

# Ontogenetic transformations of the ethmoidal region in Muroidea (Rodentia, Mammalia): new insights from perinatal stages

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## Abstract

The cartilaginous nasal capsule of mammals becomes highly modified during ontogeny by resorption and ossification that finally results in the ethmoid bone. A deeper understanding of the early ontogeny of the ethmoidal region helps to elucidate morphological patterns and homologies in the adult cranium. However, the perinatal development of the ethmoidal region is not well studied though this is a craniogenetic crucial time frame. This is especially the case in the most species-rich rodent group, the Muroidea. In order to elucidate the perinatal transformation of the nasal capsule histological serial sections of 23 muroid species, one dipodid species, and two geomyoid species were investigated, some of which are represented by more than one ontogenetic stage. In addition adult crania of selected Muroidea were analyzed by  $\mu$ CT. The muroid grundplan of the ethmoidal region is already determined at birth and comprises a general pattern of six olfactory turbinals (two frontoturbinals, three ethmoturbinals, one interturbinal between the first two ethmoturbinals). Apomorphic patterns are restricted to the number of turbinals in the frontoturbinal recess: three in *Abrothrix longipilis*, one in *Apodemus flavicollis*, *Apodemus sylvaticus*, *Micromys minutus*, *Mus musculus*, and *Rattus norvegicus*.

Perinatal stages of all altricial muroid species under study have a less mature ethmoidal region compared to precocial rodents e.g., caviomorphs. However, in muroids resorption of the nasal capsule and ossification of the turbinals, nasal septum and lamina cribrosa already start around birth and follow a distinct pattern observed in many other rodents. In around 14 days old stages of some investigated muroids the paries nasi and tectum nasi are almost completely resorbed except for the anterior nasal cartilages and those parts that become ossified and part of the ethmoid bone (e.g., roots of turbinals). Surprisingly, the precocial *Sigmodon hispidus* and *Acomys* sp. resemble generally the developmental pattern of altricial muroids although e.g., paries nasi resorption starts clearly earlier in *Acomys*. Furthermore, the perinatal maturity of *Mesocricetus auratus* that has the shortest gestation period among placental mammals corresponds to that of other altricial muroids. This observation supports an accelerated development in the golden hamster.

## Key words

*Acomys*; altricial; chondrification; ethmoid bone; *Mesocricetus auratus*; nasal cavity; ossification; *Peromyscus maniculatus*; precocial; *Sigmodon hispidus*; turbinals.

## Introduction

Adult cranial morphology can hardly be understood without taking early ontogenetic stages into account as knowledge of the primordial cranium and craniogenetic processes is essential for identification of homologies and elucidating evolutionary transformations (e.g., GAUPP, 1906; DE BEER, 1937; MAIER, 1993b; NOVACEK, 1993;

MAIER & RUF, 2014; HÜPPI *et al.*, 2018). However, the investigation of the chondrocranium, the cartilaginous skeletal structure of the fetal skull, is subject to limited access to prenatal stages in most mammalian species as well as to technical limitations. Thus, in many mammalian orders little is known about the fate of certain cartilaginous

structures and the ossification patterns. This applies in particular for the ethmoidal region (nasal region) and its delicate internal structures, the turbinals (turbinates, conchae). Great parts of the anterior chondrocranium serve as a placeholder until the covering dermal skull bones are fully developed while the anteriormost cartilages are present the entire life as they are involved in supporting the rhinarium (MAIER, 2002, 2020; MAIER & RUF, 2014; HÜPPI *et al.*, 2018).

Although a great number of comparative ontogenetic studies on the mammalian ethmoidal region covering almost all extant orders exists, many of them are restricted to very early up to mid-fetal stages (e.g., GAUPP, 1906; VOIT, 1909; FAWCETT, 1917; DE BEER, 1937; REINBACH, 1952a, b; KUHN, 1971; ZELLER, 1987, 1989). These studies are primarily based on a fully developed and still complete chondrocranium, the so-called stadium optimum (MAIER & RUF, 2014). Before the advent of non-invasive imaging techniques like micro computed tomography ( $\mu$ CT) the comprehensive work of PAULLI (1900a, b, c) on the turbinal skeleton of mammals is one of the rare cases of investigating fully ossified specimens. Nowadays the studies on the ethmoidal region in mammals are generally based on  $\mu$ CT analyses (mostly adult stages) and cover both comparative anatomy (e.g., SMITH & ROSSIE, 2008; MACRINI, 2012; RUF, 2014; RUF *et al.* 2015) as well as morphofunction (e.g., VAN VALKENBURGH *et al.*, 2004, 2014; SMITH *et al.*, 2007; MARTINEZ *et al.* 2018, 2020; WAGNER & RUF, 2019).

Basically, the delicate bony lamellae inside the nasal cavity have a two-fold function: thermoregulation and olfaction (HILLENUS, 1992, 1994). The anteriormost turbinals (turbinates, conchae) inside the vestibulum nasi, the marginoturbinal and parts of the atrioturbinal are covered by keratinous epithelium; the maxilloturbinal and nasoturbinal support respiratory epithelium and are responsible for moistening and warming inhaled air; the posterior turbinals, the fronto-, ethmo- and interturbinals, are covered by olfactory epithelium carrying the olfactory receptors. However, the exact distribution of the two types of epithelium in the transition region varies among species and may also depend on the ontogenetic stage (LE GROS CLARK, 1951; RUF, 2004; SMITH *et al.*, 2004; SMITH & ROSSIE, 2008). For instance, the olfactory epithelium can also cover the posterior part of the nasoturbinal, the nasal roof between the ethmoturbinals as well as the lamina semicircularis that is primarily separating two compartments of the nasal cavity (RUF, 2004).

The ontogenetic transformation from the simple fetal cartilaginous nasal skeleton to the complex ethmoid bone has not yet been the focus of most craniogenetic studies and thus, there is still a large gap of knowledge which structures of the ethmoidal region exactly ossify and finally contribute to the ethmoid bone in the adult skull. The ethmoid bone of the adult cranium is supposed to comprise the lamina cribrosa that transmits the fila olfactoria (CN I), the lamina perpendicularis (the ossified septum nasi), the crista galli (median ridge for attachment of the falx cerebri, not present in all species), and the laby-

rinthus ethmoidalis (ethmoturbinals) (SCHALLER, 1992). Depending on the reproduction strategy of the respective species (precocial = born fully developed with open eyes, altricial = born naked with closed eyes) the crucial time slot for these major transformations may differ; furthermore the gestation and development of a precocial large artiodactyl cannot be compared to those of an altricial small rodent. Nevertheless, especially in altricial species major transformations of the primordial ethmoidal region continue into postnatal stages (MAIER & RUF, 2014).

Rodentia is the most species-rich mammalian order and its systematic and evolution is still discussed (WILSON & REEDER, 2005; FLYNN *et al.*, 2019). Recent phylogenetic studies completely rely on molecular data and revealed three suborders, a phylogeny that differs significantly from the previous six to seven suborders based on morphological data (see FLYNN *et al.*, 2019 for review). Today three major clades, the squirrel-related clade (Eusciurida according to FLYNN *et al.*, 2019), the Ctenohystrica, and the mouse-related clade (Supramyomorphia according to D'ELIA *et al.*, 2019) are accepted (HUCHON *et al.*, 2002, 2007; BLANGA-KANFI *et al.*, 2009). The early craniogenesis of a great number of rodent species has been investigated so far representing members of all three major clades: squirrel-related clade e.g., FRAHNERT (1998); Ctenohystrica e.g., STRUTHERS (1927), RAJTOVA (1972a), DIERBACH (1985a, b), SCHRENK (1989), MESS (1995, 1997, 1999a), DA SILVA NETO (2000); mouse-related clade e.g., FAWCETT (1917), ELOFF (1948, 1951a, b), YOUSSEF (1966), FRICK (1986), HAUCK (1987), KADAM (1972, 1973a, b, 1976), RAJTOVA (1972b), VIDIC *et al.* (1972). However, most studies are restricted to a single species and very few prenatal stages which is especially the case in the by far most species-rich clade, the Muroidea (hamsters, voles, mice, rats, gerbils) (WILSON & REEDER, 2005). Among muroids most studies are restricted to the easily accessible laboratory animal species *Mesocricetus auratus*, *Mus musculus*, and *Rattus norvegicus*.

Here for the first time a comprehensive comparative morphological and ontogenetic study of the ethmoidal region of 23 muroid species is presented in order to elucidate the timing of resorption and ossification of the nasal capsule and to contribute to a deeper understanding of the craniogenesis in rodents. In addition morphological characters that should be included in future systematic and phylogenetic studies are presented. These species some of which are represented by varying fetal and perinatal stages have been investigated in detail within an unpublished diploma thesis (RUF, 1999) and PhD thesis (RUF, 2004). In addition new data from adult crania are considered in the present study. For outgroup comparison further members of the mouse-related clade, *Jaculus jaculus* (Dipodidae), *Dipodomys heermanni* (Heteromyidae), and *Thomomys* sp. (Geomysidae), whose craniogenesis has not been investigated so far, are included in the study (RUF, 2004).

Particular attention is given to *Mesocricetus auratus* due to its peculiar development: this species has the



shortest gestation period (15–17 days) among placental mammals (NOWAK, 1991). *Sigmodon* and *Acomys* show a precocial reproduction pattern (BRUNJES, 1990; NOWAK, 1991), which is quite rare among muroid rodents. The results are also discussed in the light of the different developmental maturity at birth in precocial and altricial rodents.

## Material and methods

For the present study transversal histological serial sections of perinatal stages of 23 muroid species, one dipodoid and two geomyoid species were investigated (Table 1, see RUF 1999, 2004). The observations on the chondrocranium are complemented by considering  $\mu$ CT scans of adult crania of selected species based on macerated skulls and one wet specimen (Table 2). Further outgroup comparison is based on literature data on the ethmoidal region of other rodent clades and members of Euarchontoglires. According to MUSSER & CARLETON (2005), the specimens labeled as *Akodon longipilis* belong in fact to *Abrothrix longipilis* and the one labeled as *Dendromus kivu* belongs to the species *nyasae*. The age of the 21 mm HL (head length) stage of *Sigmodon hispidus* has not been available. Based on size comparison and on the fact that its eyes are already open it is determined as at least neonatal.

The histological serial sections are housed in the histological collection of the Institut für Evolution und Ökologie, Universität Tübingen; the *Dendromus nyasae* specimen is a permanent loan by the Museum für Naturkunde Berlin and the histological serial sections of *Mus musculus* are loaned by the Anatomische Anstalt, Universität München. Adult specimens are housed in the mammal collection (SMF) of Senckenberg Forschungsinstitut und Naturmuseum Frankfurt, Frankfurt am Main, except for the wet *Mesocricetus auratus* specimen that is deposited in the collection of Wolfgang Maier at the Institut für Evolution und Ökologie, Universität Tübingen.

The systematical subdivision of the investigated muroid species follows MUSSER & CARLETON (2005) and the underlying phylogenetic concept of muroid taxa is based on MICHAUX *et al.* (2001) and JANSÁ & WEKSLER (2004). Nomenclature of turbinals follows MAIER & RUF (2014) and RUF (2014). In order to make the text more readable only the genus names are used except for *Apodemus* that is represented by two species. Furthermore, histological serial sections representing ontogenetic series of one species are numbered accordingly (see Table 1).

Histological serial sections of late fetal stages of *Peromyscus maniculatus*, *Rattus norvegicus*, and *Jaculus jaculus* were used to produce plate models made out of styrofoam with the help of a microscope camera lucida. This method is according to BORN (1883) and was modified by W. Maier (pers. comm.). Digital images of selected histological serial sections were taken with a Zeiss

Axio Imager.A1m. Adult specimens were scanned with two different  $\mu$ CT devices. The wet specimen of *Mesocricetus auratus* was scanned with a Wälischmiller RayScan 200 CT scanner located at Steinbeis-Transferzentrum Gießerei Technologie Aalen, Fachhochschule Aalen, the macerated skulls were scanned with a GE phoenix|x-ray nanotom 180 s housed at the Institut für Geowissenschaften at the Goethe-Universität, Frankfurt am Main. For scan parameters like resolution (isotropic voxel size), current, voltage, and timing see Table 2. The  $\mu$ CT data were used for creating virtual 3D models of the turbinal skeleton with the manual segmentation tool of the software Avizo 9 (Thermo Fisher Scientific FEI).

## Comparative description

In the following general morphological patterns and major ontogenetic transformations of the ethmoidal skeleton in muroid rodents are described and compared to *Jaculus*, *Dipodomys*, and *Thomomys*; detailed descriptions of skeletal and soft tissue structures are given in RUF (1999) and RUF (2004). In addition, data from further previous descriptions of the craniogenesis in muroids are included here for a more comprehensive comparison: *Mesocricetus auratus* (RAJTOVA, 1972b; KADAM, 1976), *Phodopus sungorus* (HAUCK, 1987; same specimen as in the present study), *Lemmus lemmus* (SCHRENK, 1989; same specimen as in the present study), *Arvicola terrestris* (FAWCETT, 1917), *Tatera indica cuvieri* (KADAM, 1972, 1973a, b), *Otomys tropicalis* (ELOFF, 1948), *Rhabdomys pumilio* (ELOFF, 1951b), *Mus musculus* (KADAM, 1976; FRICK, 1986), *Rattus norvegicus* (YOUSSEF, 1966; KADAM, 1976). Short definitions of the cartilaginous structures that are considered in this study are presented at the beginning of each subchapter in order to provide a general overview and introduction to the described characters. If not otherwise stated, all generalizations in the description only refer to the species and stages listed in Table 1.

### Cupula nasi anterior

**Definition.** The mammalian cupula nasi anterior remains cartilaginous throughout live and projects anteriorly through the piriform aperture of the osteocranium (DE BEER, 1937). It comprises the cartilagine cupulares whose medial and lateral lamellae form the anterior end of the nasal cavity and embrace the fenestra narina (STURM, 1936; STARCK, 1967; KUHN, 1971). Between both cartilages the dorsal sulcus suprasetalis meets the sulcus ventralis (GAUPP, 1908; FRICK, 1954). The ventral boundary of the fenestra narina is formed by the processus cupularis (= processus alaris inferior according to GAUPP, 1908; FRICK, 1954), that is located posterior to the cartilago cupularis, and the processus lateralis ventralis (= processus lateralis inferior according to FISCHER, 1901, = processus lateralis anterior according to MEAD, 1909),

**Table 1.** Transversal histological serial sections of prenatal to early postnatal stages of Rodentia considered in the present study. The specimens were described in detail in Ruf (2004), *Rattus norvegicus* in Ruf (1999). Numbering of specimens refers to order of ontogenetic stages. The *Mus musculus* specimens of fetal and unspecific age were sorted according to their developmental maturity of the structures. Abbreviations: CRL, crown-rump length; dpc, days post conception; dpn, day(s) post natum; HBL, head-body length; HL, head length.

Taxon	HL	CRL	HBL	Slice thickness	Age
<b>Muroidea</b>					
<b>Cricetidae</b>					
<b>Arvicolinae</b>					
<i>Lemmus lemmus</i>	14 mm	30 mm	unknown	10 µm	fetal
<i>Microtus californicus</i>	10.5 mm	20 mm	unknown	10 µm	fetal
<b>Cricetinae</b>					
<i>Cricetus cricetus</i>	20 mm	42 mm	unknown	10 µm	fetal
<i>Mesocricetus auratus</i> 1	12 mm	22 mm	unknown	10 µm	fetal
<i>Mesocricetus auratus</i> 2	15 mm	29 mm	35 mm	10 µm	neonatal
<i>Mesocricetus auratus</i> 3	17.5 mm	34 mm	42 mm	15 µm	4 dpn
<i>Mesocricetus auratus</i> 4	19 mm	42 mm	48 mm	10/15 µm	7 dpn
<i>Mesocricetus auratus</i> 5	23 mm	50 mm	60 mm	20 µm	11 dpn
<i>Mesocricetus auratus</i> 6	28 mm	unknown	72 mm	20 µm	14 dpn
<i>Phodopus sungorus</i>	11.5 mm	25 mm	unknown	10 µm	1 dpn
<b>Neotominae</b>					
<i>Peromyscus maniculatus</i> 1	7.5 mm	12.5 mm	unknown	10 µm	fetal
<i>Peromyscus maniculatus</i> 2	11.5 mm	21 mm	unknown	10 µm	fetal
<i>Peromyscus maniculatus</i> 3	14.5 mm	25 mm	unknown	10 µm	neonatal
<i>Peromyscus maniculatus</i> 4	25 mm	65 mm	unknown	20/30 µm	juvenile
<b>Sigmodontinae</b>					
<i>Abrothrix longipilis</i> 1	10.5 mm	18,5 mm	unknown	10 µm	fetal
<i>Abrothrix longipilis</i> 2	16.5 mm	25 mm	unknown	10/15 µm	fetal
<i>Auliscomys micropus</i>	17 mm	26 mm	unknown	15 µm	fetal
<i>Geoxus valdivianus</i>	15.5 mm	22 mm	unknown	10 µm	fetal
<i>Phyllotis</i> sp.	16 mm	26 mm	unknown	10 µm	fetal
<i>Rhipidomys</i> sp.	16.5 mm	29 mm	unknown	10 µm	fetal
<i>Sigmodon hispidus</i> 1	10.5 mm	16.5 mm	unknown	10 µm	fetal
<i>Sigmodon hispidus</i> 2	14 mm	31 mm	unknown	10 µm	fetal
<i>Sigmodon hispidus</i> 3	19 mm	36 mm	unknown	12 µm	fetal
<i>Sigmodon hispidus</i> 4	21 mm	42 mm	unknown	12 µm	> neonatal
<b>Muridae</b>					
<b>Deomyinae</b>					
<i>Acomys</i> sp. 1	20 mm	36 mm	41 mm	10 µm	fetal, 18 dpc
<i>Acomys</i> sp. 2	22 mm	unknown	45 mm	10 µm	neonatal, 35 dpc
<b>Gerbillinae</b>					
<i>Meriones unguiculatus</i>	14.5 mm	28 mm	unknown	10 µm	fetal
<i>Gerbillus perpallidus</i>	10 mm	16 mm	unknown	10 µm	fetal
<b>Murinae</b>					
<i>Apodemus flavicollis</i>	7.8 mm	12.8 mm	unknown	10 µm	fetal
<i>Apodemus sylvaticus</i>	12 mm	20 mm	unknown.	10 µm	fetal
<i>Lophuromys sikapusi</i>	10.9 mm	unknown	unknown	10 µm	fetal
<i>Micromys minutus</i>	7 mm	10.5 mm	unknown	10 µm	fetal
<i>Mus musculus</i> 1	unknown	18.5 mm	unknown	unknown	fetal
<i>Mus musculus</i> 2	unknown	22 mm	unknown	unknown	fetal
<i>Mus musculus</i> 3	unknown	25 mm	unknown	10 µm	unknown
<i>Mus musculus</i> 4	unknown	29 mm	unknown	unknown	unknown
<i>Mus musculus</i> 5	unknown	unknown	unknown	10 µm	6 dpn
<i>Mus musculus</i> 6	17.2 mm	unknown	unknown	15 µm	10 dpn
<i>Rattus norvegicus</i> 1	14.5 mm	28 mm	unknown	10 µm	fetal
<i>Rattus norvegicus</i> 2	15.5 mm	32 mm	unknown	10 µm	fetal
<i>Rattus norvegicus</i> 3	19 mm	39 mm	unknown	10 µm	neonatal
<i>Rattus norvegicus</i> 4	26 mm	59 mm	unknown	15 µm	7 dpn
<i>Rattus norvegicus</i> 5	34 mm	unknown	74 mm	20 µm	14 dpn
<i>Rhabdomys pumilio</i>	11 mm	20 mm	unknown	10 µm	fetal

Table 1 continued.

Taxon	HL	CRL	HBL	Slice thickness	Age
<b>Nesomyidae</b>					
<i>Dendromus nyasae</i>	19 mm	35 mm	unknown	15 µm	postnatal
<b>Dipodoidea</b> <b>Dipodidae</b>					
<i>Jaculus jaculus</i>	14 mm	29 mm	unknown	10 µm	fetal
<b>Geomyoidea</b> <b>Heteromyidae</b>					
<i>Dipodomys heermanni</i>	15 mm	32 mm	unknown	unknown	fetal
<b>Geomyidae</b>					
<i>Thomomys</i> sp.	unknown	36 mm	unknown	10 µm	fetal

Table 2. Investigated adult stages of Muroidea based on µCT scans of macerated skulls. The *Mesocricetus auratus* specimen from the collection W. Maier is a fixed head including soft tissue. Resolution is given as isotropic voxel size.

