Vertebrate Zoology 60 (1) 2010
37–72
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Chondrocranium and dermal bones of the Lowland Streaked Tenrec *Hemicentetes semispinosus* (Afrosoricida, Tenrecidae) and their comparison with *Potamogale* and other insectivoran-grade placental mammals

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Received on December 4, 2009, accepted on January 16, 2010.

> Abstract

Mammals of the insectivoran grade have always roused considerable interest, mainly because of their presumed similarity to the first ancestors of this group. While the morphology of adult specimens is relatively easy to access and thus well investigated embryos are rare and much less studied, in spite of their multiplicity of attributes. In order to provide additional morphological characters the ontogeny of the skull of *Hemicentetes semispinosus* was investigated using three serial sections through the heads of embryos and neonates respectively. The chondrocranium with cartilage replacing bones and dermal bones of the youngest embryo as well as the larger arteries in the posterior region of the heads of *Hemicentetes semispinosus* and *Potamogale velox* were graphically reconstructed. The findings of 70 skull and cranial artery characters were compared mainly with data from literature on several insectivore species. Already published hypotheses on phylogenetic relationships could be partially corroborated. Investigations of more primitive tenrecs and otter shrews on one hand and on e.g. golden moles and elephant shrews on the other hand are required in order to further evaluate differences and possible synapomorphies.

> Zusammenfassung

Insectivore Säugetiere haben schon immer großes Interesse geweckt, vor allem aufgrund ihrer Ähnlichkeit mit den ältesten Vorfahren der Gruppe. Während die Morphologie adulter Individuen relativ einfach zugänglich und daher gut untersucht ist, sind Embryonen selten und trotz der Vielzahl an Merkmalen deutlich weniger erforscht. Um die Datenbasis zu vergrößern, wurde die Schädelontogenese von *Hemicentetes semispinosus* anhand von drei Schnittserien der Köpfe von Embryonen bzw. Neonaten untersucht. Das Chondrocranium mit Ersatz- und Deckknochen des jüngsten Embryos sowie die größeren Arterien im hinteren Kopfbereich von *Hemicentetes semispinosus* und *Potamogale velox* wurden graphisch rekonstruiert. Die Daten von 70 Schädel- und Arterien-Merkmalen wurden hauptsächlich mit Literaturdaten von mehreren insectivoren Arten verglichen. Bereits publizierte Hypothesen bezüglich phylogentischer Verwandtschaftsverhältnisse konnten teilweise unterstützt werden. Zukünftig sind Untersuchungen an ursprünglicheren Tenreks und Otterspitzmäusen einerseits sowie an z.B. Goldmullen und Rüsselspringern andererseits erforderlich, um Unterschiede und mögliche Synapomorphien besser bewerten zu können.

> Key words

Skull ontogeny, cranial arteries, mammalian phylogeny.

Introduction

The history of the systematic relationships of the 'Insectivora' is intricate. Traditionally seen as representing a relatively primitive developmental state they were the most likely 'waste basket' within Eutheria. HAECKEL (1866) introduced the 'Lipotyphla', including tenrecs, otter shrews, golden moles, shrews, moles, hedgehogs, and Solenodontidae after exclusion of the Scandentia and Macroscelididae (BUTLER 1956, 1972). A common division split the group in 'Zalambdodonta' and 'Dilambdodonta' according to the crown pattern of the molar teeth (GILL 1885). Tenrecidae, Chrysochloridae, and Solenodontidae formed the 'Zalambdodonta'; Soricidae, Talpidae, and Erinaceidae the 'Dilambdodonta', a division that was also discussed (DE WITTE & FRECHKOP 1955; MCDOWELL 1958; SZALAY 1977; BUTLER 1988).

Furthermore the relationships within the 'Zalambdodonta' did not easily find agreement. BROOM (1915, 1916, 1927) postulated a separate order Chrysochloroidea for the golden moles, while most other authors placed them close to the tenrecs and otter shrews (MCDOWELL 1958; EISENBERG 1981; BUTLER 1988). The Solenodontidae were considered to be the sister group of the Tenrecidae and Potamogalidae with (GREGORY 1910; WEBER 1928; STORCH & WELSCH 1986) or without the Chrysochloridae (SIMPSON 1945; SABAN 1954, 1958; HEIM DE BALSAC & BOURLIÈRE 1955; BUTLER 1956; VAN VALEN 1967; THENIUS 1969; EISENBERG 1981; STARCK 1995) as well as being the sister group of the tenrecs (MIVART 1871), otter shrews (ALLMAN 1863), shrews (MCDOWELL 1958) or shrews and moles (BUTLER 1972, 1988; THENIUS 1979, 1980; EISENBERG 1981).

Finally molecular data suggested a completely new mammalian phylogeny with shrews, moles, and hedgehogs being a monophylum within the Laurasiatheria, which also includes artiodactyls, perissodactyls, whales, carnivores, and bats; while tenrecs, otter shrews, and golden moles form the Afrosoricida (or Tenrecoidea, see ASHER *et al.* 2009), united with elephant shrews, aardvarks, elephants, hyraxes, and manatees in the Afrotheria (e.g. STANHOPE *et al.* 1998; ASHER 1999, 2001, 2005; ASHER *et al.* 2002, 2008; AMRINE-MADSEN *et al.* 2003; DOUADY & DOUZERY 2003). However, some morphological and molecular data still contradict each other (e.g. ASHER, 2001; ASHER *et al.* 2002, 2003; ASHER & HOFREITER 2006).

