

# Ontogeny and morphofunctional implications of the ethmoidal region in the semiaquatic *Potamogale velox* (Afrotheria, Mammalia)

IRINA RUF<sup>1,\*</sup>, HENDRIK BEHRENS<sup>2</sup> & ULRICH ZELLER<sup>2</sup>

<sup>1</sup> Senckenberg Forschungsinstitut und Naturmuseum Frankfurt, Abteilung Messelforschung und Mammalogie, Senckenberganlage 25, 60325 Frankfurt am Main, Germany — <sup>2</sup> FG Spezielle Zoologie, Lebenswissenschaftliche Fakultät, Albrecht Daniel Thaer-Institut für Agrar- und Gartenbauwissenschaften, Humboldt-Universität zu Berlin, Unter den Linden 6, 10099 Berlin, Germany — Corresponding author: irina.ruf@senckenberg.de

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## Abstract

Afrotheria is a diverse clade in terms of morphofunction and ecology. Although its phylogeny is well supported by molecular data, morphological and ontogenetic analyses are still demanded. This holds especially true for cranial structures that can also provide a deeper insight into sensory and ecological adaptations e.g., the ethmoidal region that houses the sense of smell as well as structures involved in thermoregulation. Here we provide a comparative description of the ethmoidal region of the semiaquatic tenrecoid *Potamogale velox* based on histological serial sections of the fetal chondrocranium and  $\mu$ CT data of the adult skull. The chondrocranium of *Potamogale velox* generally resembles the placental morphotype showing a prominent and well-developed cupula nasi anterior with a large processus alaris superior. The nasoturbinal is developing later in ontogeny. The number of olfactory turbinals is already determined before birth and shows a common pattern among small placental mammals: two frontoturbinals, three ethmoturbinals, one interturbinal between ethmoturbinal I and II. Apomorphic characters of *Potamogale velox* that are related to its semiaquatic mode of life are as follows: proportionally small olfactory turbinal skeleton and a reduced lamina cribrosa, loss of ductus nasolacimalis, and an enlarged foramen epiphaniale due to the enhanced sensory innervation of the snout. Although the maxilloturbinal, that is involved in thermoregulation, is proportionally larger than in the terrestrial Tenrecoidea its morphological complexity is not significantly increasing from the fetus to the adult. Our results prove once again the importance of a deeper understanding of the cranial ontogeny for morphological studies of the mammalian skull.

## Key words

Chondrocranium; ethmoid bone; nasal capsule; nasal cavity; ossification; turbinals.

## Introduction

Potamogalidae (otter shrews) are semiaquatic carnivorous-insectivorous Tenrecoidea (Afrosoricida according to STANHOPE *et al.*, 1998) represented by two genera and three species (*Potamogale velox*, *Micropotamogale lamottei*, *Micropotamogale ruwenzorii*) known from western and central Africa (WILSON & REEDER, 2005). Within Tenrecoidea, otter shrews and the terrestrial insectivorous tenrecs are generally accepted as sister groups (SCHUNKE & ZELLER, 2010; EVERSON *et al.*, 2016) and were classi-

fied within different subfamilies under the term “Tenrecomorpha” (BUTLER, 1972; GIERE *et al.*, 2001). EVERSON *et al.* (2016) re-evaluated the African otter shrews to family rank placed as a sister family to Tenrecidae (Malagasy tenrecs) based on morphological and molecular analyses (but see ASHER & HELGEN, 2010 for taxonomic review and justification of subfamily level).

This relationship and the fact that Tenrecoidea are nested within Afrotheria including the monophyly of the

latter are supported by molecular but also morphological evidence (SEIFFERT, 2007; MEREDITH *et al.*, 2011). However, the monophyly of Potamogalidae has been challenged by SEIFFERT (2007: figure 2) based on molecular as well as morphological and fossil data. For a general overview of afrotherian systematics and phylogeny see also the reviews in TABUCE *et al.* (2008), ASHER & HELGEN (2010) and ASHER & SEIFFERT (2010).

Anatomical support for afrotherian and especially tenrecoid phylogeny is increasing by recent morphological studies (e.g., SÁNCHEZ-VILLAGRA *et al.*, 2007; ASHER & LEHMANN, 2008; BROCKLEHURST *et al.*, 2016). However, the entire ethmoidal region of Tenrecoidea has been barely taken into account although few studies on mostly selected nasal structures exist (e.g., ASHER, 2001, 2005; SCHUNKE & ZELLER, 2010). Until the end of the last century members of the Tenrecoidea were considered to be closely related to Soricidae, Talpidae, Erinaceidae, and Solenodontidae (all Lipotyphla) forming the order Insectivora (e.g., BUTLER, 1988; MACPHEE & NOVACEK, 1993). Thus, several previous comparative cranial studies including Tenrecoidea were based on misleading systematic assumptions (e.g., DE BEER, 1937 and references therein; BUGGE, 1972).

Within Mammalia, adaptations towards a semiaquatic mode of life resemble a striking example for convergence and evolved independently among various mammalian taxa (STARCK, 1995), including monotremes (*Ornithorhynchus anatinus*), marsupials (e.g., *Lutreolina crassicaudata*), Lipotyphla (e.g., *Desmana moschata*, *Neomys fodiens*), Rodentia (e.g., *Castor fiber*), Carnivora (e.g., *Lutra lutra*), and Artiodactyla (e.g., Hippopotamidae) among others.

As a semiaquatic mammal *Potamogale velox*, the giant otter shrew, shows several adaptations to this specific mode of life and locomotion: a laterally flattened tail, lateral flaps on the hindfeet, long and stiff vibrissae, specialized fur, small eyes and nostrils, which can be closed during diving (NOWAK, 1991; MONADJEM, 2018). Semiaquatic (as well as aquatic) mammals also show distinct adaptations in their sense organs. For instance, in *Potamogale velox*, like in other semiaquatic species compared to their terrestrial counter parts, the trigeminal system (tactile sense, associated with vibrissae) is well developed as revealed by enlargement of the foramen infraorbitale in contrast to the olfactory system, which appears to be reduced due to a smaller anterior cranial fossa (SÁNCHEZ-VILLAGRA & ASHER, 2002). Furthermore, *Potamogale velox* shows a unique stapedia arteries pattern and a vascular plexus in the neck region that may support heat exchange (BROCKLEHURST *et al.*, 2016). Recent studies on Rodentia and Carnivora revealed that in semiaquatic species the olfactory turbinals (fronto-, ethmo- and interturbinals) are proportionally smaller than in terrestrial species (VAN VALKENBURGH *et al.*, 2011; MARTINEZ *et al.*, 2020). In contrast, the turbinals in the anterior part of the nasal cavity, the nasoturbinal but especially the maxilloturbinal that are involved in thermoregulation in terms of exchange of heat and mois-

ture are significantly enlarged in semiaquatic rodents and carnivorans (HILLENIUS, 1992, 1994; VAN VALKENBURGH *et al.*, 2011; MARTINEZ *et al.*, 2020). As thermoregulation is a major challenge for aquatic and semiaquatic mammals, the ethmoidal region and especially the turbinal pattern of *Potamogale velox* is of special interest to get a deeper understanding of its semiaquatic adaptations.

However, the cranial morphology of adults can be challenging due to great ontogenetic modifications that often mask the original pattern and homology of characters. Thus, it is demanding to take early ontogenetic stages into account in order to identify homologies and for a better understanding of craniogenetic transformations from the chondrocranium to the adult skull; this holds particularly true for the ethmoidal region (e.g., MAIER & RUF, 2014; RUF, 2020). A recent study on the ethmoidal region of paenungulate Afrotheria (*Loxodonta africana*, *Orycteropus afer*, *Procavia capensis*) could not confirm the suitability of this cranial region for higher systematic relationships (STÖSSEL *et al.*, 2010). However, this study may have suffered from the fact that the sampling comprises two highly specialized macrosmatic species, *Loxodonta africana* and *Orycteropus afer*. Furthermore, the structures of the ethmoidal region may not be stand-alone characters for supporting higher taxa but this part of the cranium can well support relationships within lower taxa as observed e.g., in Lagomorpha and Rodentia (RUF, 2014, 2020).

The overall objective of our study is to conduct a “morphological-functional character polarization” against the background of recent phylogenies (e.g., MEREDITH *et al.*, 2011; EVERSON *et al.*, 2016). We aim at examining the chondrocranium of *Potamogale velox* with particular focus on the nasal region in order to discuss the functional-morphological adaptations against the background of a semiaquatic mode of life. The goal is to identify and eliminate autapomorphic characters of the ethmoidal region associated with the semiaquatic mode of life in order to detect synapomorphic characters within Potamogalidae and contribute to the Afrotheria discussion. The work is based on the unpublished medical dissertation on a fetal stage by BEHRENS (1998; considered for comparison in SCHUNKE & ZELLER, 2010) and supplemented by  $\mu$ CT analyses of an adult specimen. Unfortunately the dissertation thesis by YOUSSEF (1959) on the skull development of *Potamogale velox* is not available for further comparison.

## Material and methods

The fetus of *Potamogale velox* has a 105 mm crown-rump-length (CRL) and a 20 mm head length (HL). The length of the cranium is 15 mm which is  $\frac{1}{4}$  of the total body length. It is housed as specimen 2a (donated by H. Stephan, now part of the U. Zeller collection) in the Division of Systematic Zoology of Humboldt-Univer-

sität zu Berlin, Germany. This specimen was collected on January 18th, 1984 in today's Democratic Republic of Congo, former Republic of Zaire. The specimen has been fixed in Bouin and preserved in 70% ethanol. Its head has been embedded in paraffin and sectioned at 10 µm. Every second section has been Azan stained and photographed. Based on these pictures a 42.5 magnified paper 3D model was created according to the plate model technique of BORN (1883; more details in ZELLER, 1989). A second fetus of 25 mm HL was collected on January 19th 1984 at the same location and used for comparison. The 3D model of the fetal stage of *Potamogale velox* comprises the chondrocranium, bones as well as the removable outline of the head and was used as template for selected drawings (BEHRENS, 1998).

The adult stage of *Potamogale velox* is represented by a macerated skull (SMF 77080) that is housed in the mammal collection of Senckenberg Forschungsinstitut und Naturmuseum Frankfurt, Frankfurt am Main, Germany. The adult specimen was scanned with the v|tome|x s (GE phoenix|x-ray) µCT device at the Institut für Geowissenschaften und Meteorologie, Universität Bonn, Germany. Scan parameters are 110 kV, 130 µA, 500 ms exposure time, 1000 projections, and 28.9128 µm isotropic voxel size. Based on the µCT data a virtual 3D model of the turbinal skeleton has been created with the help of the manual segmentation tool of the software Avizo 9.01 (Thermo Fisher Scientific FEI).

The observations on *Potamogale velox* are compared to ontogenetic descriptions of further members of Afrotheria (e.g., ASHER, 2001; SCHUNKE & ZELLER, 2010; IHLAU, 2011; STÖSSEL *et al.*, 2010) based on recent phylogenies (MEREDITH *et al.*, 2011: fig. 1; EVERSON *et al.*, 2016: figure 4; HÜPPI *et al.*, 2018: fig. 13).

## Description

### General overview

The entire chondrocranium of *Potamogale velox* is described in detail by BEHRENS (1998). Thus, here we just give a short general overview on the cranium for a better understanding of the developmental pattern of the ethmoidal region in relation to the braincase. A detailed comparison of the orbitotemporal and occipital region with *Hemicentetes semispinosus* is given in SCHUNKE & ZELLER (2010). Further information on the rostrum (especially the vomeronasal complex) and cranial arteries of a fetal *Potamogale velox* (17 mm head length) is provided in ASHER (2001).

