A neglected part of the mammalian skull: The outer nasal cartilages as progressive remnants of the chondrocranium

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Abstract

A rostrum equipped with a rhinarium, diverse mechanoreceptors and a set of vibrissae are apomorphic characters of therian mammals. Together, they constitute a tactile sensory organ that has also been named 'rostral organ'. The rhinarium and the outer nasal openings are supported by a well-defined system of outer nasal cartilages; these cartilages can be actively moved by facial muscles. Because the structures of the rostrum are mainly composed of cartilage and soft tissues, fossils cannot contribute much information on its phylogenetic origin. Therefore, one has to rely on comparative anatomy of extant mammals. Because the cartilages are known to grow and differentiate well into juvenile and even subadult stages, embryological evidence is not too rewarding either. However, the microscopic anatomy of the rostrum of postnatal stages is difficult to study for various technical reasons, and it is hoped that modern imaging techniques will improve our knowledge.

Here, I provide a preliminary overview of the structural diversity of the outer nasal cartilages in selected taxa of placental mammals. The outer nasal cartilages of moles (Talpidae) and shrews (Soricidae) are relatively well-known and can serve as references. The soricids present a unique mode of retracting and telescoping the nasal cartilages; these peculiar structures are differentiated only postnatally by a sort of apoptosis. Several Afrotheria show a peculiar commissura alatransversalis and a specialized processus alaris superior, which are considered to be synapomorphies of Afroinsectiphilia (Afrotheria) at least. The peculiar trachea-like structure of the outer nasal cartilage of macroscelidids is also postnatally realized by an apoptotic morphogenetic mode.

Finally, the presented data are interpreted within the context of evolutionary biology of early mammals: First it is shown, that the paired outer nares of early synapsids fuse into a wide nasal aperture within true mammaliaforms, but only after the reduction of the prenasal processes of the premaxillaries. It is important to note that hatchlings of the monotreme *Tachyglossus* still retain the prenasal process, because it supports the egg-tooth. It is only after the reduction of this membrane bone, that the rostral organ could expand and diversify - and to become the new and functionally important tactile organ ('rostral organ') of therian mammals. Whereas small arboreal mammals show relatively simple outer nasal cartilages, they tend to become a specialized probe in terrestrial and fossorial taxa.

Key words

Introduction

The early ontogenetic skeleton of the head of amniotes consists of heterogeneous components (Fig. 1). In the vicinity of the brain and sense organs, we find a cartilaginous endocranium or chondrocranium: Brain capsule, nasal capsule, sclera of the eye, labyrinth capsule; at the posterior end of the brain capsule, we find attached and then incorporated three vertebrae (occipitocranium). Ventrolaterally branchial elements are loosely attached to the neurocranium: Mandibular arch (pink) and the hyoid (first yellow bar). Some parts of the chondrocranium ossify secondarily as replacement bones (ethmoid, sphenoid, petrosal, occiput, ear ossicles), others become re-
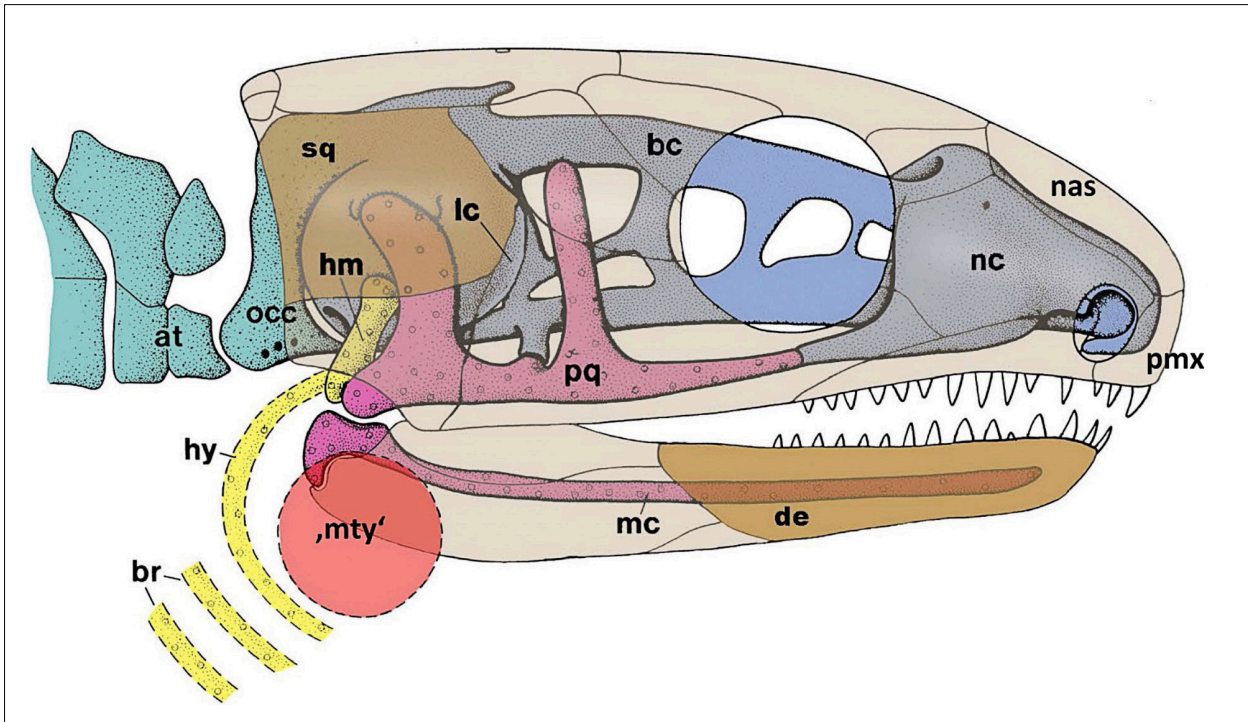
Fig. 1. Schematic 'bauplan' of the amniotic skull designed for merely didactical purposes. The exocranium (brown) is taken from the Permian *Captorhinus*, the endocranial components (blue, green, pink, yellow) are hypothetical and they are tentatively derived from fetal skulls of extant sauropsids (after various sources). The small external nasal cartilages are fitted into the small nasal openings separated by the prenasal process of the premaxillary. Modified from Maier (1993) and Maier & Werneburg (2014). Abbreviations: **at** – atlas, **bc** – braincase, **br** – branchial arches, **de** – dentary, **hm** – hyomandibula, **hy** – hyal arch, **lc** – labyrinth capsule, **mc** – Meckel's cartilage, '**mty**' – future tympanic membrane in mammals, **nas** – nasal, **nc** – nasal capsule, **occ** – occipital, **pmx** – premaxillary, **pq** – palatoquadrate, **sq** – squamosal.

sorbed. Only the rostralmost parts of the chondrocranium survive into juvenile and adult stages, and postnatally, they become even progressively elaborated as outer nasal cartilages and as nasal floor cartilages. Primarily, the anterior cupula of the nasal capsule may serve as elastic buffer of the rostrum, but then the external cartilages become a more or less mobile and complex support for the rostrum; the posterior parts of the nasal capsule ossify and are then called ethmoid or sphenethmoid. (Starck, 1967; 1979).

Naturally, the anatomy of the chondrocranium in a fossil must be speculative, because only few parts ossify and are preserved in the fossil record. The chondrocranium, as depicted in Fig. 1, is taken from extant lepidosaurs, as reconstructed by Gaupp (1900), DeBeer (1937), Bellairs & Kamal (1980) and many others. It is doubtful, whether the skulls of lepidosaurs can provide an adequate model, because their kinetic construction (streptostyly) also affects the endocranium. In any case, we can be sure that the rostralmost parts of the nasal capsule have somehow framed the nasal apertures of the osteocranium on both sides and that these openings were separated by broad prenasal processes of the premaxillaries (also processus dorsalis), i.e. there existed an immobile bony rostrum covered by a dry and horny skin.

The endocranial structures are enclosed in a bony capsule, the exocranium. The exocranium ossifies direct-ly within the connective tissue of the skin (intramembraneous ossification), i.e. it is in fact no shell but also an 'endocranium' s.l. The exocranium, which normally consists of a mosaic of well-defined bony plates shows a few openings for the nostrils, the lateral eyes and for a small parietal (pineal) eye. Otherwise, in early taxa of amniotes the exocranium is a closed bony capsule, but in some, the temporal region becomes convergently opened by one or two temporal windows; by these windows some taxa are defined, the most important ones are the diapsids and synapsids (Maier, 2008; Werneburg, 2019).

As shown by Fig. 2, in extant therian mammals the cartilaginous turbinals at the outer nasal aperture were mainly adapted to regulate the airflow entering the nasal capsule with high speed (Zhao & Jiang, 2014). During normal breathing it is most important to canalize the airstream with a minimum of friction, but by active sniffing, it is swirled and can be directed either to the opening of the vomeronasal organ (Jacobson´s organ) or dorsolaterally towards the olfactory epithelium of the ethmoturbinals (Craven et al., 2007; Van Valkenburgh et. al., 2014).