One of the most frequently accepted monophylies is the position of tenrecs and otter shrews as sister groups. Both taxa are in practically all systematic papers united in a group, which facultatively also includes the Chrysochloridae and/or the Solenodontidae (see above). On the basis of fossil material BUTLER (1972) introduced the term 'Tenrecomorpha' for the Tenrecidae and Potamogalidae, which are now generally united in the family Tenrecidae with the subfamily Potamogalinae and the tenrecs with the subfamilies Tenrecinae, Oryzorictinae, and Geogalinae (e.g. BRONNER & JENKINS 2005). Most of the tenrecs discussed in the present paper belong to the Tenrecinae. The study examined the chondrocrania of two tenrec and one otter shrew species and compared them with embryos and juveniles of other insectivoran grade placental mammals. For the polarisation of the character states generally assumptions derived from other mammals were used as cited or concluded from own observations.

Materials and methods

Histological sections from the following embryos of tenrecs and otter shrews were investigated (Figs. 1–3):

1. *Hemicentetes semispinosus* (CUVIER, 1798)
   a) head length 14 mm (M47e)
   b) head length 23 mm (M155b)
   c) head length 23 mm (M169)

2. *Potamogale velox* (DU CHAILLU, 1860)
   a) head length 20 mm (2a)
   b) head length 25 mm (1a)

3. *Tenrec ecaudatus* (SCHREBER, 1778)
   head length 48 mm

For comparison the following representatives of Soricomorpha and Erinaceomorpha could be examined:

1. *Sorex araneus* (LINNAEUS 1758), subadult (168)

2. *Suncus* "*indicus*" (=*murinus*, LINNAEUS 1766), juvenile, head length 20 mm (M51b)

3. *Talpa europaea* (LINNAEUS 1758), embryo, head length 12 mm (M1215)

4. *Erinaceus europaeus* (LINNAEUS 1758), embryo, head length 10 mm (M5284)

Most of the specimens were donations to U. Zeller from the Max Planck Institute for Brain Research in Frankfurt, Germany (*Hemicentetes*, *Potamogale*, *Sun-*

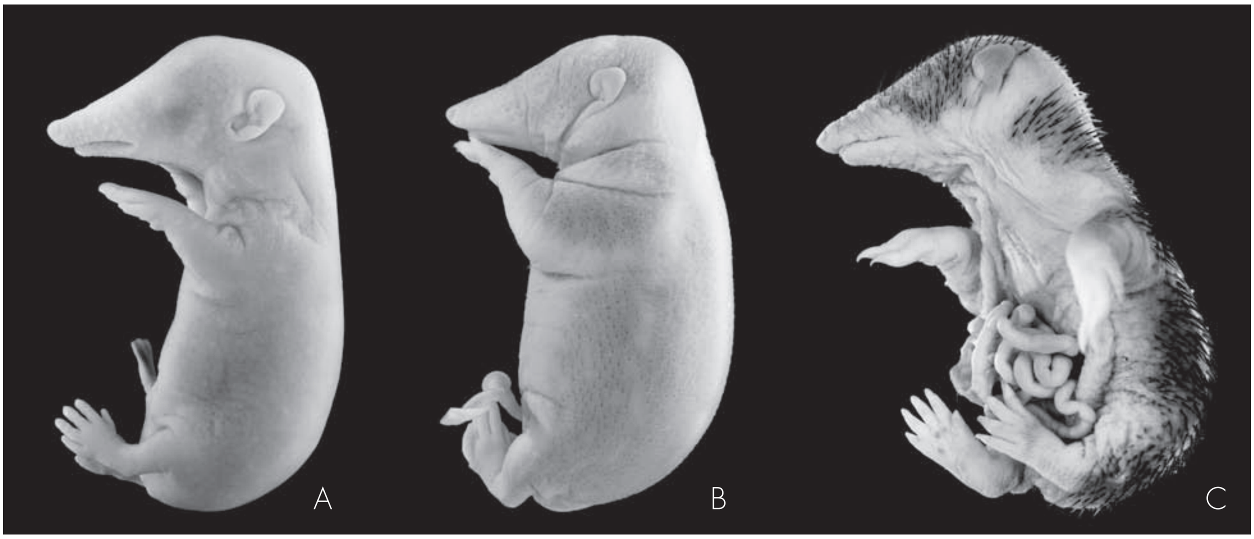

Fig. 1. *Hemicentetes semispinosus*, examined specimens in lateral view. **A**: head length 14 mm, **B**: head length 23 mm, **C**: head length 23 mm.

Fig. 2. *Tenrec ecaudatus*, examined specimen in lateral view, head length 48 mm.