Taxon	Specimen ID	Current	Voltage	Timing	Resolution
<b>Cricetidae</b> <b>Cricetinae</b>					
<i>Cricetus cricetus</i>	SMF 62024	90 µA	100 kV	1000 ms	0.01280483 mm
<i>Mesocricetus auratus</i>	SMF 82131	100 µA	100 kV	1000 ms	0.009299 mm
<i>Mesocricetus auratus</i>	Coll. W. Maier	unknown	unknown	unknown	0.0557 mm
<b>Neotominae</b>					
<i>Peromyscus maniculatus</i>	SMF 72827	37 µA	130 kV	500 ms	0.011765 mm
<b>Sigmodontinae</b>					
<i>Sigmodon hispidus</i>	SMF 87320	40 µA	120 kV	750 ms	0.014853 mm
<b>Muridae</b> <b>Murinae</b>					
<i>Mus musculus</i>	SMF 63500	37 µA	130 kV	500 ms	0.011618 mm

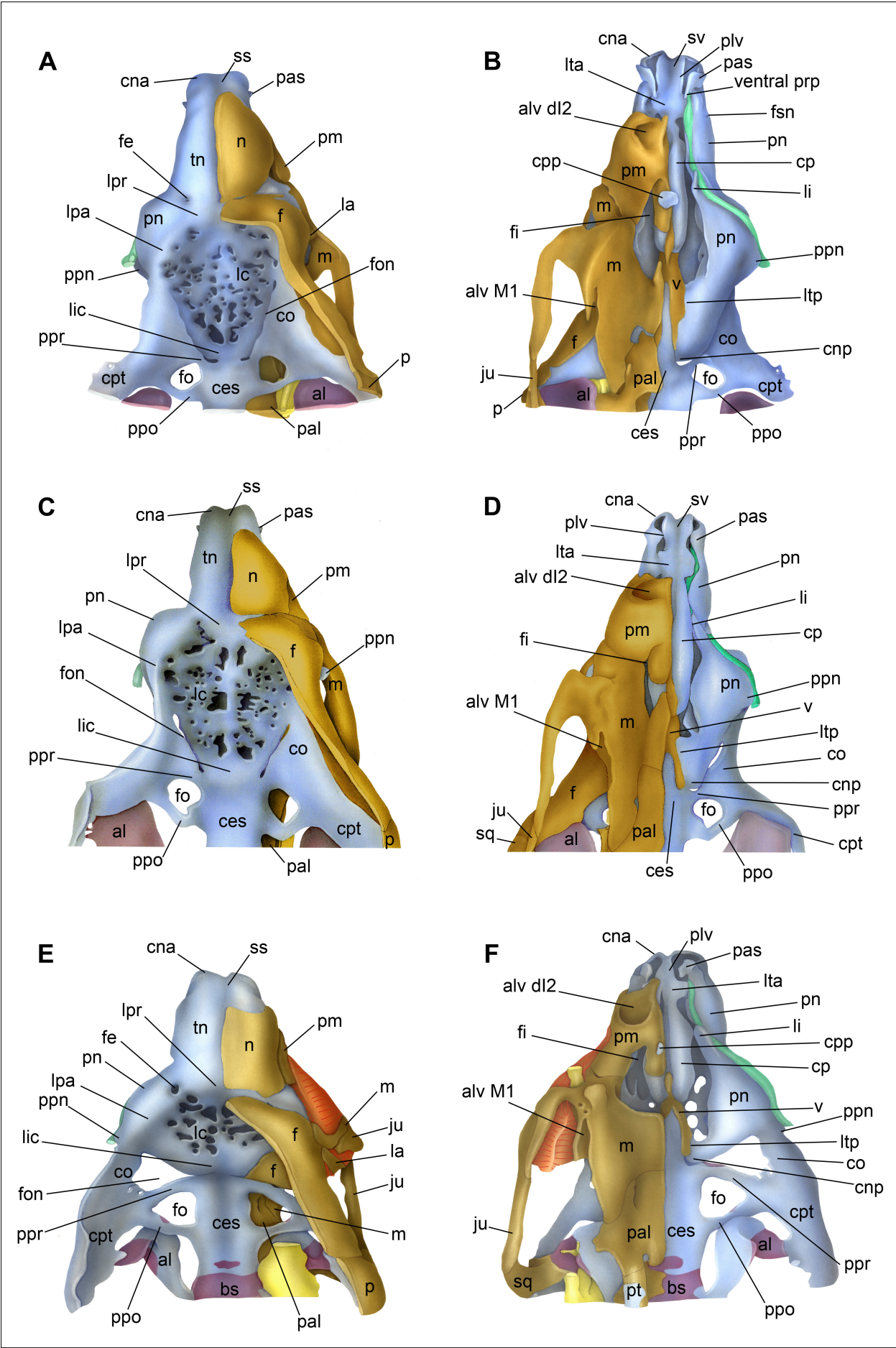
that projects ventrolaterally from the septum nasi (SPATZ, 1964; ZELLER, 1983).

**Description.** All species show a well developed cupula nasi anterior (Figs. 1, 2, 3). In the geomyoids it is rostrally closed by a broad area internarica that results in a ventrolateral to lateral orientation of the apertura nasi externa. Some muroids (*Peromyscus*, *Sigmodon* 2, *Geoxus*, *Abrothrix* 2, *Mesocricetus* 1+2, *Cricetus*) also show a broad area internarica. All other stages and species (especially murids) have a narrower area internarica and their apertura nasi externa opens more anteriorly and ventrolaterally (FAWCETT, 1917; ELOFF, 1948, 1951b; YOUSSEF, 1966; KADAM, 1972, 1973a, b; RAJTOVA, 1972b; contra FRICK 1986; pers. obs). *Phodopus* (HAUCK, 1987; pers. obs.), *Tatera* (KADAM, 1972, 1973a, b), and *Jaculus* have quite reduced cartilagine cupulares and thus an anteriorly orientation of the nasal openings.

Only *Rhabdomys* shows a distinct processus cupularis (ELOFF, 1951b; pers. obs.). Apart from that all other species show a much reduced process confluent with the processus lateralis ventralis (FAWCETT, 1917; ELOFF, 1948; YOUSSEF, 1966; KADAM, 1972, 1973a, b, 1976; RAJTOVA, 1972b; FRICK, 1986; HAUCK, 1987; pers. obs). *Gerbillus*, *Meriones* and *Jaculus* lack a distinct processus cupularis.

All species except for the Gerbillinae and *Jaculus* have well developed processus laterales ventrales that continue posteriorly into the lamina transversalis anterior (FAWCETT, 1917; ELOFF, 1948, 1951b; YOUSSEF, 1966; KADAM, 1972, 1973a, b; RAJTOVA, 1972b; FRICK, 1986; HAUCK, 1987; pers. obs) (Figs. 1B, D, 4A–C, 5A, B). However, shape and orientation of these processus are variable and show a puzzling pattern. In *Gerbillus* and *Meriones* the processus laterales ventrales are oriented ventrally and fuse to form a ventral extension of the septum nasi (Fig. 5C, D); *Jaculus* has reduced processus laterales ventrales (Figs. 1F, 4D). Thus, in these three species the sulcus ventralis is almost completely reduced.

In *Apodemus flavicollis*, *Micromys* and *Gerbillus* the cupula nasi anterior is still at least partly precartilaginous. A fetal stage of *Acomys dimidiatus* (21 days post conception stage) has still a precartilaginous cupula nasi anterior, whereas its paries nasi, tectum nasi and septum nasi are already chondrified (HÜPPI *et al.*, 2018). A 7.5 mm HL stage of *Mesocricetus* still shows blastematous processus laterales ventrales (KADAM, 1976). In *Tatera* the cupula nasi anterior chondrifies later than the adjacent structures of the nasal capsule (KADAM, 1972, 1973a, b). The early postnatal stages as well as *Acomys* show a thinning of the cartilage of the cupula nasi anterior as well as of the processus lateralis ventralis and the con-



nection of the former to the paries nasi and tectum nasi becomes resorbed (Figs. 4B, C, 5A, B). Resorption can also be observed inside the processus lateralis ventralis at its transition into the lamina transversalis anterior in *Peromyscus* 3+4 and *Mesocricetus* 4. The adult crania under study do not give any information on the cupula nasi anterior due to the fact that its cartilage is not preserved in the macerated skulls or hardly visible in the  $\mu$ CT scans of wet specimens.

## Processus alaris superior

**Definition.** The processus alaris superior is a plug-like anteroventral projection of the paries nasi. This process subdivides the primary fenestra narina into an anterior situated apertura nasi externa and a posterior fenestra narina accessoria which is closely associated with the ductus nasolacrimalis. The processus alaris superior develops relatively late in prenatal ontogeny and is quite diverse in shape and size among mammals (GAUPP, 1906; REINBACH, 1952a, b; SPATZ, 1964; KUHN, 1971; MAIER, 1980; SCHRENK, 1989).

**Description.** All investigated species possess a well-developed processus alaris superior that supports the apertura nasi externa (except for *Phodopus*, *Micromys*, *Thomomys*) (FAWCETT, 1917; ELOFF, 1948, 1951b; YOUSSEF, 1966; RAJTOVA, 1972b; KADAM, 1972, 1973a, b, 1976; FRICK, 1986; HAUCK, 1987; pers. obs.) (Figs. 1, 2, 4, 5). In most species the processus alaris superior gets close to the processus lateralis ventralis of the cupula nasi anterior (Figs. 1B, D, 4A, B, 5B). The proximal part of the processus alaris superior is formed by a thin stem, the radix processus alaris superior. Anteriorly the processus alaris superior continues as a blade-like structure, the ala processus alaris superior, that develops a deep dorsal sulcus especially in the older stages (KADAM, 1972, 1973a, b; HAUCK, 1987; pers. obs.). The murids under study show a more shallow sulcus. The sulcus is roofed medially by an alar outgrowth. However, in *Gerbillus* and *Meriones* this roof is partly separated by a fissure and the former continues posteriorly into a short channel that opens on the ventral side of the ala; here, the medial

rim of the ala rolls up dorsolaterally and is hook-shaped in cross-section (Fig. 5C).

The processus alaris superior can show a dorsal and ventral posterior process (Figs. 1B, 1A, 5A). Except for *Abrothrix* and *Geoxus* the processus alaris superior of all Sigmodontinae, *Peromyscus*, Cricetinae and *Lemmus* has a dorsal and ventral posterior process. HAUCK (1987) describes for *Phodopus* only the ventral process. The Gerbillinae possess only the ventral process that is continuous with the hook-like outgrowth of the ala (KADAM, 1972, 1973a, b; pers. obs.) (Fig. 5D). All other species show a puzzling pattern. *Apodemus flavicollis* and *Micromys* do not have a processus posterior which might be due to their immature stage.

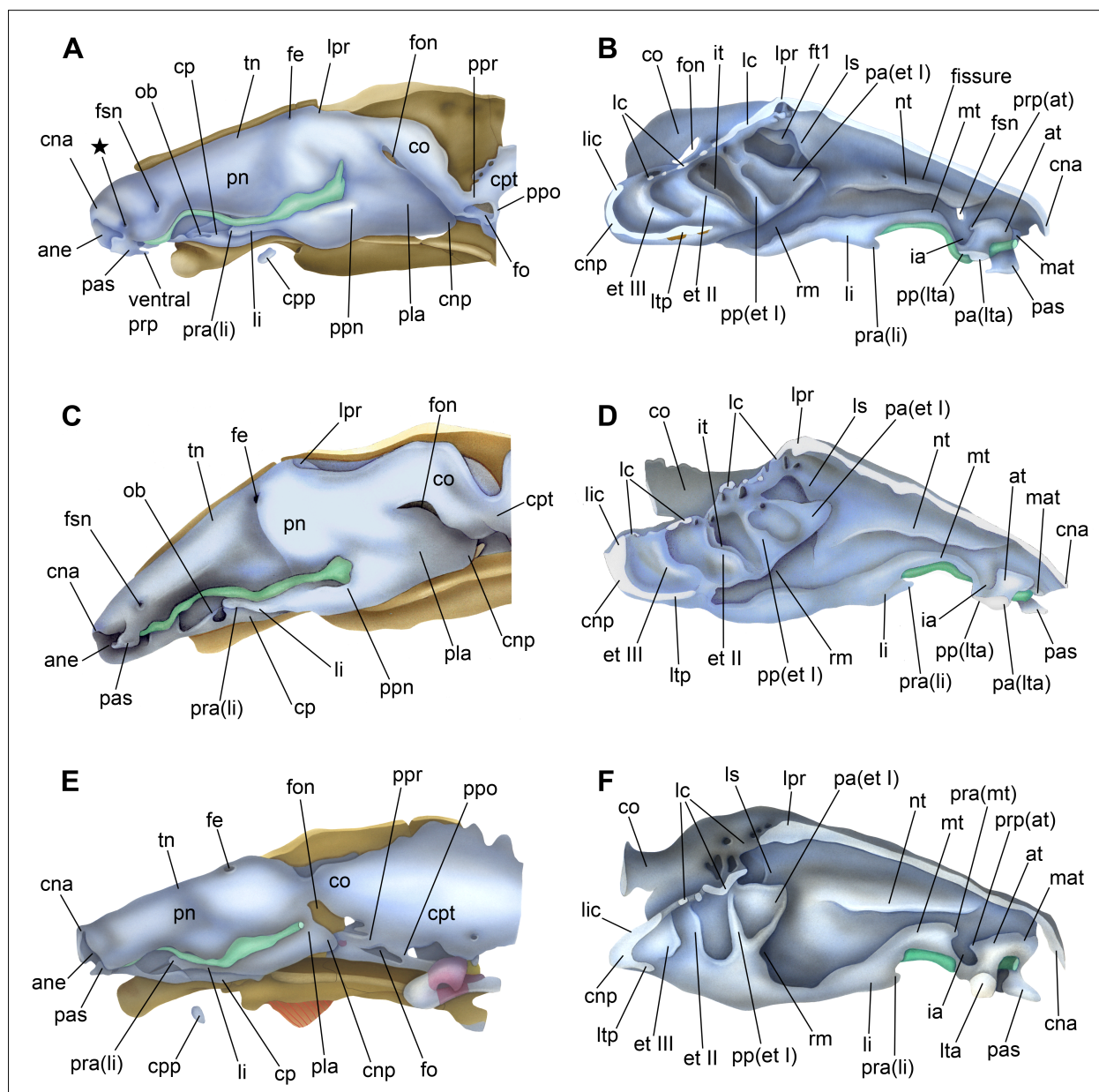
In the very early stages (*Peromyscus* 1, *Mesocricetus* 1, *Rattus* 1, *Micromys*) the processus alaris superior is still precartilaginous. The previously investigated earlier stages of *Mesocricetus*, *Tatera* and *Acomys dimidiatus* also show a blastematous processus alaris superior (KADAM, 1972, 1973a, b, 1976; HÜPPI *et al.*, 2018). The cartilaginous process becomes loosely attached or isolated in postnatal stages by proximal resorption of the paries nasi (Figs. 4B, 5B). In *Mesocricetus* 6 resorption causes a hollow space inside the processus alaris superior (Fig. 4C). As the processus alaris superior remains cartilaginous throughout life it is not visible in the  $\mu$ CT scans of the adult stages.

## Tectum nasi and lamina cribrosa

**Definition.** The precerebral roof of the prenatal nasal cavity is formed by the tectum nasi. Between tectum nasi and paries nasi the foramen epiphaniale transmits the ramus externus of the nervus ethmoidalis anterior. The subcerebral part is covered by the lamina cribrosa (considered as part of the tectum nasi), a sieve-like structure which transmits the fila olfactoria of CN I, and the lamina infracribrosa (GAUPP, 1906; VOIT, 1909; TERRY, 1917; KUHN, 1971). The latter forms the roof of the cupula nasi posterior. The limbus praecribrosus marks the border between these two parts of the nasal roof. It can give rise to a posterior process, the spina mesethmoidalis whose origin is still discussed (STARCK, 1941; SPATZ, 1964; ZELLER, 1983, 1989; SCHRENK, 1989; MAIER, 1993a). The crista

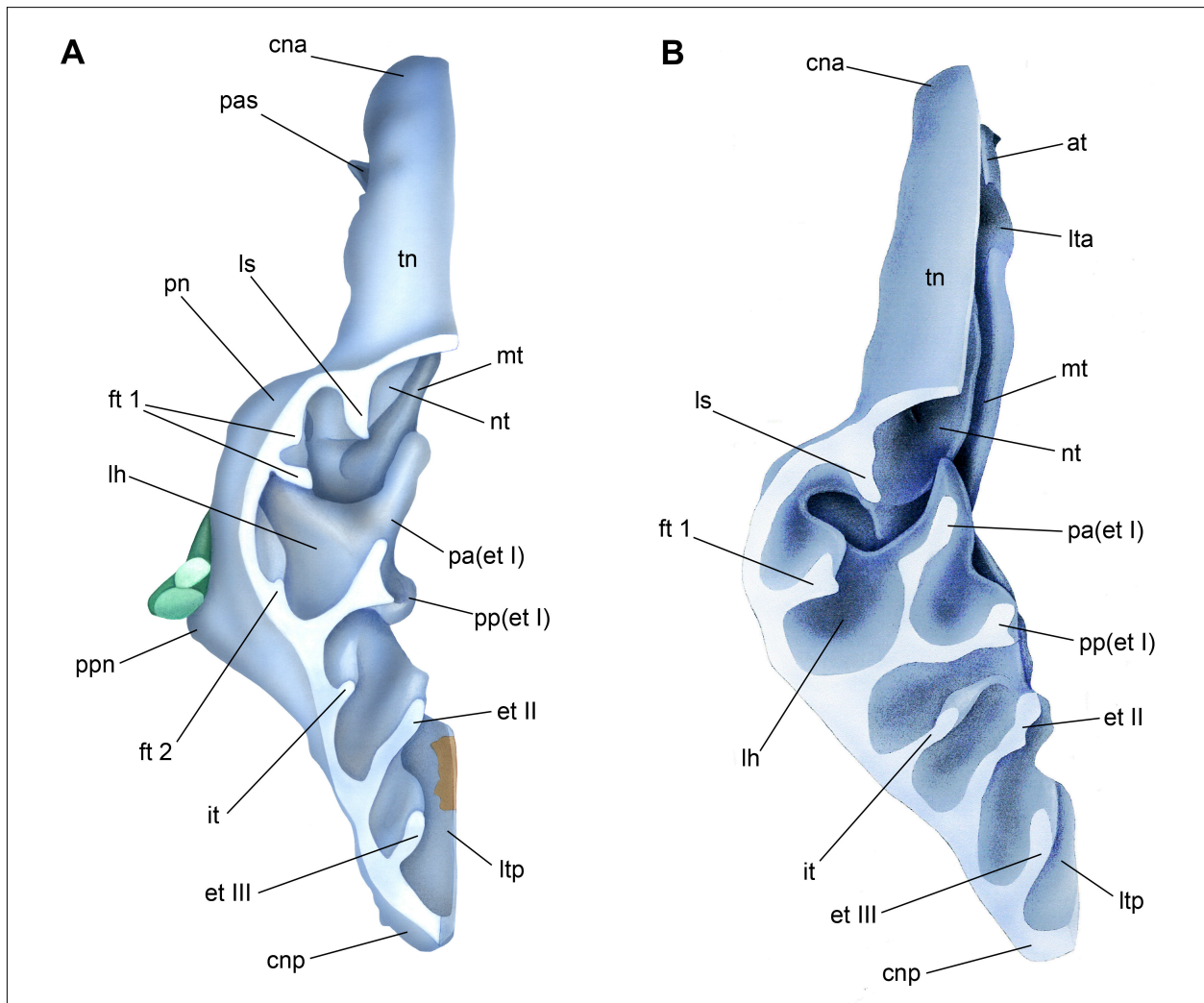
← **Fig. 1.** Plate reconstruction models of the ethmoidal region of selected Myodonta based on histological serial sections in dorsal (A, C, E) and ventral (B, D, F) view. Left dermal bones not reconstructed. A, B *Peromyscus maniculatus*, stage 2, 11.5 mm HL. C, D *Rattus norvegicus*, stage 2, 15.5 mm HL. E, F *Jaculus jaculus*, 14 mm HL. Colour code: blue, cartilage; brown, dermal bone; green, ductus nasolacrimalis; purple, endochondral bone; red, musculus masseter medialis (reconstructed only in *Jaculus jaculus*); yellow, ganglion trigeminale and nervus maxillaris of cranial nerve V. Abbreviations: al, alisphenoid bone; alv, alveolus; bs, basisphenoid bone; ces, central stem; cna, cupula nasi anterior; cnp, cupula nasi posterior; co, commissura orbitonasalis; cp, cartilago paraseptalis anterior; epp, cartilago papillae palatinae; cpt, commissura parietotectalis; di2, deciduous upper incisor 2; f, frontal bone; fe, foramen epiphaniale; fi, foramen incisivum; fon, fissura orbitonasalis; fo, foramen opticum; fsn, fenestra superior nasi; HL, head length; ju, jugal bone; la, lacrimal bone; lc, lamina cribrosa; li, lamina infraconchalis; lic, lamina infracribrosa; lpa, limbus paracribrosus; lpr, limbus praecribrosus; lta, lamina transversalis anterior; ltp, lamina transversalis posterior; m, maxillary bone; M1, upper molar 1; n, nasal bone; p, parietal bone; pal, palatine bone; pas, processus alaris superior; plv, processus lateralis ventralis; pm, premaxillary bone; pn, paries nasi; ppn, processus paranasalis; ppo, pila postoptica; ppr, pila praeoptica; prp, processus posterior; pt, pterygoid bone; sq, squamosal bone; ss, sulcus suprasetalis; sv, sulcus ventralis; tn, tectum nasi; v, vomer. Not to scale. Modified after RUF (1999) (C, D) and RUF (2004) (A, B, E, F).





**Fig. 2.** Plate reconstruction models of the ethmoidal region of selected Myodonta based on histological serial sections in lateral view (A, C, E) and medial aspect of the left nasal cavity (B, D, F). Left dermal bones not reconstructed. A, B *Peromyscus maniculatus*, stage 2, 11.5 mm HL. C, D *Rattus norvegicus*, stage 2, 15.5 mm HL. E, F *Jaculus jaculus*, 14 mm HL. Colour code: blue, cartilage; brown, dermal bone; green, ductus nasolacrimalis; purple, endochondral bone; red, musculus masseter medialis (reconstructed only in *Jaculus jaculus*). Star (★) indicates first resorption of the paries nasi. Abbreviations: ane, apertura nasi externa; at, atrioturbinale; cna, cupula nasi anterior; cnp, cupula nasi posterior; co, commissura orbitonasalis; cp, cartilago paraseptalis anterior; cpp, cartilago papillae palatinae; cpt, commissura parietotectalis; et I–III, ethmoturbinale I–III; fe, foramen epiphaniale; fo, foramen opticum; fon, fissura orbitonasalis; fsn, fenestra superior nasi; ft I, frontoturbinale I; HL, head length; ia, incisura atriomaxilloturbinalis; it, interturbinal; lc, lamina cribrosa; li, lamina infraconchalis; lic, lamina infracribrosa; lpr, limbus praecribrosus; ls, lamina semicircularis; lta, lamina transversalis anterior; ltp, lamina transversalis posterior; mat, marginoturbinale; mt, maxilloturbinal; nt, nasoturbinale; ob, outer bar; pa, pars anterior; pas, processus alaris superior; pla, planum antorbitale; pn, paries nasi; pp, pars posterior; ppn, processus paranasalis; ppo, pila postoptica; ppr, pila praeoptica; pra, processus anterior; prp, processus posterior; rm, recessus maxillaris; tn, tectum nasi. Not to scale. Modified after RUF (1999) (C, D) and RUF (2004) (A, B, E, F).