The odour molecules caught and dissolved by the moist surface of the rhinarium are at least in parts transported by the tongue to the anterior roof of the mouth through the groove of the philtrum. Here the two ductus nasopalatini open, which pass through the foramina
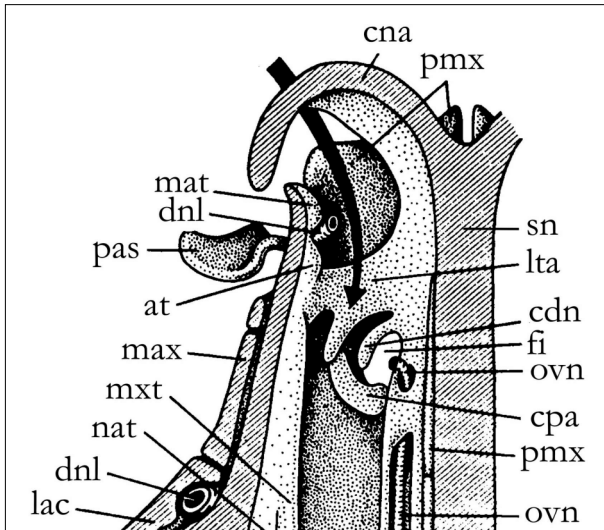
Fig. 2. Schematic drawing of the anteriormost portion of the nasal capsule of therian mammals. The nasal capsule is sectioned horizontally to show the ventral structures in more detail. Modified after MAIER (1993). Abbreviations: **at** – atrioturbinale, **cdn** – cartilago ductus nasopalatini, **cna** – cupula nasi anterior, **cpa** – cartilago palatina, **dnl** – ductus nasolacrimalis, **fi** – foramen incisivum, **lac** – lacrimal, **lta** – lamina transversalis anterior, **mat** – marginoturbinale, **max** – maxillary, **mxt** – maxilloturbinale, **nat** – nasoturbinale, **ovn** – organon vomeronasale (Jacobson's organ), **pas** – processus alaris superior, **pmx** – premaxillary, **sn** – septum nasi.

incisiva (Fig. 2). The vomeronasal organs usually open into these ducts, and the mucus loaded with pheromones and other odour molecules are sucked into these sensory organs (SCHILLING, 1970; MAIER, 1980). In most ancestral mammalian taxa, the philtrum is in function, and it prevents the median gap of the upper incisal tooth row to become closed (MAIER, 1980). Only in those taxa where the median incisors have become important for ingestion of food, the median incisors interrupt the pathway between rhinarium and the organ of Jacobson. These taxa, mainly Glires and anthropoid primates, also tend to reduce and even to lose the rhinarium (MAIER, 1980; ADE, 1998).

Morphological studies should always be embedded in a phylogenetic-systematic framework (HENNIG, 1982; WÄGELE, 2000). Phylogenetic systematics of mammals have undergone many dramatic changes during the last 25 years. This was mainly due to the contributions of molecular systematics and cladistic methods. Most important for understanding many evolutionary transformations have been the disappearance of 'Insectivora' and establishment of new monophyletic units (cf. SIMPSON, 1945): The tenrecs (Tenrecoidea) were removed with good arguments from the old 'Insectivora' and put into the newly identified African monophylum Afrotheria. Chrysochloridae, Macroscelididae, Paenungulates, Hyracoidea, and Sirenia also belong to the Afrotheria. Most molecular analyses consider the Afrotheria to be the first
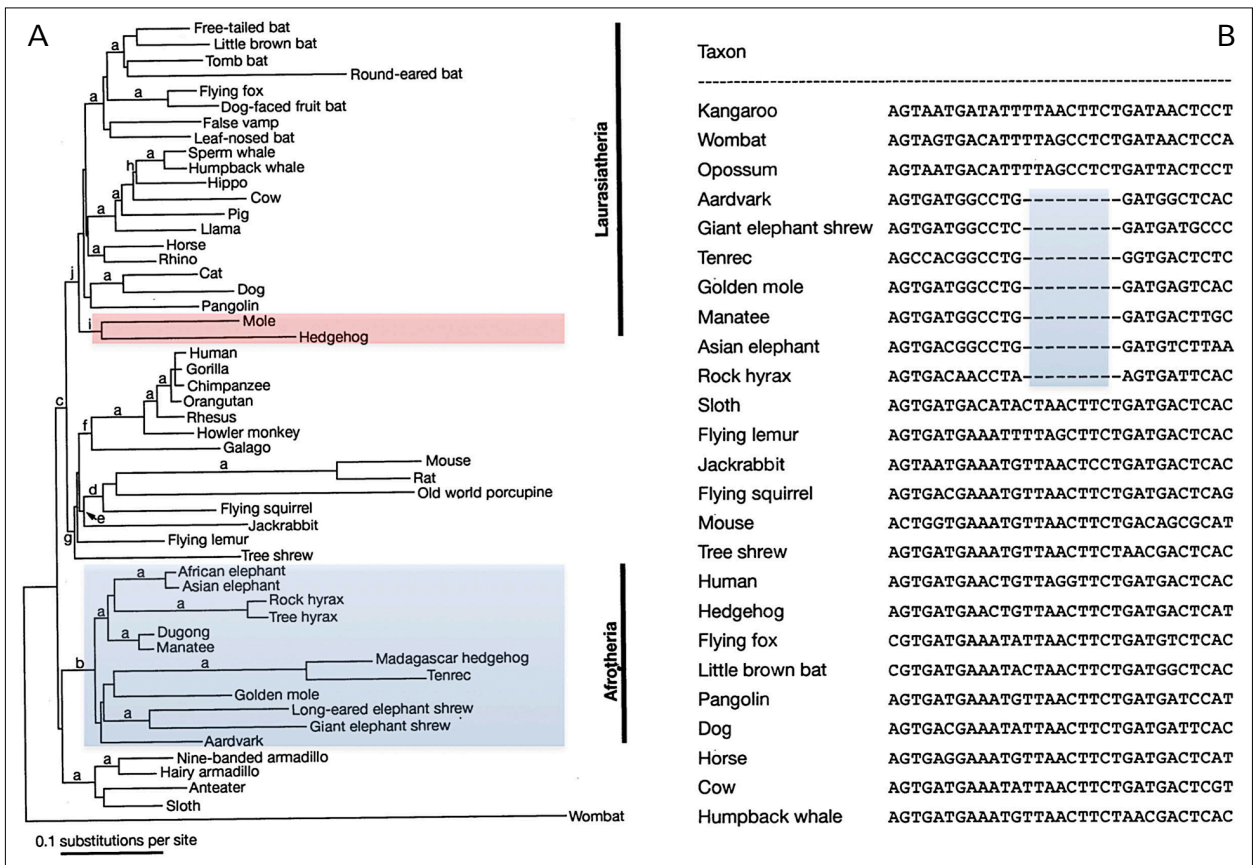

Fig. 3. A) Cladogram of placental mammals based on molecular data; the blue field comprises the Afrotheria, the red field the Eulipotyphla, of which only few members are considered here. — B) Nucleotide-sequences from the BRCA1-Gene (breast cancer) of selected placental mammals; all afrotherians are characterized by the deletion of nine homologous nucleotids. Modified from Madsen et al. (2001).

sidebranch of the Eutheria. The remaining Lipotyphla are mostly put as a more or less coherent taxon Eulipotyphla within the Laurasiatheria; Erinaceidae (hedgehogs) and Solenodontidae (solenodons) appear to belong to the Eulipotyphla, but the exact relationships within this taxon are still disputed (SPRINGER et al., 1997; STANHOPE et al., 1998; MOUCHATY, 1999; MADSEN et al., 2001; BECK et al., 2006, and many others). For heuristic reasons, I start with the eulipotyphlans, because they are better known morphologically than the afrosoricids. The Xenarthra of South America, whose position within the Placentalia is still disputed, is not considered in this study.

I confine the descriptions to a few taxa of placental mammals. Marsupials are completely omitted, but at least the Didelphidae (- opossums such as *Monodelphis domestica* -) have very simple and generalized outer nasal cartilages. Big mammals tend to show very derived and simplified structures, but the relationships with the mammalian groundplan is normally easy to comprehend (STURM, 1936). Of the haplorhine primates, most of the neotropic Platyrrhini show a progressive expansion of the outer nasal cartilages, whereas the Catarrhini of the Old World have simplified them (SCHULTZ, 1935; MAIER, 1980). The external nose as part of the face has become a component of a complex visual signal in social communication. Extremely modified conditions are found in many Chiroptera, in which the elaborated 'leafs' around the nasal openings serve for sound emission; however, this taxon certainly urgently needs further morphological and functional studies (GOEBBEL, 1998, 2000, 2002). Recently, HÜPPI et al. (2018) collated the available data on the anatomy of the outer nasal cartilages; their main purpose was a character mapping of mammals based on this evidence. To me, this study shows that the available data are still too scanty and heterogeneous to enable robust conclusions.

Materials and Methods

The present study is not strictly morphological and has no systematic purpose. It is rather meant as a study of evolutionary biology indicating the functional and adaptational importance of a structural complex: The 'rostral organ' consisting of the outer nasal cartilages and its facial muscles as well as the rhinarium and the vibrissae, that was newly acquired by therian mammals in the earlier Mesozoic. However, this new tactile organ is not neomorphic strictly speaking, because it mostly consists of elaborations of structures pre-existent in the amniote forerunners. The systematic potential of this newly differentiated structural complex is shown in an exemplary manner in some soricids, of which a broader sample of taxa has been available (cf. MAIER, 2002). Otherwise, extremely specialized external nasal cartilages of a few selected placental taxa are demonstrated. Terminological details are only given for some of the taxa.

In the eighties and nineties of the 20th century, I made some efforts to produce 3D-models of a number of mammalian taxa; some data on adult soricids were published in MAIER (2002). Here, I present some of these models without going into morphological details. All sectional series on which the plate reconstructions are based, are housed in the histological collection of the former Department of Zoology of the University of Tübingen. Unfortunately, the models were lost meanwhile.

Descriptions

Non-Afrotheria

A) Erinaceidae

Hedgehogs are here represented by *Erinaceus europaeus*, which is probably derived in its anatomy of the rostrum. Related taxa like *Hylomys* or *Echinosorex* were not available for this study. Fig. 4A shows the snout of an adult hedgehog with its peculiar rhinarium. The external nasal openings (nares) are bounded at their posterior side by a flap of naked skin with comb-like free margin; this flap is supported by the prominent processus alaris superior (Fig. 4B, C). The outer nasal cartilages are connected with the vertical nasal septum inside the bony nasal cavity by a round cartilaginous beam which allows free movements of the anterior rostrum to all sides. The details of the involved facial muscles have yet been studied only in outlines (WHIDDEN, 2000, 2002). Fig. 4C shows that the outer nasal cartilages are not yet fully differentiated in a neonate hedgehog. Although WHIDDEN (2002, p. 162) had stated that the "proboscis is not especially large in erinaceids", Fig. 4B clearly demonstrates that in the adults it is well developed anatomically. It would certainly be worthwhile to study by slow-motion whether the movements of the snout of hedgehogs also show the characteristics of 'active sensing' (MUNZ et al., 2010). In any case, the outer nasal cartilages protrude through a single nasal aperture of the osteocranium, i.e. the two openings are fused and the prenatal process of the premaxillary no longer exists.