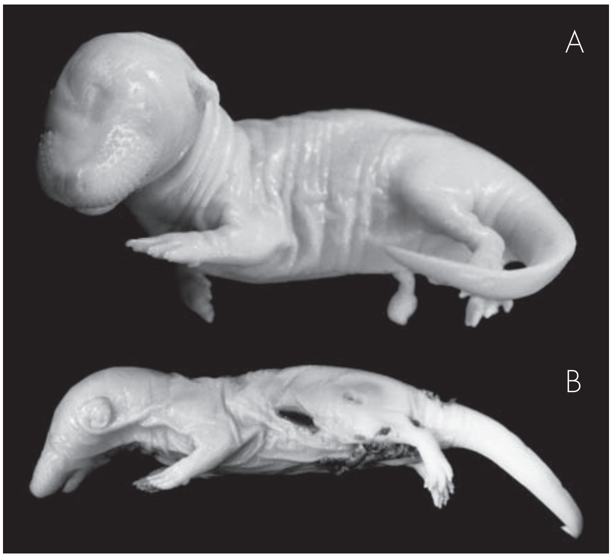

Fig. 3. *Potamogale velox*, examined specimens in lateral view. a. head length 20 mm, b. head length 25 mm.

cus, *Talpa*, and *Erinaceus*), the *Tenrec* was donated by D. Starck and the *Sorex* a loan from the Hubrecht Institute, Utrecht, Netherlands (Hubrecht Collection currently located at the Museum für Naturkunde, Berlin).

The heads were cut in frontal orientation. In most specimens the sections were made at a distance of 7 µm to 15 µm, the head of the *Tenrec* was cut with 35 µm. The sections were stained with AZAN.

From the youngest embryo of *Hemicentetes* graphical reconstructions with a 1 : 35.7 scale were made (Figs. 4–7). Therefore a photo was taken from every eighth section of the series cut with 7 µm. On the 35.7 times enlarged photos the cartilaginous structures and the cartilage replacing bones were marked, additionally on the left side the dermal bones. All markings were controlled microscopically on the stained sections. In the posterior part of the head the larger arteries were marked and separately reconstructed (Figs. 8 and 9). Figure 10 shows the position of 15 representative cross-sections (Figs. 11–24) and Figures 25–27 coronal sections at the sphenopalatinal ganglion of *Hemicentetes*, *Tenrec*, and *Potamogale*, respectively.

The two older specimens of *Hemicentetes* have head lengths of 23 mm, but in the presumably older one the spines are already visible. It is probably an animal that was a few days old, as the spines emerge postnatal (Eisenberg & Gould 1970). Additionally, the replacement of cartilage by bony tissue is further advanced. In order to describe the ontogeny of the skull as completely as possible, ‘the 23 mm specimen’ refers to the older one, unless explicitly stated otherwise.

The findings from the *Hemicentetes* embryos were compared with drawings of a model constructed by H. Behrens (Behrens 1998) in Göttingen for the younger embryo of *Potamogale velox*.