The chondrocranium of the fetus is well developed and consists of hyaline cartilage enveloped in a dermal synchondrium: dental, premaxillary, maxillary, nasal, palatine, frontal, parietal, squamosal, pterygoid, lacrimal, vomer, tympanicum, and gonial. Interparietal and jugal are lacking as is the zygomatic arch (Figs. 1–3).

Cartilage is already replaced by enchondral ossification (“Ersatzknochen”) in the following regions: alisphenoid, basisphenoid, basioccipital, and exoccipital (Figs. 1–3).

The primary wall of the braincase in the orbitotemporal region is incomplete; a commissura orbitoparietalis is lacking (Figs. 1, 4). The lamina parietalis of the otic region faces far in the medio-dorsal direction (Fig. 4). The foramen opticum is relatively small, but the openings for the branches of the trigeminal nerve (foramen epiphaniale, foramen rotundum, foramen ovale) are relatively large, as the trigeminal nerve and ganglion are expanded for the innervation of the hypertrophied vibrissal apparatus (Figs. 1, 2).

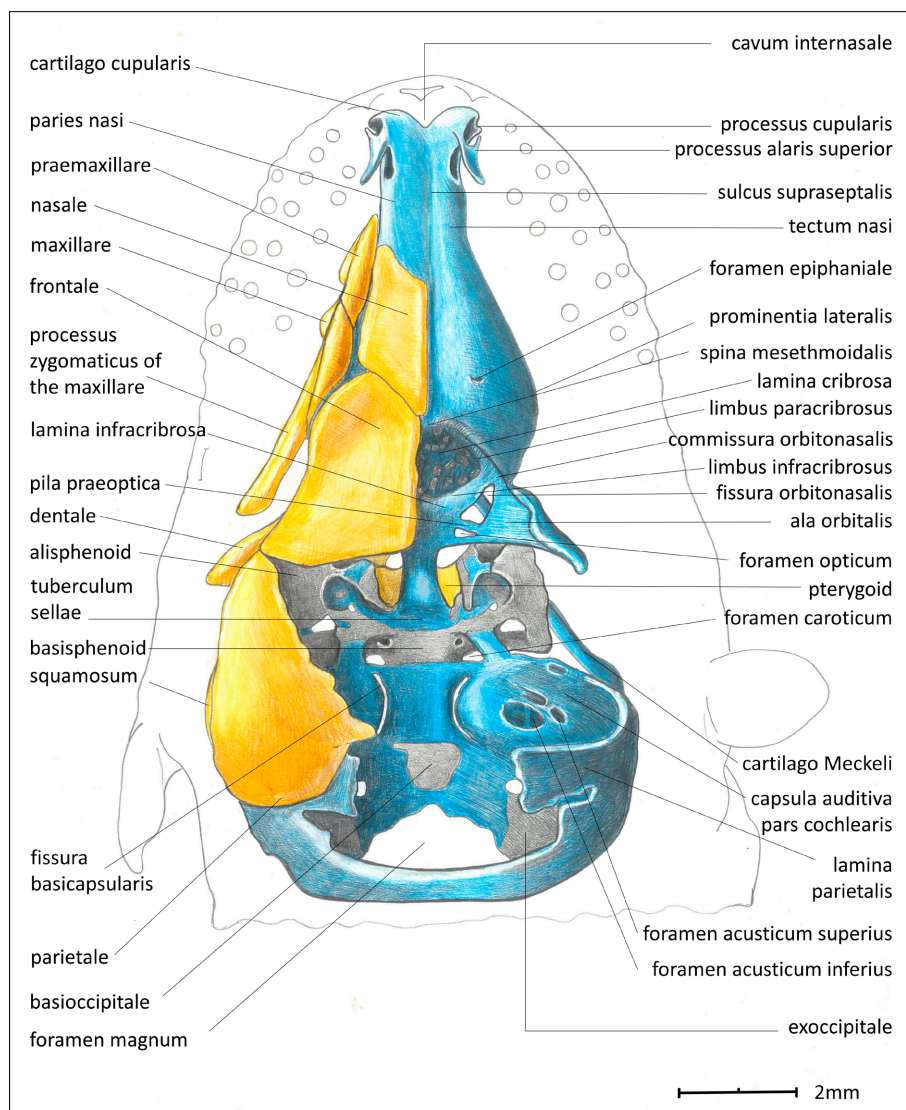
### Ethmoidal region

The nasal capsule of the fetal *Potamogale velox* shows no resorption yet; resorption and ossification of ethmoidal structures can start in late fetal stages as observed in many mammals (see RUF, 2020). The fetal nasal capsule is airohynchic, i.e. elevated against the skull base (Figs. 4, 5). From the cupula nasi anterior to the cupula nasi posterior the fetal ethmoidal region is about 8 mm in length; the length of the skull base *sensu strictu* (behind the nasal capsule) against the length of the nasal capsule is about 1 : 1.3.

The anterior part of the nasal cavity is relatively long compared to the lateral (intermediate) and posterior parts containing the turbinates covered by olfactory epithelium (Fig. 7). Accordingly, the lamina cribrosa allowing the fila olfactoria of the 1<sup>st</sup> cranial nerve to enter the cranial cavity is relatively small and short (Figs. 1, 6, 7). Similar proportions can be observed in the adult skull when taking the cartilaginous rostral cartilages of the rhinarium into account (Fig. 11A).

The fetal nasal capsule is connected to the rest of the chondrocranium by the nasal septum to the trabecular plate of the basicranium and the commissurae orbitonasales to the primary wall of the braincase (Figs. 1, 3). The commissura orbitonasalis connects the nasal capsule to the ala orbitalis and is a relatively narrow cartilaginous crest in an almost upright position. The triangular space between the nasal capsule and the ala orbitalis is the fissura orbitonasalis. A septum interorbitale, the posterior elongation of the septum nasi between the orbits, is lacking in the fetus as well as in the adult (Figs. 1, 6).

The septum nasi is fully developed and extends throughout the entire nasal capsule (Figs. 6, 8B–D, 9). Its greatest height is at the anterior edge of the foramen olfactorium; its ventral edge is drop-shaped in the vertical section. Almost the entire ventral edge is embraced by the vomer (Figs. 2, 6, 10B–D), which is also the case in the adult (Fig. 12A). A septoturbinal and a fenestra internasalis anterior (or posterior) are lacking in the fetus. If these structures develop later in ontogeny cannot be verified in the adult specimen as the anterior part of the nasal septum remains cartilaginous. The posterior third of the septum nasi from the level of the second upper molar on



**Fig. 1.** *Potamogale velox* (2a; 105 mm CRL), color plate of the fetal skull in dorsal view; anterior to the top. The paired dermal bones are visualized only on the left side of the skull. The outer silhouette reflects the shape of soft tissues. Color code: blue, cartilage; grey, cartilage replacement bones; yellow, dermal bones.

becomes ossified and part of the ethmoidal bone of the adult skull (Fig. 12B).

The anterior end of the nasal capsule is formed by the cupula nasi anterior, namely the crescent shaped cartilagine cupulares and the processus laterales ventrales (Figs. 1–5, 8, 9A). Together with the processus alaris superior on both sides, parts of the tectum and paries nasi as well as the lamina transversalis anterior, this part of the nasal capsule remains cartilaginous as the outer nasal cartilagine in the adult skull forming the skeleton of the rhinarium and the associated vibrissal apparatus (see MAIER, 2020).

The fenestra narina is facing dorso-laterally and is caudally bordered by the processus alaris superior. The latter is connected to the tectum nasi as well as to the processus cupularis by a cartilaginous bridge (commissura alicupularis). Behind both bridges and medial to the processus alaris superior lies the fenestra nasi superior (Figs. 4, 5, 8, 9A, B).

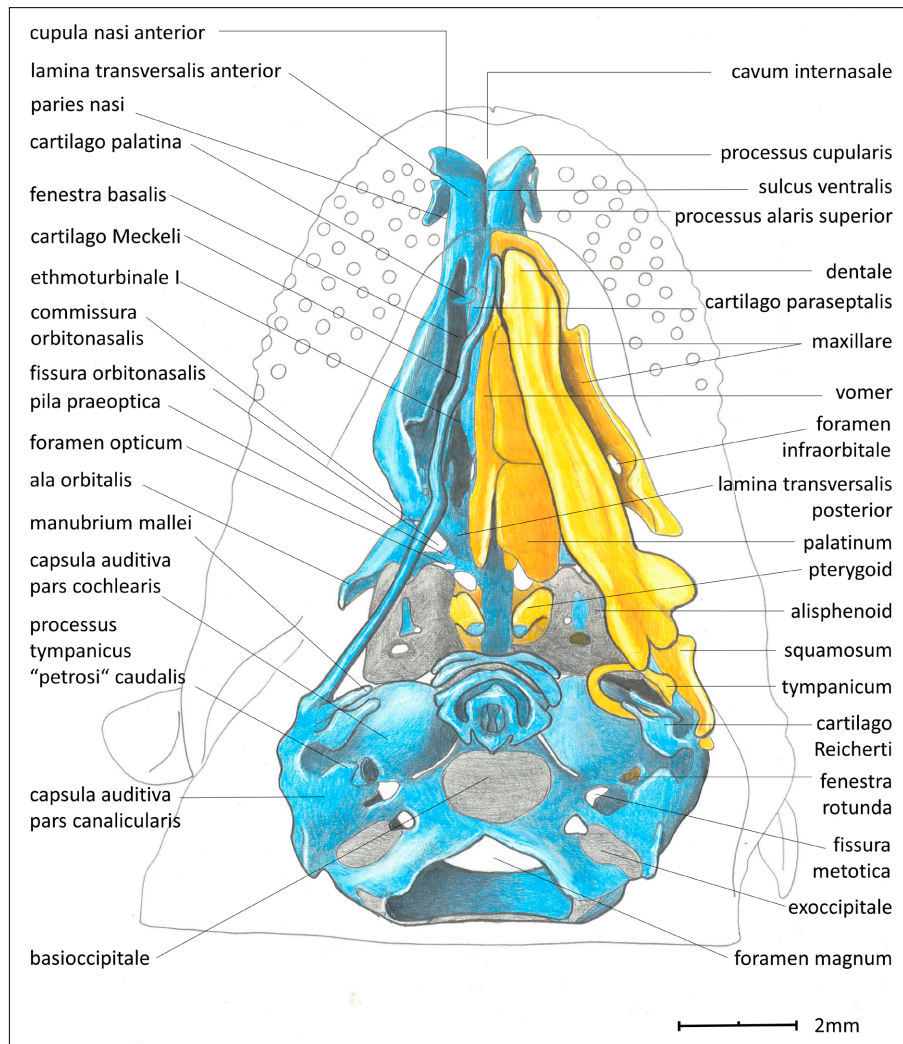
The processus alaris superior is remarkably large and covers almost completely the fenestra nasi superior. It forms a cartilaginous plate in an almost vertical position

slightly removed laterally (Figs. 5, 8, 9B). Ventrally to the fenestra narina the cartilago cupularis extends into a small cartilaginous process connected to the processus alaris superior by the commissura alicupularis.

The deep space between the cartilagine cupulares, the cavum internasale, is ventrally continuous to the sulcus ventralis. In its rostral part the lamina transversalis anterior is deep in the sulcus ventralis connected to the ventral edge of the septum nasi (Figs. 2, 9B). Further caudally however, this connection is opened up; the sulcus ventralis is transformed into an opening and the ventral edge of the septum nasi is free. Up to this point the lamina transversalis anterior is part of the border of the fenestra basalis. Medially it is connected to the cartilago paraseptalis.