B) Soricidae

The outer nasal cartilages of various adult soricids were studied by MAIER (2002). Of course, soricids are well known by their protruding and actively moved muzzles and their mobile vibrissae (MUNZ et al., 2010). Because these movements occur at about 15 Hz, the input of this 'active sensing' can possibly be integrated by their brains into holistic representations of the outside objects. As in *Erinaceus*, the nasal septum is transformed into a round central beam near the aperture of the osteocranium (Fig. 5), which allows great moveability of the rostrum.
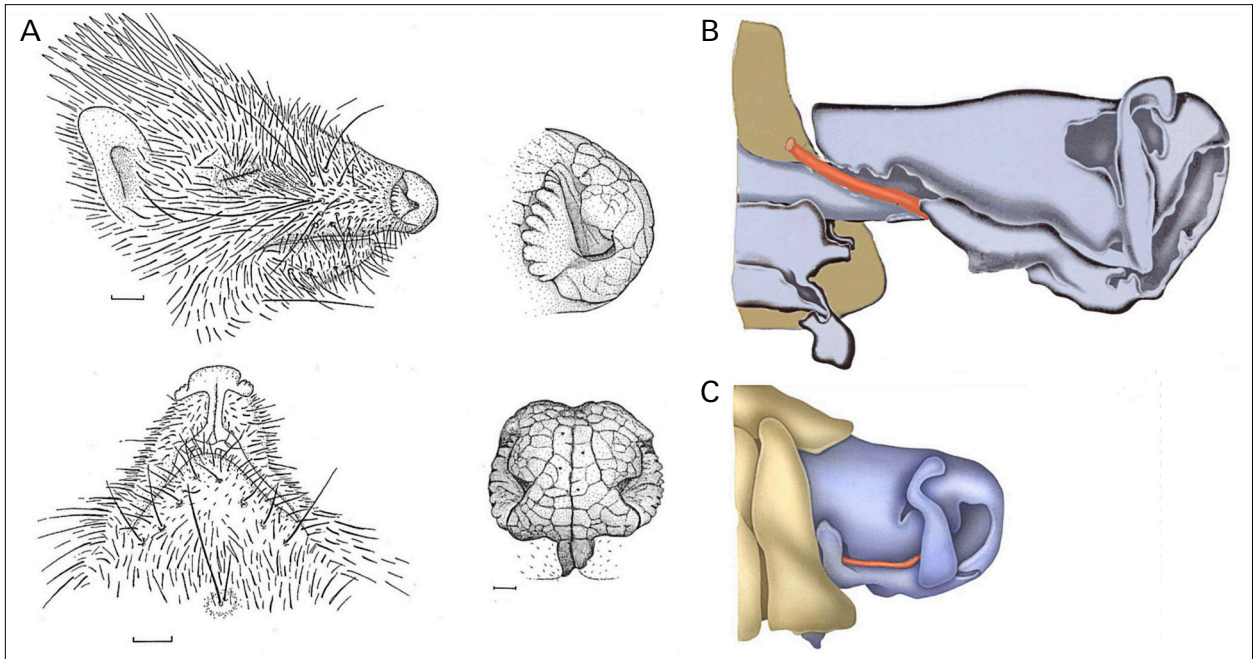
Fig. 4. A) Rostrum and rhinarium of an adult hedgehog (*Erinaceus europaeus*). Note that the rhinarium is connected with the anterior roof of the mouth by the philtrum. – B) External nasal cartilages of an adult hedgehog after removal of the facial bones of the right side. – C) External nasal cartilages of a neonatal hedgehog. Band C not to scale. (A – unpublished drawings of M. Ade; B and C are drawn by airbrush after 3D models based on plate reconstructions; W. Maier, original)
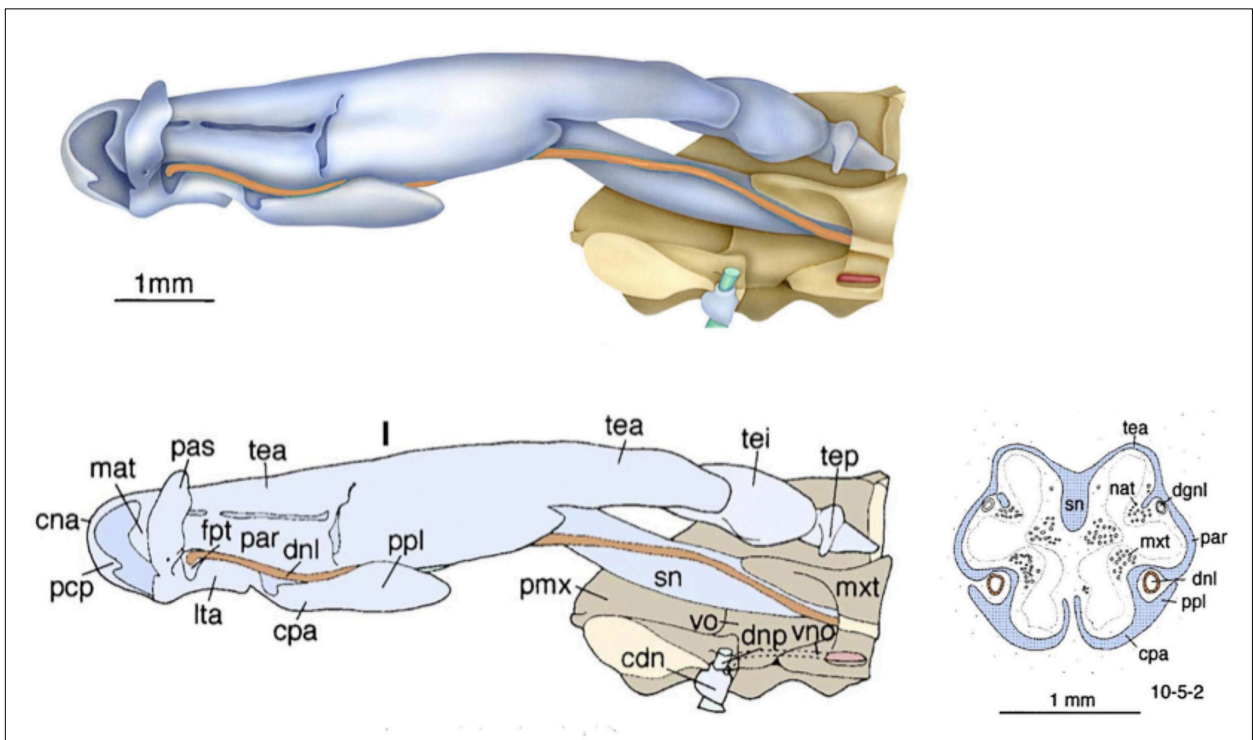

Fig. 5. Rostral nasal cartilages of an adult specimen of *Neomys fodiens* (Crocidurinae) seen from the left side; the dermal bones of the left side are removed. In the transitional zone, the nasal septum is transformed into a central beam which allows bending of the rostrum to all sides. The nasolacrimal duct runs outside the paries nasi within a deep sulcus lateralis; in its midth it is laterally framed by a processus para-lacrimalis (ppl), which is an outgrowth of the prolonged cartilago paraseptalis anterior (cpa). Modified from Maier (2002). Abbreviations: **cdn** – cartilago ductus nasopalatini, **cna** – cupula nasi anterior, **cpa** – cartilago paraseptalis anterior, **dgnl** – ductus glandulae nasi lateralis, **dnl** – ductus nasolacrimalis, **dnp** – ductus nasopalatinus (Steno), **ftp** – foramen praetransversalis, **lta** – lamina transversalis anterior, **mat** – marginoturbinal, **mxt** – maxilloturbinale, **nat** – nasoturbinale, **par** – paries nasi, **pas** – processus alaris superior, **pcp** – processus cupularis, **pmx** – praemaxillare, **ppl** – processus paralacrimalis, **sn** – septum nasi, **tea** – tectum nasi anterius, **tei** – tectum nasi intermedium, **tep** – tectum nasi posterius, **vno** – organon vomeronasale (Jacobson's organ), **vo** – vomer.
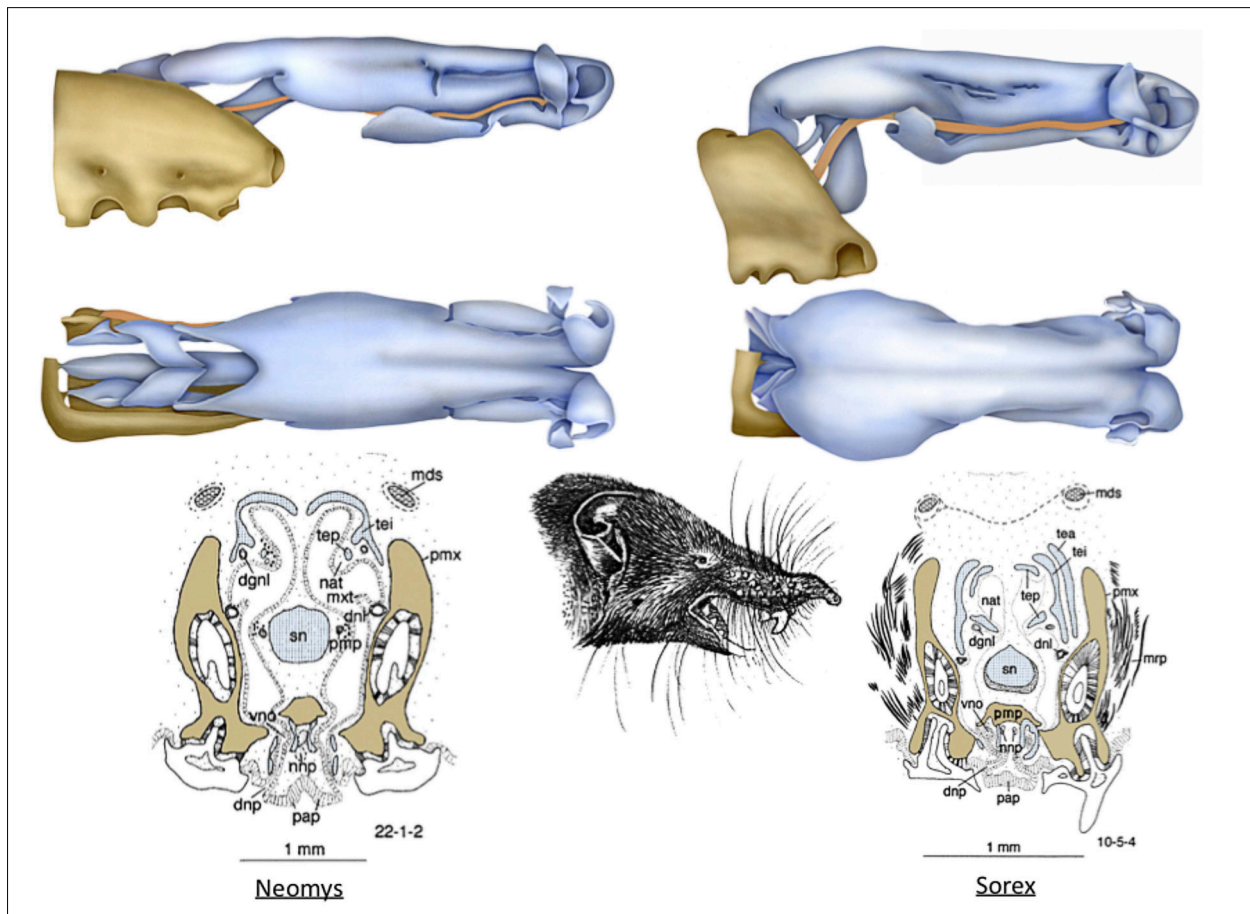
Fig. 6. Outer nasal cartilages of two adult soricids. Left row: *Neomys fodiens* in extended state. Right column: *Sorex araneus* in retracted position. Each side from above to below: Rostrum from right side, from dorsal side, cross section at the level of the opening of the vomeronasal organ. Note that in the retracted position of the isolated posterior elements of the nasal roof are telescoping against one another, the rounded nasal septum is bent S-like. The retraction is caused by the musculus retractor proboscidis (mrp), a specialized facial muscle. The inset, copied from a drawing of KINGDON (1974), shows a shrew retracting its rostrum when biting with the exposed front teeth – thereby protecting the structures of the rostrum. Abbreviations as in Fig. 5.