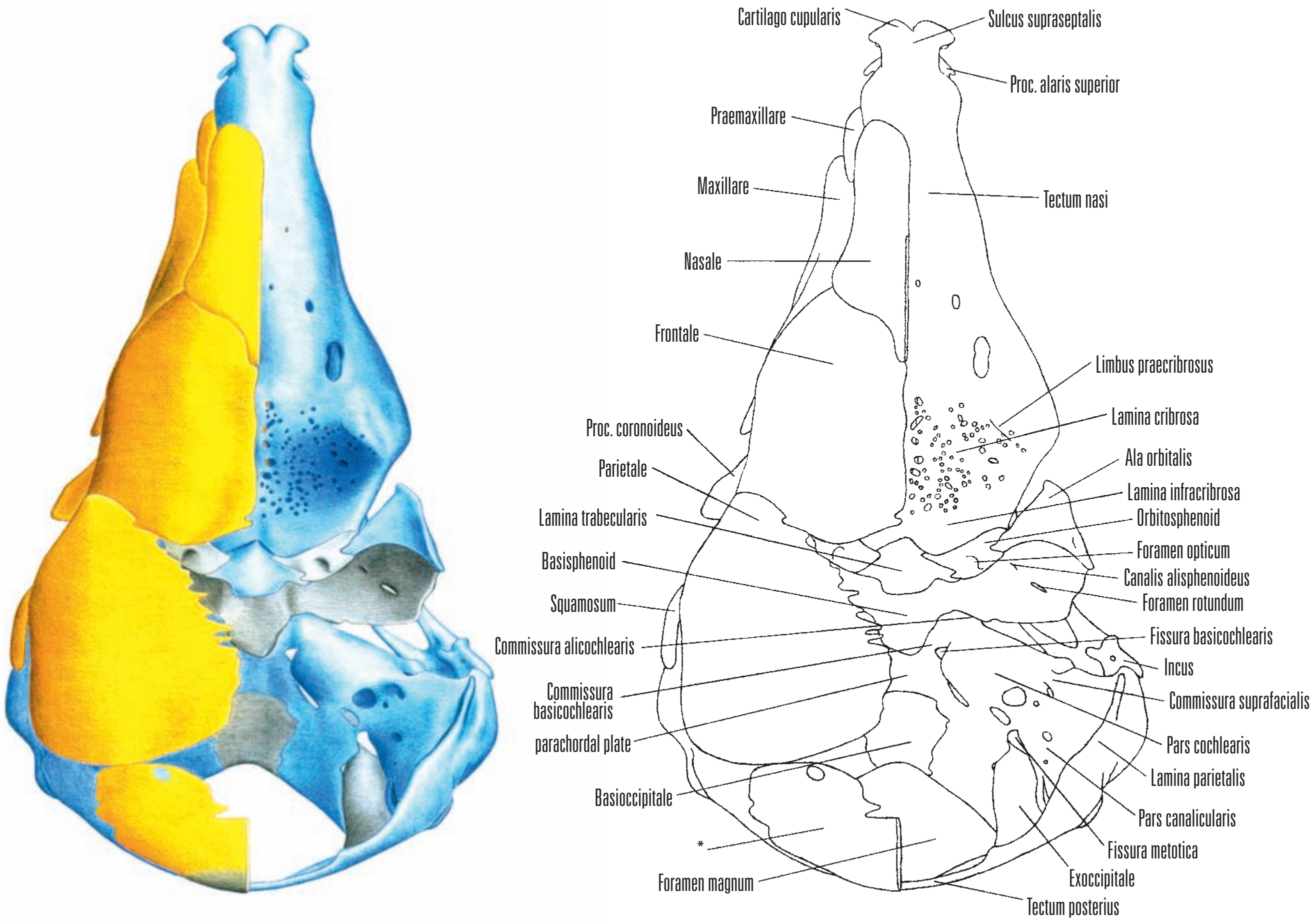

Fig. 4. *Hemicentetes semispinosus*, embryo, head length 14 mm. Graphical reconstruction and outlines of the skull in dorsal view. Blue: cartilage, yellow: dermal bones, grey: cartilage replacing bones; dermal bones of right half not drawn. *: fused interparietal and supraoccipital bones.

Description

1. Regio ethmoidalis

Hemicentetes semispinosus has a large nasal region with an ethmoidal region which extends far in caudal direction. The relation of the nasal region to the total skull length is 0.70 : 1 for the embryo and 0.76 : 1 for the adult.

The **septum nasi** is complete in the 14 mm specimen. Its ventral margin is, mainly rostrally and caudally, strongly thickened. In these areas it is drop-shaped in cross-section (Figs 14, 19). After resorption of the thin, dorsal part of the septum in the 23 mm specimen a cylindrical cartilaginous bar is visible in the rostral and caudal area. The specimen has no **fenestra internasalis**.

The rostral border of the nasal capsule is formed by the **cupula nasi anterior**, with the rostralmost part consisting of the **cartilagines cupulares** (Fig. 11). These cartilages are connected far rostral in *Hemicentetes*, leaving a small **cavum internasale** in between. Medioventrally from the cupular cartilage lies the caudally directed **processus cupularis**, which is very narrow in *Hemicentetes* (Figs 5, 6). Further caudally the **processus lateralis ventralis** originates and forms the ventral border of the cupula nasi anterior. It has the same shape as the cupular process and is connected with the nasal septum (Figs 5, 6). No **sulcus ventralis nasi** is visible (Figs 12, 13). Due to the lateroventrally directed opening of the **fenestra narina** no anterior wall is formed in *Hemicentetes* (Fig. 6).

Dorsally and slightly lateral of the fenestra narina is the **fenestra superior** located (Figs 6, 12) above the **ductus glandulae nasi lateralis** which terminates in the medial part of the opening. On the cartilaginous bar which separates the fenestra narina and the fenestra superior originates the **processus alaris superior** (Figs 4, 6). It is dorsolaterally orientated and covers the fenestra superior partially from lateral direction. The processus alaris superior is relatively small in *Hemicentetes*.

No **commissura alicupularis** which connects the processus alaris superior with the cupular process is visible in the investigated specimen, but the distance