The ventral part of the cupula nasi anterior is formed by lateral extensions of the septum nasi, the processus laterales ventrales, which are situated in caudal direction continuously connected to the lamina transversalis anterior (Figs. 5, 8). Inside the nasal capsule, the processus lateralis ventralis is giving rise to the marginoturbinale (Figs. 7, 9B).





**Fig. 2.** *Potamogale velox* (2a; 105 mm CRL), color plate of the fetal skull in ventral view; anterior to the top. The paired dermal bones are visualized only on the left side of the skull. The outer silhouette reflects the shape of soft tissues. Color code: blue, cartilage; grey, cartilage replacement bones; yellow, dermal bones.

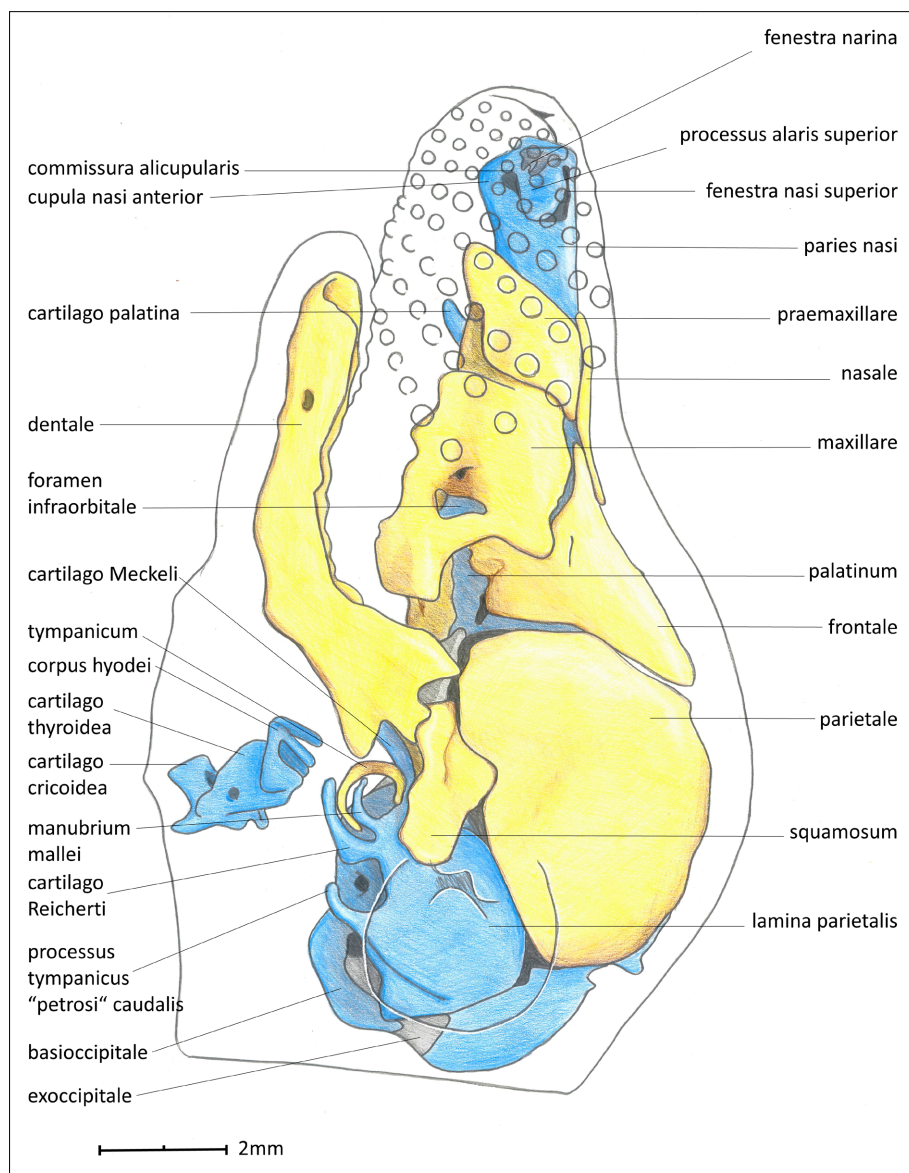
The tectum nasi forms the roof of the nasal capsule. This is a horizontal cartilaginous plate achieving its greatest width at the limbus praecribrosus just in front of the lamina cribrosa (Fig. 1). In between both halves of the tectum and along the median lineage, a shallow groove (sulcus suprasedalis) is clearly visible which is confluent with the cavum internasale between the anterior cupular cartilages and is caudally connected to the spina mesethmoidalis. Externally the sulcus suprasedalis indicates the position of the septum nasi (Figs. 1, 9B–D, 10A, B).

The tectum nasi is laterally confluent with the paries nasi and rostrally with the cartilagine cupulares. The border between paries and tectum nasi is indicated by the sulcus horizontalis.

Caudally to the tectum nasi the roof of the nasal capsule of mammals is open to the cranial cavity via the foramen olfactorium advehens, which is incompletely closed by the lamina cribrosa supplemented caudally by the lamina infracribrosa, already being part of the cupula nasi posterior (Figs. 1, 6; see ZELLER, 1989: Abb. 3). As in other mammals, the nervus ethmoidalis uses the foramen cribroethmoidale to enter the nasal cavity. The lamina cribrosa of *Potamogale velox*, as in other mam-

mals, lies in a deeper plane than the foramen olfactorium advehens that is the ancestral common opening for the fila olfactoria and the nervus ethmoidalis (ZELLER, 1988). Thus, a part of the nasal cavity is incorporated into the cranial cavity, i. e. the recessus supracribrosus. The margins of the foramen olfactorium advehens are still demarcated by the limbus prae-, para- and infracribrosus (Fig. 1). The crista galli formed by the septum nasi, to which the lamina cribrosa is attached, is relatively small. The spina mesethmoidalis is short (Fig. 1). In the adult stage the tectum nasi is completely resorbed; only the lamina cribrosa, the adjacent limbi and most probably the root of the nasoturbinal are ossified. Neither a crista galli nor a spina mesethmoidalis are clearly detectable.

The paries nasi, i.e. the lateral wall of the nasal capsule, can be subdivided in the anterior, lateral and posterior division. The relative large foramen epiphaniale can be found between the anterior and lateral division (Figs. 1, 4). This opening allows the ramus externus nervi ethmoidalis (cranial nerve V) to leave the nasal capsule. In the adult most of the paries nasi has been resorbed except for the roots of the turbinals, the lamina semicircularis and the lamina horizontalis (see below).



**Fig. 3.** *Potamogale velox* (2a; 105 mm CRL), color plate of the fetal skull (left side) in lateral view; anterior to the top. The outer silhouette reflects the shape of soft tissues. Color code: blue, cartilage; grey, cartilage replacement bones; yellow, dermal bones.

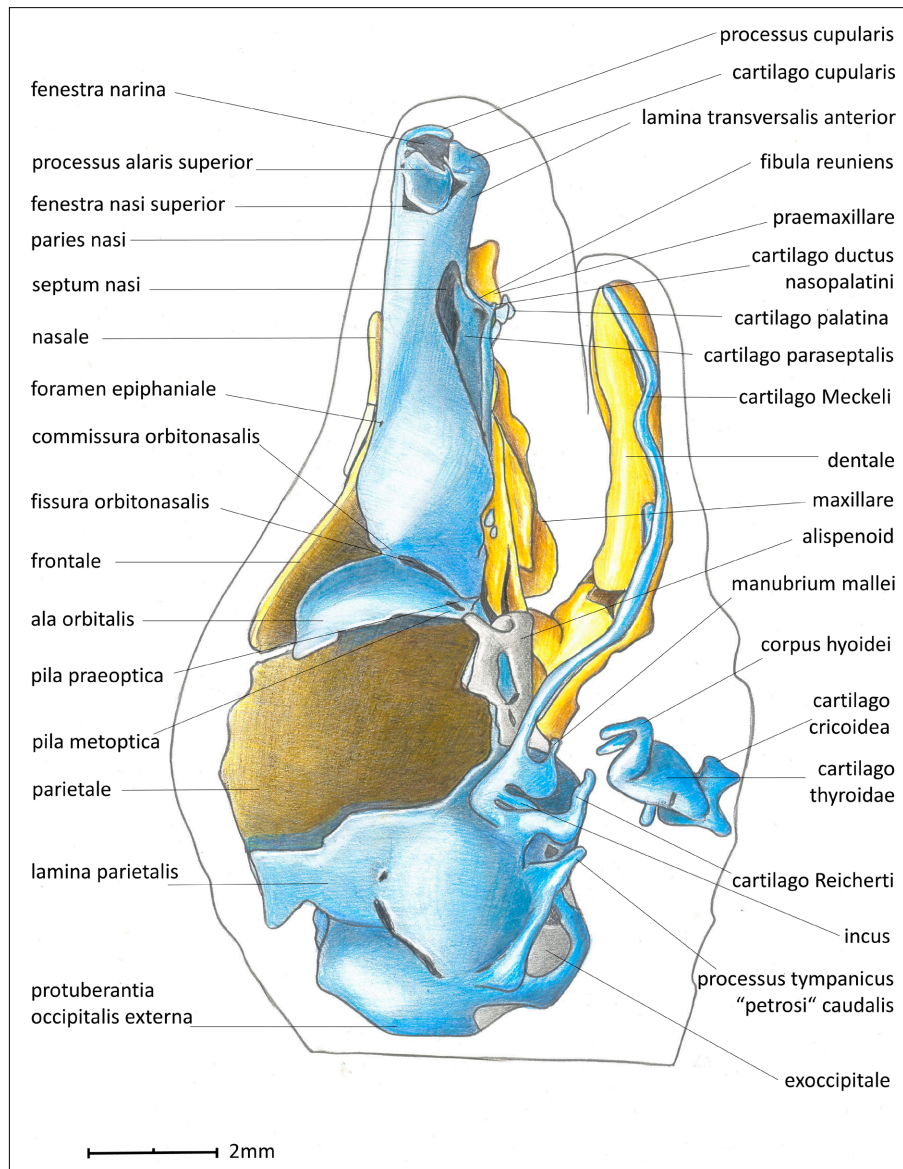
The incomplete floor of the nasal capsule is formed by the lamina transversalis anterior, the cartilago paraseptalis anterior and the lamina transversalis posterior (Figs. 2, 6, 8, 9B, C).

The Lamina transversalis anterior subdivides the fissura rostroventralis into the fenestra narina and the fenestra basalis. The latter also forms the apertura nasalis interna, the primary connection between nasal and oral cavity, which is later closed by membrane bones of the secondary palate (premaxillary, maxillary, palatine).

The lamina transversalis anterior is relatively long and broad and laterally connected to the paries nasi (Figs. 2, 6, 8, 9B, C). A sulcus ductus nasolacimalis is lacking as is the ductus nasolacimalis. In rostral direction the lamina is connected to the processus lateralis ventralis and in caudal direction to the cartilago paraseptalis anterior. As the lamina transversalis anterior remains cartilaginous it is not visible in the  $\mu$ CT images.

