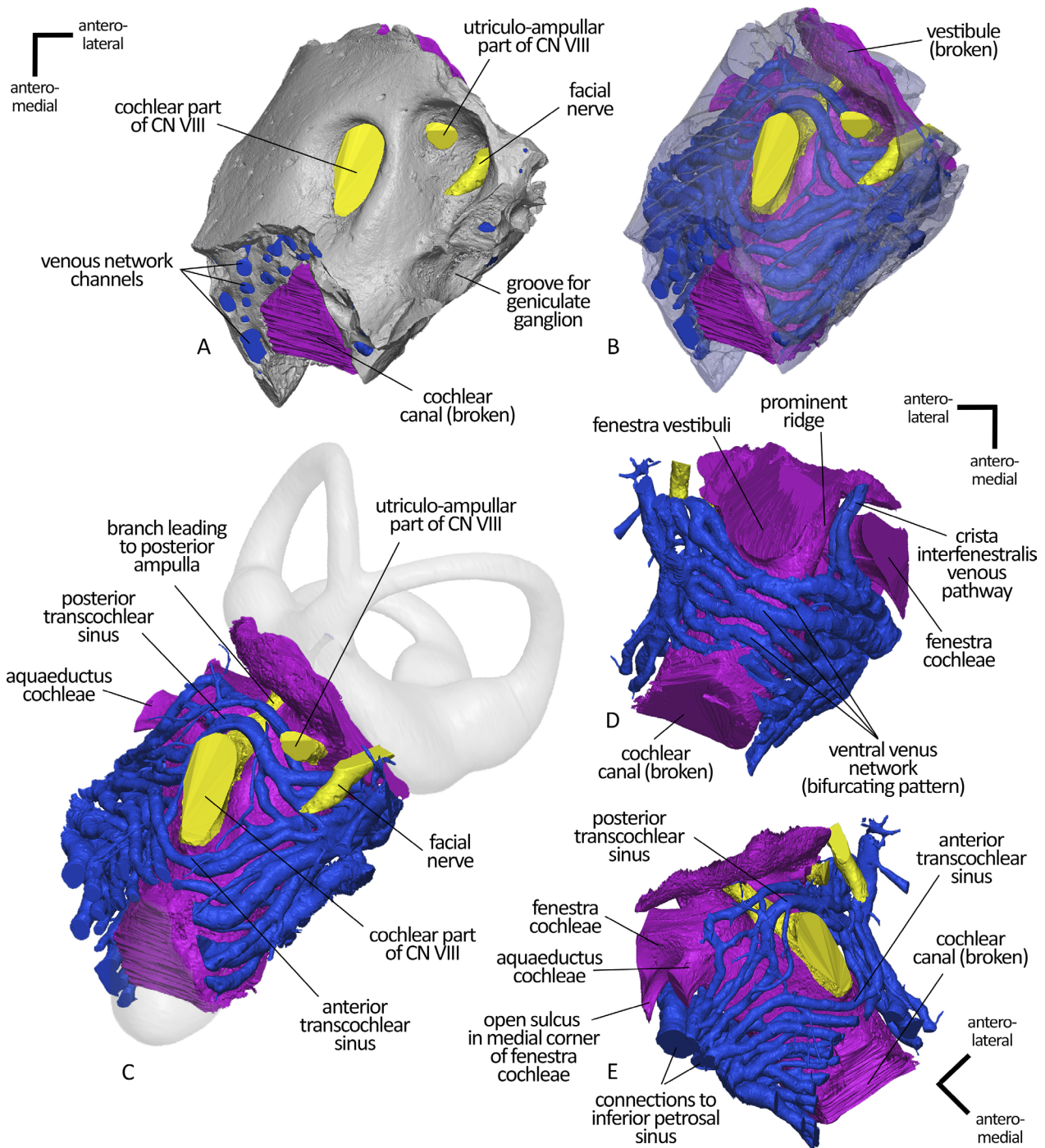


Figure 3. 3D reconstruction of soft tissue parts of the Teete petrosal. **A)** Dorsal (endocranial) view of the internal acoustic meatus of the petrosal with reconstructed soft tissue parts of the cochlear endocast (pink), venous pathways (blue), and innervation areas (yellow). **B)** Same view as A with translucent bone parts to illustrate the high degree of vascularity of the circum-promontorial region. **C)** Same view as A and B, reconstructed soft tissue parts (cochlear endocast pink, venous pathways blue, innervation areas yellow) enclosed in the petrosal bone with indicated missing parts of the inner ear (vestibular region and cochlear apex in shaded gray). **D)** Ventral view of the bifurcating venous pathways. **E)** Dorsomedial view of the reconstructed soft tissue parts (cochlear endocast pink, venous pathways blue, innervation areas yellow).