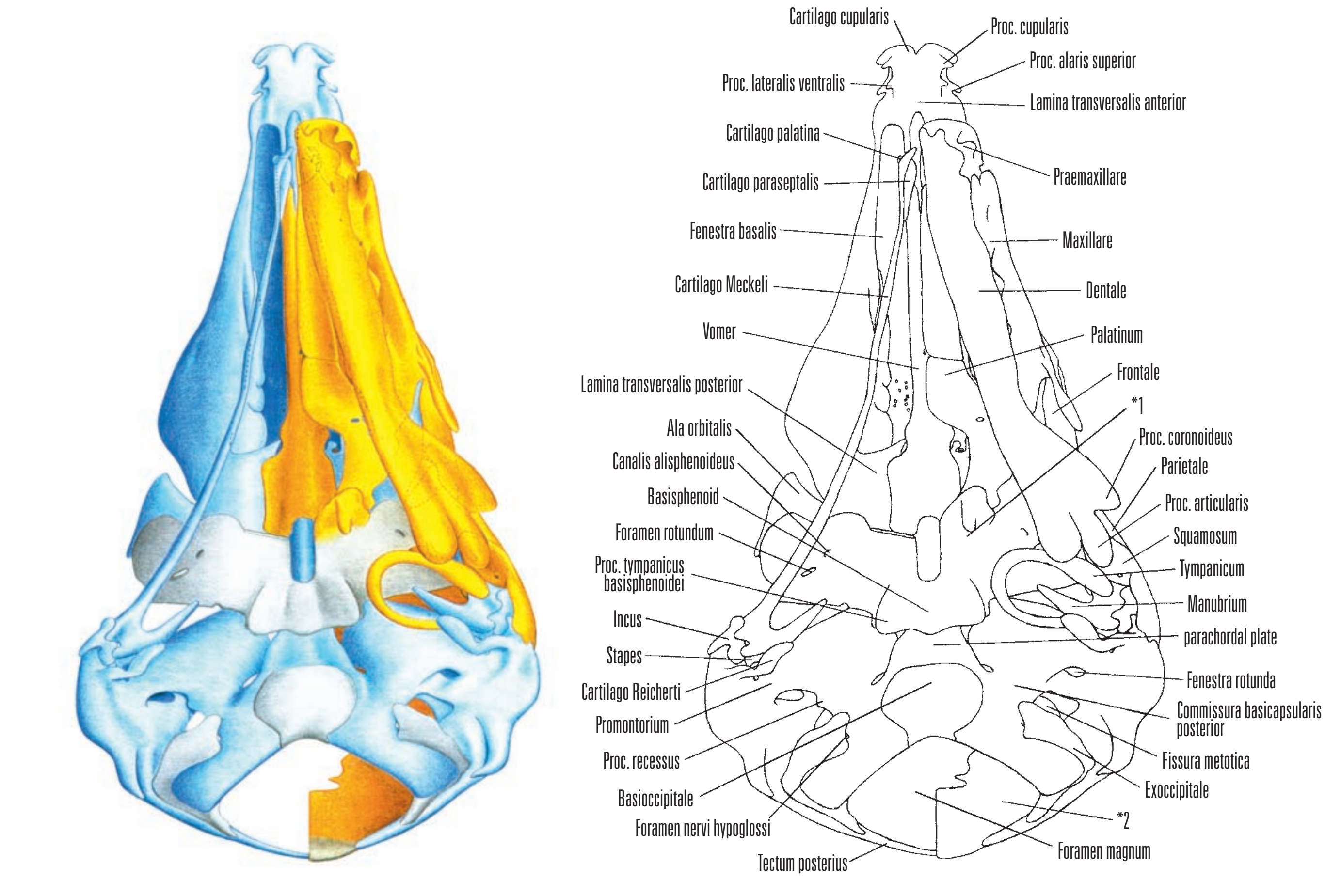

Fig. 5. *Hemicentetes semispinosus*, embryo, head length 14 mm. Graphical reconstruction and outlines of the skull in ventral view. Blue: cartilage, yellow: dermal bones, grey: cartilage replacing bones; dermal bones of right half not drawn. *1: fused pterygoid and alisphenoid bones, *2: fused interparietal and supraoccipital bones.

between the two processes is very small (Fig. 6). Thus the **primary fenestra narina** is incompletely divided in two. The rostrodorsal part encloses the **apertura nasalis externa** (Gaupp 1905a; Figs 11, 12). This opening is the **secondary fenestra narina**. The **ductus nasolacrimalis** terminates on the caudal border of the caudoventral part of the **vestibulum nasi**. The 23 mm specimen shows an alicupular commissure. The cupula nasi anterior is separated from the rest of the nasal capsule by a clearly visible lateral constriction in the area of the processus alaris superior (Figs 4, 5).

The **tectum nasi**, the roof of the nasal capsule (Fig. 4), is divided in a precerebral and a subcerebral part. The precerebral part ascends towards the **limbus praecribrosus** (Fig. 4), where the subcerebral area begins. The limbus praecribrosus is only in the lateral parts represented by a low cartilaginous ridge, medially exists a smooth transition into the **lamina cribrosa** (Fig. 4). Very little relief structure is visible on the tectum surface. The **sulcus supraseptalis** is shallow and only formed in the area of the cupula nasi anterior (Fig. 12). The caudal part is medially slightly flattened, but there is no groove (Figs 13–16). No **sulcus horizontalis** is visible.

The roof of the nasal capsule shows three openings in the 14 mm specimen (Fig. 4). The anteriormost, next to the nasal septum, exists only on the right side of the skull. One small branch of the arteria cerebri anterior leaves the cavum nasi there and continues in rostral direction. The middle foramen is pierced by another branch of the arteria cerebri anterior (Fig. 16), which lies lateral from and parallel to the other. The caudalmost and far laterally placed opening is probably due to resorption in the already far developed specimen. This is supported by the fact that neither nerves nor blood vessels penetrate this opening.

The **foramen epiphaniale** as opening for the **ramus nasalis externus** of the **nervus ethmoidalis** is absent in *Hemicentetes*. The ethmoidal nerve runs dorsal above the lamina cribrosa towards the **foramen cribroethmoidale** where it enters into the nasal capsule. In the 14 mm specimen it lies ventrally of the nasal tectum and runs rostral without leaving the nasal capsule.

At the highest point of the nasal capsule the nasal tectum shows a short, caudally spine-like elongated **crista galli** (Figs. 6, 17). No **spina mesethmoidalis** as an extension of the nasal tectum is visible.