**Description.** In all species the tectum nasi shows a very similar pattern (Figs. 1A, C, E, 2A, C, E, 3, 4, 5, 6A–C, 7, 8A, B, D, 9A, C, D). Rostrally the tectum nasi is very thick, has a broad connection to the septum nasi and a shallow sulcus supraseptalis. The latter becomes deeper



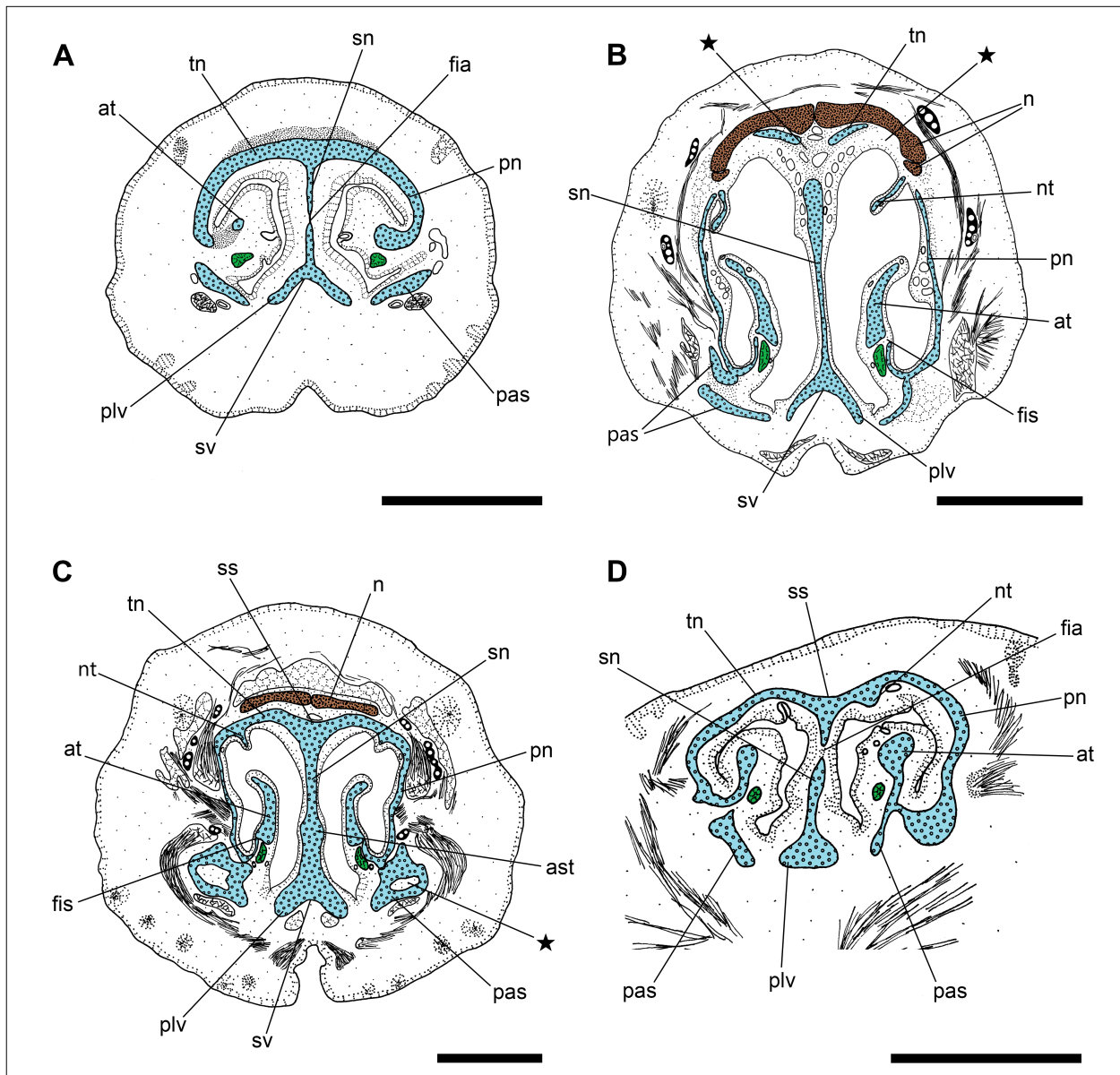
**Fig. 3.** Plate reconstruction models of the ethmoidal region of selected Muroidea based on histological serial sections. Dorsal view into the recessus frontoturbinis and ethmoturbinis of the left nasal cavity. Left dermal bones not reconstructed. **A** *Peromyscus maniculatus*, stage 2, 11.5 mm HL. **B** *Rattus norvegicus*, stage 2, 15.5 mm HL. Colour code: blue, cartilage; brown, dermal bone; green, ductus nasolacrimalis. Abbreviations: at, atrioturbinal; cna, cupula nasi anterior; cnp, cupula nasi posterior; et I–III, ethmoturbinal I–III; ft 1–2, frontoturbinal 1–2; HL, head length; it, interturbinal; lh, lamina horizontalis; ls, lamina semicircularis; lta, lamina transversalis anterior; ltp, lamina transversalis posterior; mt, maxilloturbinal; nt, nasoturbinal; pa, pars anterior; pas, processus alaris superior; pn, paries nasi; pp, pars posterior; ppn, processus paranasalis; tn, tectum nasi. Not to scale. Modified after RUF (1999) (**B**) and RUF (2004) (**A**).

between the lamina transversalis anterior and the limbus praecribrus which results in a dome shaped tectum nasi on each side (FAWCETT, 1917; ELOFF, 1948, 1951b; YOUSSEF, 1966; RAJTOVA, 1972b; KADAM, 1972, 1973a, b, 1976; FRICK, 1986; HAUCK, 1987; pers. obs) (Figs. 8A, B, D, 9C, D). The foramen epiphaniale is present in all investigated specimens except for *Thomomys* and always transmits the ramus externus of the nervus ethmoidalis anterior (Figs. 1A, E, 2A, C, E). It has also been observed in the previously described muroid species (FAWCETT, 1917; ELOFF, 1948, 1951b; YOUSSEF, 1966; RAJTOVA, 1972b; KADAM, 1972, 1973a, b, 1976; FRICK, 1986; HAUCK, 1987). In *Micromys* it is very small, in *Jaculus* very large (Fig. 1E). ELOFF (1948, 1951b) describes for *Otomys* and *Rhabdomys* that only a small artery runs through the foramen epiphaniale; this could not be verified for *Rhabdomys* by the present study.

A spina mesethmoidalis is present in many species, either as a crista or as a true spine. The previously described stages of *Mesocricetus*, *Arvicola*, *Mus*, *Rattus*, and *Rhabdomys* (FAWCETT, 1917; YOUSSEF, 1966; RAJTOVA, 1972b; KADAM, 1976; FRICK, 1986) as well as *Peromyscus* 1+2, *Abrothrix*, *Phyllotis*, *Geoxus*, *Rhipidomys*, *Mesocricetus* 1, *Microtus*, *Gerbillus*, *Apodemus sylvaticus*, *Rattus*, *Mus* 1–4, *Dendromus* and *Jaculus* lack a spina mesethmoidalis. This pattern may indicate a later development of the spina.

All investigated species show a well developed lamina cribrosa (FAWCETT, 1917; ELOFF, 1948, 1951b; YOUSSEF, 1966; RAJTOVA, 1972b; KADAM, 1972, 1973a, b, 1976; FRICK, 1986; HAUCK, 1987; pers. obs); due to the reduced posterior nasal cavity the lamina cribrosa of *Jaculus* is reduced in length (Figs. 1A, C, E, 2 B, D, F). The shape of the lamina cribrosa differs among the inves-

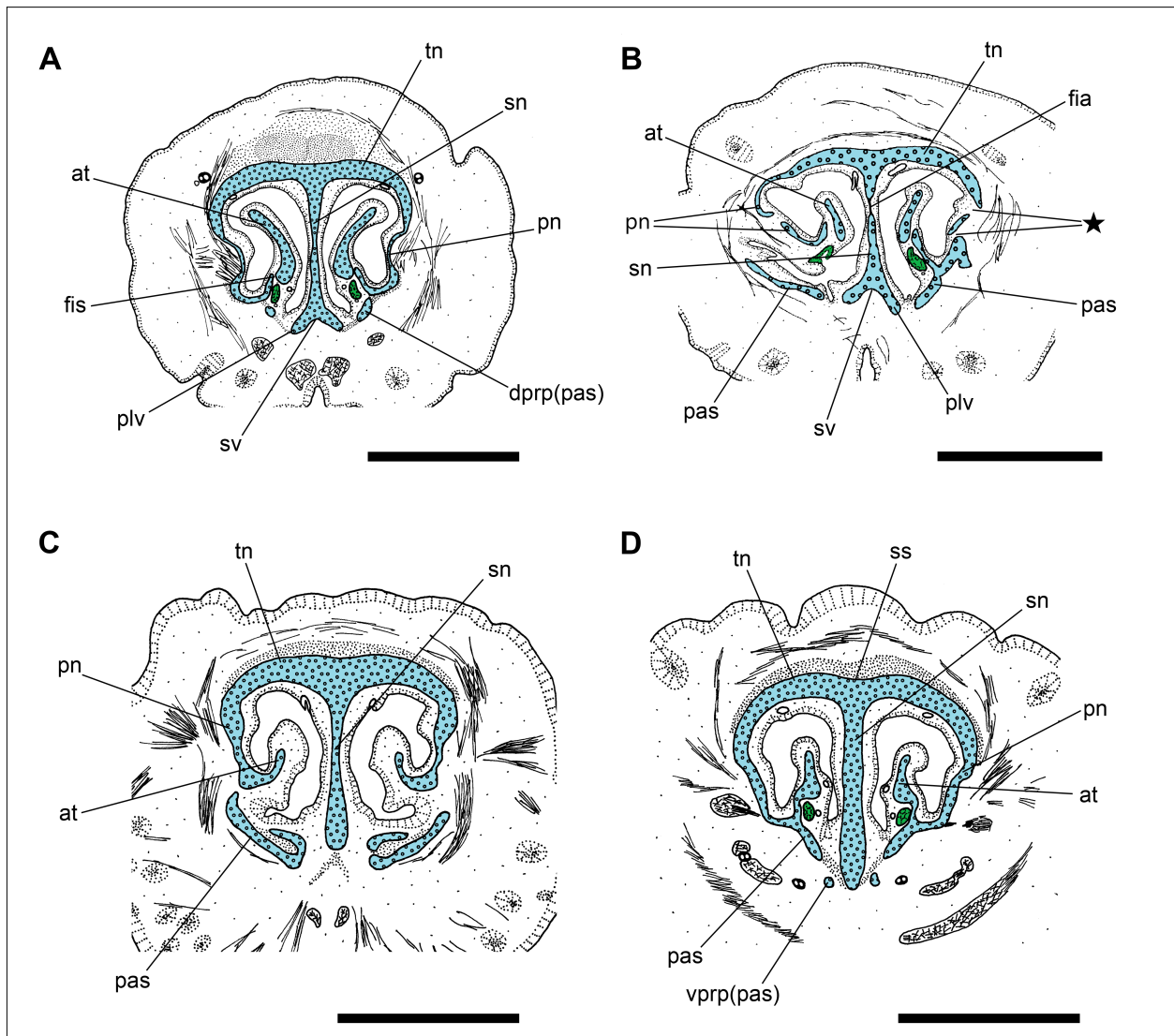




**Fig. 4.** Line drawings of transversal histological sections through the cupula nasi anterior. **A** *Peromyscus maniculatus*, stage 1, 7.5 mm HL, slice 2-3-1; **B** *Peromyscus maniculatus*, stage 4, 25 mm HL, slice 4-6-2; **C** *Mesocricetus auratus*, stage 6, 28 mm HL, slice 6-1-2; **D** *Jaculus jaculus*, 14 mm HL, slice 3-3-2. Colour code: blue, cartilage; brown, dermal bone; green, ductus nasolacrimalis. Stars (★) indicate areas of resorption. Abbreviations: ast, anterior septoturbinal; at, atrioturbinal; fia, fenestra internasalis anterior; fis, fissure; HL, head length; n, nasal bone; nt, nasoturbinal; pas, processus alaris superior; plv, processus lateralis ventralis; pn, paries nasi; sn, septum nasi; ss, sulcus suprasedentalis; sv, sulcus ventralis; tn, tectum nasi. Scale bars: 1 mm. Modified after RUF (2004).

tigated species from being mostly concave to rarely convex or straight (Figs. 10B, C, 11). However, in all species the origin of ethmoturbinal I at the lamina cribrosa is funnel-shaped; its depth is increasing during ontogeny (Fig. 10C). The development from a low and minor to a prominent crista galli can be observed in the ontogeny of *Mesocricetus* (RAJTOVA, 1972b; pers. obs.). Such a well-developed crista galli is also present in *Microtus*, *Lemmus*, *Tatera*, and *Acomys* 2 (KADAM, 1972, 1973a, b; pers. obs.) (Fig. 10C). *Rhipidomys*, *Abrothrix* 2, *Geoxus*, *Dendromus*, *Apodemus*, and *Mus* are lacking the crista galli. In all other investigated species the crista galli is not well pronounced.

In *Peromyscus* 1, *Gerbillus*, *Micromys*, and *Apodemus flavicollis* the tectum nasi is still at least partly blastematos or precartilaginous. KADAM (1972, 1973a, b, 1976) describes a blastematos tectum nasi in the very young stages of *Mesocricetus* (6 mm HL) and *Tatera* (4.5 mm HL). In *Peromyscus* the anteriormost part of the tectum nasi chondrifies at latest. Thus, the tectum nasi chondrifies later than the paries nasi. In contrast, in *Sigmodon* it is vice versa. In the younger stages the tectum nasi is thicker than the paries nasi and thus both parts of the nasal capsule can be easily distinguished. Thinning of the tectum nasi and first areas of resorption occur underneath the nasals that project deep into the sulcus suprasedentalis



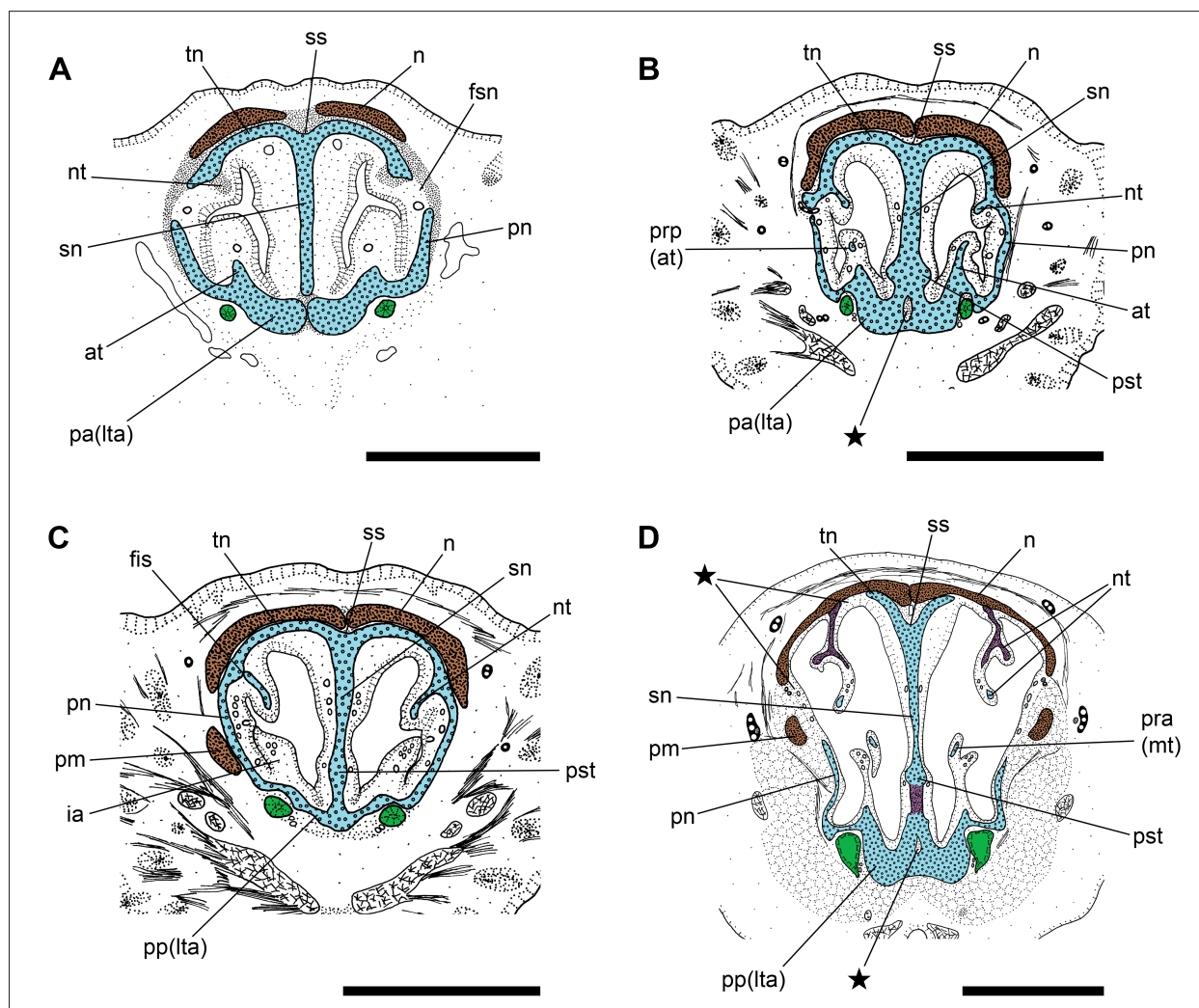
**Fig. 5.** Line drawings of transversal histological sections through the cupula nasi anterior. **A** *Acomys* sp., stage 1, 20 mm HL, slice 7-1-3; **B** *Acomys* sp., stage 2, 22 mm HL, slice 4-3-5; *Meriones unguiculatus*, 14.5 mm HL, slice 2-2-1 (**C**) and slice 2-4-2 (**D**). Colour code: blue, cartilage; brown, dermal bone; green, ductus nasolacrimalis. The star (★) indicates areas of resorption. Abbreviations: at, atrioturbinal; dprp, dorsal processus posterior; fia, fenestra internasalis anterior; fis, fissure; HL, head length; pas, processus alaris superior; plv, processus lateralis ventralis; pn, paries nasi; sn, septum nasi; ss, sulcus suprasedimentalis; sv, sulcus ventralis; tn, tectum nasi; vprp, ventral processus posterior. Scale bars: 1 mm. Modified after RUF (2004).

and finally cover the entire tectum nasi from the lamina transversalis anterior to the limbus praecribrosus (KADAM, 1972, 1973a, b; pers. obs.) (Figs. 7, 8A, B, D, 9B, C). Resorption starts in late fetal stages as it can be observed in neonates and occurs along the fenestra nasalis superior, in separate areas above the lamina transversalis anterior and more caudolaterally (e.g., *Peromyscus* 3+4) (Figs. 6D, 8C). Finally, the only cartilaginous tectum nasi is the anterior most portion behind the cupula nasi anterior. Ossification also starts in perinatal stages. Ossified remnants of the precerebral tectum nasi constitute the origin of the nasoturbinal, the limbus praecribrosus and the spina mesethmoidalis (Fig. 6D). In *Peromyscus* 4, *Cricetus* and *Acomys* 2 further ossified fragments of the precerebral tectum nasi can be observed (Fig. 8C). The adult stages show ossified remnants of the tectum

nasi between septum nasi and lamina semicircularis and at the origins of the frontoturbinals (Fig. 15B–E).

In all species the limbus praecribrosus becomes increasingly covered by the frontals and ossifications starts medially as observed in *Sigmodon* 3+4, *Mesocricetus* 6 and *Acomys*. In *Lemmus* and *Mus* 5 the tip of the spina mesethmoidalis ossifies first and from here the area of ossification continues onto the limbus praecribrosus.

A quite late development of the lamina cribrosa inside the fenestra olfactoria has been described in *Mus*, *Mesocricetus* and *Tatera* (RAJTOVA, 1972b; KADAM, 1972, 1973a, b; FRICK, 1986); in *Gerbillus* the lamina cribrosa is still completely precartilaginous. In *Apodemus flavicollis* the anterior part of the lamina cribrosa is still precartilaginous, whereas in the posterior part only the precartilaginous roots of the turbinals are present. A 10 mm



**Fig. 6.** Line drawings of transversal histological sections through the lamina transversalis anterior of *Peromyscus maniculatus*. **A** stage 1, 7.5 mm HL, slice 2-6-6; **B** stage 2, 21 mm HL, slice 3-3-5; **C** stage 2, 21 mm HL, slice 3-5-5; **D** stage 4, 25 mm HL, slice 5-6-2. Colour code: blue, cartilage; brown, dermal bone; green, ductus nasolacrimalis; purple, endochondral bone. Stars (★) indicate areas of resorption. Abbreviations: at, atrioturbinal; fis, fissure; fsn, fenestra superior nasi; HL, head length; ia, incisura atriomaxilloturbinalis; lta, lamina transversalis anterior; mt, maxilloturbinal; n, nasal bone; nt, nasoturbinal; pa, pars anterior; pm, premaxillary bone; pn, paries nasi; pp, pars posterior; prp, processus posterior; pst, posterior septoturbinal; sn, septum nasi; ss, sulcus suprasetalis; tn, tectum nasi. Scale bars: 1 mm. Modified after RUF (2004).

HL stage of *Mesocricetus* shows a completely chondrified lamina cribrosa (KADAM, 1976). The lamina cribrosa chondrifies from rostral to caudal and medial to lateral. This can be observed in *Peromyscus*, *Sigmodon*, *Abrothrix*, *Micromys*, *Mus*, and *Rattus* (Fig. 10A).