The cartilago paraseptalis anterior forms a trough, is "C"-shaped in cross section and lodges Jacobson's organ

(vomeronasal organ), which opens into the ductus nasopalatinus (Figs. 6, 9D, 10A–C). The paraseptal cartilage is closely attached to the ventral edge of the septum nasi, but separated from the latter by the fissura septoparaseptalis and posteriorly also by the vomer. Rostrally it is connected to the lamina transversalis anterior. The caudal end of the cartilago paraseptalis reaches about two thirds of the nasal capsule; it does not reach the lamina transversalis posterior (Fig. 6). From its middle part on, the vomer is closely attached to the paraseptal cartilage. Only the anterior end of the cartilago paraseptalis is closed to form a tube by a narrow cartilaginous bar, the fibula reuniens (outer bar) (Figs. 4, 6). During ontogeny the cartilago paraseptalis anterior and the fibula reuniens become resorbed and replaced by the processus palatinus medialis of the maxillary. In the adult this process forms a deep trough that opens dorsally (Fig. 12A); as in the fetus its anterior half is significantly separated from the septum nasi although the vomer extends more rostrally in the adult stage. The trough for Jacobson's organ extends



**Fig. 4.** *Potamogale velox* (2a; 105 mm CRL), color plate of the fetal skull (right side) in lateral view; anterior to the top. The outer silhouette reflects the shape of soft tissues (rows of vibrissae not depicted). Color code: blue, cartilage; grey, cartilage replacement bones; yellow, dermal bones.

from the posterior border of the foramen incisivum (at level of third upper incisor) to the level of the second upper molar; it remains unclear from the  $\mu$ CT images if Jacobson's organ is as long as the trough.

At the junction between the lamina transversalis anterior and the cartilago paraseptalis anterior the cartilago ductus nasopalatini supports from the medial aspect the ductus nasopalatinus, the remaining communication between nasal and oral cavity. Ventrolaterally the ductus is supported by the cartilago palatina (Fig. 2–6, 9D, 10A). This small cartilage is isolated from the remaining chondrocranium rostro-lateral to the paraseptal cartilage. None of these cartilages is visible in the  $\mu$ CT images.

The lamina transversalis posterior forms the nasal floor in the posterior part of the nasal capsule, namely the caudal third of the recessus ethmoturbinalis (Fig. 6–8). It is a horizontal cartilaginous plate medially connected to the nasal septum and laterally to the paries nasi. In caudal direction it is confluent with the cupula nasi posterior

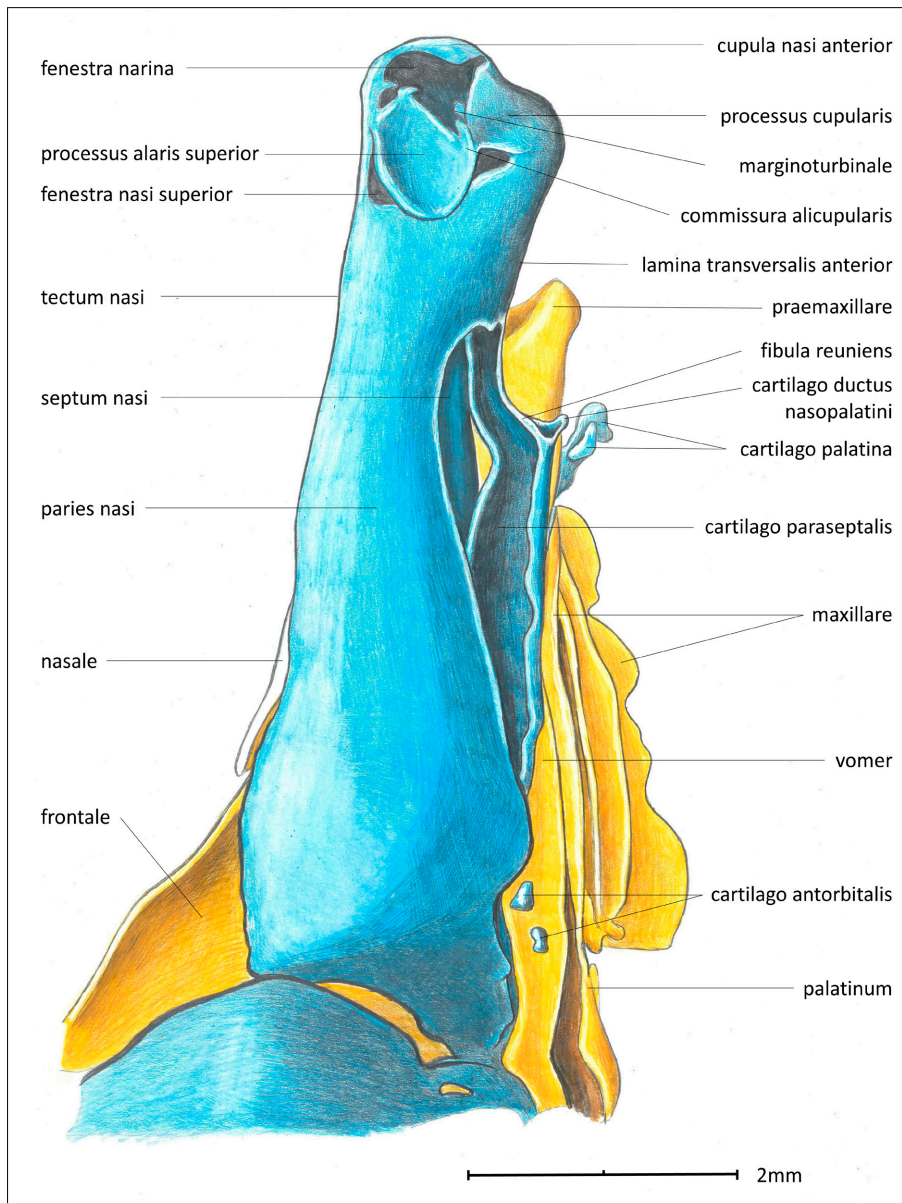
(Figs. 6, 7). In the adult the lamina is synossified with the vomer and forms the lamina terminalis which is part of the ethmoid bone. The lamina terminalis has a concave anterior rim and separates the posterior nasal cavity from a large ductus nasopharyngeus (Fig. 12B).

The interior of the nasal capsule can be subdivided into the (1) pars anterior, (2) pars intermedia (*sive* lateralis), (3) pars posterior and (4) recessus paraseptalis (VOIT, 1909; REINBACH, 1952a, b; ZELLER, 1987).

The pars anterior, mainly involved in respiratory function, reaches from the cupula nasi anterior up to the lamina semicircularis. Its anterior part appears like a tube subdivided by the septum nasi in two halves and is relatively long. Further caudally, the nasal cavity opens up like a funnel (Figs. 7, 8).

The anteriormost turbinal is the marginoturbinal arising from the lateral edge of the processus lateralis ventralis in mediodorsal direction (Fig. 7, 9B). Caudally it is connected to the ventral root of the processus alaris superior. The atrioturbinal is lacking. As these two turbi-





**Fig. 5.** *Potamogale velox* (2a; 105 mm CRL), color plate of the fetal nasal capsule (right side) in lateral view; anterior to the top. The paired dermal bones are visualized only on the left side of the specimen. Color code: blue, cartilage; yellow, dermal bones.

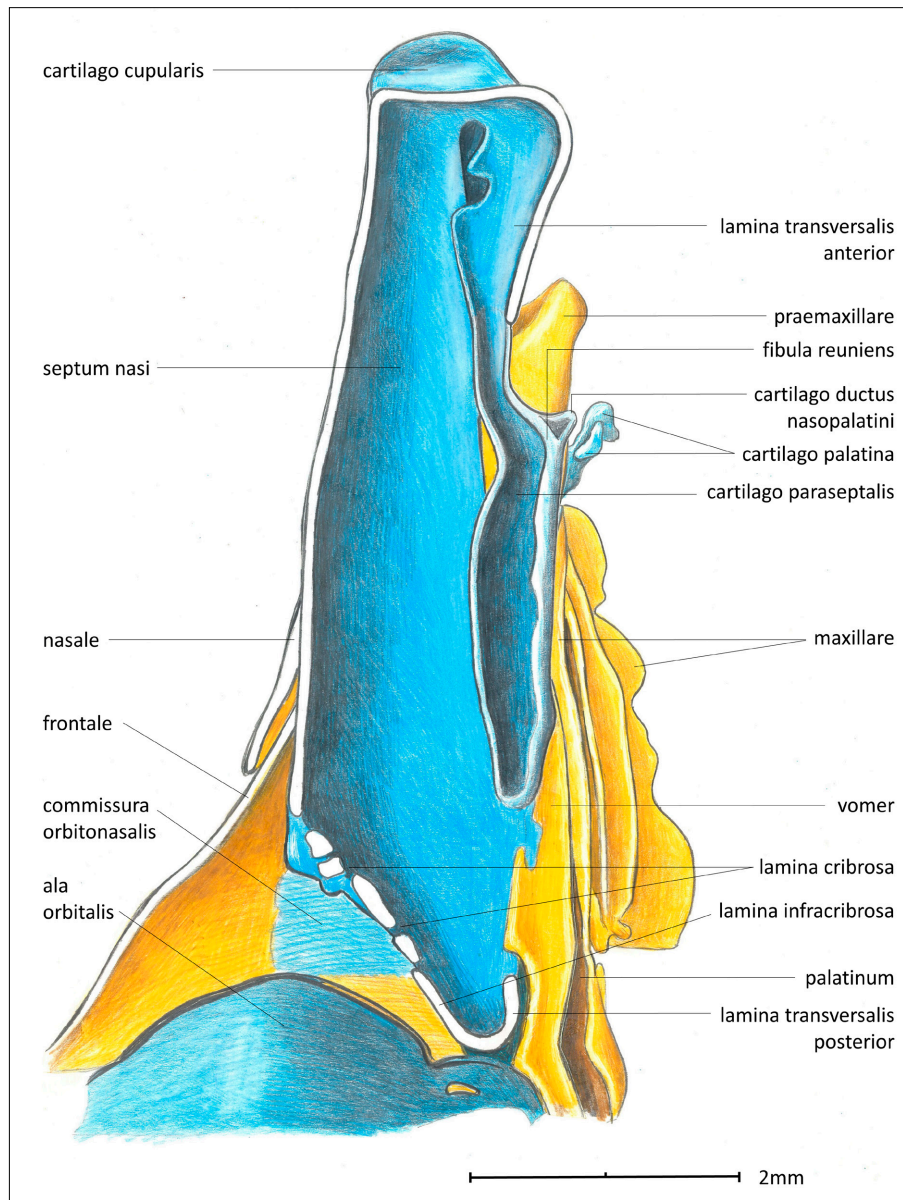
nals remain cartilaginous throughout life their pattern in the adult skull cannot be investigated by  $\mu$ CT.

The maxilloturbinal arises from the ventral edge of the paries nasi (Fig. 7, 9D, 10A, B). Together with the paries nasi it forms the boundaries of the sulcus supraconchalis. At the external face of the paries nasi this corresponds to the prominentia supraconchalis. The maxilloturbinal of the fetus is a simple straight lamella projecting medio-dorsally. Further posteriorly its free edge turns ventrally (Fig. 10B). The adult maxilloturbinal is more complex and consists of a low straight dorsal and a complex laterally infold ventral lamella (Fig. 11B, C). The ventral lamella bears an epiturbinal on its medial surface and on the lower edge (Fig. 12A). The maxilloturbinal extends in the posterior  $\frac{3}{4}$  of the pars anterior of the adult nasal cavity and overlaps slightly with ethmoturbinal I (Fig. 11A).

In the fetus the nasoturbinal is almost lacking and appears only as a weak cartilaginous crest (Fig. 7). In contrast, the adult stage clearly shows a distinct nasoturbinal

that is a slightly laterally curved lamella located dorso-medial of the maxilloturbinal (Figs. 11B, C, 12A). It is almost as long as the latter.