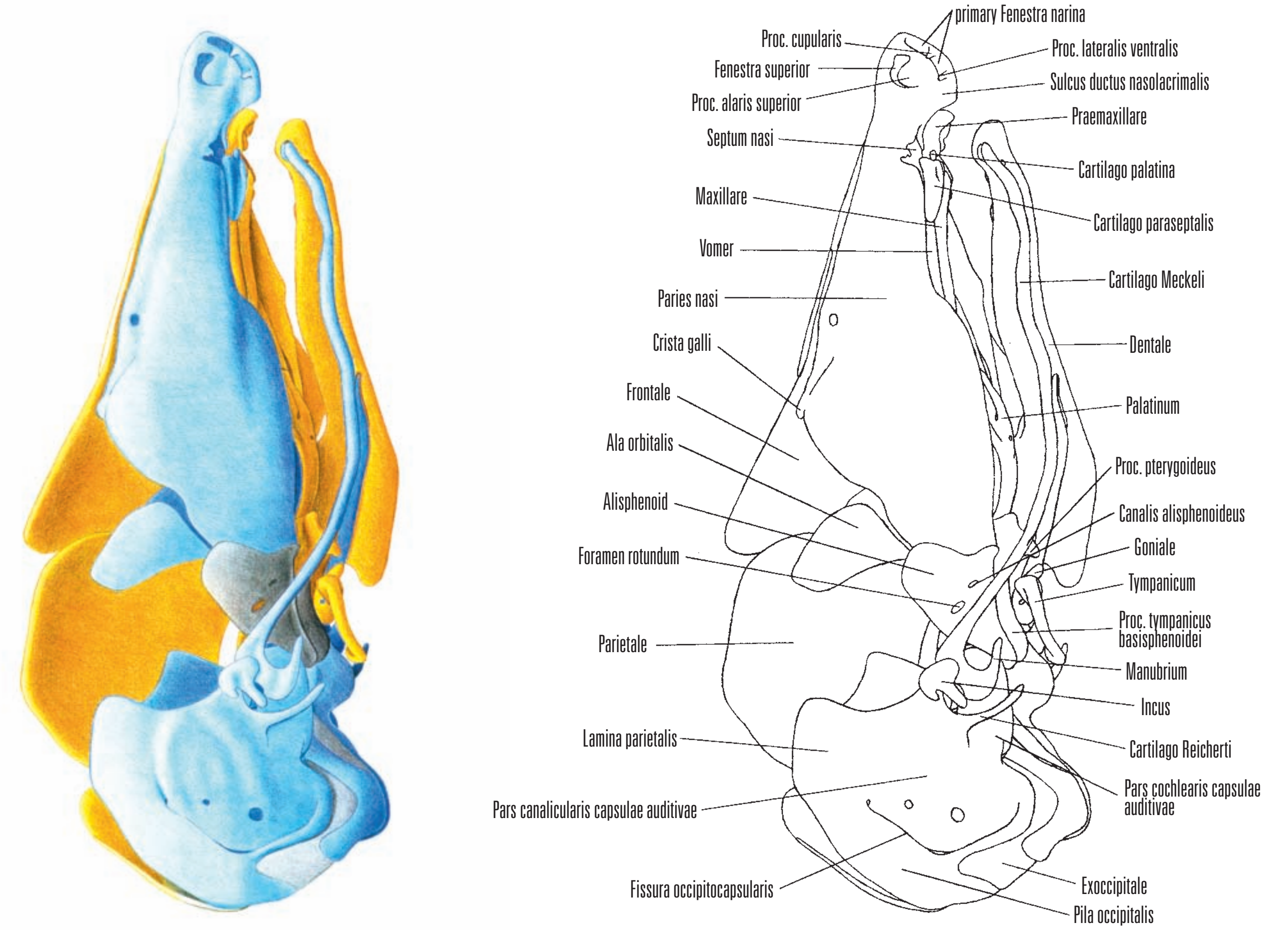

Fig. 6. *Hemicentetes semispinosus*, embryo, head length 14 mm. Graphical reconstruction and outlines of the skull in right lateral view. Blue: cartilage, yellow: dermal bones, grey: cartilage replacing bones; dermal bones of right half not drawn.

The major part of the subcerebral area of the nasal capsule is formed by the **lamina cribrosa** (Fig. 4). This structure is in *Hemicentetes* relatively wide with numerous small **foramina olfactoria**, which extend rostrally and laterally up to the limbus praecribrosus. The rostral part of the lamina cribrosa is steep, in caudal direction it becomes increasingly flat. The nasal capsule terminates caudally with the **cupula nasi posterior** which extends in *Hemicentetes* posteriorly almost to the hypophysal plate. In the caudalmost area the cupula nasi posterior is separated from the nasal septum and is located laterally of it.

The lateral part of the nasal capsule is formed by the **paries nasi** (Fig. 6). In the examined specimen no resorption is visible and the paries nasi is in continuous connection with the tectum nasi. **Sulci laterales anteriores** or **posteriores** are not visible. A moderate **prominentia lateralis** exists, but no **impressio orbitalis**. In *Hemicentetes* the eye is very small (Fig. 18) and still closed in the 14 mm specimen.

Except for a shallow groove for the **ductus nasolacrimalis** in the medial and ventral area the paries nasi has a rather smooth surface. The ductus nasolacrimalis passes in *Hemicentetes* through an incision in the caudal border of the maxilla and continues in a groove between the cartilaginous nasal capsule and the maxilla (Figs 15, 16). In the middle of the nasal capsule it passes around the ventral border of the paries nasi and runs ventrally of the lateral border rostrad (Fig. 14). In the zona anularis area it lies within the sulcus ductus nasolacrimalis (Fig. 13). Rostral from the zona anularis it terminates in the vestibulum nasi.