The pattern of ossification of the lamina cribrosa is somewhat variable among the investigated species, in terms of timing as well as location of the first ossification centers. Ossification can be observed in *Peromyscus* 3+4, *Sigmodon* 3+4, *Cricetus*, *Mesocricetus* 4-6, *Acomys*, *Mus* 4-6, *Rattus* 4+5, and *Dendromus* (Figs. 10B, C, 11A). One ossification center is located right behind the spina mesethmoidalis and continues caudally and laterally. This ossification may spread to the limbus paracribrosus. In most species a second posteromedial ossification center can be observed where the ossification of the lamina cribrosa most probably starts (e.g., *Mesocricetus* 4+5). BEATTY

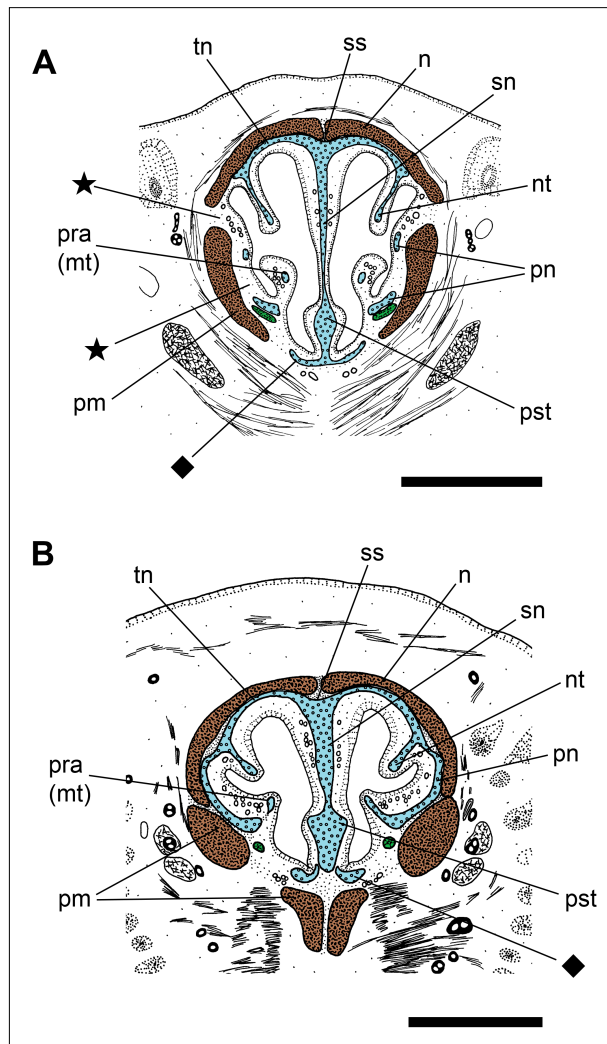
& HILLEMANN (1950) describe paired lateral and smaller scattered ossification centers of the lamina cribrosa in a six day old *Mesocricetus*. In *Rattus* ossification of the lamina cribrosa follows the same pattern as its chondrification, from anterior to posterior and from medial to lateral.

## Paries nasi

**Definition.** The paries nasi forms the sidewall of the nasal cavity and can be subdivided into three parts (VOIT, 1909; TERRY, 1917; DE BEER, 1937; REINBACH, 1952a, b; STARCK, 1967; ZELLER, 1983):

- (i) The pars anterior comprises the anterior third of the paries nasi, from the fenestra narina to the sulcus lateralis anterior, which corresponds to the origin of





**Fig. 7.** Line drawings of transversal histological sections through the ethmoidal region between lamina transversalis anterior and cartilago paraseptalis anterior. **A** *Acomys* sp., stage 1, 20 mm HL, slice 10-5-3; **B** *Dipodomys heermanni*, 15 mm HL, slice 7-4-2. Colour code: blue, cartilage; brown, dermal bone; green, ductus nasolacrimalis. The diamond (◆) indicates the connection between lamina transversalis anterior and cartilago paraseptalis anterior. Stars (★) indicate areas of resorption. Abbreviations: HL, head length; mt, maxilloturbinal; n, nasal bone; nt, nasoturbinal; pm, premaxillary bone; pn, paries nasi; pra, processus anterior; pst, posterior septoturbinal; sn, septum nasi; ss, sulcus supraseptalis; tn, tectum nasi. Scale bars: 1 mm. Modified after RUF (2004).

In many mammals the caudal paries nasi shows a prominent processus paranasalis that is associated with the ductus nasolacrimalis as well as adjacent dermal bones and represents the origin of the musculus obliquus inferior (e.g., TERRY, 1917; DE BEER, 1937; REINBACH, 1952a, b).

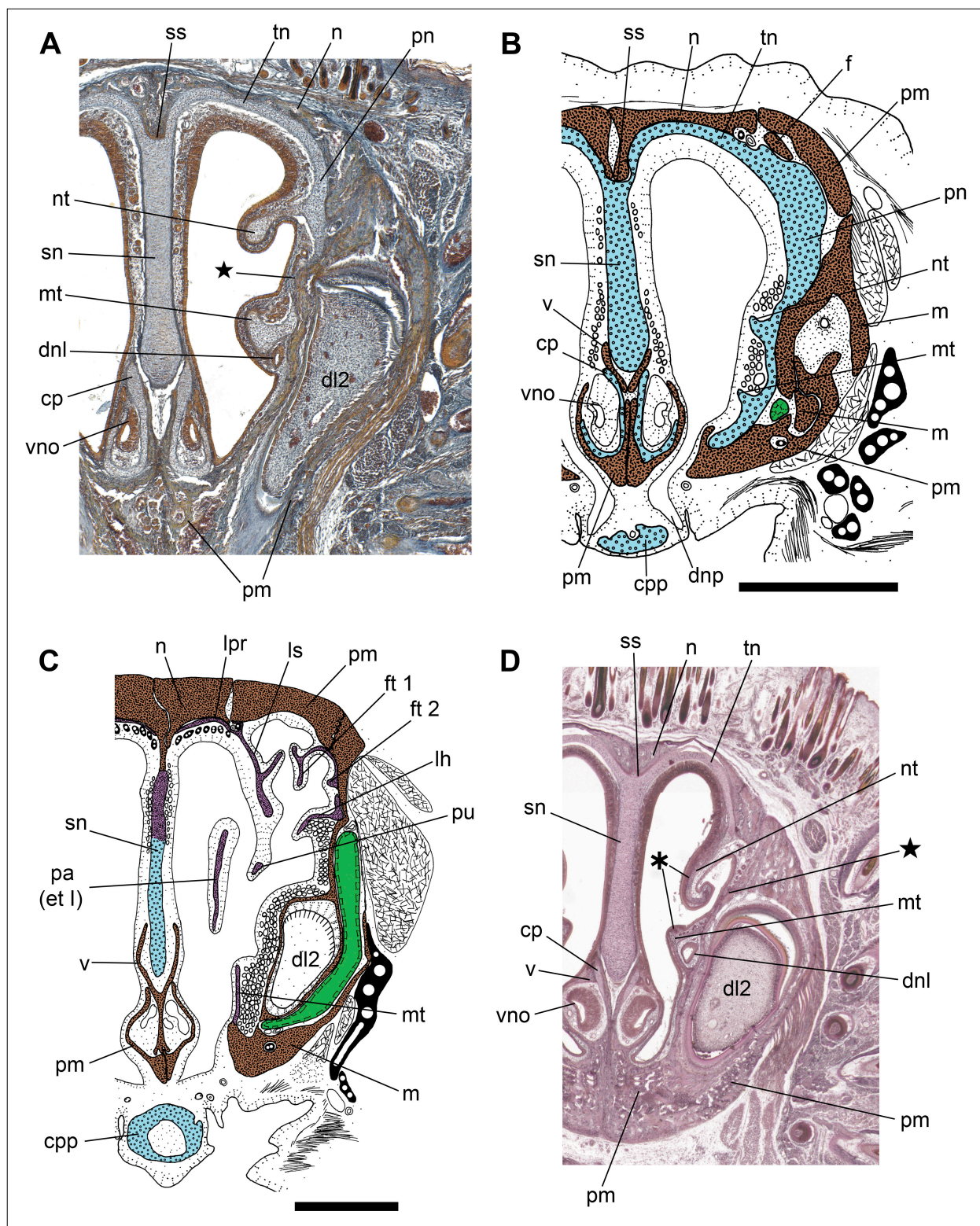
Except for the anteriormost part adjacent to the cupula nasi anterior and the bases of the turbinals, the paries nasi becomes resorbed and replaced by the surrounding dermal bones. Resorption of the paries nasi is induced by the adjacent dermal bones (STARCK, 1967).

**Description.** Generally, all species show a similar pattern of the paries nasi (Figs. 1, 2A, C, E). The fenestra superior nasi is present in all investigated species and stages except for *Gerbillus*, *Jaculus* and *Dipodomys* (contra ELOFF, 1951b; FRICK, 1986: fenestra lateralis; contra HAUCK, 1987) (Figs. 1B, 2A, C, E, 6A). In all investigated stages of *Rattus* two fenestrae per side can be observed. The fenestra superior nasi is located in the pars anterior of the paries nasi roughly above the lamina transversalis anterior. In *Lemmus* and *Microtis* the fenestra superior nasi is very small. All species and stages show a well-developed lamina infraconchalis; it has an anterior process except in *Lemmus*, *Arvicola*, *Gerbillus*, *Meriones*, *Apodemus flavicollis*, *Mus* 5, *Micromys* and *Thomomys* (FAWCETT, 1917; ELOFF, 1948, 1951b; YOUSSEF, 1966; RAJTOVA, 1972b; KADAM, 1972, 1973a, b, 1976; contra FRICK, 1986; contra HAUCK, 1987; pers. obs.) (Figs. 1B, D, F, 2, 8B, D, 9A, C, D).

In early ontogenetic stages the paries nasi is posteriorly continuous with a commissura orbitonasalis in almost all species (FAWCETT, 1917; ELOFF, 1948, 1951b; YOUSSEF, 1966; RAJTOVA, 1972b; KADAM, 1972, 1973a, b, 1976; FRICK, 1986; HAUCK, 1987; pers. obs.) (Figs. 1, 2, 12A). However, according to KADAM (1976) the commissura orbitonasalis of *Mesocricetus* projects from the cartilago sphenethmoidalis. *Tatera* has a commissure that is completely made up by the cartilago paranasalis, in *Arvicola* at least partly (FAWCETT, 1917; KADAM, 1972, 1973a, b, 1976). An ala minima, the connection between commissura orbitonasalis and limbus paracribrus, is present in *Peromyscus* 1, *Sigmodon* 1, *Otomys*, *Rhabdomys*, *Apodemus*, *Mus* (10 mm HL stage), and

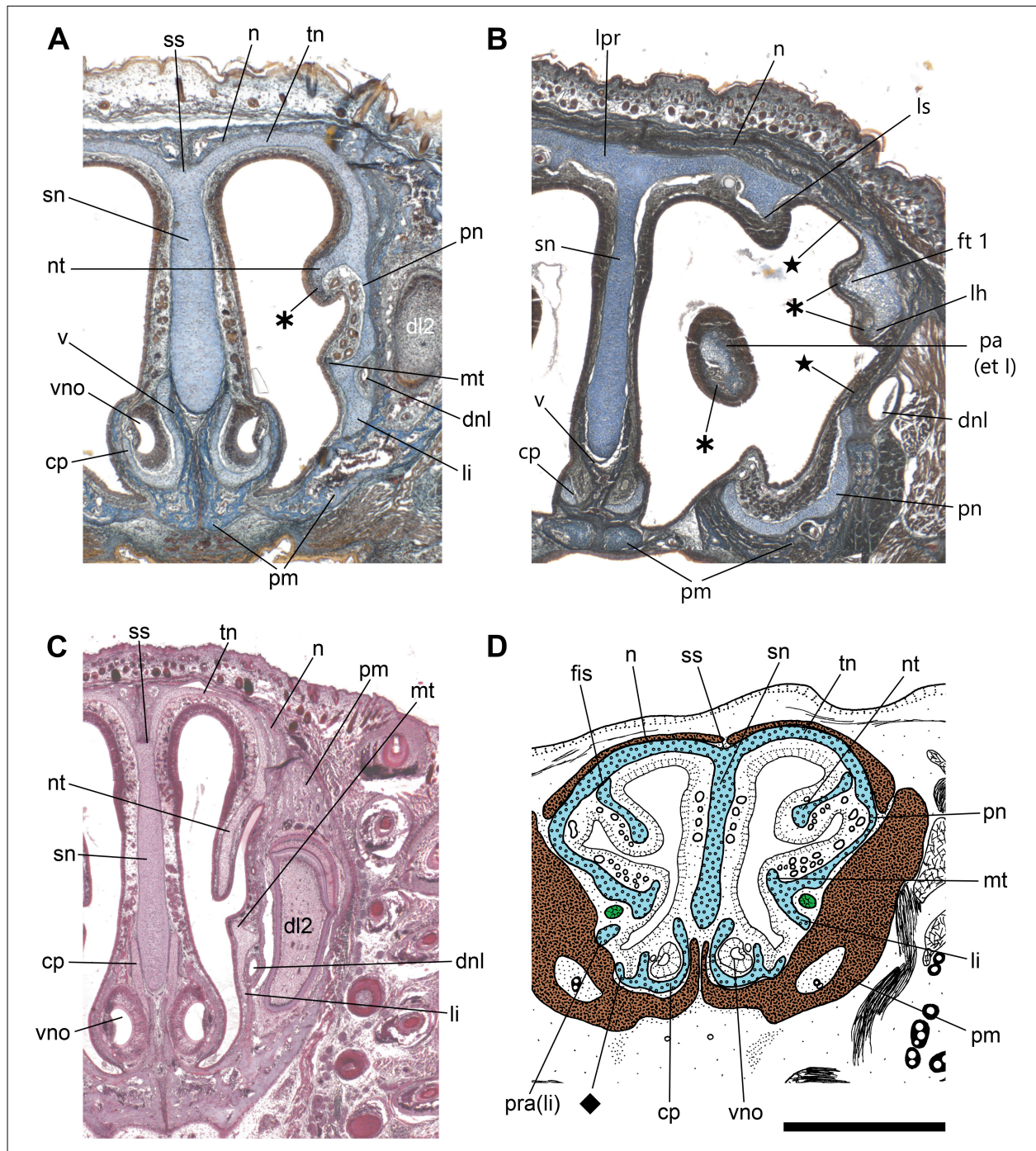
the lamina semicircularis inside the nasal cavity. The lateral bulge is the prominentia supraconchalis. Ventrally it is confluent with the lamina infraconchalis that is located below the maxilloturbinal. The lamina infraconchalis contributes to the canalis nasolacrimalis. In many mammals a persisting fenestra superior nasi occurs between pars anterior and tectum nasi.

- (ii) The pars lateralis forms a more or less prominent lateral outgrowth and is located between sulcus lateralis anterior and sulcus lateralis posterior, which corresponds to the root of ethmoturbinal I. The latter belongs to the pars posterior but expands anteriorly and thus pars lateralis and pars posterior overlap. Dorsally the pars lateralis houses the recessus frontoturbinalis and ventrally the recessus maxillaris.
- (III) The pars posterior extends from the sulcus lateralis posterior to the posterior end of the nasal capsule. Strictly speaking, the cupula nasi posterior and the lamina transversalis posterior belong to the paries nasi. The lateral and vertical wall of the paries nasi above the lamina transversalis posterior is the planum antorbitale.



**Fig. 8.** Line drawings and digital images of transversal histological sections through the ethmoidal region showing the housing of the vomeronasal organ in selected Cricetidae. **A–C** *Peromyscus maniculatus*: **A** stage 3, 14.5 mm HL, slice 7-4-3; **B** same specimen, slice 10-1-3; **C** stage 4, 25 mm HL, slice 17-3-2. **D** *Sigmodon hispidus*, stage 4, 21 mm HL, slice 17-3-2. Colour code for line drawings: blue, cartilage; brown, dermal bone; green, ductus nasolacrimalis; purple, endochondral bone. Stars (★) indicate resorption of the paries nasi. The asterisk (\*) indicates ossification of the naso- and maxilloturbinal. Abbreviations: cp, cartilago paraseptalis anterior; cpp, cartilago papillae palatinae; dl2, deciduous upper incisor 2; dnl, ductus nasolacrimalis; dnp, ductus nasopalatinus; et I, ethmoturbinal I; f, frontal bone; ft 1–2, frontoturbinal 1–2; HL, head length; lh, lamina horizontalis; lpr, limbus praecribrosus; ls, lamina semicircularis; m, maxillary bone; mt, maxilloturbinal; n, nasal bone; nt, nasoturbinal; pa, pars anterior; pm, premaxillary bone; pn, paries nasi; pu, processus uncinatus; sn, septum nasi; ss, sulcus suprasedalis; tn, tectum nasi; v, vomer; vno, vomeronasal organ. Scale bars: 1 mm. **A**, **D** not to scale. **B**, **C** modified after RUF (2004).





**Fig. 9.** Line drawing and digital images of transversal histological sections through the ethmoidal region showing the housing of the vomeronasal organ in selected Myodonta. **A–B** *Mesocricetus auratus*: **A** stage 2, 15 mm HL, slice 8-1-1; **B** stage 3, 17.5 mm HL, slice 13-1-5; **C** *Acomys* sp., stage 2, 22 mm HL, slice 16-4-3. **D** *Jaculus jaculus*, 14 mm HL, slice 8-3-3. Colour code for line drawing: blue, cartilage; brown, dermal bone; green, ductus nasolacrimalis. Asterisks (\*) indicate areas of ossification. Stars (★) indicate resorption of the paries nasi. The diamond (◆) indicates the lateral trough at the cartilago paraseptalis anterior that most likely represents a cartilago ductus nasopalatini. Abbreviations: cp, cartilago paraseptalis anterior; dl2, deciduous upper incisor 2; dnl, ductus nasolacrimalis; et I, ethmoturbinal I; fis, fissure; ft 1, frontoturbinal 1; HL, head length; lh, lamina horizontalis; li, lamina infraconchalis; lpr, limbus praecribrosus; ls, lamina semicircularis; mt, maxilloturbinal; n, nasal bone; nt, nasoturbinal; pa, pars anterior; pm, premaxillary bone; pn, paries nasi; pra, processus anterior; sn, septum nasi; ss, sulcus supraseptalis; tn, tectum nasi; v, vomere; vno, vomeronasal organ. Scale bar: 1 mm. **A–C** not to scale. **D** modified after RUF (2004).

*Rattus* (ELOFF, 1948, 1951b; KADAM, 1976; pers. obs.). Most of the investigated species possess a more or less pronounced processus paranasalis (KADAM, 1972, 1973a,

b; pers. obs.) (Figs. 1A–D, 2A, C, E, 3A, 10A). In *Apodemus flavicollis*, *Mus* 2, *Rattus*, *Lophuromys*, and in the geomyoids a crista is present in this position. In con-

trast, *Phyllotis*, *Auliscomys*, *Arvicola* (FAWCETT, 1917), *Microtus* and *Meriones* only show a more or less pronounced kink of the paries nasi in this area. Due to the shortening of the nasal cavity in *Jaculus* its processus paranasalis is situated more posteriorly and thus does not show the same topology compared to the other species (Figs. 1E, F, 2E). In prenatal stages of *Peromyscus*, *Sigmodon*, *Abrothrix*, *Geoxus*, *Lemmus*, all murids (except for *Apodemus flavicollis*), and *Dipodomys* the processus or crista paranasalis projects deeply into the foramen infraorbitale.

The separate chondrification of the three paries nasi sections has been observed in *Mesocricetus*, *Tatera*, and *Otomys* (ELOFF, 1948; KADAM, 1972, 1973a, b, 1976). In contrast RAJTOVA (1972b) observed in *Mesocricetus* a successive chondrification of the paries nasi from anterior to posterior. In *Peromyscus* 1, *Sigmodon* 1+2, *Gerbillus*, *Lophuromys*, *Apodemus flavicollis*, *Mus* 1+2 and *Micromys* the pars anterior in front of the lamina transversalis anterior chondrifies from caudal and dorsal and later than the other parts of the paries nasi. However, FRICK (1986) described a homogeneous chondrification of the paries nasi in *Mus*. The chondrification of the lamina infraconchalis occurs later than that of the adjacent paries nasi as it is still blastematous in *Apodemus flavicollis* or it consists of precartilage as in *Sigmodon* 1 and *Micromys* (KADAM, 1972, 1973a, b, 1976; pers. obs.); in a 7.5 mm HL stage of *Mesocricetus* the lamina infraconchalis chondrifies separately although a common anlage with the rest of the paries nasi has been observed (KADAM, 1976).

One or two fissures between paries nasi and margino- and atriortubinal, that cause the separation of the ventromedial part of the paries nasi in this area, are present in all species and stages except for *Peromyscus* 1, *Sigmodon* 1, *Micromys*, *Apodemus flavicollis*, *Rhabdomys*, *Mus* and *Dipodomys* (Figs. 4B, C, 5A, B, D); these fissures become longer with increasing age. Older prenatal and perinatal stages show thinning of the paries nasi and a common resorption pattern among Muroidea that occurs in several areas simultaneously (FAWCETT, 1917; ELOFF, 1948, 1951b; YOUSSEF, 1966; RAJTOVA, 1972b; KADAM, 1972, 1973a, b, 1976; FRICK, 1986; HAUCK, 1987; pers. obs.) (Figs. 4B, C, 5A–C, 6B–D, 7A, 7C, 8A, C, D, 9A, C, D). In *Peromyscus* 4, *Sigmodon* 3+4, *Rhipidomys*, *Cricetus*, *Acomys*, *Mus* 5+6, *Rattus* 5 and *Lophuromys* the fenestra superior nasi is posteriorly continuous with an area of resorption. In addition, further smaller or larger areas of resorption can be observed in the pars anterior in a variable pattern (FAWCETT, 1917; pers. obs.). Generally, two more areas of resorption are located in the pars lateralis, especially the sidewall of the recessus maxillaris as observed in *Peromyscus* 4, *Mesocricetus* 2, *Cricetus*, *Dendromus*, *Acomys* and *Mus* 3–6 (Figs. 9B, 10B, C). In *Phodopus* a third area of resorption can be observed in the pars lateralis (HAUCK, 1987; pers. obs.). Resorption of the pars posterior starts later than in the other two parts of the paries nasi (Fig. 11). In contrast, in *Rattus* 3 and in the geomyoids resorption of the paries nasi starts in the pars lateralis. In

comparison in *Cricetus* and *Acomys* the resorption of the paries nasi obviously begins in earlier prenatal stages. The oldest stages of *Mesocricetus*, *Tatera*, *Rattus* and *Mus* show an almost completely resorbed paries nasi that is replaced by the adjacent dermal bones except for the anterior part in front of the cartilago paraseptalis anterior (KADAM, 1972, 1973a, b; pers. obs.). Prenatal ossification of the lamina infraconchalis can be observed in *Sigmodon* 3+4, *Cricetus*, and *Acomys* 2, postnatal in *Peromyscus* 4, *Mesocricetus* 5+6, *Dendromus*, and *Mus*. The pattern is always a rostral area of ossification but the direction (ventral, dorsal) or the number of areas is variable. The commissura orbitonasalis becomes increasingly resorbed as observed in *Peromyscus* 3+4, in which only a processus orbitonasalis is left. Ossified remnants of the paries nasi are its ventral edge, the lamina infraconchalis, the origin of the turbinals and the processus orbitonasalis (e.g., *Peromyscus* 4) (Figs. 8C, 11A, 14, 15). In *Peromyscus* 4 and *Mesocricetus* 6 the ossified lamina infraconchalis has a medially projecting epitubinal.