MAIER (2002) studied the rostral nasal cartilages of two adult specimens of *Neomys fodiens* and *Sorex araneus*. The snouts of these specimens were serially sectioned and plate models were prepared from these histological series. The posterior pieces of cartilage show a peculiar position: When the snout is fixed in a retracted posion as in the *Sorex* specimen under study, the cartilages are aligned telescopically; a facial muscle of considerable size, the newly named musculus retractor proboscidis (Fig. 5), was found to be responsible for this peculiar mode of retraction, which may be useful during biting with front teeth as suggested by a drawing of KINGDON (1974). Unfortunately, no slow-motion study of prey capture behavior in adult shrews seems to exist.

With the dated postnatal series of several soricid species, provided generously by the late Peter Vogel, it can be shown that this peculiar arrangement of the cartilages of the posterior paries nasi is realized only about 7−9 days after birth. It is suspected that mechanical strain caused by the action of the strong retractor proboscidis muscle is causing the fragmentation of the tectum nasi, i.e it is probably an example of pure epigenetic morphogenesis.

The chondrocranium of early ontogenetic stages of soricids were studied by DEBEER (1929) in fetuses of about 9 mm length (Fig. 6A). Their cartilaginous nasal capsules are still almost complete, i.e the anterior parts are in continuity with its posterior, intracranial portions. The external nasal cartilages protrude only moderately from the nasal aperture. In his study of African 'Insectivores', ROUX (1946) had available various fetuses of *Suncus orangiae*. He noticed that the external nasal cartilages begin to become separated from the posterior parts by gaps, but he did not realize its meaning, because he did not consider the adult condition (Fig. 6B). In his specimens, the outer nasal cartilages had become increasingly elongated in relation to the osteocranium.

The ductus nasolacrimalis in the two soricine (red-toothed shrews) taxa *Neomys* and *Sorex* runs at the lateral side of the paries nasi within a well-pronounced sulcus horizontalis. In contrast, the processus paralacrimalis of *Crocidura* and *Suncus*, as members of Crocidurinae, fuses with the tectum nasi, and the nasolacrimal duct is enclosed in a channel, which may open toward the nasal cavity (Fig. 8A−D). Outgroup comparison with many
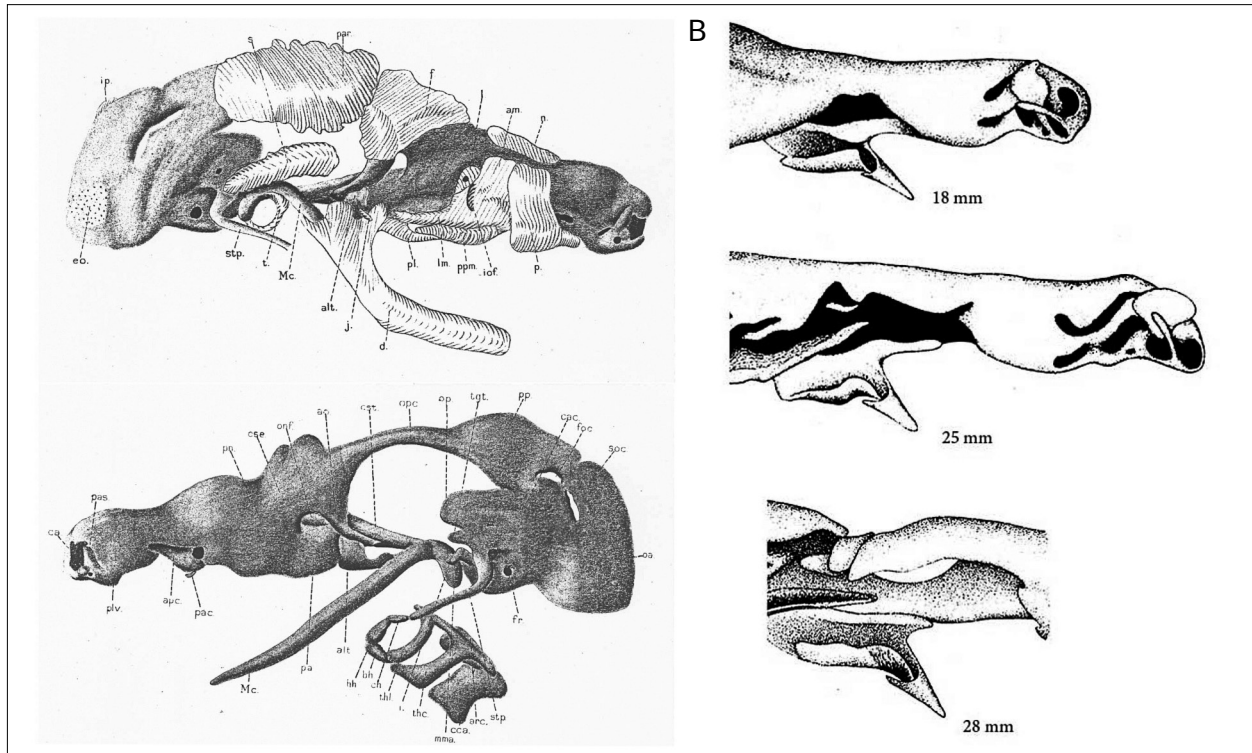
Fig. 7. A) Reconstruction of the cranium of a fetal *Sorex araneus* of 11 mm CR-length (reproduced from DeBeer, 1929). The chondro-cranium is near its maximal completeness. Left side with the exocranial bones removed. The protrusion of the external nasal cartilages is moderately pronounced. — B) Nasal cartilages of different stages of fetuses of *Suncus orangiae* showing different stages of segregation of the outer nasal cartilages (Roux, 1947).
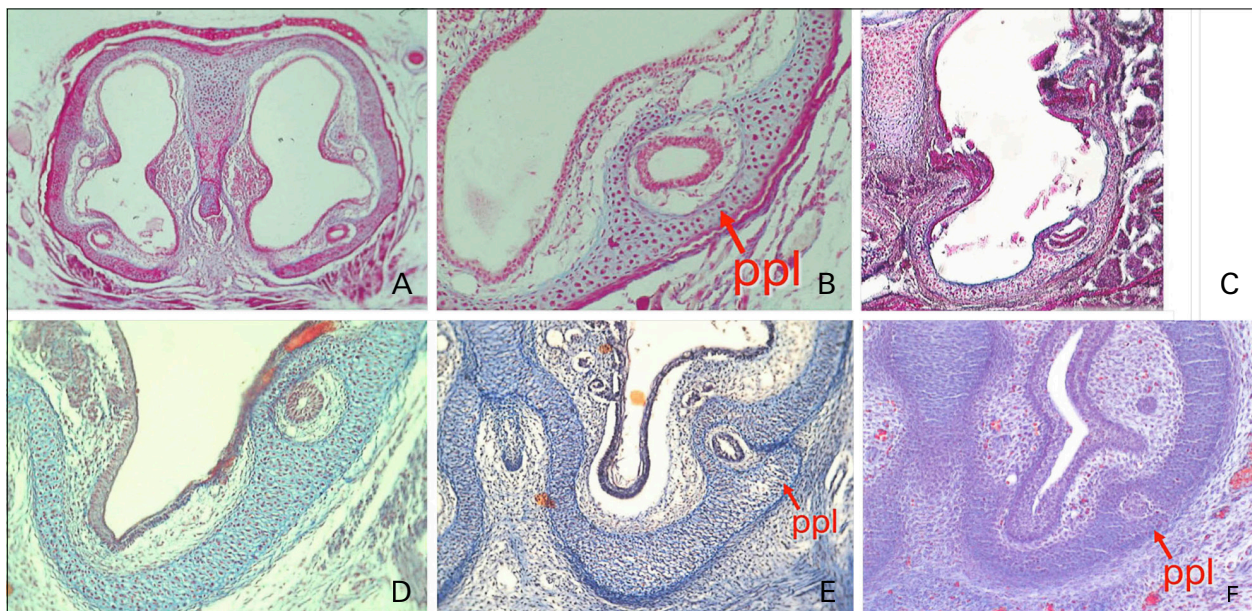