The pars lateralis of the nasal capsule encloses the recessus frontalis and frontoturbinalis, which together form the recessus lateralis superior (VOIT, 1909) dorsal to the pars obecta (lamina horizontalis and lamina verticalis *sensu* SCHLIEMANN, 1966) of the paries conchalis and the septum frontomaxillare (REINBACH, 1952a, b; ZELLER, 1983). The latter is the rostral extension of the pars obecta of the paries conchalis. It is an almost horizontal cartilaginous plate separating the rostral extension of the recessus maxillaris, the recessus lateralis inferior anterior, from the recessus lateralis superior (Fig. 10B). A septum frontoturbinalis is lacking in *Potamogale velox*. Caudal of the septum frontomaxillare all recessus of the pars intermedia are confluent. The recessus maxillaris is a space situated ventral to the pars obecta and septum frontomaxillare and in mediorostral direction it is confluent with the



**Fig. 6.** *Potamogale velox* (2a; 105 mm CRL), color plate of the fetal nasal capsule (right side) after paramedian section and removal of the right half in lateral view; anterior to the top. The paired dermal bones are visualized only on the left side of the specimen. Color code: blue, cartilage; white, cutting surface; yellow, dermal bones.

recessus glandularis (Figs. 10B, C). In the adult a septum frontomaxillare cannot be discerned.

The recessus lateralis superior contains two frontoturbinalia in the fetus and in the adult (Figs. 7, 10C, 11B, C). In the fetus the frontoturbinals already show a mushroom-shape in cross-section. Frontoturbinal 1 arises from the lateral sidewall (pars libera of paries conchalis), frontoturbinal 2 from the lamina horizontalis (Fig. 10C). In the adult the frontoturbinals are well-developed double-scrolls and frontoturbinal 2 arises anteriorly from the lamina horizontalis and posteriorly from the sidewall of the nasal cavity (Figs. 11B, 12B).

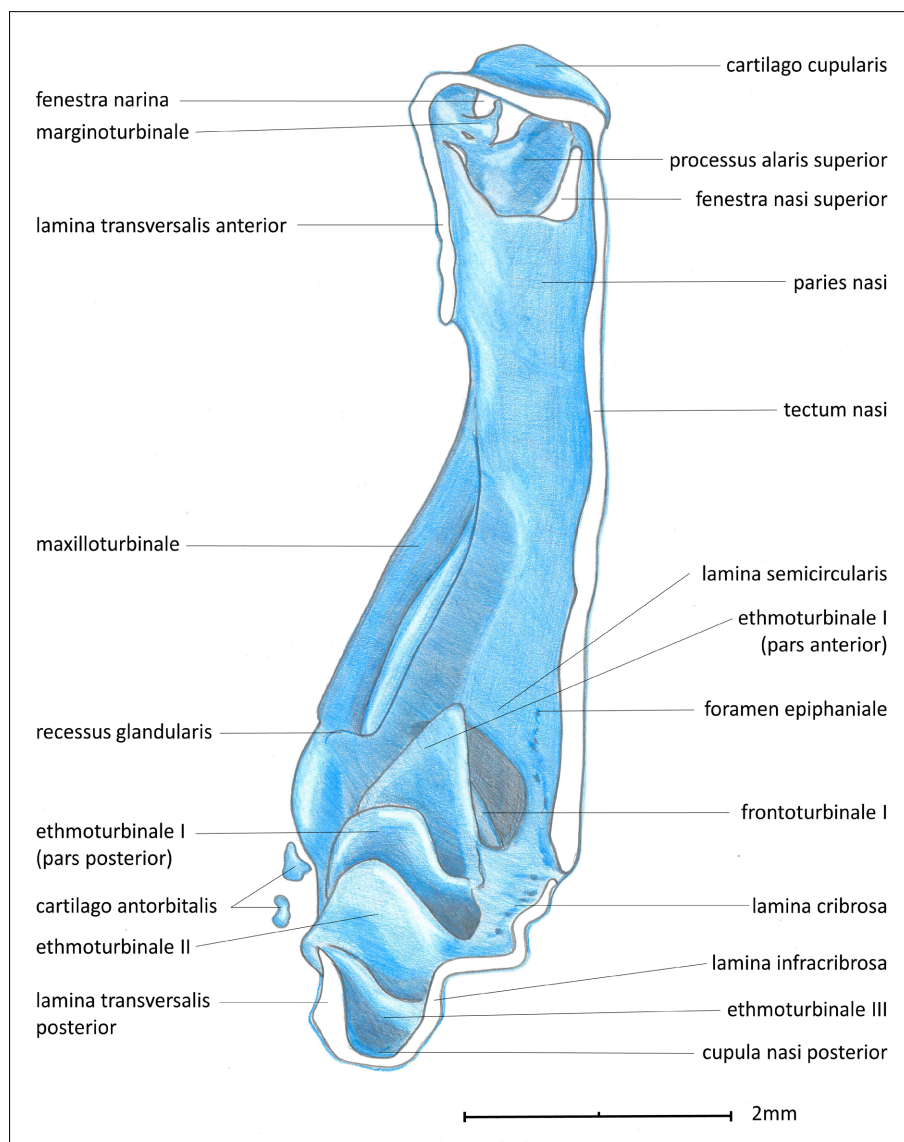
The lamina semicircularis is also involved in olfaction although it is not a turbinal by origin. Instead it is an outgrowth of the anterior paries nasi partly separating the pars intermedia from the rest of the nasal cavity (VOIT, 1909; REINBACH, 1952a, b). In the fetal *Potamogale velox* the lamina semicircularis is a sickle-shaped wall obliquely oriented from dorsomedially to ventrolaterally

(Figs. 7, 10B). Its dorsocaudal end is connected to the lamina cribrosa. In the adult the lamina semicircularis is completely ossified and its dorsal edge is elongated in anterior-posterior direction. Anteriorly the lamina contacts the posterior end of the nasoturbinal. The anterior part of the lamina semicircularis forms a lateral open cavity (Fig. 11B, C). Both stages are lacking a processus uncinatus (Figs. 7, 11B).

The pars posterior of the nasal capsule comprises the recessus ethmoturbinalis, mainly involved in olfactory function. In both investigated stages of *Potamogale velox* it contains three ethmoturbinals as well as an interturbinal between ethmoturbinal I and II (Figs. 7, 10B–D, 11B, C, 12B). Only ethmoturbinal I and the anterior tip of the interturbinal (as well as frontoturbinal 2) arise from the lamina horizontalis that ossifies during ontogeny.

In the fetus, ethmoturbinal I is relatively short and has the shape of a half-cone cut off at its median plane with the tip facing in rostral direction. It can be subdivided





**Fig. 7.** *Potamogale velox* (2a; 105 mm CRL), color plate of the right part of the fetal nasal capsule after paramedian section in medial view; anterior to the top. Color code: blue, cartilage; white, cutting surfaces.

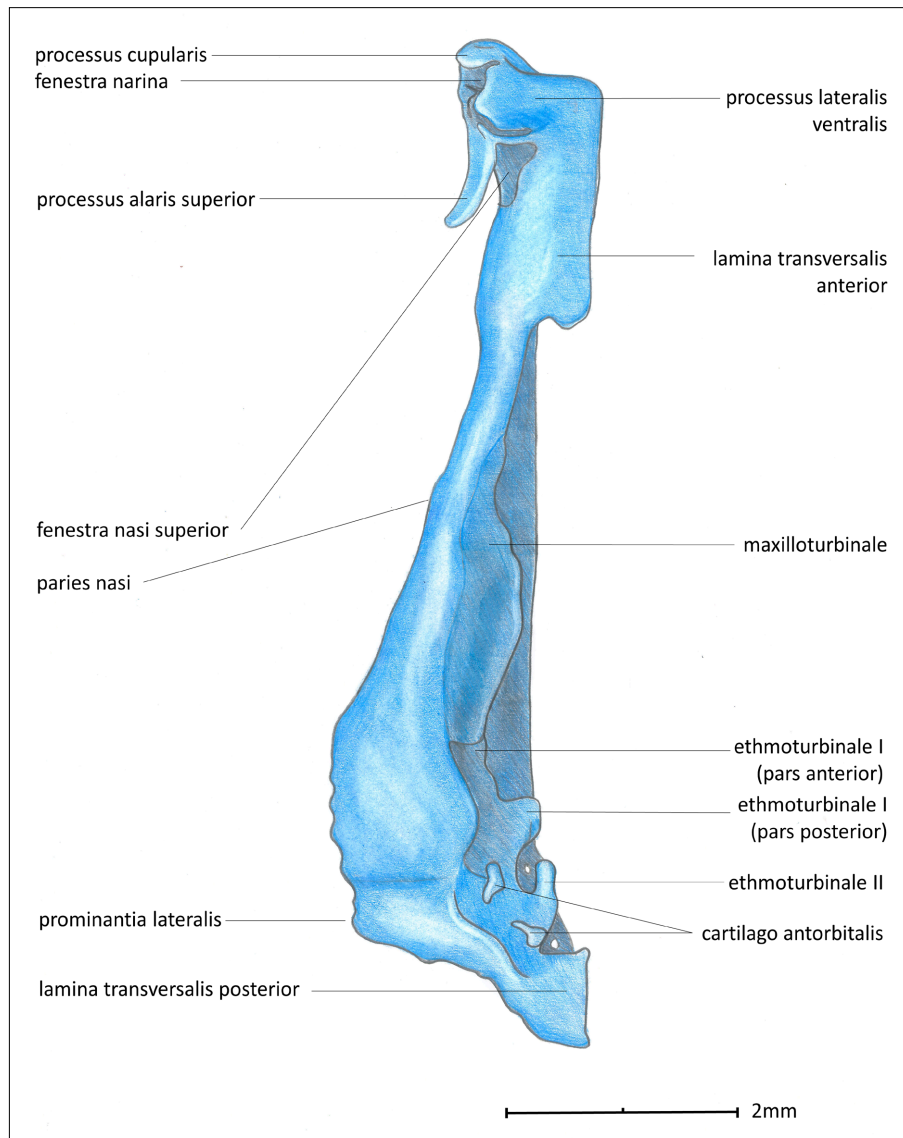
into an anterior and a posterior part (Fig. 7). The anterior part forms most of the half-cone and is deeply concave in medial direction. Its rostral end forms a short processus anterior (Fig. 10B). It does not reach far beyond the caudal edge of the lamina semicircularis. Dorsally ethmoturbinal I touches the lamina cribrosa forming the crista intercribrosa. The pars posterior of ethmoturbinal I is caudally attached to the pars oblecta of the paries conchalis. Its anterior end reaches into the cave of the pars anterior. In the adult the anterior process of the pars anterior of ethmoturbinal I projects into the pars anterior of the nasal cavity; it starts at the level of the posterior end of the nasoturbinal and the anterior tip of the lamina semicircularis respectively (Fig. 11C). The pars anterior of ethmoturbinal I remains a curved lamella forming a medial cavity that houses the laterally scrolled pars posterior (Figs. 10C, 12B). Both parts are attached to the lamina cribrosa.

In the fetus ethmoturbinal II is a cartilaginous plate in almost sagittal position and slightly convex in medial direction. Rostrally it ends free in a semilunar crest, ven-

trocaudally it is connected to the paries conchalis and dorsally to the lamina cribrosa (Fig. 7). Lateral to ethmoturbinal II and totally hidden from the medial aspect, an epiturbinal can be found as a cartilaginous ridge rising from a caudodorsal into a rostroventral position (Fig. 10D). In the adult the still hidden epiturbinal has become a double-scroll (Fig. 12B). The main body of ethmoturbinal II shows an anterior process.

The space between ethmoturbinal I and II lodges an interturbinal, which from the medial aspect is totally hidden by ethmoturbinal II. The interturbinal is a sickle-shaped cartilaginous plate in an almost vertical position (Fig. 10D). Dorsally it touches the lamina cribrosa. In the adult the interturbinal is scrolled laterally (Fig. 12B).