The incomplete floor of the ethmoidal region is formed by the **solum nasi**. Its rostralmost part is the **lamina transversalis anterior** (Figs. 5, 12, 13) which is subdivided into the **pars horizontalis** and the **pars verticalis**. The pars horizontalis is a flat plate which is connected rostrally with the processus laterales ventrales and further caudally with the nasal septum. The **sulcus ventralis nasi** is in *Hemicentetes* only in the rostralmost area visible. The pars verticalis shows a laterodorsal orientation and is connected with the paries nasi. This connection leads in this area to the formation of the **zona anularis**, a closed cartilaginous ring in the nasal capsule. The border between the lamina transversalis anterior and the paries nasi is marked by the **sulcus ductus nasolacrimalis** (Fig. 13). Caudally the lamina transversalis anterior continues in two

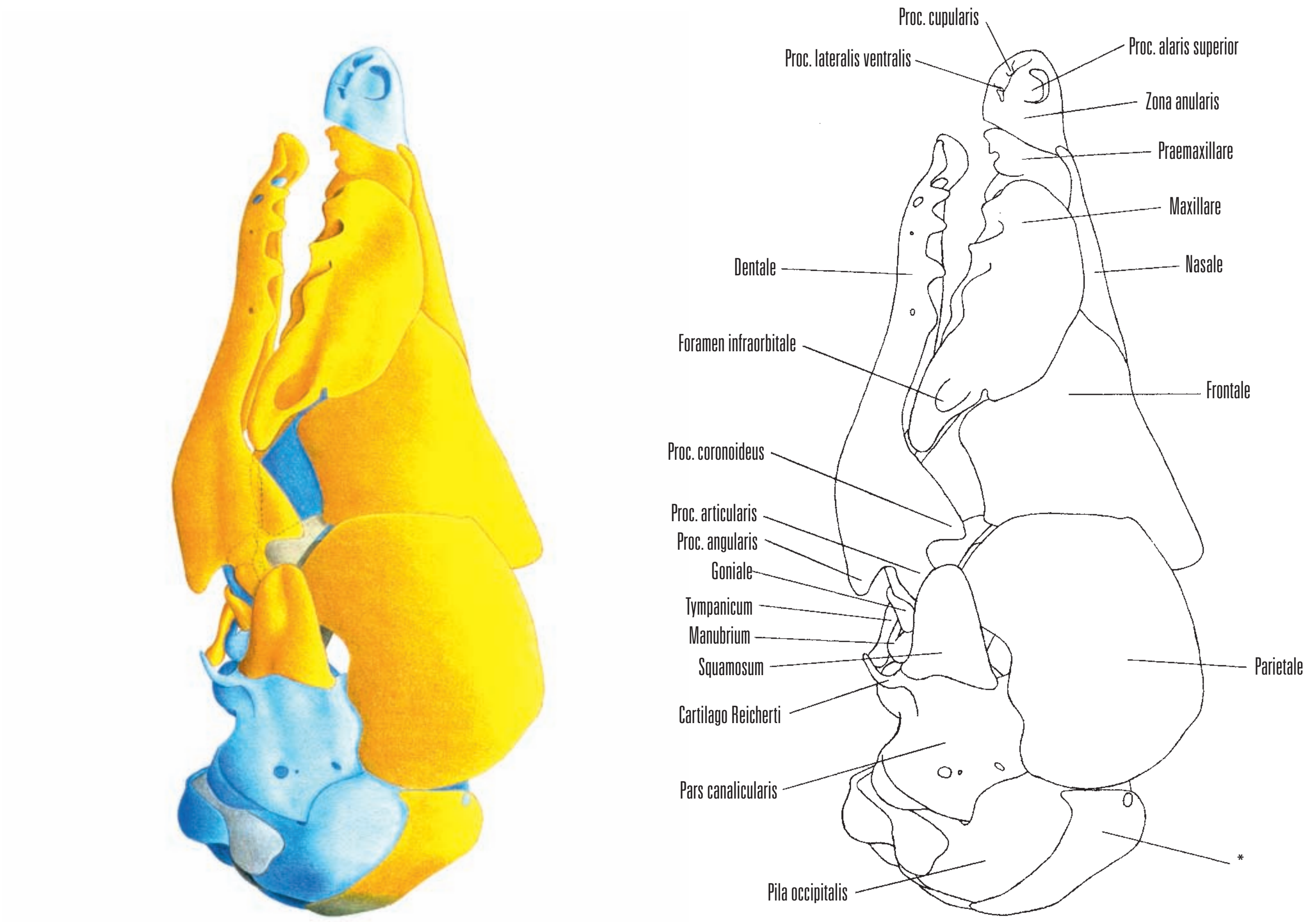

Fig. 7. *Hemicentetes semispinosus*, embryo, head length 14 mm. Graphical reconstruction and outlines of the skull in left lateral view. Blue: cartilage, yellow: dermal bones, grey: cartilage replacing bones; dermal bones of right half not drawn. *: fused interparietal and supraoccipital bones.

processes lateroventral of the nasal septum which are caudally orientated (Fig. 5). The lamina transversalis anterior divides the **fissura rostroventralis** into the fenestra narina and the ventral **fenestra basalis**.

The **cartilago palatina** consists in the 14 mm specimen of two small, ovally shaped cartilages whose rostral borders are close to the caudal borders of the processes of the lamina transversalis and slightly lateral and ventral of them (Figs 5, 6). In the 23 mm specimen the palatine cartilage extends further ventrally and caudally. It has the shape of a flat plate in a medial-ventral to lateral-dorsal orientation. Neither a **cartilago papillae palatinae** nor a **cartilago ductus nasopalatini** are visible.