Fig. 8. A, B) Histological cross sections of *Crocidura russula* (15 d) at the level of the paralacrimal process. – C) Cross section of the outer nasal cartilages of an adult *C. russula*. – D) Cross section of a late fetus of *Suncus etruscus*. – E) The African taxon *Myosorex afer* is reminiscent in this character of the soricine condition, which is considered as plesiomorphic. – F) A young fetus of *C. russula* still shows the plesiomorphic soricine condition, i.e. probably it is an example of ontogenetic recapitulation. Not to scale.

other mammals suggests that the outside position of the nasolacrimal duct as in the soricids is the plesiomorphic condition, whereas the 'inside course' in all studied crocidurine (white-toothed shrews; studied were here only

Crocidura and *Suncus*) must consequently be considered as derived (apomorphic). It is of systematic interest that the African genus *Myosorex*, which is commonly aligned with the white-toothed Crocidurinae, retains the plesio-
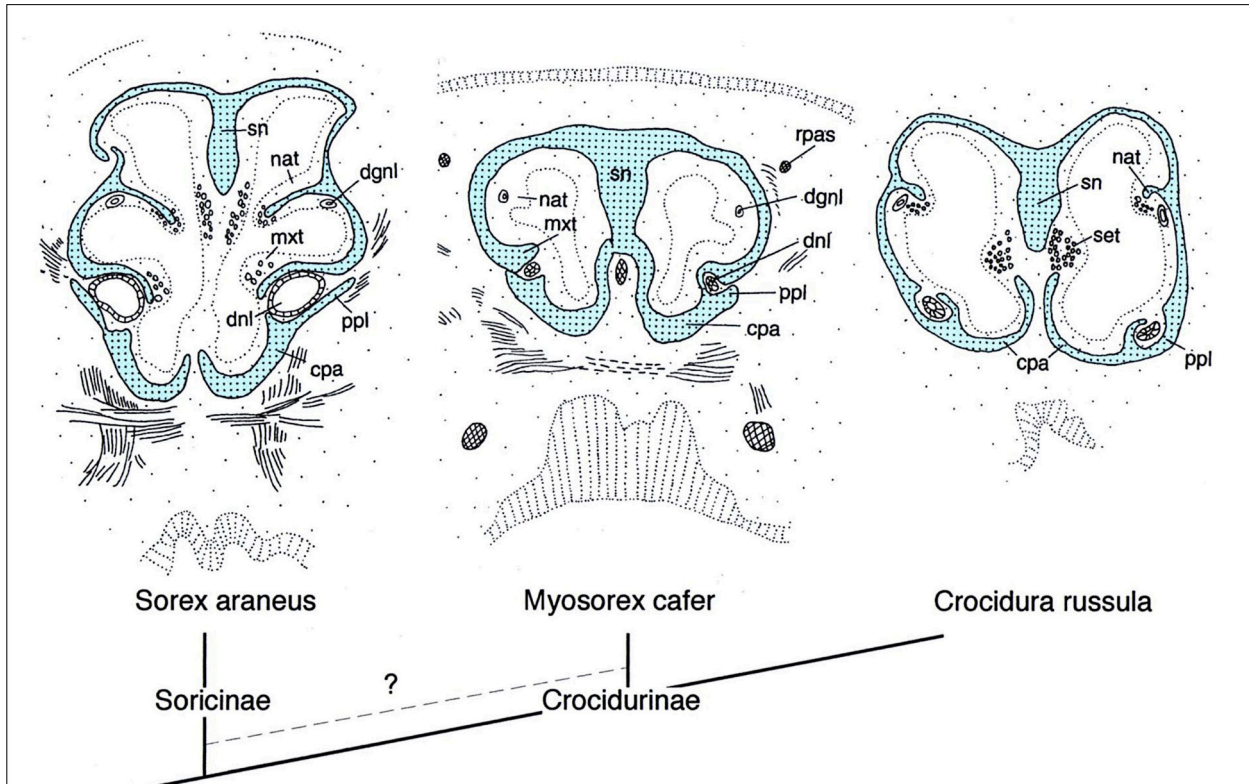
Fig. 9. The channel of the nasolacrimal duct and its relevance for the systematics of the Soricidae. In the Soricinae (red-toothed shrews), the nasolacrimal duct is laterally incompletely covered by the paralacrimal process of the cartilago paraseptalis anterior. In the Crocidurinae (white-toothed shrews s.l.) the duct is completely enclosed by the lateral wall of the anterior nasal capsule. *Myosorex cafer* (darkfooted, white-toothed shrew of Southern Africa), which is usually more or less closely allied with the Crocidurinae, shows the same incomplete enclosure of the nasolacrimal duct as the Soricinae. However, this arrangement is most probably a symplesiomorphic character state. Anyhow, this example of comparative anatomy demonstrates the principal potential of the outer nasal cartilages for phylogenetic systematics. Abbreviations as in Fig. 5. Not to scale.

morphic nasal structures of the Soricinae. Provided that *Crocidura* and *Suncus* represent the apomorphic state, *Myosorex* could be considered as their sister-group (Fig. 8E). This in accordance with modern systematics, which often classifies *Myosorex* as own subtaxon Myosoricinae (WILLOWS-MUNRO & MATTHEE, 2009; TAYLOR et al., 2011). It is noteworthy, that young fetuses of *Crocidura* ‚repeat' the soricine condition (Fig. 8F).

C) Talpidae

A fetal stage of *Talpa europaea* is shown by the original halftone plate of FISCHER (1901), which was the first craniogenetic study based on serial sectioning and wax-plate models (Fig. 10A, B). The chondrocranium is almost completely developed (so-called ‚stadium optimum'), and shows neither endochondrial ossifications nor resorptions. The external nasal cartilages are confluent with the rest of the nasal capsule; the dermal bones of the nasal and the premaxillary are still small and do not yet cover the cartilage of the endocranium. Seen from above, the external nasal cartilages already have the form of a protruding double-tube. The rhinarium, which is supported by the cupula nasi is often depicted by pho-

tos, but the rhinoglyphic pattern and the facial muscles of the external nose have not yet been adequately studied in moles. However, it is known that the outer nose of subterranean and fossorial moles is not actively involved in digging, but that it mainly serves mechanosensitive functions (HALATA, 1975, 1990). According to MORLOCK (1983), the outer nasal cartilages of the Talpidae have not evolved extreme specializations of the rostrum - but see *Condylura cristata*.

D) Solenodontidae

The geographically isolated solenodons (*Solenodon* spp.) of the Greater Antilles are relatively big inhabitants of the forest floor. They are among other characters distinguished by their prominent and mobile snout (Fig. 11), with which they explore the forest floors. Although the external nasal cartilages are several centimeters long, the outer wall is not segmented in any way; however, the nasal septum is a rounded beam of cartilage near the exit from the osteocranium, allowing considerable mobility. WHIDDEN (2002) described the facial muscles that actively move the rostrum. The systematic position of the solenodontids was subject to controversial discussions in
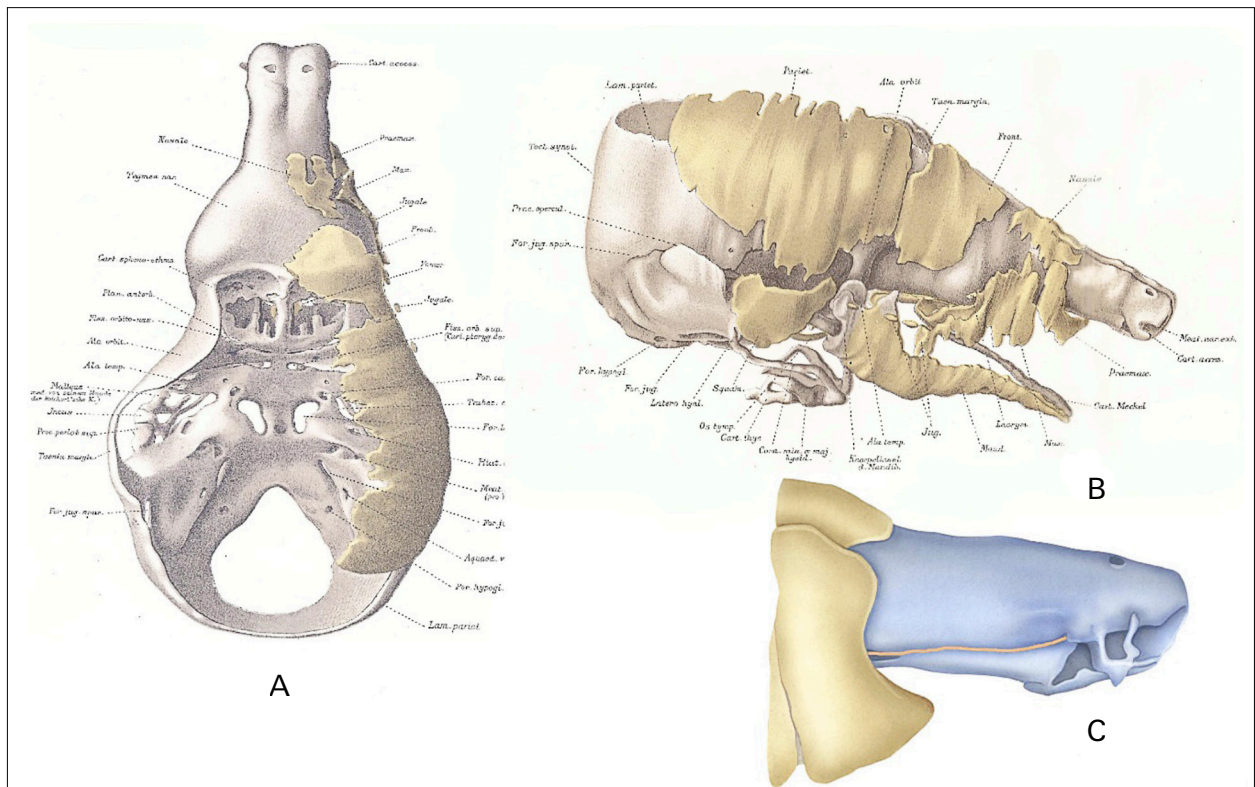
Fig. 10. A, B) Chondrocranium of a fetal *Talpa europaea* (adopted and slightly modified from Fischer, 1901). — C) Outer nasal cartilage of a juvenile *Talpa*. The nasolacrimal duct runs lateral to the cartilago paraseptalis throughout. (Drawing after a plate reconstruction; original). Not to scale.

the past, but there seems to be consensus now to put them into the Eulipotyphla (Whidden & Asher, 2001). In museum specimens, dried remnants of the outer nasal cartilages sometimes stick to the cleaned skull (cf. Wible, 2008; fig. 4).