Three connections of the circumpromontorial plexus preserved on the ventral side of the cochlear canal show an bifurcating pattern (Fig. 3D). The connections to the prootic sinus are documented by the direct bony opening to the prootic canal in this area. All vessels on the lateral side lead in posterior direction. Interestingly, the connections of the circumpromontorial plexus on the

ventral side of the cochlear canal are much thicker than the dorsal transcochlear sinuses. We report the finding that two larger channels run through the crista interfenestralis connecting to the complex venous system. And these two channels, called the crista interfenestralis venous pathways (Fig. 3), are inside the bone between the fenestra vestibuli and the fenestra cochleae (Fig. 3D). To

our knowledge, this is the first case that two channels in the crista interfenestralis have been described. Since the posterior part of the petrosal is lost due to breakage, it is possible that a connection of the two channels and the paroccipital sinus existed.

Discussion

Although broken anteriorly and posteriorly, the mammalian petrosal (PIN 5614/25) from the Teete locality shows a number of striking features: 1) the co-existence of an open sulcus in the medial corner and a separated aquaeductus cochleae near the fenestra cochleae which is uncommon for non-mammalian mammaliaforms; other non-mammalian mammaliaforms either have an open sulcus, or a canal of the aquaeductus cochleae, but not both; 2) a straight cochlear canal (for the part that is preserved) with a shallow groove and a prominent ridge in the same position as a base of the secondary lamina, on the ventral aspect of the cochlear canal endocast; 3) a well developed, venous channel network in the bone of the pars cochlearis, consisting of vessels of large diameters; and 4) connected to the venous channel network in the pars cochlearis are two large channels inside the crista interfenestralis.

Remains of several mammalian morphs have been reported for the Teete locality so far, including the tritylodontid *Stereognathus kolosovi*, the euharamiyidan *Cryoharamiya tarda*, the tegotheriid docodontan *Khotherium yakutense*, and the eutriconodontan *Sangarotherium aquilonium* (Lopatin and Agadjanian 2008; Averianov et al. 2017, 2018, 2019), and a yet undescribed gobiconodontid.

A tritylodontid origin for the Teete petrosal can be excluded, because the bony housing of the cochlear canal in tritylodontids is lacking an inflated promontorium and retains the basisphenoid wing, a primitive feature of many cynodonts (Luo 2001). The Teete petrosal is a clearly fused single bone with an inflated promontorium and no obvious bone sutures or facets for the overlapping basisphenoid wing. This morphology suggests that this petrosal (PIN 5614/25) is not of a tritylodontid origin.

In the morganucodontan *Morganucodon*, the docodontans *Haldanodon* and *Boreolestes*, multituberculates, and the monotreme *Ornithorhynchus* an open sulcus (for the perilymphatic duct) leads from the jugular notch to enter the inner ear through an opening, also termed the perilymphatic foramen (Lillegraven and Hahn 1993; Zeller 1993; Hurum 1998; Ruf et al. 2013; Panciroli et al. 2019). Wible (1990) interpreted that the perilymphatic duct was contained within a well-developed groove on the petrosal that runs between the jugular fossa and fenestra cochleae in non-mammalian mammaliaforms like morganucodontids, as in case of extant monotremes. With the enlargement of the pars cochlearis, and the better segregation of the inner ear from the middle ear cavity in derived mammals, a bony separation (the processus recessus) developed to enclose the perilymphatic duct, a transfor-