Ethmoturbinal III is a semilunar cartilaginous lamella bent to a lateral concave position (Fig. 7). In the adult it is laterally scrolled and ends at the lamina cribrosa. The posterior end of ethmoturbinal III continues as a straight lamella that subdivides the nasal cavity spanning from the nasal floor or ventral nasal septum to the roof behind the lamina cribrosa (Fig. 11B, C).



**Fig. 8.** *Potamogale velox* (2a; 105 mm CRL), color plate of the right part of the fetal nasal capsule after paramedian section in ventral view; anterior to the top. Color code: blue, cartilage.

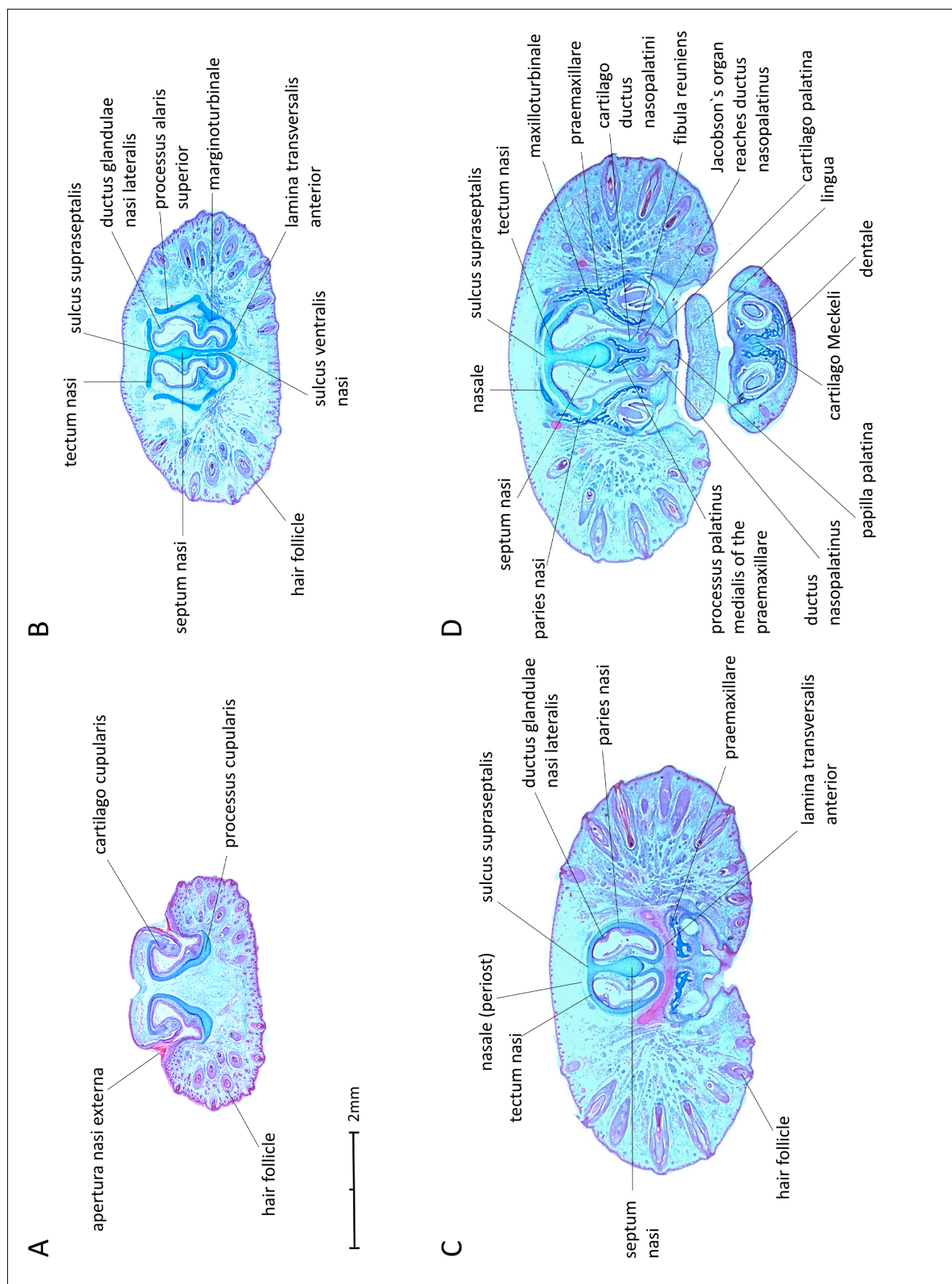
## Discussion

The overall shape or *gestalt* of the skull of *Potamogale velox* is influenced by its semiaquatic mode of life. This holds especially true for the ethmoidal region. A detailed comparison of the morphological observations on the ethmoidal region of *Potamogale velox* compared to *Hemicentetes semispinosus*, *Tenrec ecaudatus* as well as several Lipotyphla is provided in SCHUNKE & ZELLER (2010). Thus, here we refer to new systematic and morphofunctional implications that can be drawn from the presented data as well as recent cranial studies.

In his comprehensive study on the anterior ethmoidal region (especially the vomeronasal complex) and cranial vasculature of Tenrecoidea ASHER (2001) describes a slightly younger stage of *Potamogale velox* (17 mm head length). In general our observations are in concordance with those of ASHER (2001). However, our interpretation of the cartilages that support the ductus nasopalatinus is somewhat different in that the cartilago palatina corre-

sponds to the generally named nasopalatine duct cartilage of ASHER (2001); for further discussion on other structures see below.

The nasal capsule of the fetal *Potamogale* is relatively short (ratio length of the skull base against length of the nasal capsule = 1 : 1.3), compared to fetal stages of the related terrestrial Tenrecidae. In *Hemicentetes semispinosus* this ratio is 1 : 2.5 (fetus) and 1 : 3.2 (adult), in *Tenrec ecaudatus* it is 1 : 1.7 (fetus) (converted from SCHUNKE & ZELLER, 2010). However, in *Tupaia belangeri* the proportional size of the ethmoidal region is increasing with age from 1 : 0.6 (fetus, 25 days after perception) to 1 : 0.9 (neonate) to 1 : 1.5 (adult) (SPATZ, 1964; ZELLER, 1983). A late fetal stage of *Rattus norvegicus* (15.5 mm head length) shows a ratio of 1 : 0.9 (calculated from RUF, 1999). Thus, the investigated Tenrecoidea have a proportionally larger rostrum already in prenatal stages. However, compared to Tenrecidae *Potamogale velox* has a relatively short rostrum. If this resembles a plesiomorphic pattern for Tenrecoidea or Afrotheria in general has to be elucidated based on a broader taxon sampling.



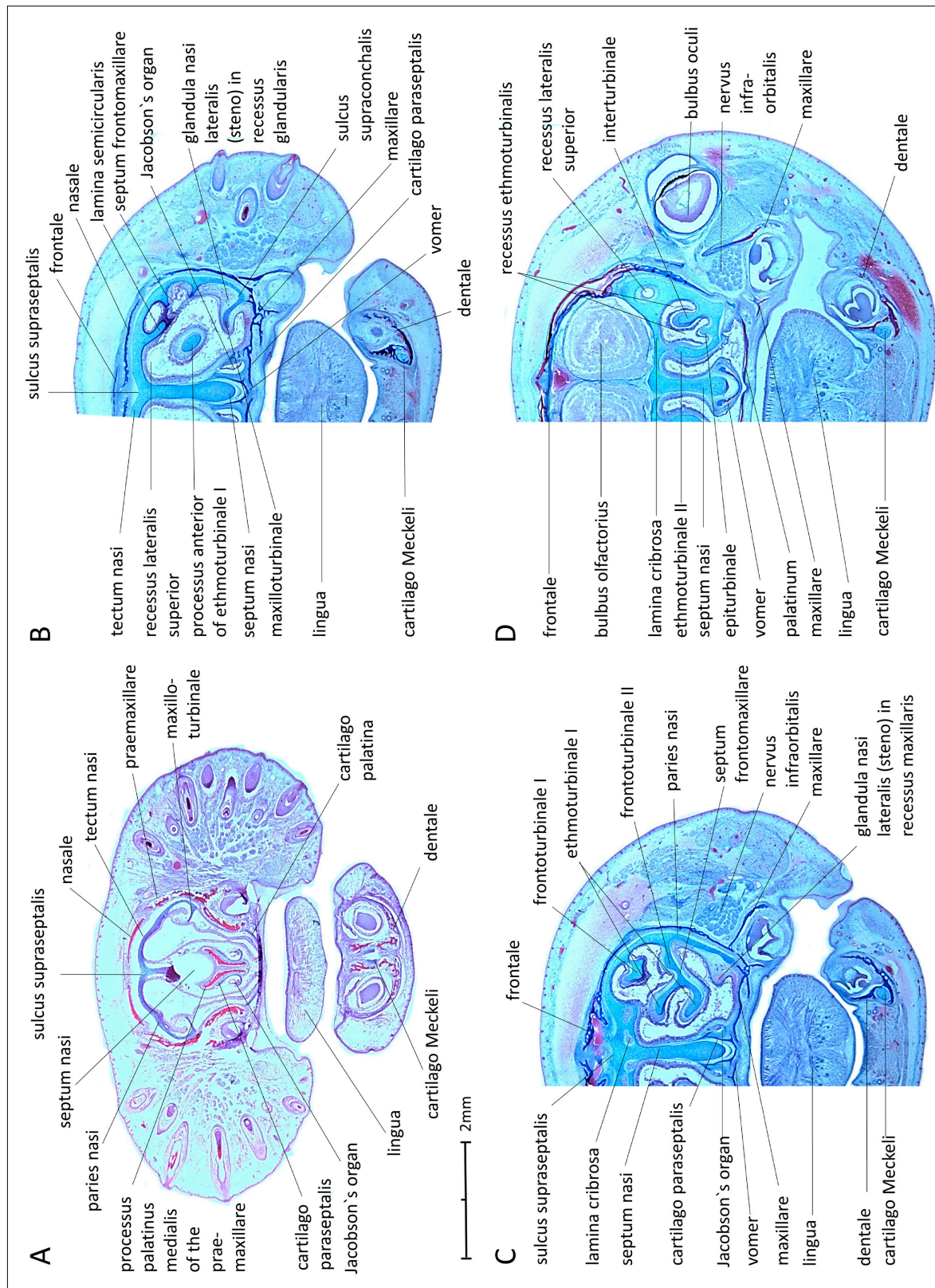
**Fig. 9.** Transversal histological sections through the pars anterior of the ethmoidal region of *Potamogale velox* (2a; 105 mm CRL), from anterior (**A**) to posterior (**D**).

When comparing the proportions of the three major compartments of the nasal cavity (pars anterior, lateralis, posterior) it is evident that in *Potamogale velox* (fetus and adult) the pars anterior is significantly longer than the other two parts compared to other Afrotheria and mammals e.g., Scandentia and Lagomorpha (SCHUNKE &

ZELLER, 2010; STÖSSEL *et al.*, 2010; RUF, 2014; RUF *et al.*, 2015).