Afrotheria

Relatively recently, Poulakakis & Stammatakis (2010) reviewed the internal relationships of the Afrotheria. The first four of the mentioned taxa are classified together as subgroup Afroinsectiphilia, the last three as subgroup Paenungulata; only the Afroinsectiphilia are here considered, because the members of the other taxa show highly specialized outer noses.

A) Tenrecidae

The Madegassean 'hedgehogs' (Tenrecidae) are represented by quite diverse ecomorphic adaptation types. Closer inspection of the cross sections indicates that the processus alaris superior of the group is quite different from what is known from other therian mammals. It appears to originate with a broad basis from the anterior end of the paries nasi and only the tip of the processus alaris superior (painted pink) is freely ending and thus corresponds to the common processus alaris superior.

From the lower end of the paries, a slender cartilage bar originates and is connected with the cartilago paraseptalis anterior (Fig. 12); I name this connection commissura lateroventralis. In *Micropotamogale*, this commissure runs very obliquely. The studied specimens, which all represent late fetal stages, are otherwise not very specialized - but we do not yet know the cartilages of the adult rostrum. *Orycteropus* and *Macroscelides* also show a slender bar (see below), but it originates at the processus alaris superior and therefore, the homology of these cartilages remains doubtful.

B) Orycteropidae

I had a neonate specimen of the aardvark (deadborn from the Frankfurt Zoolocical Garden) available for histological processing. The snout of the adult *Orycteropus afer* was described by Pocock (1924) (see Fig. 13). The outer nasal cartilages are relatively stout and they support a rhinarium which is extensively used when sniffing in ant and termite heaps. For the thematic context it seems important to note that the free processus alaris superior is also connected with the anterior paraseptal cartilage by a relatively strong connection tentatively named commissura alatransversalis (cat). Stössel *et al.* (2010) published a study on the comparative anatomy of the ethmoidal region of *O. afer*, *Loxodonta africanus* and *Procavia capensis*. It is not surprising that their description of
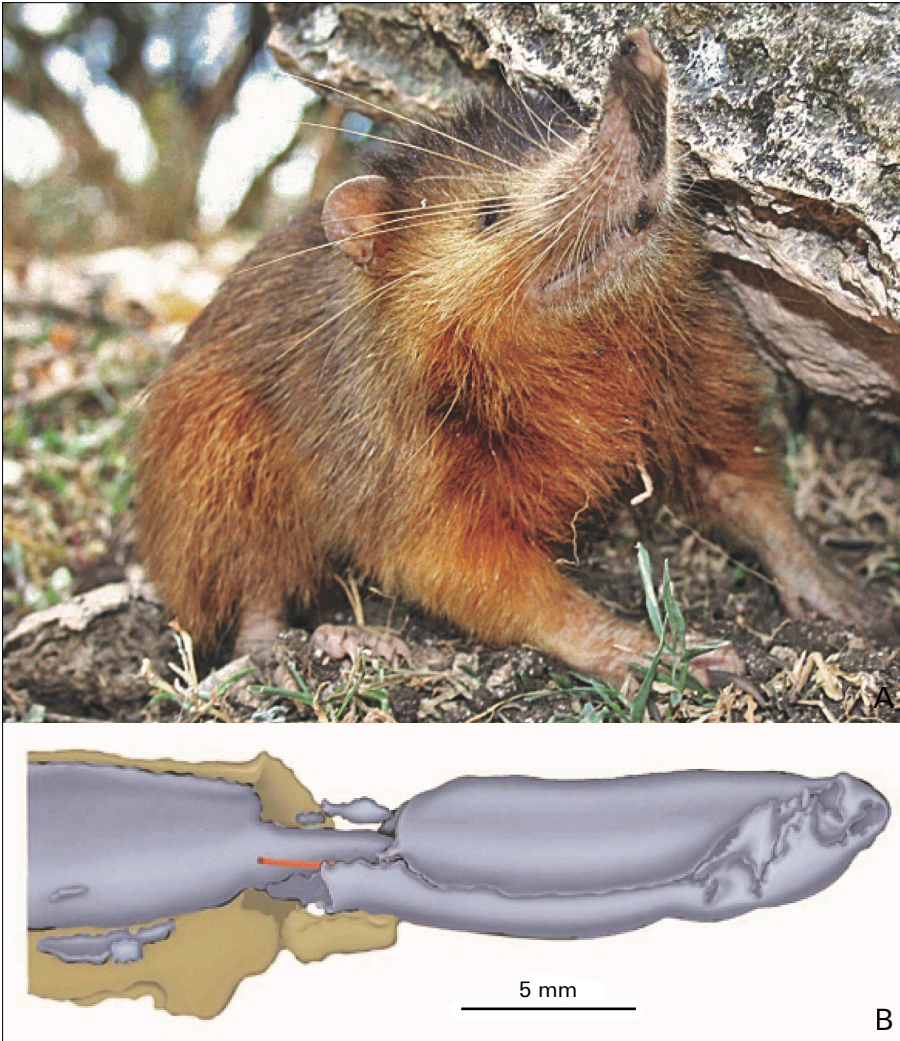
Fig. 11. A) Habitus of an adult specimen of *Solenodon paradoxus* (Wikimedia, photo by „Seb az86556"). — B) Rostral nasal cartilages reconstructed from an adult *S. paradoxus* (original from W. MAIER). The nasal septum is forming a central beam ('biegsame Zentralachse' according to NACHTIGALL, 1971), which allows bending of the whole rostrum to all sides. Not to scale.
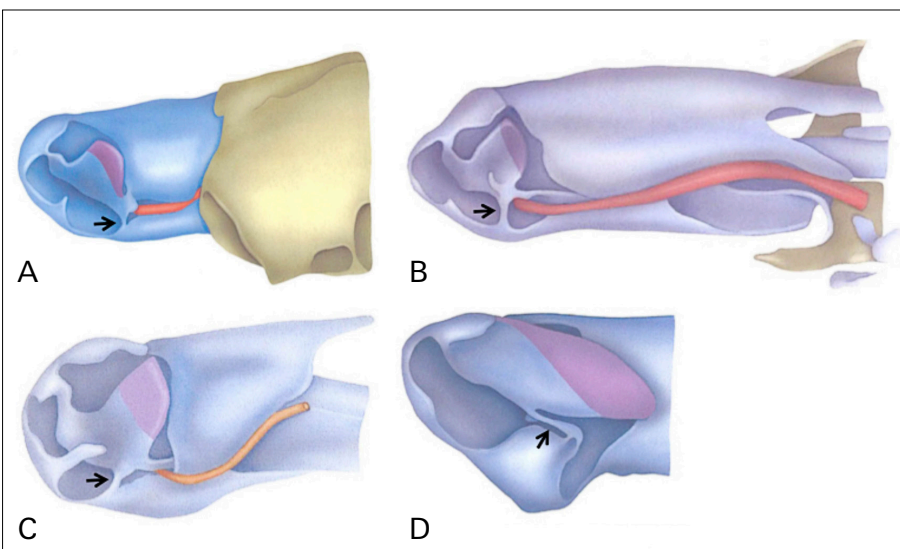

Fig. 12. Selected members of Afrosoricida (different ontogenetic stages): — A) *Echinops telfairi* (Tenrecidae); — B) *Microgale pusilla* (Tenrecidae); — C) *Setifer setosus* (Tenrecidae); — D) *Micropotamogale lamottei* (Potamogaleidae). The taxa show synapomorphies in details: In all taxa the processus alaris superior (pink colour) has a broad origin at the anterior paries nasi, and the paries nasi is always connected with the processus lateralis ventralis a narrow cartilaginous bridge (arrows), here named commissura lateroventralis. Not to scale.

*O. afe*r does not differ significantly from the presented picture in Fig. 13B, because both are based on the same serial section housed in Tübingen. Hyraxes, elephants, and manatees have too derived external nasal cartilages to warrant comparison.