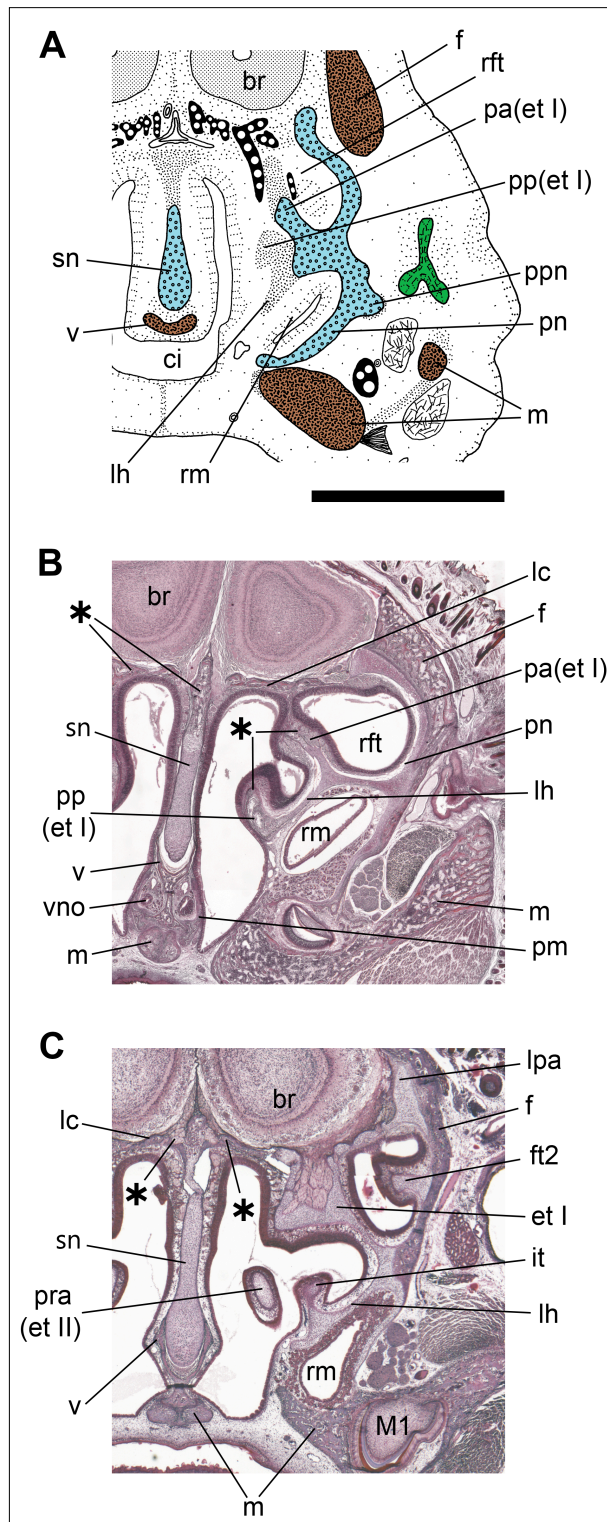
The processus or crista paranasalis becomes overgrown by the maxillary (e.g., *Sigmodon*) or the lacrimal (e.g., *Abrothrix*) and finally resorbed. Generally, the process/crista serves as the origin of the musculus obliquus inferior in younger ontogenetic stages (KADAM, 1972, 1973a, b; pers. obs.). However, in *Auliscomys* the muscle origin lies on the paries nasi wall and in *Thomomys* it lies dorsal to the processus paranasalis. Finally, after resorption of the paries nasi the musculus obliquus inferior originates from the lacrimal and maxillary and as in *Acomys* also from the frontal; in *Jaculus* only the latter is involved. The ontogenetic series of *Peromyscus* and *Rattus* clearly demonstrate that the origin of the musculus obliquus superior also moves from the planum antorbitale (in many stages/species a crista is present here) to the frontal bone that replaces this area of the nasal capsule. This transition occurs perinatally.

## Cupula nasi posterior

**Definition.** The cupula nasi posterior forms the posterior boundary of the nasal cavity. Its side walls are built by the posterior planum antorbitale of the paries nasi and its floor is continuous with the lamina transversalis posterior, that separates the posterior nasal cavity from the ductus nasopharyngeus; the lamina infracribrosa forms the roof of the cupula nasi posterior (TERRY, 1917; MAIER, 1986; ZELLER, 1989).

**Description.** All studied and described species show a well-developed cupula nasi posterior (Fawcett, 1917; Eloff, 1948, 1951b; YOUSSEF, 1966; RAJTOVA, 1972b; KADAM, 1972, 1973a, b, 1976; FRICK, 1986; HAUCK, 1987; pers. obs.) (Figs. 1, 2, 3). However, in *Jaculus* it is less prominent due to the reduction of the caudal nasal cavity. Generally, the cupula nasi posterior shows deep sulci on the ventral side which correspond to the medial rim of the





**Fig. 10.** Line drawing and digital images of transversal histological sections through the pars posterior of the nasal cavity of selected Muroidea. **A** *Peromyscus maniculatus*, stage 1, 7.5 mm HL, slice 5-5-4; **B** *Sigmodon hispidus*, stage 4, 21 mm HL, slice 35-2-3; **C** *Acomys* sp., stage 2, 22 mm HL, slice 29-2-2. Colour code for line drawing: blue, cartilage; brown, dermal bone; green, ductus nasolacrimalis. Asterisks (\*) indicate centers of ossification. Abbreviations: br, brain; ci, communicatio internasalis; et I–II, ethmoturbinal I–II; f, frontal bone; ft2, frontoturbinal 2; HL, head length; it, interturbinal; lc, lamina cribrosa; lh, lamina horizontalis; lpa, limbus paracribrosus; M1, first upper molar; m, maxillary bone; pa, pars anterior; pm, premaxillary bone; pn, paries nasi; pp, pars posterior; ppn, processus paranasalis; pra, processus anterior; rft, recessus frontoturbinalis; rm, recessus maxillaris; sn, septum nasi; v, vomer; vno, vomeronasal organ. Scale bar: 1 mm. **B** and **C** not to scale. **A** modified after RUF (2004).

eral in *Phodopus*. In addition, *Phyllotis* has a short dorsal processus posterior. The posterior end of the cupula nasi posterior and its process are highly variable among the investigated species. In almost all investigated species the cupula ends anterior to the pila praeoptica (Fig. 1B, D, F), in *Abrothrix* 1, *Phyllotis*, *Mesocricetus*, *Lemmus*, and *Microtus* below the radix/pila praeoptica. In *Micromys* the posterior end of the cupula nasi posterior is situated dorsal to the pila praeoptica; in *Gerbillus* and in a 10 mm HL stage of *Mus* (KADAM, 1976) the posterior end is close to the foramen opticum and dorsal to the central stem. In the geomyoids the cupula nasi posterior shows a shorter ventral and a longer dorsal process; the cupula ends far anterior from the pila praeoptica.

The shape of the cupula nasi posterior in cross-section is variable. *Jaculus* and the geomyoids have an extremely wide and box-shaped cupula; in *Peromyscus* and *Lophuromys* it is spade-shaped with the septum nasi being the dorsalmost point (Fig. 12A, B); *Sigmodon* shows a deep and wide sulcus on the dorsal side.

In early stages like *Peromyscus* 1, *Phyllotis* and *Gerbillus* the cupula nasi posterior is not yet continuous with the lamina infracribrosa and the septum nasi and therefore ends as isolated cartilaginous cones (Fig. 12A). During ontogeny the cupula nasi posterior becomes modified by resorption and ossification. In *Sigmodon* 4, *Mus* 5 and *Acomys* 2 resorption of the lateral wall of the cupula nasi anterior (part of the planum antorbitale) starts ventrally. Thus, in the oldest stages under study most of the planum antorbitale is already resorbed (Fig. 12C). Ossified parts of the cupula nasi posterior are (besides the lamina terminalis) the lamina infracribrosa and the dorsalmost part of the planum antorbitale. This pattern is evident in *Peromyscus* 4, *Mesocricetus* 6, *Mus* 6, and *Acomys* 2. *Rattus* 5 shows a strip of ossified planum antorbitale that runs from the posterior end of ethmoturbinal III into the posterior nasal capsule. In *Sigmodon* 4 only the dorsolateral rim of the cupula nasi posterior is already ossified. The posterior end of the cupula nasi posterior becomes surrounded and replaced by the frontal, pala-

lamina transversalis posterior. Vomer and palatine extend into these sulci (Figs. 1B, D, F, 12A, B). The cupula nasi posterior of *Peromyscus*, all Sigmodontinae, Cricetinae, *Lemmus*, *Microtus*, *Gerbillus*, *Acomys*, *Mus* 3+4 and *Jaculus* ends on each side as a processus posterior that is supported by the palatine. This process is very long in *Mesocricetus* 1+2, *Phodopus*, *Lemmus* and *Microtus* and ends ventral to the foramen opticum. The processus posterior is situated medial to the palatine in *Lemmus* and lat-

tine and vomer, in Cricetinae, *Microtus* and *Dendromus* also by the maxillary (Fig. 12C). Thus, the still cartilaginous processus posterior of *Sigmodon* 3, *Mesocricetus* 4–6 and *Acomys* 2 projects as a cone into the frontal, in *Geoxus* into the palatine, in *Phodopus* into the processus ascendens of the palatine and into the frontal (HAUCK, 1987; pers. obs.).

## Lamina transversalis anterior

**Definition.** The lamina transversalis anterior forms the anterior nasal floor and in most mammals it is continuous with the paries nasi forming the so-called zona annularis (GAUPP, 1900, 1908; KUHN, 1971; ZELLER, 1989; HÜPPI *et al.*, 2018). It remains cartilaginous through life although it can become modified in size and shape (SCHRENK, 1989).

**Description.** The lamina transversalis anterior of all species is relatively long and forms at least temporarily a zona annularis (FAWCETT, 1917; ELOFF, 1948, 1951b; YOUSSEF, 1966; RAJTOVA, 1972b; KADAM, 1972, 1973a, b, 1976; FRICK, 1986; HAUCK, 1987; pers. obs.) (Figs. 1B, D, F, 6B–D). In *Jaculus* the lamina transversalis anterior is significantly shorter. All muroids and *Dipodomys* show a lamina transversalis anterior that is divided into a thick pars anterior and a thin pars posterior (KADAM, 1973a: Fig. 19; FRICK, 1986: Fig. 9; HAUCK, 1987: figs. 10 and 11; pers. obs.) (Figs. 2B, D, 6B, C). The pars anterior of *Meriones* and *Lophuromys* has a processus posterior on each side. *Phyllotis* and *Geoxus* have a very short pars posterior. The sulcus ventralis varies on the pars anterior from deep (*Sigmodon*, *Mesocricetus*, *Cricetus*, *Tatera* (KADAM, 1972, 1973a, b); *Micromys*, *Rhabdomys*) to shallow (Arvicolinae, *Acomys*); in *Jaculus* and *Thomomys* no sulcus is present on the lamina transversalis anterior (Fig. 1B, D, F). Medially, the pars posterior ends with a processus posterior that is continuous with the cartilago paraseptalis (ELOFF, 1951b; KADAM, 1976: processus paraseptalis anterior; pers. obs.) (Fig. 7).

Observations on the origin of the lamina transversalis anterior are controversial. In *Otomys* and *Rattus* the lamina is a medial outgrowth of the paries nasi (ELOFF, 1948; YOUSSEF, 1966). In contrast, *Tatera* has a blastematous anlage of the lamina transversalis anterior that is separated from the paries nasi and the septum nasi but connected to the cartilago paraseptalis anterior; this anlage fuses to the blastematous cartilago parietotectalis and forms a zona annularis in a 9 mm HL stage, which chondrifies up to the 13 mm HL stage (KADAM, 1972, 1973a, b). In early ontogenetic stages as *Peromyscus* 1, *Mus* 1+2, *Micromys* and *Lophuromys* the lamina transversalis anterior is at least partly separated from the septum nasi by a fissure on each side (Fig. 6A). Here the cartilage of the lamina is more mature than that of the paries nasi but the connection to the cartilago paraseptalis anterior is still precartilaginous.

In many species the connection between lamina transversalis anterior and septum nasi is very thin. Older

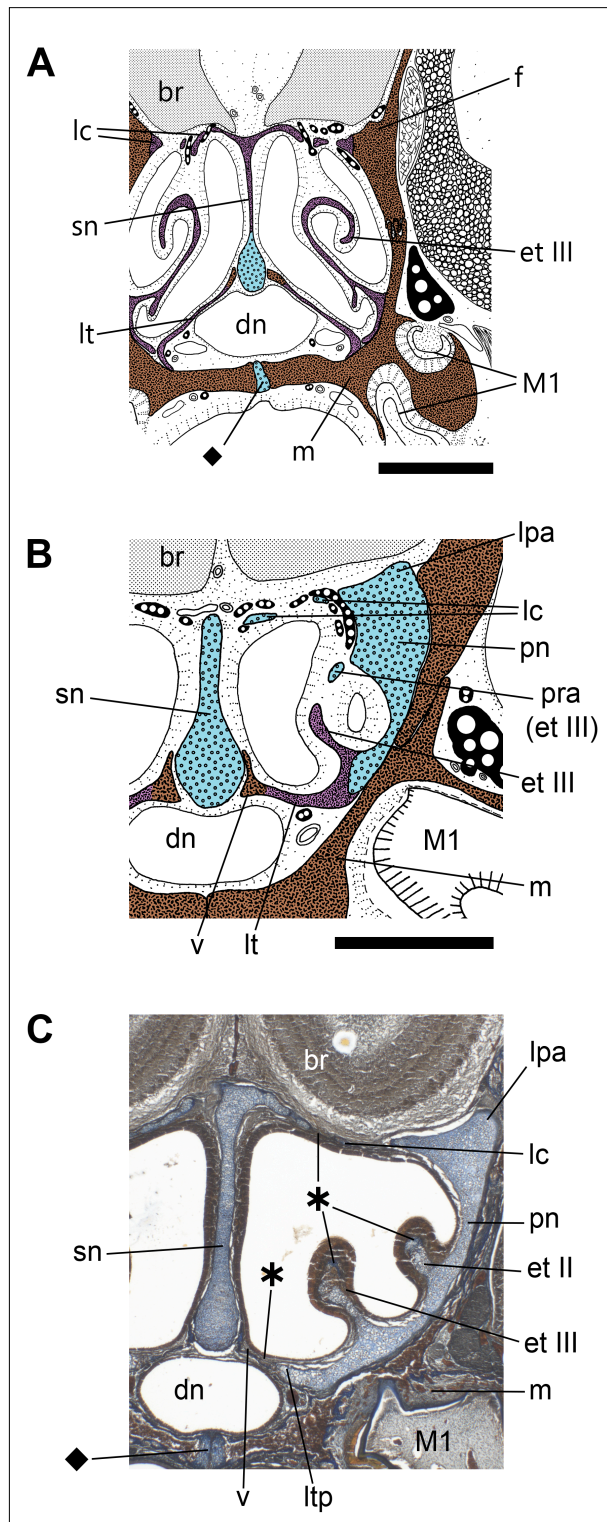
stages such as *Peromyscus* 4, *Mesocricetus* 6, *Mus* 6, *Rattus* 5 and *Dendromus* show a fissure that separates the pars posterior of the lamina from the septum nasi. In *Peromyscus*, *Mus* and *Rattus* this fissure separates a cartilaginous bar caudolaterally. In *Peromyscus* 2–4 the anterior part of the lamina transversalis anterior shows a central resorption and in stage 4 the lamina becomes almost completely resorbed and replaced by adipose tissue (Fig. 6B, D).

## Cartilages of the vomeronasal complex

**Definition.** The cartilago paraseptalis communis is a paired structure situated below the nasal septum and separated from the latter by the fissura septoparaseptalis on each side. In many mammals it is subdivided into the cartilago paraseptalis anterior and the cartilago paraseptalis posterior which is connected to the lamina transversalis posterior (GAUPP, 1906; TOEPLITZ, 1920; DE BEER, 1937; STARCK, 1967; KUHN, 1971; ZELLER, 1983, 1989). Due to the expansion of the vomer the latter can be reduced to a processus paraseptalis posterior attached to the lamina transversalis posterior or even completely missing (TOEPLITZ, 1920; KUHN, 1971).

The cartilago paraseptalis anterior forms a tube-like structure that houses the vomeronasal organ (Jacobson's organ). Above the entrance into the ductus nasopalatinus the outer bar (fibula reuniens) is present (BROOM, 1896; REINBACH, 1952a, b). In many mammals the ductus nasopalatinus and the palatine papilla between the incisive foramina can be supported by further cartilaginous elements, the cartilago papillae palatinae and the cartilago ductus nasopalatini as well as the cartilago palatina (STURM, 1936; STARCK, 1967; KUHN, 1971; MAIER, 1980). Due to the enlarged incisive alveolae the ductus nasopalatinus of rodents is shifted posteriorly (WÖHRMANN-REPPENING, 1984a, b; MESS, 1997).

**Description.** A cartilago paraseptalis communis, the continuous connection of the cartilago paraseptalis to the lamina transversalis anterior and posterior, is only present in *Arvicola* (FAWCETT, 1917) and *Dipodomys*. In all species a well-developed cartilago paraseptalis anterior can be observed and in Myodonta it generally shows a very similar pattern (FAWCETT, 1917; ELOFF, 1948, 1951b; YOUSSEF, 1966; RAJTOVA, 1972b; KADAM, 1972, 1973a, b, 1976; FRICK, 1986; HAUCK, 1987; pers. obs.) (Figs. 1B, D, F, 2A, C, E, 8A, B, D, 9). In all investigated species the transition from the lamina transversalis anterior to the cartilago paraseptalis is bean-shaped in cross-section, and in front of the latter it forms a trough (Fig. 7). Generally, the cartilago paraseptalis anterior is hook-shaped in cross-section, with a higher medial lamina and a broad dorsolateral opening (Figs. 8A, B, D, 9A, C, D). In *Mus*, *Rhabdomys* and in the geomyoids the cartilago paraseptalis anterior forms an almost closed tube with a thin dorsal fissure. *Lemmus* possesses a posterior process that projects from the dorsal rim of the cartilago paraseptalis anterior and overlays the



**Fig. 11.** Line drawings and digital image of transversal histological sections through the pars posterior of the nasal cavity of selected Cricetidae. **A** *Peromyscus maniculatus*, stage 4, 25 mm HL, slice 29-1-1; **B** *Sigmodon hispidus*, stage 4, 21 mm HL, slice 49-2-1; **C** *Mesocricetus auratus*, stage 4, 19 mm HL, slice 22-1-4. Colour code for line drawings: blue, cartilage; brown, dermal bone; purple, endochondral bone. The diamonds (◆) indicate secondary cartilage within the suture between both maxillary bones. Asterisks (\*) indicate areas of ossification. Abbreviations: br, brain; dn, ductus nasopharyngeus; et II–III; ethmoturbinal II–III; f, frontal bone; HL, head length; lc, lamina cribrosa; lpa, limbus paracribrus; lt, lamina terminalis; ltp, lamina transversalis posterior; M1, first upper molar; m, maxillary bone; pn, paries nasi; pra, processus anterior; sn, septum nasi; v, vomer. Scale bars: 1 mm. **C** not to scale. **A**, **B** modified after RUF (2004).

(*Peromyscus* 1, *Sigmodon* 1, *Abrothrix* 1, *Gerbillus*, *Apodemus flavicollis*, *Micromys*, *Mus* 1) it can be observed that the chondrification of the cartilago paraseptalis anterior starts in the middle part and continues anteriorly and posteriorly. In *Tatera* the connection to the lamina transversalis anterior chondrifies later than the cartilago paraseptalis anterior (KADAM, 1972, 1973a, b). In *Mesocricetus* the chondrification of the cartilago paraseptalis anterior proceeds from medial to lateral (KADAM, 1976). Furthermore, during ontogeny the cartilago paraseptalis anterior exceeds the vomeronasal organ posteriorly. Thinning and resorption of the cartilago paraseptalis anterior as well as replacement by dermal bones follows the same pattern in the muroids (Figs. 8, 9). Already in late fetal stages the processus palatinus medialis of the praemaxillary projects medial to the cartilago paraseptalis anterior and seems to induce the resorption of the latter (Figs. 8A, B, D). This process starts in the middle part of the cartilaginous trough and continues anteriorly and posteriorly (KADAM, 1972, 1973a, b; HAUCK, 1987; pers. obs.). *Cricetus* and *Acomys* appear to be much more developed than comparable stages of the other species (Fig. 9C). The premaxillary, maxillary and vomer together form an almost complete tube with a small dorsal fissure as also clearly visible in the adult stages under study (Figs. 8C, 14B, D, E). This fissure becomes also closed except for some nutritive and nerval foramina. However, the dorsal edge of the medial lamella of the cartilago paraseptalis anterior becomes thicker and persists quite long into postnatal stages; in *Cricetus* it ossifies but the rest of the cartilago paraseptalis anterior becomes resorbed.

All species have an outer bar, a connection – continuous in most specimens – running ventrolaterally from the medial to the lateral lamella (ELOFF, 1951b; KADAM, 1972, 1973a, b; HAUCK, 1987; pers. obs.) (Fig. 2A, C, E). In *Mesocricetus* 1, *Meriones*, *Acomys* 1, *Rattus* 1+2, *Lophuromys* and *Jaculus* it consists of two cartilaginous projections that are connected by blastematos tissue in the middle. In *Mesocricetus* 2–6 and *Lophuromys* an overlap of these two separate parts of the outer bar can be observed. According to the observation of blastematos

vomer. In *Rattus* 1–3, *Jaculus* and *Thomomys* a processus paraseptalis posterior can be observed.

The anlage of the cartilago paraseptalis anterior has been described in very early stages of *Mesocricetus* (10 mm and 13 mm HL stages) in which it develops separately from the lamina transversalis anterior and septum nasi (RAJTOVA, 1972b). In contrast, KADAM (1972, 1973a, b) describes a very early common anlage of all these three structures in *Tatera*. In the younger stages



tissue or precartilaginous at the anterior end of the outer bar in *Abrothrix* 1, *Gerbillus*, *Apodemus flavicollis*, *Micromys*, *Mus* 1 and *Rattus* 1+2 the outer bar obviously develops from posterior to anterior. In *Tatera* it is the other way round (KADAM, 1972, 1973a, b). In *Dendromys* the outer bar is still completely blastematos. The outer bar also undergoes resorption, from posterior to anterior as observed in *Peromyscus*, *Mesocricetus*, *Phodopus*, *Acomys*, and *Rattus*. In *Phodopus* the missing posterior part of the outer bar is replaced by an anterior process of the processus palatinus medialis of the praemaxillary (HAUCK, 1987; pers. obs.). In the other species this anterior process increases in length prenatally and overlays the outer bar dorsolaterally. Thereby it closes the dorsal gap of the cartilago paraseptalis anterior. In the geomyoids the outer bar forms a broad plate that forms a short closed tube.