mation that has also separated the fenestra cochleae from the perilymphatic foramen in therians (Zeller 1985). The perilymphatic foramen of non-mammalian mammaliaforms can therefore be regarded as a shared opening of the presumptive fenestra cochleae and the perilymphatic duct in an open sulcus. With the bony separation, the open sulcus for the perilymphatic duct is transformed into a canal and thus the true fenestra cochleae does not show a sulcus. The difference between a perilymphatic foramen and a fenestra cochleae is defined by the presence of an osseous processus recessus (de Beer 1929; Zeller 1985), which walls off the perilymphatic duct from the middle ear cavity into a canal called the cochlear canaliculus for the aquaeductus cochleae (Rougier and Wible 2006). The cochlear canal of the Teete petrosal shows an unusual co-existence of both the canaliculus for the aquaeductus cochleae and a posteromedial opening of a fully separated aquaeductus cochleae from the fenestra cochleae, and an open sulcus in the medial corner of the fenestra cochleae leading to the jugular notch. A perilymphatic foramen as shared opening of fenestra cochleae and perilymphatic duct and the presence of an open sulcus for the perilymphatic duct are considered to be two ancestral characters of mammalian morphs (Kermack et al. 1981; Crompton and Luo 1993; Lillegraven and Hahn 1993; Wible and Hopson 1993, 1995; Rougier et al. 1996; Luo et al. 2001), but the occurrence of a well separated aquaeductus cochleae and a fenestra cochleae is regarded as a derived character for the cladotherians including living therians (Wible 1990; Wible et al. 2001; Ekdale 2013; Luo et al. 2016; Harper and Rougier 2019; Luo and Manley 2020). The preserved sulcus in the medial corner of the fenestra cochleae of the Teete petrosal might be a pathway for a vein that formerly was the accompanying vein of the perilymphatic duct. A perilymphatic foramen is also found in the eutriconodontan *Priacodon* (Rougier et al. 1996; Harper and Rougier 2019), but an additional separated aquaeductus cochleae like in the Teete petrosal is not present in *Priacodon*. Interestingly, in both a tentatively assigned gobiconodontid and a trechnotherian petrosal (i.e., Höövör 1 and 2 in Harper and Rougier 2019) from the Lower Cretaceous of Mongolia a fully separated aquaeductus cochleae was observed using virtual 3D endocast reconstruction (Harper and Rougier 2019). In an earlier work the trechnotherian petrosal was described to lack an aquaeductus cochleae (Rougier et al. 1996), but this was corrected by Harper and Rougier (2019). In both taxa the separated canal lies in a similar position like in the Teete specimen. It is important to note, that the bony segregation of the fenestra cochleae from its confluent sulcus of the perilymphatic duct is seen only in advanced stem therians (“cladotherians”). It has been described for example for the cladotherians *Vincelestes*, *Dryolestes*, *Henkelotherium* and other dryolestoids, and is present in the vast majority of therians (Wible 1990; Rougier et al. 1992; Wible et al. 2001; Ladevèze, 2004, 2007; Ruf et al. 2009; Luo et al. 2012; Ekdale 2013; Hughes et al. 2015). Because a separate aquaeductus cochleae is present in more derived taxa, it probably represents an apomorphic cladotherian character (Ruf et al. 2009; Luo et al. 2012),

which may also occur in some trechnotherians according to the latest study by Harper and Rougier (2019). However, in the modern mysticete cetacean *Eschrichtius robustus* with a teardrop shaped fenestra cochleae a confluence with the perilymphatic foramen exists (Ekdale et al. 2011).

The fenestra vestibuli is severely broken in the Teete petrosal, but the remnants of its edges suggest a shape closer to circular rather than oval. It is known from other eutriconodontan petrosals that the fenestra vestibuli is close to circular (stapedial ratio 1.2, see Harper and Rougier 2019), but the specimen described here is too damaged to calculate a ratio for comparison.

Because the pterygoparoccipital foramen is broken in the Teete petrosal it is not clear if it was fully closed (as in cladotherians) or a simple open notch (as in non-mammalian mammaliaforms). The superior ramus of the stapedial artery passes through the pterygoparoccipital foramen in early mammaliaforms and extant mammals (Wible 1990; Rougier et al. 1992; Wible and Hopson 1995). In non-mammaliaform cynodonts and the morganucodontid *Morganucodon* the pterygoparoccipital foramen is an open notch, which is considered to be the plesiomorphic condition (Kermack et al. 1981; Rougier et al. 1992).

The internal acoustic meatus (IAM) of the Teete petrosal shows three major openings. The IAM of the eutriconodontan *Priacodon* was first described to have three foramina (Rougier et al. 1996) and later was revised to have four foramina (Harper and Rougier 2019). The transverse crest in the IAM of the Teete petrosal is quite prominent resembling the pattern of the eutriconodontan *Priacodon* (Harper and Rougier 2019). There is no sign of a small opening in the prominent transverse crest of the Teete petrosal for a separate innervation of the saccular macula like in recently described tentatively assigned docodontan and haramiyidan petrosals from western Siberia (Schultz et al. 2021). A well-separated and larger area for the innervation of the saccular macula is also found in the monotreme *Tachyglossus* (Schultz et al. 2017). In comparison, in the monotreme *Ornithorhynchus* the saccular innervation lies in a narrow sulcus branching off of the cochlear branch close to the utriculo-ampullar branch (Schultz et al. 2017). We therefore hypothesize that in the Teete specimen the innervation of the saccular macula either might have shared the same canal of the utriculo-ampullar branch or branched off of the cochlear branch inside the cochlear canal suspended in soft tissue.