The proportionally smaller size of the olfactory turbinal skeleton housed in the pars lateralis and posterior in *Potamogale velox* can be regarded as an adaptation to the semiaquatic mode of life. A recent study on the size

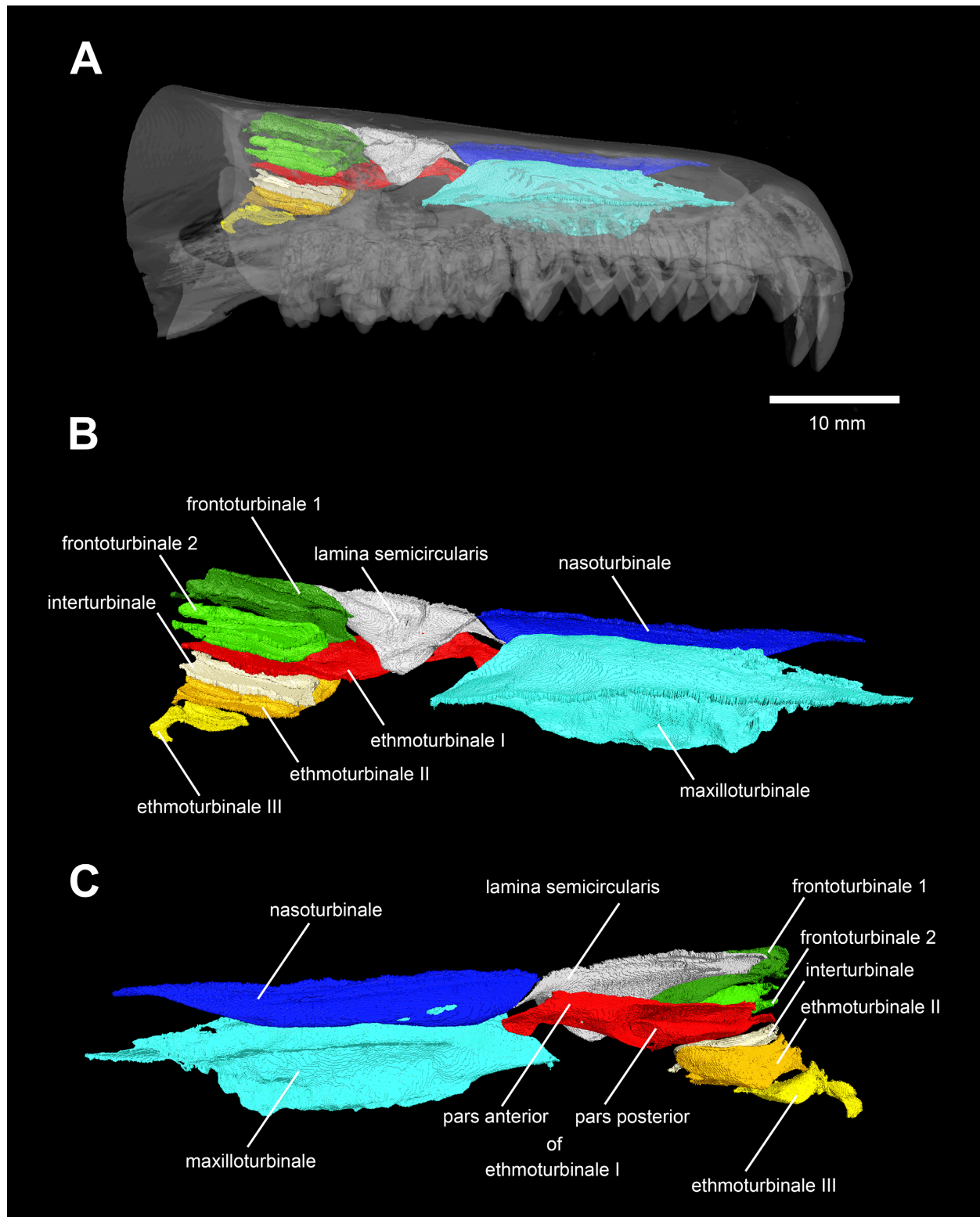




**Fig. 10.** Transversal histological sections through the ethmoidal region of *Potamogale velox* (2a; 105 mm CRL). **A**, pars anterior; **B**, transition of pars anterior and pars lateralis; **C**, pars lateralis and pars posterior; **D**, pars posterior.

of the respiratory and olfactory turbinal skeleton in terrestrial and semiaquatic small mammals (Tenrecoidea, Rodentia, Lipotyphla) shows a trade-off between the respiratory and olfactory capacity in the latter; their olfactory turbinal skeleton is smaller than in their terrestrial counterparts (MARTINEZ *et al.*, 2020). In the sampling of

semiaquatic tenrecoids *Potamogale velox*, *Micropotamogale lamottei* and *Limnogale mergulus* (= *Microgale mergulus*, see STEPHENSON *et al.*, 2019) have a smaller relative surface area of the olfactory turbinals and greater relative surface area of the respiratory turbinals than the terrestrial Tenrecidae *Tenrec ecaudatus*, *Hemicentetes se-*

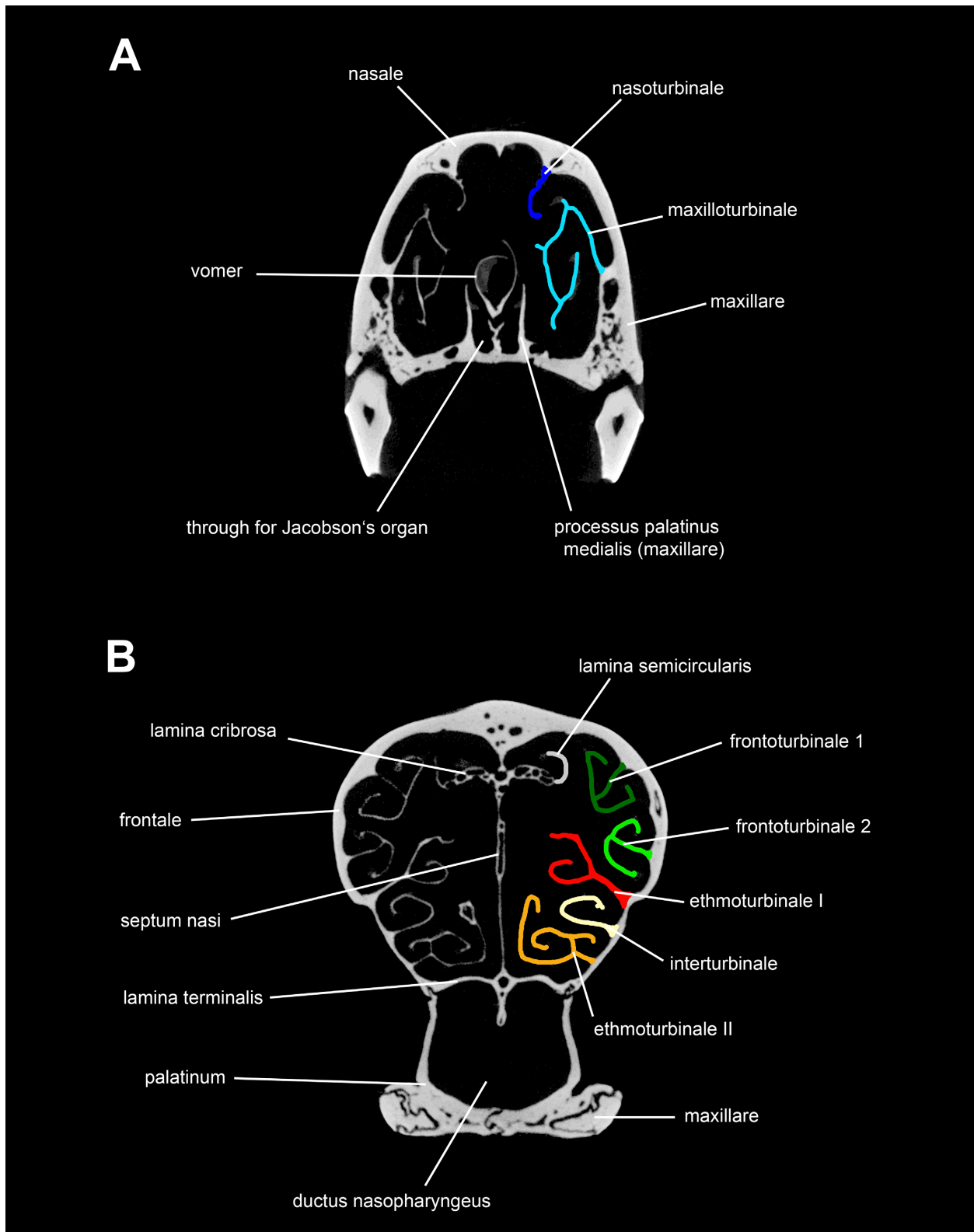


**Fig. 11.** *Potamogale velox* (SMF 77080), virtual 3D model of the adult turbinal skeleton (left side, mirrored for comparison). Rostrum in lateral view (A); the skull bones are made transparent. Turbinal skeleton in lateral (B) and medial (C) view. Anterior to the right in A and B, and to the left in C. B and C not to scale.

*mispinosus*, *Setifer setosus*, and *Echinops telfairi*. This supports the adaptation to a higher respiratory capacity and lower olfactory performance in the semiaquatic species. A similar pattern can be observed in terrestrial versus semiaquatic Carnivora (VAN VALKENBURGH *et al.*, 2011). However, *Potamogale velox* still has a larger

relative surface area of the olfactory turbinals than the other two semiaquatic species (MARTINEZ *et al.*, 2020). This indicates a still relative high olfactory performance level, which is supported by the fact that a septum interorbitale is missing in *Potamogale velox* as well as in *Hemicentetes semispinosus* (SCHUNKE & ZELLER, 2010).





**Fig. 12.** *Potamogale velox* (SMF 77080), transversal  $\mu$ CT images of the adult ethmoidal region through the anterior (A) and posterior (B) nasal cavity. Color code of turbinals refers to Fig. 11. Not to scale.

In contrast, in *Tenrec ecaudatus* and *Loxodonta africana* a septum interorbitale has been observed (LEIMGRUBER, 1939; STÖSSEL *et al.*, 2010: fig. 2). Presence of the septum interorbitale like in *Tupaia* or Primates is regarded to be associated with reduction of the posterior nasal capsule and less olfactory capacity in favour of higher

importance of the optic sense. However, while the septum interorbitale in moderate microsmatic Lipotyphla is a plesiomorphic mammalian structure, the one in microsmatic primates should be regarded as derived from the mammalian *grundplan* (see discussion in RUF *et al.*, 2015).

The reduction of the olfactory turbinal complex is supported by the fact that the lamina cribrosa of *Potamogale velox* is proportionally smaller and the number of openings for the fila olfactoria is less than in the investigated Tenrecidae (SCHUNKE & ZELLER, 2010). This observation corresponds to the fact that *Potamogale velox* has a smaller brain than other investigated insectivorous mammals of the lipotyphlan grade (STEPHAN, 1967). In contrast, *Potamogale velox* has a very large accessory bulbus olfactorius that correlates with the large size of Jacobson's organ in that species; in *Micropotamogale lamottei* both structures are comparably small (STEPHAN *et al.*, 1991; ASHER, 2001). However, the young age of the investigated *Potamogale velox* specimen might affect the proportions of these structures (ASHER, 2001; SÁNCHEZ-VILLAGRA & ASHER, 2002).

A recent study across all major mammalian clades shows that the size of the lamina cribrosa in the adult corresponds to the number of olfactory gene receptors and thus, can be used as a proxy for the olfactory capacity (microsmatic, macrosmatic) in the respective species (BIRD *et al.*, 2018). The reduction of the lamina cribrosa is also known from semiaquatic (e.g., *Ornithorhynchus anatinus*) and aquatic (e.g., odontocetes) species (ZELLER, 1988, 1989; BIRD *et al.*, 2018). In the latter the lamina cribrosa is restricted to the passage of small fibres of the nervus vomeronasalis.