The cartilago papillae palatinae that supports the papilla palatina between both ductus nasopalatini can be observed in almost all species; generally it occurs late in prenatal or in perinatal ontogeny (ELOFF, 1948; KADAM, 1972, 1973a, b, 1976; WÖHRMANN-REPPENING, 1982, 1984a, b; HAUCK, 1987; pers. obs.) (Figs. 1B, 2A, C, 8B, C). The investigated stages of *Arvicola* (FAWCETT, 1917), *Microtus*, *Apodemus flavicollis*, *Gerbillus*, and *Thomomys* do not show a cartilago papillae palatinae; in *Lophuromys* and *Rhabdomys* a mesenchymal condensation is present in the respective area (ELOFF, 1951b: prenasal cartilage; pers. obs.). The shape of this cartilage is highly variable.

Some species show structures that can be interpreted as a reduced cartilago ductus nasopalatini or its remnants. These are a lateral trough next to the outer bar as observed in *Gerbillus*, *Meriones* and *Jaculus* (although no contact to the ductus nasopalatinus is present due to the posterior displacement of the latter) and a ventral crista located lateral at the cartilago paraseptalis anterior in *Lophuromys* and associated with the ductus nasopalatinus (Fig. 9D). In *Sigmodon* 3+4 cartilaginous elements are present anterior and lateral to the ductus. A cartilago palatina that is located posterior to the ductus nasopalatinus is only present in *Peromyscus* 4 and *Mesocricetus* 6.

## Lamina transversalis posterior

**Definition.** The lamina transversalis posterior develops relatively late in ontogeny by the medial bending of the lower margin of the posterior paries nasi and thus forms the floor of the posterior recessus ethmoidalis (FAWCETT, 1917; DE BEER, 1937; STARCK, 1967; KUHN, 1971). The lamina can be connected to the paraseptal cartilages. In many mammals the vomer that projects between septum nasi and lamina transversalis posterior synossifies with the latter to form the lamina terminalis (FUCHS, 1909; KUHN, 1971).

**Description.** All investigated species have a well-developed lamina transversalis posterior except for *Tatera*, *Otomys*, and *Jaculus* in which it is reduced in length

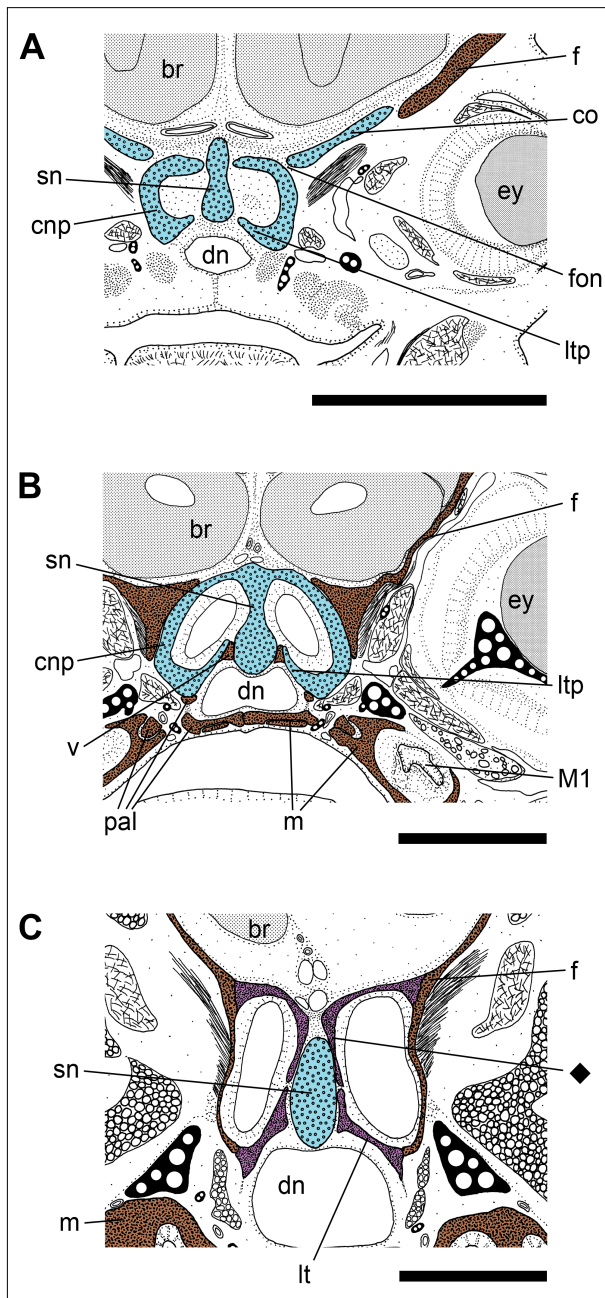
(Figs. 1B, D, F, 2B, D, F, 3, 11C, 12A, B); the lamina transversalis posterior is always separated from the septum nasi except for its hindend at the cupula nasi posterior (FAWCETT, 1917; ELOFF, 1948, 1951b; YOUSSEF, 1966; RAJTOVA, 1972b; KADAM, 1972, 1973a, b, 1976; WÖHRMANN-REPPENING, 1982; FRICK, 1986; HAUCK, 1987; pers. obs.). However, in a 15 mm HL stage of *Tatera* the fusion of the lamina transversalis posterior and the septum nasi has been observed (KADAM, 1972, 1973a, b). The processus paraseptalis posterior is described above. The cartilago paraseptalis communis of *Dipodomys* is situated between septum nasi and a medial processus anterior of the lamina transversalis posterior. Such a medial anterior process is also present in *Sigmodon* 3. However, it remains questionable if this process can be homologized with the processus paraseptalis posterior. The anterior edge of the lamina shows a lateral processus anterior in *Rhipidomys*; in *Mus* 4 the lamina has a ventrolateral process that is projecting caudally. *Rattus* shows a ventral process that becomes ossified and then is deeply nested in the palatine.

In *Peromyscus* 1 and *Apodemus flavicollis* the lamina transversalis is still mostly precartilaginous. During ontogeny the cartilaginous lamina elongates anteriorly (as observable in *Peromyscus*, *Mesocricetus*, *Rattus*, *Mus*) and develops a concave anterior edge. Already in prenatal stages the alae of the vomer fuse to the anterior edge of the lamina and embrace the septum nasi ventrally (Figs. 1B, 3A). Increasing of the length and induction of ossification of the lamina transversalis posterior by the vomer can be observed (FAWCETT, 1917; ELOFF, 1948, 1951a, b; YOUSSEF, 1966; RAJTOVA, 1972b; KADAM, 1972, 1973a, b, 1976; HAUCK, 1987; pers. obs.). The ossification of the lamina transversalis posterior starts anteriorly and medially until both structures are completely synossified and form the lamina terminalis (Figs. 11, 12C, 15A, D, E). The ossification of the lamina transversalis posterior obviously starts relatively earlier in muroids than in *Jaculus* and in geomyoids as most fetal stages of the former already show extensive ossification of the lamina transversalis posterior.

## Septum nasi

**Definition.** The septum nasi occurs early in ontogeny and divides the nasal cavity into left and right airway; the septum is fused to the tectum nasi, cupula nasi anterior, cupula nasi posterior, and in many mammals to the lamina transversalis anterior (DE BEER, 1937; STARCK, 1967; NOVACEK, 1993). Septoturbinals and a rostral fenestra internalis, that remains covered by the nasal epithelium, can be observed in variable patterns in many taxa (STARCK, 1941; KUHN, 1971; MESS, 1995, 1997). During ontogeny at least the posterior third of the septum nasi becomes ossified as lamina perpendicularis of the ethmoid bone (SCHALLER, 1992).

**Description.** Generally, all investigated species show the same pattern in septum nasi morphology (FAWCETT, 1917;



**Fig. 12.** Line drawings of transversal histological sections through the cupula nasi posterior of *Peromyscus maniculatus*. **A** stage 1, 7.5 mm HL, slice 6-6-5; **B** stage 3, 14.5 mm HL, slice 19-3-3; **C** stage 4, 25 mm HL, slice 33-2-2. Colour code: blue, cartilage; brown, dermal bone; purple, endochondral bone. The diamond (◆) indicates the ossified part of the cupula nasi posterior. Abbreviations: br, brain; cnp, cupula nasi posterior; co, commissura orbitonasalis; dn, ductus nasopharyngeus; ey, eye; f, frontal bone; fon, fissura orbitonasalis; HL, head length; lt, lamina terminalis; ltp, lamina transversalis posterior; M1, first upper molar; m, maxillary bone; pal, palatine bone; sn, septum nasi; v, vomere. Scale bars: 1 mm. Modified after RUF (2004).

A single anlage of the septum nasi has been described for *Rattus* and *Mus* (VIDIC *et al.*, 1972; FRICK, 1986). The dorsal part of the septum nasi of *Peromyscus* 1, *Mus* 1 and *Micromys* is still precartilaginous below the lamina cribrosa (Fig. 10A). Anteriorly, in a 6 mm HL stage of *Mesocricetus* (KADAM, 1976) and in *Peromyscus* 1 the septum is still blastematos and precartilaginous respectively, and in *Rattus* 1 it is made up by hyaline cartilage. Ossification of the septum nasi can be observed in prenatal stages of *Sigmodon*, *Cricetus* and *Acomys*, and in neonate stages of *Peromyscus*, *Mesocricetus*, *Mus* and *Rattus*. The ossification of the septum follows a common pattern. It starts dorsally at the septum below the anterior part of the lamina cribrosa and proceeds caudally and ventrally (Fig. 10B, C). Once the subcerebral ossification is completed this process continues rostrally (Fig. 8C, 11A). The adult stages show that in the pars anterior the septum nasi is still mostly cartilaginous as only remnants or no septal structures are visible in the  $\mu$ CT images (Fig. 14).

All species show – depending on the maturity of the stages – a specific pattern of septoturbinals and fenestrations or thinning of the septum nasi in the pars anterior. *Peromyscus* 1, *Phodopus*, *Arvicola*, *Lemmus*, *Acomys*, *Mus* (10 mm HL stage) and *Jaculus* show an opening in the anterior septum nasi that is covered by nasal epithelium and located next to the processus alaris superior (FAWCETT, 1917: foramen internasale; KADAM, 1976; contra HAUCK, 1987; SCHRENK, 1989; pers. obs.) (Figs. 4A, D, 5B). This opening should be named fenestra internasalis anterior. For *Acomys dimidiatus* a fenestration in the region of the cupula nasi anterior is described (HÜPPI *et al.*, 2018). In all species except for *Lemmus* the fenestra is also closed by the lamina membranacea. It appears to be a primary opening as it is not present in older stages, although the cartilage might still be thin in this area. Between the posterior part of the lamina transversalis anterior and the cartilago paraseptalis, the middle part of the septum nasi is thinner. This feature can be observed in *Peromyscus*, Sigmodontinae (except for *Rhipidomys* and *Geoxus*), Cricetinae, Gerbillinae, Muridae, and *Dipodomys* (FRICK, 1986; SCHRENK, 1989; pers. obs.) (Figs. 6C, D, 7). This area becomes extremely thin which can result in a secondary opening of the nasal sep-

ELOFF, 1948, 1951b; YOUSSEF, 1966; RAJTOVA, 1972b; KADAM, 1972, 1973a, b, 1976; FRICK, 1986; HAUCK, 1987; pers. obs.). The septum nasi has its maximum height below the limbus praecribrosus. The cartilaginous septum nasi is continuous with the cupula nasi anterior, processus lateralis ventralis, lamina transversalis anterior, cupula nasi posterior, and tectum nasi; it shows a swollen ventral rim especially in the pars posterior (Figs. 4, 5, 6, 7, 8A, B, D, 9, 12B). However, as described above in the Gerbillinae and in *Jaculus* the septum nasi extends ventrally posterior to the cupula nasi anterior (Fig. 5C, D). A septum interorbitale i.e., the extension of the septum nasi posterior to the cupula nasi posterior is only present in *Sigmodon* 3+4, *Phyllotis*, *Mesocricetus* 5+6, *Acomys* 1, *Mus* 5, *Micromys*, *Rhabdomys*, *Gerbillus*, and in geomyoids. In *Micromys* the septum nasi ends with a posterior process.

tum as observed in *Mus* 5+6 and *Rattus* 5 that should be named fenestra internasalis posterior. In *Sigmodon*, *Cricetinae*, *Apodemus sylvaticus*, *Acomys*, *Jaculus* and *Thomomys* a prominent anterior septoturbinal is situated in front of to the lamina transversalis anterior (Fig. 4C). The anterior septoturbinal of *Jaculus* is located ventral to the fenestra internasalis anterior (Fig. 4D). *Abrothrix*, *Phyllotis*, *Arvicolinae*, *Gerbillinae*, and *Dipodomys* have only a small anterior septoturbinal. Almost all species show a posterior septoturbinal that is situated between lamina transversalis anterior and at least posteriorly below the fenestra internasalis posterior or the corresponding thin area of the septum nasi respectively; it runs more or less caudoventrally and ends in the ventral swelling of the nasal septum (FAWCETT, 1917; SCHRENK, 1989; pers. obs.) (Figs. 6B–D, 7). In *Lemmus*, *Jaculus* and *Dipodomys* the posterior septoturbinal is extremely prominent. *Rhipidomys*, *Apodemus flavicollis* and *Micromys* have no distinct posterior septoturbinal but the epithelium forms a ridge in the respective area. In *Gerbillus* the posterior septoturbinal ends blastemateously and in the geomyoids the septoturbinal is partly an isolated cartilaginous bar attached to the septum nasi. In *Abrothrix*, *Dendromus*, *Mus*, *Acomys* and *Jaculus* the posterior septoturbinal starts anteriorly as two converging ridges of which the ventral one is much more prominent. In *Abrothrix*, *Phyllotis*, *Auliscomys*, *Lemmus*, *Lophuromys* and notably in *Mus* the septum nasi ventral to the posterior septoturbinal is thinned; in *Peromyscus* 4 this area is ossified (Fig. 6D). The adult stages also show some septoturbinal-like but hollow structures in the posterior part of the septum nasi (Fig. 15).

## Turbinals and lamina semicircularis

**Definition.** The nasal cavity houses a specific number of delicate laminae that can show highly complex branching. The ventral rim of the anterior paries nasi forms three turbinals from anterior to posterior: marginoturbinal, atrioturbinal, and maxilloturbinal (VOIT, 1909; REINBACH, 1952a, b; SCHRENK, 1989). The marginoturbinal frames the fenestra narina dorsolaterally. Caudally it can be continuous with the atrioturbinal, which is often separated from the maxilloturbinal by the incisura atriomaxilloturbinalis. The maxilloturbinal can extend from the lamina transversalis anterior into the pars lateralis.

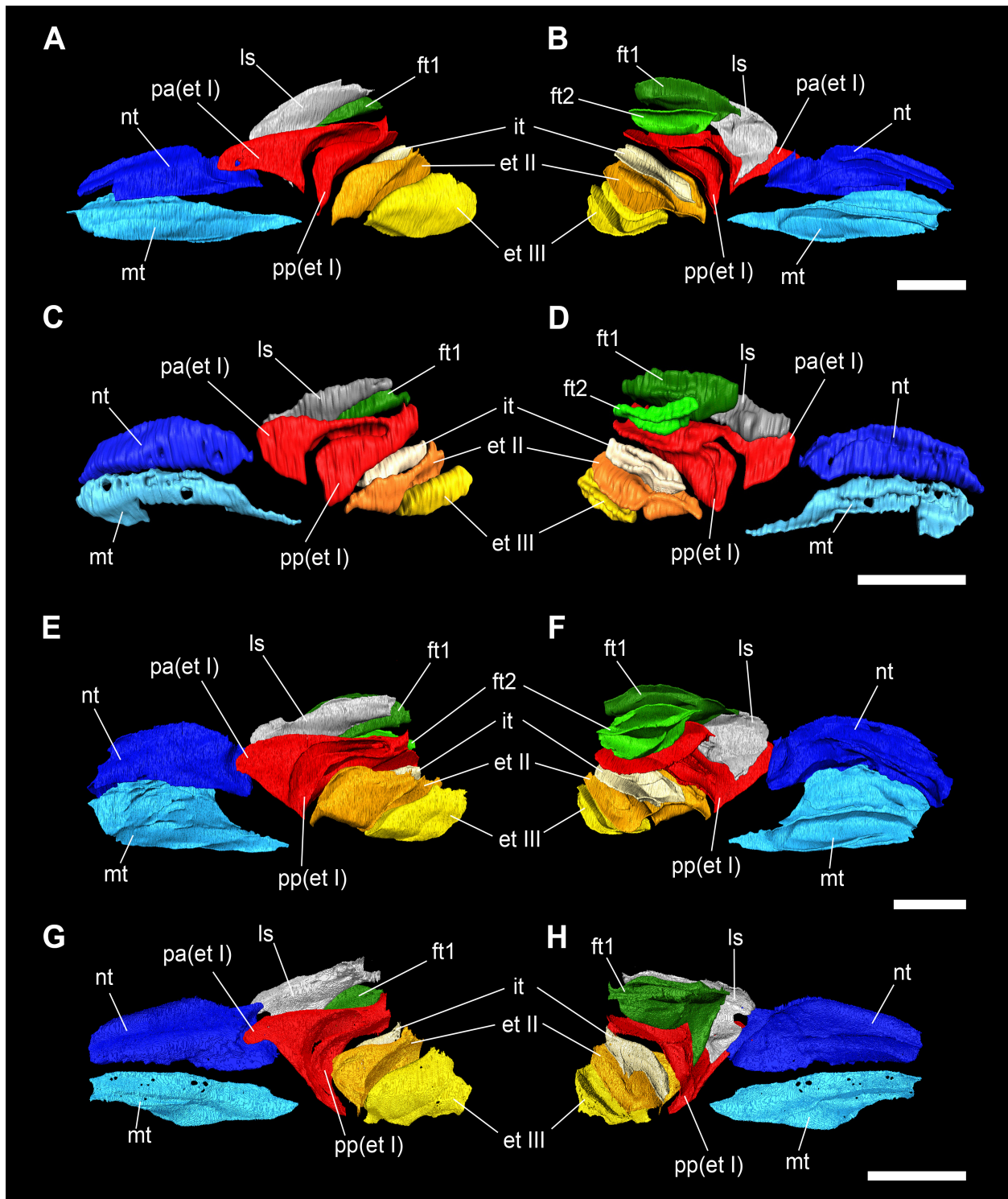
The nasoturbinal is located dorsal to the maxilloturbinal along the border between paries nasi and tectum nasi. Rostrally in some taxa it can be continuous with a rostratorturbinal; caudally it reaches the lamina semicircularis (VOIT, 1909; SCHRENK, 1989). The latter (also called crista semicircularis in earlier stages) is not a turbinal but an outgrowth of the anterior paries nasi, that separates the pars anterior and pars lateralis (pars intermedia) of the nasal cavity; however, it is also covered by olfactory epithelium (VOIT, 1909; DE BEER, 1937; REINBACH, 1952a, b; KUHN, 1971; SCHRENK, 1989; ZELLER, 1989).

The recessus frontoturbinalis of the pars lateralis houses a specific number of frontoturbinals, the recessus ethmoturbinalis of the pars posterior houses the ethmoturbinals. The frontoturbinals normally arise from the lateral sidewall of the nasal capsule; in addition, they can arise anteriorly from the lamina horizontalis, that forms the floor of the recessus frontoturbinalis and the roof of the recessus maxillaris, respectively. In both, recessus frontoturbinalis and recessus ethmoturbinalis additional turbinals, the interturbinals, can occur. They develop later in ontogeny than the main olfactory turbinals and never extend as far medially as the fronto- and ethmoturbinals (PAULLI, 1900a; VOIT, 1909; REINBACH, 1952a, b). All turbinals, except for the atrio- and marginoturbinal and sometimes the rostral tip of the maxilloturbinal, become ossified and thus part of the ethmoid bone. By appositional bone growth (Zuwachsknochen sensu STARCK, 1955) they can develop a complex pattern of further lamellae the so-called epiturbinals (PAULLI, 1900a; REINBACH, 1952a, b).

**Description.** All investigated species show a very similar pattern of turbinals in the pars anterior of the nasal cavity (Figs. 2B, D, F, 4, 5, 6, 7, 8, 13, 14). Marginoturbinal and atrioturbinal are separated by a distinct incisura marginoturbinalis. Atrio- and maxilloturbinal are separated by a long incisura atriomaxilloturbinalis which is highly reduced in *Mesocricetus* 6, *Meriones*, and *Mus* 6 and both turbinals can overlap (HAUCK, 1987; contra SCHRENK, 1989; pers. obs.). In previous studies the wrong naming of the margino-, atrio- and even maxilloturbinal leads to some confusion (see FAWCETT, 1917; ELOFF, 1948, 1951b; YOUSSEF, 1966; RAJTOVA, 1972b; Kadam, 1972, 1973a, b; FRICK, 1986). The atrioturbinal projects above the pars anterior of the lamina transversalis anterior and often has an anterior process. The atrioturbinal of all myodonts except *Tatera* and *Micromys* has a processus posterior (KADAM, 1972, 1973a, b; pers. obs.) (Figs. 2B, F, 6B); the pattern of *Arvicola* and *Otomys* remains unclear (FAWCETT, 1917; ELOFF, 1948). In the geomyoids the atrioturbinal ends as a crista that merges into the lamina transversalis anterior. As the margino- and atrioturbinal are cartilaginous throughout life no information of the adult pattern is available from the  $\mu$ CT scans.

In prenatal to early postnatal stages the maxilloturbinal forms a simple ridge or scroll (in later stages) and ends in the pars lateralis of the nasal cavity (Figs. 2B, D, F, 7C, 8A, B, D, 9A, D). In the arvicolines and geomyoids the maxilloturbinal lies rostrally lateral to the atrioturbinal. In all other species both turbinals are strictly in a row. All investigated sigmodontines (except for *Sigmodon* and *Abrothrix*), *Peromyscus*, *Mesocricetus*, *Meriones*, *Tatera*, *Dendromus*, *Apodemus sylvaticus*, *Acomys*, *Mus* 2–6, *Rattus*, *Jaculus* and *Dipodomys* have a processus anterior (KADAM, 1972, 1973a, b; pers. obs.) (Figs. 2F, 6D, 7). In *Mesocricetus* 6, *Mus* 6, and *Rattus* 6 a short and low epiturbinal projects laterally from the maxilloturbinal.