C) Macroscelididae

The proboscis-like snout of macroscelidids, which gives these animals its German vernacular name 'Rüsselspringer' ['trunk jumper'], is a very mobile touching organ for
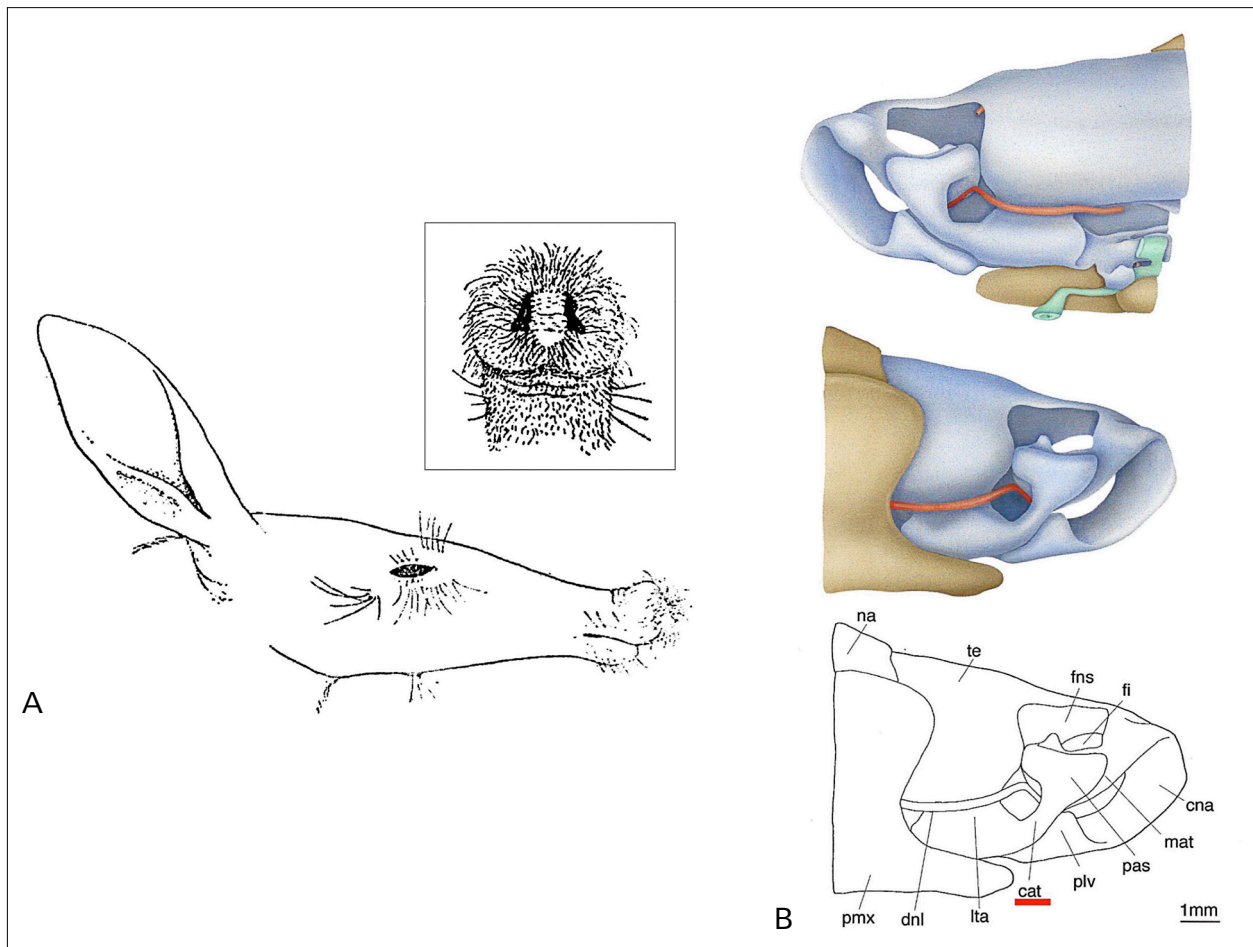
Fig. 13. Outer nasal cartilages of *Orycteropus afer*. — A) Habitus of the head and snout of an adult aardvark as depicted by Pocock (1924). — B) Plate reconstruction of a neonate of *O. afer*. In the view from the left side (top), the premaxillary and nasal are removed. The aardvark has relatively unspecialized cartilages. Abbreviations: **cat** – commissura alatransversalis, **cna** – cupula nasi anterior, **dnl** – ductus nasolacrimalis, **fi** – fenestra internasalis, **fns** – fenestra nasi superior, **fpt** – foramen praetransversale, **lta** – lamina transversalis anterior, **mat** – marginoturbinale, **na** – nasale, **par** – paries nasi, **pas** – processus alaris superior, **plv** – processus lateralis ventralis, **pmx** – premaxillare, **te** – tectum nasi.

'active sensing', whose actions need to be further studied by slow motion film. Fig. 14A is based on a deadborn neonate of *Macroscelides proboscideus* provided by the late Prof. E. Kulzer. Its sidewall is supported by cartilages, which are differentiated into rings (annuli) that are reminding a trachea. However, in fetuses, the outer nasal cartilages are complete tubes, which only begin to further differentiate around the time of birth. As shown in Fig. 14C, the separation process of the anterior tectum nasi begins behind and proceeds rostrally. The cartilages surrounding the nasal openings are not much affected by the differentiation occurring more posteriorly; one can see again a well-developed processus alaris superior, which is connected with a projecting anterior transversal lamina by a slender commissura alatransversalis (Fig. 14C). The outer nasal cartilages are stabilized posteriorly by a neomorphic cartilago externa on each side. Alltogether, Macroscelididae own the most derived external nasal cartilages of all extant mammals.

DuToit (1942) carefully described and depicted the nasal region of an embryo of *Elephantulus myurus* (CR-length 17 mm). The anterior part of the nasal capsule is still complete, but the photo of her 3D model (Plate 1, fig. 3) clearly shows sequential thickenings of the paries lateralis, which foreshadow the formation of the above described annuli. Because the author was not aware of the adult structures of the outer nasal cartilage, she did not notice this detail – nor did she observe these structures in the older embryos she had at her disposal. Kratzing & Woodall (1988) studied histological cross-sections of adult specimens of *Elephantulus brachyrhynchus* and *E. myurus*, but they did not recognize the specific morphology of the outer nasal cartilages either.

Discussion

The present paper does not pretend to provide a complete and comprehensive evolutionary story. Rather, it points out in an erratic way the scientific potential for future
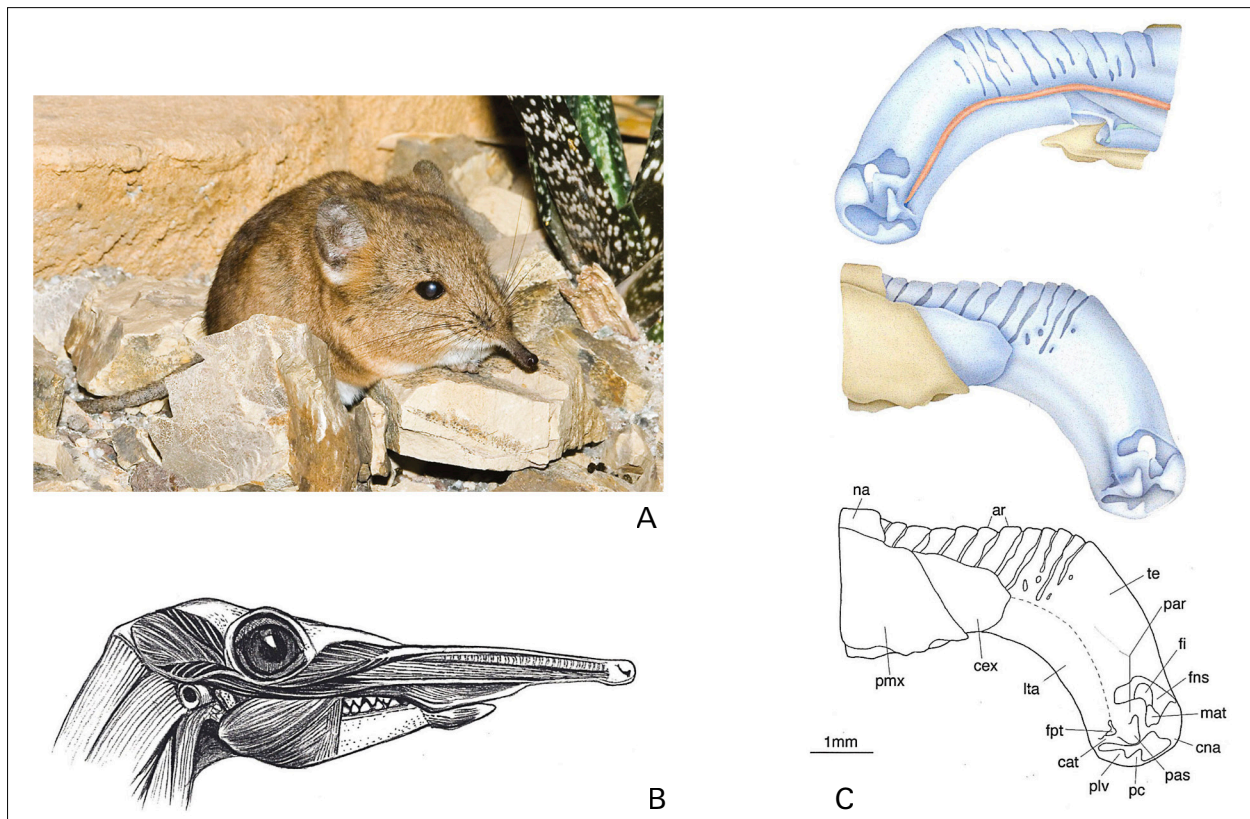
Fig. 14. 'Proboscis' of different Macroscelididae. — A) Habitus of *Macroscelides proboscideus* (Wikimedia, photo modified after „Olaf Leillinger"). — B) Skinned head of *Rhynchocyon cirnei* in right lateral view showing the segmentation of the complete external nasal cartilages - except the most rostral part (after KINGDON, 1974). — C) Plate reconstruction of the external nasal cartilages of a neonate of *M. proboscideus* (dead-born of the breeding group at the Dept. of Zoology Tübingen, donated by the late Prof. Kulzer). In the upper figure the left exocranial elements are removed. The fragmentation of the outer nasal cartilages is just beginning (After a plate model, W. Maier, original). (Abbreviations: **ar** – annuli rostrales, **cat** – commissura alatransversalis, **cex** – cartilago externa, **cna** – cupula nasi anterior, **fi** – fenestra internasalis, **fns** – fenestra nasi superior, **fpt** – foramen praetransversalis, **lta** – lamina transversalis anterior, **mat** – marginoturbinale, **na** – nasale, **par** – paries nasi, **pas** – processus alaris superior, **pc** – processus cupularis, **plv** – processus lateralis ventralis, **pmx** – premaxillare, **te** – tectum nasi.)

research on a neglected part of the mammalian skull – the outer nasal cartilages. At present, too few species are known to allow far reaching systematic conclusions to be drawn; the valuable cladistic study of HÜPPI et al. (2018) includes very different ontogenetic stages - hence its limitations.

The reason for this lack of knowledge appears to be rather trivial technical problems. First of all, the outer nasal cartilages are not preserved in cleaned museum specimens; second, the final ontogentic differentiation of the snout structures occurs only in postnatal stages, and these are difficult to handle by conventional histological techniques. I used the very time-consuming embedding in celloidine in a limited number of taxa. Hopefully, modern imaging techniques combined with new contrasting techniques will abrogate this constraint. Of course, consisting mainly of cartilage and soft tissues, this skeletal complex can receive almost no stimulus from palaeontology.

All choanate gnathostomes show one anterior nasal opening at each side of the rostrum (see Fig. 1). The anterior end of the skull is thus formed by the premaxillaries, which send a pair of prenasal processes dorsally to meet the nasal bones (JANVIER, 1996; and many other textbooks). This condition is well illustrated in extant squamates (Fig. 15A, B). In mammals, the two external nasal openings have come so close together medially that the prenasal processes of the premaxillary have disappeared and the bony skull is distinguished by a single nasal aperture. (Most turtles also have single nasal apertures in the osteocranium; however, this fusion was certainly due to different functional causes, i.e. the acquisition of a rhamphotheca; cf. GAFFNEY, 1979).