Beside reduction of surface area of the olfactory turbinals, adaptation to a semiaquatic mode of life with less constraint on the olfactory capacity can be realized by reduction of the number of these turbinals (MARTINEZ *et al.*, 2020). However, this is not the case in *Potamogale velox*. The number and pattern of olfactory turbinals (two frontoturbinals, three ethmoturbinals, one interturbinal between ethmoturbinal I and II) reflects a very common pattern among small mammals (RUF, 2014, 2020; RUF *et al.*, 2015). However, the processus anterior of ethmoturbinal I is relatively short, compared to other mammals (e.g., *Tupaia*, ZELLER, 1987). SMITH & ROSSIE (2008) observed two frontoturbinals and four ethmoturbinals in a fetal *Tenrec ecaudatus*; however, these ethmoturbinals certainly comprise ethmoturbinal I to III and the interturbinal. *Macroscelides proboscideus* and *Procavia capensis* show exactly the same olfactory turbinal number as *Potamogale velox* (STÖSSEL *et al.*, 2010; IHLAU, 2011). In *Orycteropus afer* and *Loxodonta africana* the number of these turbinals is extremely increased due to their enhanced macrosmatic performance (STÖSSEL *et al.*, 2010). Thus, we tentatively conclude that the olfactory turbinal pattern of *Potamogale velox* represents the *grundplan* of Tenrecoidea and Afrotheria in general. *Orycteropus afer* and *Loxodonta africana* would represent a derived character state compared to the afrotherian *grundplan*. The latter holds true for Sirenia due to their aquatic mode of life: *Trichechus manatus* has only four ethmoturbinals (that might comprise also interturbinals), in *Dugong dugon* the entire turbinal skeleton is reduced to one frontoturbinal and two ethmoturbinals (MATTHES, 1912, 1921).

Coming to the respiratory turbinals, *Potamogale velox* shows an unspecific pattern of complexity of the maxilloturbinal. Although the relative surface area of the respiratory turbinals appears to be increased, the maxilloturbinal remains a relative simple lamellar structure, not comparable to the extremely scrolled, multilamellar or dendritic shape observed in other mammals (VAN VALKENBURGH *et al.*, 2011; MARTINEZ *et al.*, 2020). Interestingly the nasoturbinal is not yet developed in the examined fetus but in the adult. This is an interesting case, as in placentals the nasoturbinal should be present in a comparable stage. Our observation underscores the importance of an ontogenetic series to understand nasoturbinal development in *Potamogale velox*.

Afrotheria is characterized by a robust and well-developed cupula nasi anterior (HÜPPI *et al.*, 2018). Thus, *Potamogale velox* represents the afrotherian ancestral condition. In contrast, *Hemicentetes semispinosus* shows a more delicate cartilage of the cupula nasi anterior (SCHUNKE & ZELLER, 2010). The broad cartilagineous cupulares and a well-developed processus alaris superior are regarded as the ancestral condition in Theria; thus *Potamogale velox* is plesiomorphic in this respect (DE BEER, 1937; KUHN, 1971; HÜPPI *et al.*, 2018). While *Macroscelides proboscideus* and *Orycteropus afer* also have a well-developed processus alaris superior, the process in *Hemicentetes semispinosus*, *Tenrec ecaudatus* and *Setifer setosus* is relatively small, in Sirenia, *Procavia capensis* and *Loxodonta africana* it is highly reduced or missing respectively (MATTHES, 1912, 1921; LEIMGRUBER, 1939; ROUX, 1947; STÖSSEL *et al.*, 2010; IHLAU, 2011). As the Paenungulata show different patterns of the anterior nasal cartilages it is reasonable to assume that they represent homoplastic derived character states.

Additional connections of the processus alaris superior to other parts of the anterior nasal cartilages have been described in several species. A commissura alicupularis (connection to the processus cupularis) like in *Potamogale velox* is also present in *Hemicentetes semispinosus*, *Geogale aurita* and *Procavia capensis*, as well as in most Microchiroptera, and *Ornithorhynchus anatinus* (FAWCETT, 1919; ZELLER, 1989; GÖBBEL, 2000; ASHER, 2001; SCHUNKE & ZELLER, 2010: figure 6; STÖSSEL *et al.*, 2010; HÜPPI *et al.*, 2018; MAIER, 2020). In *Sorex araneus*, *Suncus varilla* (formerly *orangiae*), and *Sus scrofa* the processus alaris superior is connected to the processus lateralis ventralis (PARKER, 1874, contra MEAD, 1909; DE BEER, 1929; ROUX, 1947). According to (ASHER, 2001) *Echinops telfairi*, *Tenrec ecaudatus* and *Setifer setosus* lack a connection of the processus alaris superior to the cupula nasi anterior; in the latter the process shows a short connection to the anterior nasal floor. However, based on the same specimens MAIER (2020) observed a ventral commissure at the processus alaris superior in *Echinops telfairi* and *Setifer setosus*. He defines the broad base of the processus alaris superior in *Micropotamogale lamottei*, *Echinops telfairi*, *Microgale pusilla*, and *Setifer setosus* as still being part of the paries nasi. MAIER (2020) names the connection between this area and the ventral

nasal cartilage that he interprets as processus lateralis ventralis, commissura lateroventralis. This pattern is hypothesized to be a synapomorphy of Tenrecoidea. However, *Micropotamogale lamottei* differs slightly from the other investigated species in MAIER (2020: figure 12) but shows a more similar pattern like *Potamogale velox* in the ventral attachment site of the commissure.

*Orycteropus afer* and *Macroscelides proboscideus* show a commissura alitransversalis, the connection between processus alaris superior and lamina transversalis anterior (STÖSSEL *et al.*, 2010; MAIER, 2020). Although the pattern is variable among Afroinsectiphilia (Tenrecoidea, Macroscelidea, Tubulidentata), it is evident that a ventral connection of the processus alaris superior to the anterior nasal cartilages is a specific character of this group. Functionally these connections support and stiffen the rim of the nostril. In concert with the well-developed processus alaris superior, to which facial muscles can be attached, it could serve as an enlarged area of facial muscle attachment (ROUX, 1947; GÖBBEL, 2000; MAIER & RUF, 2014). In the Afroinsectiphilia this would enhance the mobility of the external nasal cartilages in the significantly elongated and motile rostrum or proboscis of the respective species (ASHER, 2005; IHLAU, 2011; MAIER, 2020). Already in fetal stages the cartilage of the tectum and paries nasi of Macroscelidea shows distinct circular areas of resorption that may increase flexibility of the proboscis (KRATZING & WOODALL, 1988; IHLAU, 2011; MAIER, 2020); a distinct cartilaginous element, the cartilago lateralis, is associated with facial muscles and may be an apomorphy of Macroscelidinae (IHLAU, 2011). ASHER (2001) describes the attachment of facial muscles to the processus alaris superior in all investigated Tenrecoidea independent from the size of the process. His *Potamogale velox* fetus shows a distinct dorsal spur at the processus alaris superior that is associated with a prominent alar-cupular muscle. A comparable structure has been described in *Setifer setosus* (ROUX, 1947). Based on his study on the extrinsic musculature of the rostrum in Afrotheria and Lipotyphla WHIDDEN (2002) proposes that the mobile snout is not homologous among the investigated afrotherian species; especially Tenrecidae and Chrysochloridae differ from the other Afrotheria. *Potamogale velox* shows the same pattern of five snout muscles like Tenrecidae (and Chrysochloridae) that insert as long tendons into the mobile rostrum; movements of the rostrum, that is used as a sensory organ, are well controlled by this set of muscles (WHIDDEN, 2002). Although no distinct muscle pattern has been observed in the otter shrew, the chondrocranial characters could also be regarded as an adaptation to the demand of distinct opening and closure of the nostrils during swimming and diving.

The lack of the atrioturbinal in *Potamogale velox* cannot be discussed yet, as no information is available if this structures develops later in ontogeny. However, the lack of this structure could increase the flexibility of the vestibulum nasi when closing the nostrils during diving.

The ossified part of the septum nasi in the adult *Potamogale velox* is notably short. Thus, the long anterior cartilaginous portion supports the mobility of the anterior nasal cartilages. Like *Potamogale velox*, *Hemicentetes semispinosus*, *Setifer setosus*, *Procavia capensis*, and *Loxodonta africana* lack a fenestra internasalis anterior as well as any septoturbinals (SCHUNKE & ZELLER, 2010; STÖSSEL *et al.*, 2010). In contrast, *Orycteropus afer* has a large fenestration of the anterior septum nasi (STÖSSEL *et al.*, 2010). According to HÜPPI *et al.* (2018) the lack of a fenestra internasalis anterior is a derived feature. Thus, we tentatively conclude that the lack of the fenestra internasalis anterior is an apomorphic *grundplan* character of Afrotheria.

While in *Potamogale velox*, chrysochlorids and *Procavia capensis* the foramen epiphaniale is well-developed, it is obviously absent in *Hemicentetes semispinosus*, *Tenrec ecaudatus*, *Orycteropus afer*, *Dugong dugon*, and *Loxodonta africana* (MATTHES, 1921; SCHUNKE & ZELLER, 2010; STÖSSEL *et al.*, 2010). According to STÖSSEL *et al.* (2010) the absence of the foramen epiphaniale is an apomorphic *grundplan* character of Afrotheria. However, due to the independently highly derived nasal structures in several afrotherian clades a homoplastic reduction or loss of the foramen epiphaniale cannot be ruled out. The foramen of *Potamogale velox* is relatively large which might be due to the increased size of the ramus externus of the nervus ethmoidalis anterior that innervates the hypertrophied vibrissal apparatus. The same holds true for the large foramen infraorbitale of *Potamogale velox* that is passed by the nervus maxillaris that mainly innervates the facial vibrissae. As *Micropotamogale lamottei* and *Limnogale mergulus* also show an enlarged foramen infraorbitale (and enlarged cross-section of the nervus maxillaris) compared to terrestrial Tenrecidae this pattern is an adaptation to the semiaquatic mode of life (SÁNCHEZ-VILLAGRA & ASHER, 2002). Independently evolved enlargement of the foramen infraorbitale has also been observed in semiaquatic Lipotyphla (*Neomys fodiens*, *Desmana moschata*, *Galemys pyrenaicus*), Muridae (*Hydromys chrysogaster*, *Colomys goslingi*), Didelphidae (*Chironectes minimus*), and Monotremata (*Ornithorhynchus anatinus*) (ZELLER, 1988; SÁNCHEZ-VILLAGRA & ASHER, 2002).

Reduction or loss of the ductus nasolacrimalis is a common adaptation among aquatic and semiaquatic mammals as their lacrimal fluid apparatus is reduced (STARCK, 1982). In contrast to the other investigated Afrotheria, *Potamogale velox*, *Micropotamogale lamottei*, *Loxodonta africana* and Sirenia lack the ductus nasolacrimalis as well as the associated cartilaginous and skeletal structures (sulcus ductus nasolacrimalis) (ASHER, 2001; ASHER & HOFREITER, 2006; STÖSSEL *et al.* 2010). *Limnogale mergulus* has no foramina lacrimales, like the Potamogalidae, which also indicates a lacking ductus nasolacrimalis (SÁNCHEZ-VILLAGRA & ASHER, 2002; ASHER & HOFREITER, 2006). Although Elephantidae are terrestrial species it is discussed that the earliest Proboscidea or at least the last common ancestor of Tethytheria was

semiaquatic (FISCHER & TASSY, 1993). However, the lack of the ductus nasolacimalis in the semiaquatic Afrotheria clearly indicates an adaptation to their mode of life.

In conclusion, the overall objective of this study is to identify and eliminate autapomorphic characters of *Potamogale velox* based on the fetal chondrocranium. The following characters have been identified as apomorphic and related with the semiaquatic mode of life: short olfactory turbinal skeleton, reduced lamina cribrosa, loss of ductus nasolacimalis, enlarged foramen epiphaniale. This “morphological-functional character polarization” can be seen as an important prerequisite for further studies in order to identify synapomorphic characters of Potamogalidae and thus to contribute to the ongoing Afrotheria discussion.

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