A puzzling pattern of the anlage of the anteriormost turbinals has been described for *Tatera* and *Mesocrice-*



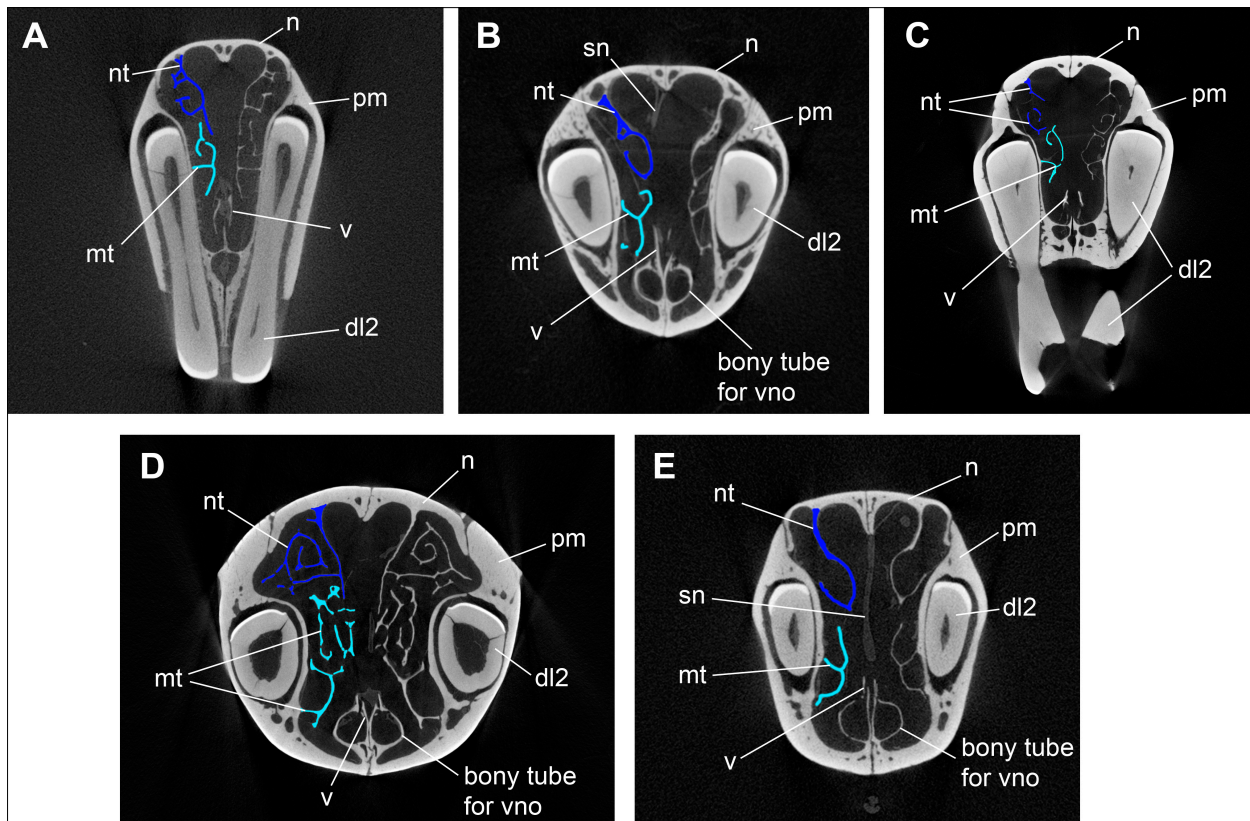
**Fig. 13.** 3D models of the adult turbinal skeleton (right side) of selected Muroidea based on  $\mu$ CT data. Medial view on the left, lateral view on the right. The single frontoturbinal of *Mus musculus* is homologized with frontoturbinal 1 of the cricetids. **A, B** *Peromyscus maniculatus* SMF 72827; **C, D** *Mesocricetus auratus*, coll. W. Maier; **E, F** *Cricetus cricetus* SMF62024; **G, H** *Mus musculus* SMF 63500. Abbreviations: et I–III, ethmoturbinal I–III; ft 1–2, frontoturbinal 1–2; it, interturbinal; ls, lamina semicircularis; mt, maxilloturbinal; nt, nasoturbinal; pa, pars anterior; pp, pars posterior. Scale bars: 5 mm.

*tus*: in the former the margino- and atrioturbinal develop earlier than the maxilloturbinal, in the latter it is the other way round (RAJTOVA, 1972b; KADAM, 1972, 1973a, b). Chondrification of the margino-, atrio- and maxilloturbinal can be observed in the very young stages and happens

from proximal to distal and in each turbinal from caudal to rostral.

The marginoturbinal and atrioturbinal remain cartilaginous throughout life; especially in older stages fissures between both turbinals but also between the atriot-





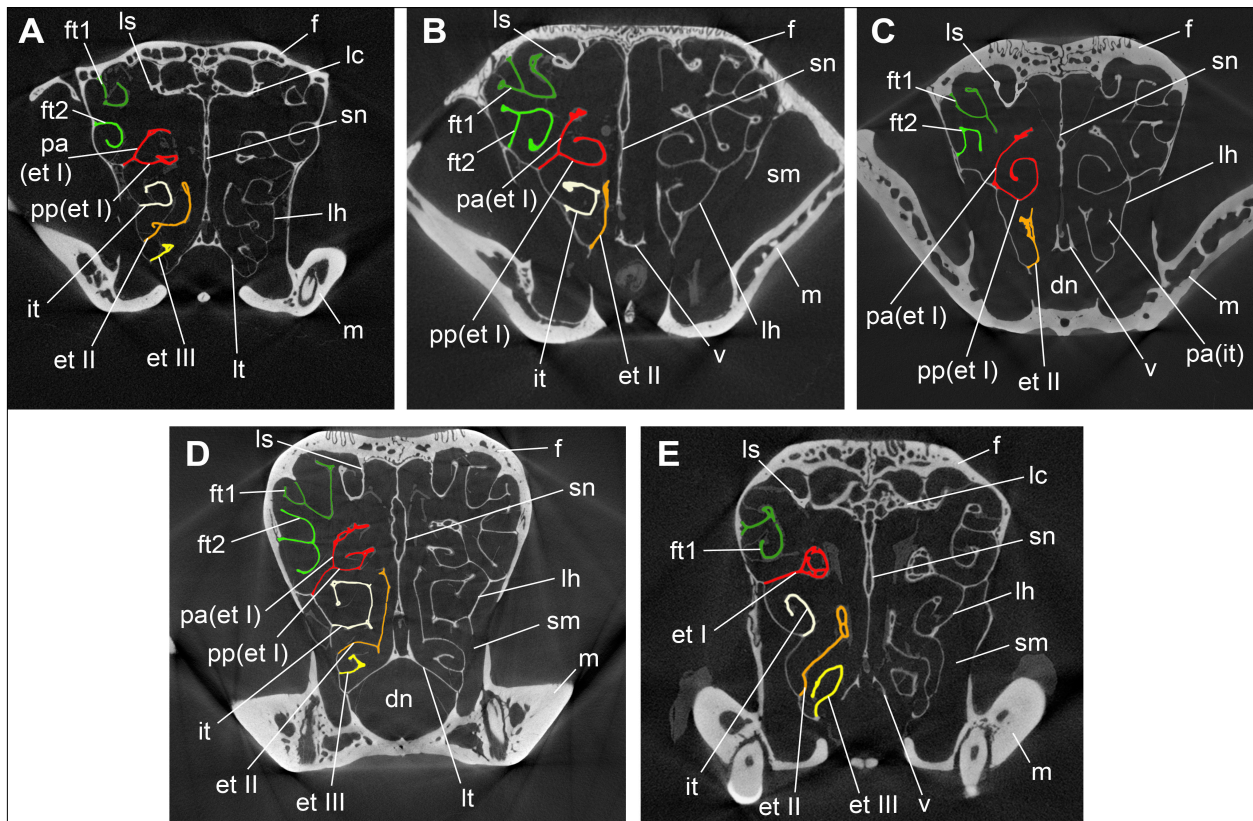
**Fig. 14.** Transversal  $\mu$ CT images through the anterior nasal cavity of adult stages of selected Muroidea. **A** *Peromyscus maniculatus* SMF 72827; **B** *Sigmodon hispidus* SMF 87320; **C** *Mesocricetus auratus* SMF 82131; **D** *Cricetus cricetus* SMF62024; **E** *Mus musculus* SMF 63500. The cartilaginous septum nasi is preserved in **B** and **E**. Colour code of the turbinal skeleton refers to Fig. 13. Abbreviations: dl2, deciduous upper incisor 2; mt, maxilloturbinal; n, nasal bone; nt, nasoturbinal; pm, premaxillary bone; sn, septum nasi; v, vomer; vno, vomeronasal organ. Not to scale.

urbinal and the paries nasi can occur. The ossification of the maxilloturbinal occurs from distal to proximal (Fig. 8D). The anterior tip can remain cartilaginous and is separated by a fissure as in *Peromyscus* (HAUCK, 1987; pers. obs.). Prenatal ossification can be observed in *Sigmodon*, *Cricetus*, and *Acomys*. The fully ossified maxilloturbinal is a simple double scroll anteriorly and a straight lamella posteriorly (Figs. 8C, 13A–D, G–H, 14A–C, E). In *Cricetus* the maxilloturbinal shows a much more complicated pattern with several additional lamellae (Figs. 13 E–F, 14D).

The nasoturbinal of all species forms a distally thickened and straight to laterally rolled-up lamella in prenatal and perinatal stages and is located dorsal and lateral to the atrio- and maxilloturbinal (FAWCETT, 1917; ELOFF, 1948, 1951b; YOUSSEF, 1966; RAJTOVA, 1972b; KADAM, 1972, 1973a, b, 1976; FRICK, 1986; HAUCK, 1987; pers. obs.) (Figs. 2B, D, F, 4B, C, 6B–D, 7, 8A, C, D, 9A, C, D). Only in *Jaculus* it is partly situated medial to the atrioturbinal. The nasoturbinal begins anterior to the lamina transversalis anterior. It ends in the pars anterior of the nasal cavity in *Rhipidomys*, *Cricetus*, *Mesocricetus*, *Arvicola*, *Meriones*, *Gerbillus*, *Apodemus*, *Rattus*, *Acomys*, *Micromys*, *Jaculus* and *Dipodomys*, in all other species it ends in the pars lateralis medial to the lamina semicircularis (FAWCETT, 1917; KADAM, 1976; HAUCK,

1987; pers. obs.) (Figs. 2B, D, F, 8B). The posterior end of the nasoturbinal is bent ventrally. In *Mesocricetus*, arvicolines, *Acomys*, *Mus*, *Rattus* 5 and *Lophuromys* it is split into two lamellae (FAWCETT, 1917; pers. obs.). In the geomyoids the nasoturbinal has a processus anterior. The nasoturbinal is fused to a crista of the nasal roof from which it is partly separated by a fissure in many species (FAWCETT, 1917; ELOFF, 1948, 1951b; KADAM, 1976; pers. obs.) (Figs. 2B, 6C, 9D). Furthermore, in some species small foramina for the transmission of blood vessels and a nerve branch can be observed (FAWCETT, 1917; KADAM, 1976; HAUCK, 1987; SCHRENK, 1989; pers. obs.). However, both patterns are quite variable among the investigated species and stages. *Peromyscus* 4, *Mesocricetus* 6, and *Mus* 6 have two ventromedial epiturbinals, *Auliscomys* has a very low one medially, *Geoxus* and *Rattus* 5 have one laterally (Fig. 6D). The adult stages under study show a common pattern in which the laterally enrolled nasoturbinal can show additional epiturbinals (Figs. 13, 14). *Cricetus* shows a much more complex nasoturbinal than *Peromyscus*, *Sigmodon*, *Mesocricetus*, and *Mus*.

The nasoturbinal develops in *Mesocricetus* after the maxilloturbinal and ethmoturbinal I (RAJTOVA, 1972b). Chondrification of the nasoturbinal occurs from proximal to distal as observed in *Sigmodon*, *Abrothrix*, *Mesocricetus*, *Gerbillus*, *Micromys*, *Rattus*, *Mus*, and *Jacu-*



**Fig. 15.** Transversal  $\mu$ CT images through the posterior nasal cavity of adult stages of selected Muroidea. **A** *Peromyscus maniculatus* SMF 72827; **B** *Sigmodon hispidus* SMF 87320; **C** *Mesocricetus auratus* SMF 82131; **D** *Cricetus cricetus* SMF 62024; **E** *Mus musculus* SMF 63500. Colour code of the turbinal skeleton refers to Fig. 13. Abbreviations: dn, ductus nasopharyngeus; et I–III, ethmoturbinal I–III; f, frontal bone; ft 1–2, frontoturbinal 1–2; it, interturbinal; lc, lamina cribrosa; lh, lamina horizontalis; ls, lamina semicircularis; lt, lamina terminalis; m, maxillary bone; pa, pars anterior; pp, pars posterior; sm, sinus maxillaris; sn, septum nasi; v, vomer. Not to scale.

lus (KADAM, 1976; pers. obs.). This process starts in the middle of the turbinal and spreads anteriorly and somewhat later posteriorly. In *Peromyscus* 1 and *Apodemus flavicollis* the nasoturbinal is still blastematous (Fig. 6A). In *Sigmodon* 1 the cartilage of the nasoturbinal is less mature than that of the paries nasi and tectum nasi. Ossification of the nasoturbinal starts rostral and proximal above a cartilaginous anteroventral remnant as observed in *Peromyscus* 4, *Sigmodon* 3+4, *Cricetus*, *Mesocricetus* 3–6, *Phodopus*, *Dendromus*, *Acomys*, *Rattus* 4+5 and *Mus* 5+6 (HAUCK, 1987; pers. obs.) (Figs. 6D, 8D); the timing varies from prenatal to postnatal. In the cricetines and *Rattus* ossification proceeds from distal to proximal, in the other above mentioned species from proximal to distal.

The lamina semicircularis is present in all species and stages (Figs. 2B, D, F, 3, 13). It is a crista in younger stages but expands during ontogeny to form a distinct lamina that is sickle-shaped and forms the anterior border of the hiatus semilunaris, the entrance into the pars lateralis of the nasal cavity. Posteriorly the lamina semicircularis continues as a dorsal lamella that contributes to the canalis cribroethmoidalis beneath the limbus praecribrosus (FAWCETT, 1917; ELOFF, 1948, 1951b; YOUSSEF, 1966; RAJTOVA, 1972b; KADAM, 1972, 1973a, b, 1976; FRICK, 1986; HAUCK, 1987; pers. obs.) (Figs. 2B, D, F, 9B). Ad-

ditionally, all Sigmodontinae (except *Auliscomys*), *Peromyscus*, *Mesocricetus* 1+2, all arvicolines, *Meriones*, *Tatera*, *Dendromus*, *Rattus* and *Thomomys* possess a ventral lamella posteriorly (FAWCETT, 1917; KADAM, 1972, 1973a, b; pers. obs.). This ventral lamella can continue into a processus uncinatus (*Peromyscus* 4, *Abrothrix*, *Phyllotis*, *Auliscomys*, *Rattus*, *Dendromus*, *Thomomys*). *Jaculus* has a very short reduced lamina semicircularis. In *Peromyscus* 4, *Abrothrix* 2, *Geoxus*, *Mesocricetus* 5+6, *Acomys*, *Rattus* 5 and *Dendromus* a dorsolateral epiturbinal can be observed (Fig. 8C).

In *Gerbillus* the ventral part of the lamina semicircularis is still precartilaginous which indicates a chondrification pattern from dorsal to ventral. The ossification of the lamina semicircularis can already be observed in late prenatal stages although the pattern varies among the different species. In *Peromyscus* 3, *Sigmodon* 3, *Geoxus*, *Abrothrix* 2, and *Dendromus* ossification starts dorsolaterally, in *Sigmodon* 4, *Cricetus*, *Mesocricetus* 2–6, *Mus* 4 and *Rattus* 4+5 it proceeds from rostral to caudal and distal to proximal. In *Mus* 5 ossification appears to proceed from proximal to distal starting in the middle of the lamina semicircularis; although *Acomys* has a completely ossified anterior lamina semicircularis, posteriorly it still shows several small centers of ossification. After resorption of the adjacent part of the tectum nasi and paries

nasi the lamina semicircularis contacts the surrounding dermal bones, in particular the nasal and the praemaxillary (Figs. 8C, 15B–D). In *Mus* 6 the lamina is enlarged rostroventrally by the maxillary bone.

The lamina horizontalis subdivides the pars lateralis into the recessus frontoturbinalis and the recessus maxillaris (Figs. 3, 8C, 10, 15). In all Muroidea (except for *Lophuromys*) and in the Geomyoidea, the lamina horizontalis is anteriorly elongated by the septum frontomaxillare (FAWCETT, 1917; radix anterior of ethmoturbinal I; ELOFF, 1948; radix anterior of ethmoturbinal I; YOUSSEF, 1966; FRICK, 1986; HAUCK, 1987; SCHRENK, 1989). During ontogeny the lamina horizontalis becomes increasingly oblique and oriented ventromedially. *Peromyscus* 1, *Micromys* and *Apodemus flavicollis* have a blastematosus to precartilaginous lamina horizontalis that chondrifies in *Micromys* from caudal to rostral. Ossification of the lamina horizontalis including the septum frontomaxillare occurs from rostral to caudal (*Peromyscus* 3+4, *Sigmodon* 3+4, *Phyllotis*, *Auliscomys*, *Rhipidomys*, *Cricetus*, *Mesocricetus* 3–6, *Acomys* 2, *Rattus* 4). In *Mus* 3 ossification of the lamina horizontalis starts in the middle.

All investigated Cricetidae, most Muridae and the Geomyoidea have two frontoturbinals (FAWCETT, 1917; RAJTOVA, 1972b; KADAM, 1972, 1973a, b, 1976; FRICK, 1986; HAUCK, 1987; SCHRENK, 1989; pers. obs.) (Figs. 3A, 8C, 9B, 10C, 13B, D, F, 15A–D). Among the murids *Otomys*, *Apodemus*, *Micromys*, *Rattus* and *Mus* have only one frontoturbinal, which is most likely frontoturbinal 1 (ELOFF, 1948; YOUSSEF, 1966; FRICK, 1986; HAUCK, 1987; SCHRENK, 1989; pers. obs.) (Figs. 3B, 13H, 15E). In *Jaculus* the frontoturbinals appear to be reduced as only an epithelial ridge (most likely frontoturbinal 1) can be observed (HAUCK, 1987; SCHRENK, 1989; pers. obs.). Interturbinals are not present in the investigated species and stages respectively. However, *Abrothrix* 2 has an additional turbinal anterior to frontoturbinal 1, that could be interpreted as an interturbinal. Generally, frontoturbinal 1 is always larger than frontoturbinal 2. The former originates anteriorly from the lamina horizontalis, the latter from the lateral side wall of the nasal cavity (paries nasi in younger stages) (FAWCETT, 1917; KADAM, 1972, 1973a, b; HAUCK, 1987; SCHRENK, 1989; pers. obs.) (Figs. 8C, 10C). In *Lophuromys* both frontoturbinals arise from the paries nasi. The caudal end of frontoturbinals merges into the paries nasi (ELOFF, 1951b; HAUCK, 1987; pers. obs.). However, the frontoturbinal 1 of *Sigmodon* 3, *Rhipidomys*, *Abrothrix* 2, *Mesocricetus*, *Dendromus*, *Acomys*, *Rattus* and *Lophuromys* merges into the lamina cribrosa caudally.

During ontogeny the frontoturbinals become increasingly rolled-up and finally form double-scrolls (Fig. 15). Chondrification of the frontoturbinals can be observed in the youngest muroid stages (e.g., *Peromyscus* 1); it starts in the middle of the frontoturbinals, proceeds distally and rostrally as well as caudally, and it is finished later than the chondrification of the paries nasi. The development of frontoturbinal 1 is generally more advanced than that of frontoturbinal 2. In contrast, ossification of the fron-

toturbinals extends from distal to proximal and rostral to caudal. It can be observed prenatally in all Sigmodontinae (except *Geoxus*) as well as in *Peromyscus*, *Cricetus* and in the neonate and early postnatal stages of *Mesocricetus*, *Dendromus*, *Acomys*, *Mus* and *Rattus*.

The number and general shape and topography of ethmo- and interturbinals in the pars posterior of the nasal cavity show a common pattern in all species (PAULLI 1900c; FAWCETT, 1917; YOUSSEF, 1966; RAJTOVA, 1972b; KADAM, 1972, 1973a, b, 1976; FRICK, 1986; HAUCK, 1987; pers. obs.) (Figs. 2B, D, F, 3, 10, 11, 13, 15). These are three ethmoturbinals and one interturbinal between ethmoturbinal I and ethmoturbinal II. However, the interturbinal of *Micromys* is represented only by an epithelial fold; *Jaculus* is lacking an interturbinal altogether. During ontogeny the ethmoturbinals and the interturbinal increase in size, overlap, and roll-up laterally as can be observed in *Peromyscus*, *Sigmodon*, *Mesocricetus*, *Cricetus*, *Mus* and *Rattus*.

Ethmoturbinals I and II and the interturbinal arise from the lamina horizontalis and increasingly with age from the lateral sidewall of the nasal cavity (paries nasi or dermal bones respectively); ethmoturbinal III originates only from the later (Figs. 3, 10, 11, 15). Caudally all ethmoturbinals merge into the lamina cribrosa, ethmoturbinal I into the funnel-shaped depression (Fig. 10C). The interturbinal is connected to the lamina cribrosa only in *Peromyscus* 4, *Sigmodon* 2+3, *Abrothrix* 2, *Mesocricetus* 5+6, *Microtus*, *Mus* 4–6, *Rattus* and *Lophuromys*. Ethmoturbinal I consists of a lateral pars anterior and a medial pars posterior (Figs. 2B, D, F, 3, 10A, B, 13, 15). With growth, the pars anterior and especially its processus anterior project far into the pars anterior of the nasal cavity (Figs. 8C, 9B, 13A, C, E, G). The interturbinal and the ethmoturbinals II and III have a processus anterior in certain species (Fig. 10C); the pattern is quite variable. In all species except for *Gerbillus* and *Micromys* the ethmoturbinals and the interturbinal become increasingly complex by epiturbinals and infolding already in prenatal stages as can be observed in many of the investigated species (HAUCK, 1987; pers. obs.). Although in detail these additional lamellae show a puzzling pattern among the investigated species the adult stages reveal a general morphology of bony scrolls in the pars posterior (Figs. 13, 15).