No sulcus or separate canal on the anterior side of the cochlear branch (of CN VIII) opening is observed in the Teete petrosal. Such a canal would lead in antero-medial direction toward a lagenar macula in the apical region of the cochlear canal like it is reported for the docodontan *Haldanodon* (Ruf et al. 2013). Thus, we infer that the lagenar macula was absent in this petrosal.

The prominent ridge associated with a parallel shallow groove on the ventral side of the cochlear canal of the Teete petrosal is in the same position where the secondary bony lamina would be in cladotherians. This structure that can be observed on the ventral side of the cochlear canal endocast in spalacotheroids and eutriconodontans is

different from the “true secondary bony lamina” of cladotherians in two characters: the secondary bony lamina is wedge-like with a sharp edge, and always co-exists with the primary bony lamina. The cochlear canal endocasts of both spalacotheroids and eutriconodontans lack both these features (Luo and Manley 2020). They are also absent in the Teete specimen. In many crown therians, the secondary bony lamina is located at the junction of the scala media and the scala tympani, one reason some authors termed this structure “the secondary lamina base without its bony edge” (e.g., Luo et al. 2016) or “scala tympani impression” (e.g., Luo and Manley 2020) in spalacotheroids or eutriconodontans. In Harper and Rougier (2019) the structure is termed “secondary (abneural) bony lamina of cochlear canal”.

The extensive and prominent network of venous channels around the cochlear canal of the Teete petrosal causes the cancellous appearance of the pars cochlearis. The channels are much larger (wider in the channel diameter) than a similar vascular channel network described for the docodontan *Borealestes*, which shows thin canals and a fine circum-promontorium plexus network on the ventral side of the cochlear canal (Panciroli et al. 2019). The Teete petrosal is similar to *Borealestes* in having an anterior and posterior transcochlear sinus crossing the cochlear canals dorsally. Harper and Rougier (2019) described similar structures for the eutriconodontan *Priacodon*, but used the terminology anterior and posterior epicochlear sinuses. The Teete petrosal differs from both *Borealestes* and *Priacodon* in having additional vessels crossing the cochlear canal dorsally. Three connections of venous pathways are also preserved on the ventral side of the cochlear canal with an unusual bifurcating pattern very different from the fine network found in *Borealestes* (Panciroli 2019). Thicker ventral connections have also been described for *Priacodon* (Harper and Rougier 2019) but those channels are far less developed than in the Teete petrosal. Schultz et al. (2021) described a similar extensive vascularization in tentatively assigned haramiyidan petrosals from western Siberia. Whether or not this extensive vascularization of the petrosal is an adaptation to the subpolar climate needs further investigation.

Two larger channels connecting to the complex venous system run through the crista interfenestralis in the Teete petrosal and therefore lie in the bone between the fenestra vestibuli and the fenestra cochleae. A single thin vessel in this area is present in *Priacodon* (Harper and Rougier 2019: page 7, fig. 3 and page 18, fig. 7) suggesting a connection to the paroccipital sinus, which can also be assumed for the Teete petrosal. Unfortunately, the whole paroccipital region is broken thus we currently cannot demonstrate the connection without a more complete specimen.

A structure described as “half-pipe shaped sulcus” in the two Höövör petrosals (one tentatively assigned to gobiconodontids, the other probably a trechnotherian; Harper and Rougier 2019) is also seen in the Teete petrosal. Harper and Rougier (2019) postulate that this half-pipe shaped sulcus is confluent with a venous canal inferred to have contained the vein of the aquaeductus cochleae.

In some therians, this vein follows a tortuous trajectory to connect to the inferior petrosal sinus (Axelsson 1988; Harper and Rougier 2019). The reconstruction of the vascular network of the Teete petrosal shows that there is a definite connection of this sulcus to a short canal, which is confluent with the venous pathways collecting on the medial side where the inferior petrosal sinus is located (Figs 2D, 3E).

We tentatively assign the Teete petrosal to be of eutriconodontan origin, because of the similarities to the petrosal of *Priacodon* and also the shared features of gobiconodontids.

Conclusion

The petrosal from Teete displays striking similarities to that of the eutriconodontan *Priacodon* and also shares features that are known from a gobiconodontid petrosal from the Lower Cretaceous of Mongolia. Like *Priacodon fruitaensis* from the Upper Jurassic of North America, the Teete petrosal has an oval shaped and deep fenestra cochleae as well as a straight cochlear canal with a ridge on the ventral side. The unusual thick blood vessels, however, resemble the situation recently reported for possible haramiyidan petrosals from Middle Jurassic of western Siberia (Russia). Eutriconodontan, gobiconodontan, and haramiyidan remains are known from the Teete locality and therefore an assignment of the petrosal to one of these taxa is probable.

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