Once the prenasal bones had disappeared, the cartilages could expand rostrally and become the support of a rostrum. Normally some facial muscles are associated with the external nasal cartilages, and it thus can become very mobile. At least in therian mammals, the anteriormost nasal cartilages became covered by a rhinoglyphic skin; this rhinarium is equipped with diverse tactile receptors, which make the external rostrum an important tactile organ (HALATA, 1975, 1990). Together with the vibrissae, the rostrum became an important sense organ, which was named 'rostral organ' by KLAUER (1984) that was principally able to perform 'active sensing'. It is es-
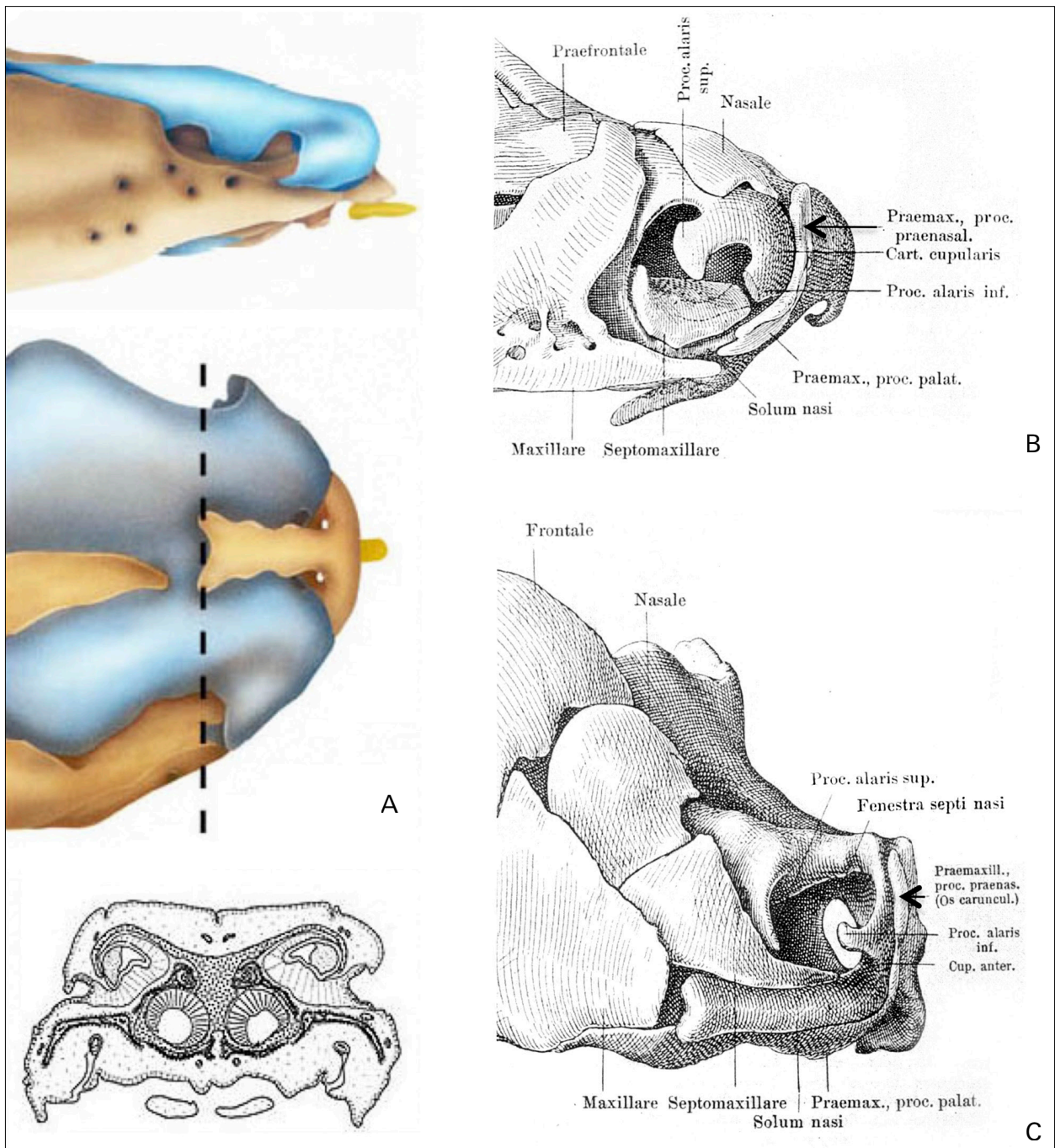
Fig. 15. A) Rostrum of a late fetus of *Heloderma suspectum* ('Gila Monster', head length 18.8 mm). The almost completed chondrocranium shows the anterior nasal cupulae of considerable size. However, these cupulae are separated by an unpaired processus praenasalis (ascendens) of the premaxillary. The egg-tooth is fixed to the lower end of the prenasal process. The stippled line indicated the position of the cross-section below. — B) Rostrum of a late fetal stage of *Lacerta agilis* (47 mm CRL) in right lateral view showing the processus praenasalis of the premaxillary (arrow). — C) Rostrum of a fetus of *Tachyglossus aculeatus* in oblique lateral view with a still persisting processus praenasalis supporting the 'caruncula' (egg-tooth), but not contacting the nasal bone (arrow). Not to scale. (A from BERNSTEIN, 1997; B and C modified from GAUPP, 1905).

pecially important in many small terrestrial and fossorial mammals. In larger mammals, the rhinarium, which is kept moist by special glands, collects pheromones which are normally transported in different ways to the vomeronasal organ. Modifications in this form-function-complex can be closely correlated with the ecomorphology of a taxon (ADE, 1999). The comparison between the taxa presented in this paper shows, that most structural elements of the outer nasal cartilages, as depicted in Fig. 2, are always present, but that they vary considerably in size and proportions. It is obvious, that the prominence of the rostrum has increased several times independently. Soricids and macroscelidids have evolved the outer nasal cartilages to extremes.

Preliminary systematic comparisons seem to indicate that the mobile rostrum belongs to the 'groundplan' of therian mammals, i.e. it must have existed in the last common ancestor of this monophylum (see also HÜPPI *et al.*, 2018). The evidence in extant monotremes is less clear, because their rostrum is very specialized (GAUPP, 1905; KUHN, 1971); ZELLER (1989) suspects that the rostrum of extant monotremes may be secondarily simplified. However, GAUPP (1905) showed that hatchlings of *Tachyglossus* 'recapitulate' a prenasal process, which supports the egg-tooth (caruncula) at its upper end (Fig. 15 C). Shortly after hatching, both bony process and caruncula are resorbed.

GAUPP (1905) had named the ascending process of the premaxillary as processus praenasalis, and I have adopted this term. Paleontological literature also uses other names: processus dorsalis, processus nasalis, processus ascendens, and others. In early amniotes as well as in synapsids up to cynodonts the rostral nasal aperture remained subdivided medially by the paired prenasal processes of the premaxillaries, which contact the anterior ends of the nasals (Figs. 1, 15). BROOM (1932), KEMP (2005), and many others have shown that the nasal openings are separate in cynodonts. PUSCH et al. (2019) demonstrate that the processus praenasalis is very narrow in the cynodont *Galesaurus*. According to KIELAN-JAWOROWSKA *et al* (2004), fossil taxa such as *Sinoconodon* and *Morganucodon* still have external nares which are separated by prenasal processes of the premaxillaries. In the docodont *Haldanodon*, the prenasal process (called processus dorsalis) appears to be incomplete (LILLEGRAVEN & KRUSAT, 1991). However, for *Morganucodon*, KERMACK *et al*. (1981) stated: "In no specimen is there a trace of a median dorsal process. It is, therefore, most probably that the external nares were confluent as in tritylodonts and – according to our interpretation – *Sinoconodon rigneyi*" (p. 2). This is in contrast to the later publications of *Sinoconodon changchiawaensis* by CROMPTON & SUN (1985), CROMPTON & LUO (1993), and KEMP (2005). Tritylodontids such as *Kayentatherium* have been shown to have medial ascending processes (SUES, 1986). The early mammaliaform *Hadrocodium* is tentatively reconstructed with two separate nasal openings (LUO et al., 2001). This short and incomplete list of fossil taxa demonstrates that the delicate dorsal processes of the premaxillaries are usually not well preserved in fossils - and hence reports are sometimes contradictory. However, the literature seems to indicate that the prenasal processes tend to become reduced in late therapsids and early mammaliaforms.

The prenasal processes of the premaxillaris develop as pairs, but they tend to fuse, and in hatchlings, they support the os carunculae ('Eizahn', egg tooth). Gaupp (1905) clearly pronounced that the reduction and loss of the processus praenasalis in mammals most probably is connected "mit der Ausbildung der 'äußeren Nase' der Säuger; während bei den niederen Wirbeltieren das knorpelige Nasenskelett bis zu seiner Spitze von Deckknochen überlagert ist, wird diese Spitze bei den Säugern frei, und

damit kann der ganze vordere Teil des Ethmoidalskelettes sich selbständiger entfalten" (p. 277). ("… with the evolutionary development of the 'outer nose' of mammals; whereas in the lower vertebrates the nasal cartilages are completely covered by membrane bones, the tip of the nose became free in mammals, and was therefore able to differentiate independently", transl. W.M.). It is evident that the reduction of the prenasal processes is also functionally connected with viviparity and with suckling.

This 'rostral organ' must be conceived as an important new acquisition (apomorphy) of early mammals. As far as we understand the rostral organ of extant mammals, it seems clear that arboreal mammals show a simpler structure of the nasal cartilages (MAIER, 1980; 1993), whereas terrestrial and fossorial taxa tended to evolve more complicated and diversified rostral structures. Obviously, the litter of forest floors, containing invertebrate and small vertebrate prey, had become a new and important source of food for early mammals; advanced modes of feeding biology are also reflected by tooth morphology (MAIER, 2020). Hence, the rostral organ can also provide valuable ecomorphological data. It is an old discussion, whether basal mammals were arboreal or terrestrial (CARTMILL, 1972). The finds of mammalian fossils of the Jurassic and Cretaceaous that were made in recent years render this alternative as too simple (KIELAN-JAWOROWSKA *et al.*, 2004). Alltogether, our present knowledge of the external nasal structures of mammals are by far too incomplete to be useful for systematical and adaptational generalizations – but their potential is evident.

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