Ethmoturbinal I is the first turbinal in the recessus ethmoturbinalis that develops as described in *Tatera* and *Mesocricetus* (RAJTOVA, 1972b; KADAM 1972, 1973a, b). Chondrification starts also in ethmoturbinal I and proceeds caudally (e.g., *Peromyscus*) (Fig. 10A). The interturbinal develops after the three ethmoturbinals but its chondrification can be accelerated as observed in *Mesocricetus*, *Gerbillus*, *Apodemus flavicollis*, *Micromys*, *Rattus* and *Thomomys*. Due to their young age, in a 10 mm HL stage of *Mesocricetus* (KADAM, 1976) and in the previously investigated stages of *Rhabdomys* and *Otomys* (ELOFF, 1948, 1951b) only ethmoturbinals I and II are present; the previously investigated stages of *Mesocricetus* (RAJTOVA, 1972b) and *Rattus* (YOUSSEF, 1966)



still lack the interturbinal. The anterior process of the pars anterior chondrifies later than the rest of ethmoturbinal I (*Peromyscus*, *Sigmodon*, *Abrothrix*, *Apodemus flavicollis*, *Mus*, *Micromys*, *Gerbillus*, *Rattus*). Chondrification of the single turbinal occurs from proximal to distal.

The ossification of the turbinals can already start in late fetal stages and proceeds from rostral to caudal and distal to proximal (*Sigmodon* 3+4, *Cricetus*, *Mesocricetus* 3–6, *Dendromus*, *Acomys* 2, *Rattus* 4+5, *Mus* 4–6) (Fig. 11); in older stages as in *Sigmodon* 4 and *Acomys* 2 ossification of the ethmoturbinals is dorsally connected with ossification of the lamina cribrosa (Fig. 10B, C). The processus anterior of the pars anterior of ethmoturbinal I ossifies from ventral to dorsal (Fig. 9B).

## Discussion

Detailed discussion of morphological characters observed in the investigated Myodonta and Geomyoidea in terms of developmental patterns and systematic implications is given in RUF (2004). This takes the complete ontogenetic literature on the chondrocranium of rodents including unpublished diploma and PhD theses into account. However, it should be pointed out that many of the studied species are only represented by a single fetal stage and thus further developmental transformations or differentiations cannot be ruled out. Thus, the morphological observations often show a puzzling pattern. Nevertheless, the results comprise important and comprehensive information regarding the craniogenesis of the ethmoidal region in Rodentia and mammals in general. In the following only the most striking features are discussed.

### Morphological patterns of the ethmoidal region

A well-developed cupula nasi anterior with broad cartilagine cupulares and a well-developed processus lateralis ventralis confluent with the lamina transversalis anterior are plesiomorphic grundplan characters of Euarchontoglires and in particular Rodentia (e.g., TOEPLITZ, 1920; STURM, 1936; STARCK, 1967; KUHN, 1971; ZELLER, 1983, 1987; MESS, 1997; FRAHNERT, 1998; RUF *et al.*, 2015; HÜPPI *et al.*, 2018). Lagomorpha, the sister-group of rodents, instead shows an apomorphic pattern with a reduced cupula nasi anterior and lack of the processus lateralis ventralis (VOIT, 1909; ELOFF, 1950; FRICK & HECKMANN, 1955; FRAHNERT, 1997; MESS, 1999b). Thus, the Muroidea and especially Geomyoidea under study resemble the plesiomorphic grundplan pattern of Rodentia.

*Jaculus* is derived due to its reduced cupula nasi anterior. If this holds true for Dipodidae in general has to be verified by a larger taxon sampling. However, MESS

(1997) points out that the observation of a less developed cupula nasi anterior in fetal stages of Glires could be related to the immature condition of the anteriormost chondrocranium in the investigated species (mostly precocial) as she observed a postnatal differentiation of that area in postnatal stages of Caviomorpha. The present study clearly shows that the differentiation of the anteriormost cartilages of the ethmoidal region of muroids starts well before birth (see below). The extremely broad cupula nasi anterior described for *Mus* by FRICK (1986) cannot be verified by any of the re-studied *Mus* specimens. This specimen is obviously aberrant and deviates from the morphology observed in other house mice. Besides *Jaculus* and the Gerbillinae the processus lateralis ventralis has also been independently reduced or lost in *Ctenodactylus gundi*, *Pedetes capensis*, *Anomalurus beecrofti* (SCHRENK, 1989). Although KADAM (1972, 1973a, b) described a processus lateralis ventralis in a very young stage of *Tatera*, his figures of older stages clearly show an increasing reduction of this structure. Thus, it can be concluded that the reduction or loss of the processus lateralis ventralis is an apomorphic character of Gerbillinae but it also clearly indicates the significance of investigating an ontogenetic series.

The well-developed processus alaris superior is also present in the investigated species and can be regarded as a plesiomorphic grundplan feature of Theria (DE BEER, 1937; KUHN, 1971; ZELLER, 1987; MAIER, 1991; RUF *et al.*, 2015; HÜPPI *et al.*, 2018). Within Rodentia the processus alaris superior is reduced in *Aplodontia rufa* and the Hystricognathi (RAJTOVA, 1972a; DIERBACH, 1985a, b; MESS, 1997; FRAHNERT, 1998; DA SILVA NETO, 2000). The lamellar roofing of the processus alaris super is only known from the investigated Muroidea and thus can be regarded as an apomorphic character. If the lack of this character in *Phodopus* is a secondary derived feature or if the lamella develops later in ontogeny can only be clarified by investigation of older stages. The hook-like ventral outgrowth in *Gerbillus* and *Meriones* can be regarded as an apomorphic character of Gerbillinae.

The processus anterior of the lamina infraconchalis is only known from the Muroidea and *Dipodomys* but not from any other member of Euarchontoglires (e.g., VOIT, 1909; ZELLER, 1987; MAIER, 1991; MESS, 1997; FRAHNERT, 1998; RUF *et al.*, 2015). Therefore, it can be concluded that this process is an apomorphic character of Muroidea and possibly also of Dipodidae; its lack in Gerbillinae would be a secondary derived character due to the fact that this taxon is deeply nested within Muridae (MICHAX *et al.*, 2001; JANS & WEKSLER, 2004). The lack of this structure in *Lemmus*, *Arvicola* (FAWCETT, 1917), and *Thomomys* cannot be properly polarized without taking older stages into account.

Myodonta and Geomyoidea resemble the mammalian grundplan in having a zona annularis in which the lamina transversalis anterior is fused to the septum nasi and on the same level as the ventral edge of the latter (HÜPPI *et al.*, 2018). In contrast, *Castor fiber* and the Hystricomorpha show a ventral keel of the septum nasi below

the lamina transversalis anterior (FRAHNERT, 1998; MESS, 1999a). The separation of the lamina transversalis anterior in a thicker pars anterior and a thinner pars posterior as observed in Muroidea and *Dipodomys* has not been described for Rodentia (except Gliridae) nor Euarchontoglires (e.g., VOIT, 1909; ELOFF, 1950; ZELLER, 1987; SCHRENK, 1989; MESS, 1997; FRAHNERT, 1998); at least for Muroidea this character is apomorphic. This pattern has also been observed in Gliridae although this has to be interpreted as independently evolved due to their phylogenetic position in the squirrel-related clade (KLINGLER, 2003; BLANGA-KANFI *et al.*, 2009).

The fenestration of the cartilaginous septum nasi has been observed in several mammals although its development (primary or secondary) and topography are variable (e.g., GAUPP, 1908; STARCK, 1941; KUHN, 1971). Among Euarchontoglires a fenestra internasalis anterior, that is located far anterior to the lamina transversalis anterior, is only described in *Aplodontia rufa*, an adult *Castor fiber*, *Ctenodactylus gundi*, several Hystricognathi and *Ochotona* sp. (STRUTHERS, 1927; SCHRENK, 1989; MESS, 1997; FRAHNERT, 1998). The observed anterior fenestra can be homologized with the fenestration of the other rodents and thus most probably is a plesiomorphic character. According to HÜPPI *et al.* (2018), the presence of a fenestra internasalis anterior is an ancestral condition in Mammalia. The fenestra internasalis anterior develops very early in ontogeny. In *Ctenodactylus gundi* it develops from a fissure in the septum nasi and therefore it is a primary opening (SCHRENK, 1989); in *Erethizon dorsatum* it becomes closed during ontogeny (STRUTHERS, 1927) while in some muroids it obviously persists into postnatal stages. Here the fenestration could be responsible for a higher mobility of the cartilaginous rostrum. The fenestra internasalis posterior is located dorsocaudally of the lamina transversalis anterior and develops later in ontogeny by increasing thinning of the septum nasi. Among Glires a true fenestration has been observed in postnatal stages of *Rattus*, *Mus*, and in an adult *Glis glis* (KLINGLER, 2003). However, many muroids, *Jaculus*, *Dipodomys*, *Muscardinus avellanarius*, and *Eliomys quercinus* show thinning of the septum nasi in the respective area (KLINGLER, 2003). The fenestra internasalis posterior certainly belongs to the grundplan of Myodonta although its polarization cannot be given until further postnatal stages are investigated. Probably the thinning of the septum nasi in this area has been overlooked in many previously described species.

Varying septoturbinals have been described in several mammals (REINBACH, 1952a, b; STARCK, 1982; RUF *et al.*, 2015). However, early ontogenetic stages of *Tupaia* sp. do not show a septoturbinal but adults do (SPATZ, 1964; ZELLER, 1983; RUF *et al.*, 2015). Some Caviomorpha show an anterior septoturbinal that is located along the posterior rim of the fenestra internasalis anterior or the thinned septum nasi in this area (MESS, 1995). Due to its different position it should not be homologized with the anterior septoturbinal of Myodonta, *Dipodomys*, and *Eliomys quercinus* (KLINGLER, 2003). The anterior septoturbinal-fenestra internasalis complex of Caviomorpha can

be regarded as an apomorphic feature. In contrast, the investigated Myodonta and Geomyoidea show a different pattern of a posterior septoturbinal-fenestra internasalis complex in that the posterior septoturbinals lies ventrally to the posterior fenestra internasalis posterior (or the thinned septum nasi). This should be regarded as a common pattern among the members of the mouse-related clade. A similar but independently evolved pattern can be observed in Gliridae (KLINGLER, 2003).

The simple shape of the naso- and maxilloturbinal becomes modified during ontogeny. Compared to other rodents in Muroidea the relative simple shape of these two turbinals persists into adult stages as observed in the investigated species; this is supported by a comprehensive study on the turbinal skeleton in worm-eating Murinae (MARTINEZ *et al.*, 2018). Thus, the adult stages under study show a slightly more complex pattern which is most pronounced in *Cricetus*. However, *Cricetus* still differs from the highly branched maxilloturbinal as observed in other rodents like *Aplodontia rufa*, *Sciurus vulgaris*, *Castor fiber*, *Myocastor coypus* (FRAHNERT, 2003; MARTINEZ *et al.*, 2020). Interestingly, *Myocastor coypus* has developed an additional simple turbinal in the pars anterior between naso- and maxilloturbinal that is interpreted as an adaptation to its amphibious mode of life (MARTINEZ *et al.*, 2020).

Concerning the number of olfactory turbinals the muroid grundplan is already determined at birth and comprises two frontoturbinals, three ethmoturbinals, and one interturbinal between ethmoturbinal I and II. This pattern is confirmed by the adult stages under study as well as data from further Sigmodontinae and Deomyinae from MARTINEZ *et al.* (2018). Obviously this pattern of two frontoturbinals and three ethmoturbinals and one interturbinal between the first two ethmoturbinals is quite conserved as it is also present in most investigated rodents, many leporidae (which show an additional interturbinal between the frontoturbinals) and Scandentia and therefore can be confidently regarded as a plesiomorphic grundplan feature of Rodentia (SCHRENK, 1989; MESS, 1997; FRAHNERT, 1998; DA SILVA NETO, 2000; KLINGLER, 2003; RUF, 2014; RUF *et al.*, 2015; MARTINEZ *et al.*, 2020). However, many murine species show a derived pattern concerning the number of frontoturbinals. *Apodemus*, *Micromys*, *Mus*, and *Rattus* have only one frontoturbinal, which is most likely frontoturbinal 1. This pattern is also described for *Otomys* and many more adult stages of Murinae (ELOFF, 1948; MARTINEZ *et al.*, 2018). However, as *Otomys* also lacks a third ethmoturbinal the herein observed turbinal pattern could be due to its immature stage (ELOFF, 1948). The sigmodontine *Abrothrix* is also derived from the murid grundplan in having an interturbinal anterior to frontoturbinal 1. Compared to other mammals like primates, lagomorphs or carnivorans (MAIER & RUF, 2014; RUF, 2014; WAGNER & RUF, 2019) the number of interturbinals does not change after birth in Muroidea as it is restricted to one in the recessus ethmoturbinalis of the investigated species. An additional interturbinal is observed in the murine *Tateomys macrocerus* (MARTINEZ

*et al.*, 2018). The lack of frontoturbinals and of the interturbinal in *Jaculus* might be also due to its immature age. However, as the reduction of the posterior nasal cavity is obviously associated with proportional enlargement of the eyes the observed number of turbinals might reflect the species specific pattern; this should be verified by  $\mu$ CT investigation of adult crania.

## Resorption and ossification of the nasal capsule

Although the picture of resorption and ossification of the nasal capsule of Muroidea remains still incomplete as most species are represented by a single specimen some general patterns can be deduced from the observations. Furthermore it can be stated that in Muroidea the ethmoid bone comprises some more remnants of the former nasal capsule than previously defined (e.g., SCHALLER, 1992): the ossified part of the septum nasi, all olfactory turbinals as well as the lamina semicircularis including those parts of the tectum nasi and paries nasi to which the turbinals and the lamina are attached, lamina cribrosa, limbus praecribrosus, limbus paracribrosus, lamina infracribrosa, and the dorsalmost part of the posterior planum antorbitale. If present, the crista galli and the spina mesethmoidalis also become part of the ethmoid bone. In contrast, the ethmoid bone of Lagomorpha also comprises the nasoturbinal which contacts or even fuses to the lamina semicircularis in the adult skull (RUF, 2014).

Thinning, resorption and ossification of the cartilaginous nasal capsule already starts in late prenatal to neonatal stages in the investigated species. The paries nasi has at least two areas of resorption, in the pars anterior and in the pars lateralis. This general pattern is also observed in other rodents, in *Oryctolagus cuniculus*, *Tupaia* sp., and *Daubentonia madagascariensis* (e.g., FRICK & HECKMANN, 1955; SPATZ, 1964; MAIER, 1991; DA SILVA NETO, 2000; MESS, 1997). Thus, the cupula nasi anterior becomes increasingly isolated which is further supported by the development of fissures in this area that results in a higher mobility of the rhinarium (FRICK, 1954; KUHN, 1971; MAIER, 1980, 2002; MESS, 1999b). This is especially evident in the loosely attachment of the processus alaris superior in the older investigated stages. The paries nasi is almost completely lost after birth in Muroidea except for the anteriormost parts as well as ossified remnants at the roots of the turbinals.

In the Muroidea ossified remnants of the tectum nasi are the areas between the nasoturbinal and lamina semicircularis as well as the areas between the frontoturbinals. These remnants contribute to the ethmoid bone. In muroids the lamina cribrosa ossifies from medial to lateral. This pattern is also observed in *Glis glis* and *Octodon degus* (KLINGLER, 2003; MESS, 1997).

A recent study on the perinatal development of the sphenoethmoidal junction in Primates, *Cynocephalus volans* and *Tupaia belangeri* revealed a complete breakdown of the cartilaginous cupula nasi posterior (SMITH

*et al.*, 2017). Thus, in Euarchontoglires ossified remnants of the cupula nasi posterior are not known so far. However, the present study reveals that, at least in some muroid species, parts of the cupula as its roof (lamina infracribrosa) and the dorsal rim of the lateral wall (planum antorbitale of paries nasi) ossify and become incorporated into the ethmoid bone.

The results of this study could not confirm some previous observations on the cartilago paraseptalis anterior of *Mesocricetus* and *Rattus*. According to BEATTY & HILLEMANN (1950) and WÖHRMANN-REPENNING (1985) the cartilage ossifies to the bony tube that houses the vomeronasal organ in adults. The results on all older stages clearly show the mode of resorption of the cartilago paraseptalis anterior and replacement by the vomer as well as the processus palatinus medialis of the premaxillary bone. This is also the case in many other investigated rodents as well as in *Oryctolagus cuniculus* (FRICK & HECKMANN, 1955; WÖHRMANN-REPENNING, 1984a, b; MESS, 1997). In contrast in *Apodontia rufa* and *Sciurus vulgaris* the cartilage itself becomes ossified and in *Rattus* the cartilago paraseptalis anterior persists into the adult stage (WÖHRMANN-REPENNING, 1982; FRAHNERT, 1998).

The fusion of the ossified lamina transversalis posterior with the vomer to form the lamina terminalis is a common pattern among mammals and also among rodents (e.g., PAULLI, 1900a; ELOFF, 1951a; FRICK & HECKMANN, 1955; ZELLER, 1987; MESS, 1997; FRAHNERT, 1998; KLINGLER, 2003). Thus, this pattern can be regarded as plesiomorphic for Muroidea. The same holds true for the ossification of the septum nasi that occurs from posterior below the lamina cribrosa to anterior and from dorsal to ventral as also described for some Gliridae and *Octodon degus* (MESS, 1997; KLINGLER, 2003).

The development and ossification of the turbinals in muroids reflects some general patterns also observed in other rodents and mammals. As in muroids, the maxilloturbinal ossifies from distal to proximal in *Sciurus vulgaris*, *Ctenodactylus gundi* and *Octodon degus* (SCHRENK, 1989; MESS, 1997; FRAHNERT, 1998); the anterior tip remains cartilaginous at least into late postnatal stages. In contrast, in Cheirogaleidae the maxilloturbinal ossifies from proximal to distal (SMITH & ROSSIE, 2008). The ossification of the nasoturbinal of other rodents shows the same puzzling pattern as the investigated muroids (MESS, 1997; FRAHNERT, 1998).

The observation that the frontoturbinals as well as the ethmoturbinals develop and chondrify from anterior to posterior and proximal to distal is a common pattern among mammals; the interturbinal (if present) between ethmoturbinal I and II can develop somewhat delayed. This general pattern has also been observed in other rodents like *Ctenodactylus gundi* and *Octodon degus* as well as in *Tupaia* spp. and Cheirogaleidae (SPATZ, 1964; SCHRENK, 1989; ZELLER, 1989; MESS, 1997; SMITH & ROSSIE, 2008). Further interturbinals (not present in the investigated species of the present study except for *Abrothrix*) develop later and independent of the other olfactory turbinals (RUF, 2014; WAGNER & RUF, 2019). The ossi-

fication of the olfactory turbinals shows partly the opposite pattern to their chondrification. It starts prenatally in Muroidea and proceeds also from anterior to posterior but from distal to proximal. A similar pattern is described for the frontoturbinals of a juvenile specimen of *Sciurus vulgaris* and of *Eliomys quercinus* (FRAHNERT, 1998; KLINGLER, 2003). In a neonate stage of *Tupaia glis* the frontoturbinals are the first structures of the nasal capsule that ossify (SPATZ, 1964). It should be emphasized that after the ossification of the turbinals is completed further increase in size and complexity of the turbinals happens by appositional bone growth.

### Altricial versus precocial Muroidea

In general, muroids are altricial rodents (NOWAK, 1991). The investigated Muroidea include two precocial species: the cricetid *Sigmodon* and the murid *Acomys*. In *Sigmodon* gestation is about 27 days, in *Acomys* around 35–42 days. In comparison most altricial Muroidea show a gestation around three weeks like *Mus* and *Rattus* (NOWAK, 1991; BRUNJES, 1990). Another precocial murid is *Otomys*, in which the young are born fully furred after a gestation estimated at 40 days; they open their eyes after two days (NOWAK, 1991). Unfortunately the described stage by ELOFF (1948) is too young to contribute to the comparison with other precocial Muroidea.

Compared to precocial rodents such as the Caviomorpha it is expected that the transformation of the muroid chondrocranium is less advanced at birth; this conclusion is generally supported by the present study. For instance, in the precocial Hytricrognathi resorption of the paries nasi already starts prenatally (RAJTOVA, 1972a; DA SILVA NETO 2000; MESS, 1997). In contrast, in the altricial *Sciurus vulgaris* (Frahner, 1998) and most altricial muroids there is less resorption in late fetal stages. Furthermore the ossification of e.g., the septum nasi starts prenatally in *Sigmodon* and especially in *Acomys* but around birth in the other muroids. The transformation of the chondrocranium of *Acomys* is more advanced at birth whereas *Sigmodon* mostly resembles the altricial muroids. However, in a neonatal stage of *Octodon degus*, whose gestation is around three months, only the subcerebral part of the nasal septum has been ossified, which is less advanced than expected (NOWAK, 1991; MESS, 1997). In comparison the ethmoidal region of altricial muroids is less developed at birth than that of precocial species but not as immature as indicated by the outer anatomy of the naked, blind and deaf newborn. Resorption and ossification of the chondrocranium is in full progress. Surprisingly, the altricial *Cricetus* is by far the most advanced in its craniogenesis compared to all other muroids as resorption and ossification of the nasal capsule seems to start much earlier before birth.

In this regard the most striking muroid species is the cricetid *Mesocricetus*. With a gestation of only 15–17 days it has by far the shortest gestation among Placentalia (NOWAK, 1991). Compared to the other studied altricial

Muroidea it shows only minor delay in its maturity in perinatal stages as thinning of cartilage is evident in the neonate and resorption and ossification is already going on in a 4 days old stage. Investigation of the prenatal to early postnatal development of the entire skeleton in *Mesocricetus auratus* revealed that first ossification centers occur on day 12 of gestation rapidly increasing in number until birth (BEATTY & HILLEMANN, 1950). Although, the prenatal increase of crown-rump length from day 9 to day 16 of gestation is fairly constant, the body weight shows also an explosive acceleration from day 13 on (PURDY & HILLEMANN, 1950). To conclude, the development and transformation of the ethmoidal region of *Mesocricetus auratus* supports a unique highly accelerated perinatal and early postnatal development as revealed by previous studies. *Mesocricetus auratus* has to develop the same neonatal maturity in around only four days compared to other Muroidea (BEATTY & HILLEMANN, 1950).

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