Medially and caudally from the palatine cartilage lies the **cartilago paraseptalis**, which is extraordinarily short in *Hemicentetes* (Fig. 5) with only 1/5 of the length of the fenestra basalis. It is separated from the nasal septum by the **fissura septoparaseptalis** which contains parts of the vomer as well as the processus palatinus medialis (Fig. 15). Because of its position in the rostral third of the fenestra it must be considered to be the **cartilago paraseptalis anterior**. A **cartilago paraseptalis posterior** as caudal part of a former **cartilago paraseptalis communis** is not visible. In the 14 mm specimen the cartilago paraseptalis anterior is separated from the caudal processes of the lamina transversalis anterior by a clearly visible gap (Figs 5, 6). The separation seems to last long during the ontogeny. Only the older 23 mm specimen shows a narrow contact made by connective tissue. The cartilago paraseptalis is in this stage already partially resorbed. In the rostral part the cartilago paraseptalis forms a half-pipe with its opening orientated laterally and slightly dorsally. This groove contains **Jacobson's organ**. Caudally the groove becomes increasingly shallow until the cartilage has the form of a flat plate which is orientated slightly in medioventral to laterodorsal direction (Fig. 15). The Cartilago paraseptalis terminates clearly rostral from Jacobson's organ. A **fibula reuniens** or **„outer bar“**, which closes the cartilago paraseptalis to a complete ring, is not formed in the examined specimens of *Hemicentetes*.

The lamina transversalis posterior is not connected with the paraseptal cartilage in the examined specimens and a **processus paraseptalis posterior** as a rostral process of the lamina transversalis posterior is not visible. At its rostral border the lamina transver-

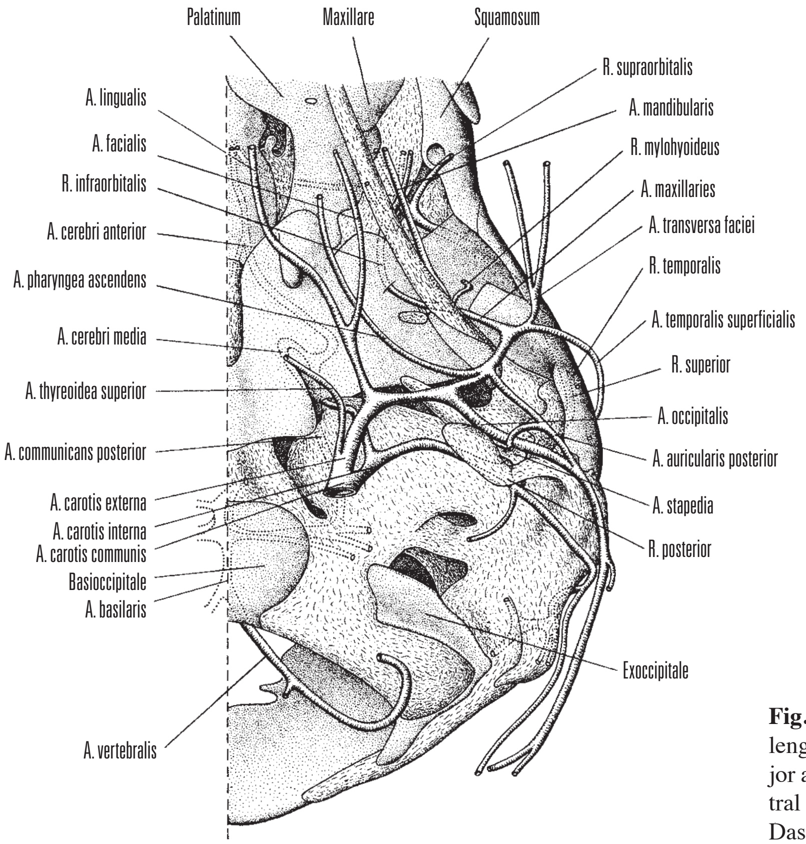

Fig. 8. *Hemicentetes semispinosus*, embryo, head length 14 mm. Graphical reconstruction of the major arteries of left posterior part of the skull in ventral view. Dentary and tympanic bone not drawn. Dashed: cartilage, dotted: bones.

salis posterior is fused with the vomer (Fig. 19) and laterally with the caudal part of the paries nasi.

2. Regio orbitotemporalis

The regio ethmoidalis, which extends far caudally, is followed posteriorly by the regio orbitotemporalis, which is very short in *Hemicentetes*. It represents no more than 1/16 of the total length of the skull between the cupula nasi posterior and the otic capsule (Fig. 4).

The basal part of the orbitotemporal region is formed by the **lamina trabecularis** (Fig. 4), which extends from the cupula nasi posterior to the **lamina hypophyseos**. The height of the lamina trabecularis decreases caudally, with a shallow crest in the middle (Fig. 20). Neither the **foramen hypophyseos** nor a **fovea hypochiasmatica** are visible in *Hemicentetes* and the **septum interorbitale** as a caudal extension of the nasal septum is absent, too. The lamina trabecularis is in *Hemicentetes* basically shaped very smoothly. A **tuberculum hypophyseos** is absent as well as a **dorsum sellae** and an isolated **cartilago dorsi sellae**. The border between lamina hypophyseos and lamina parachordalis, which often forms a **crista transversa**, does not show this structure in *Hemicentetes*.

The **orbitosphenoid** is well developed in the examined specimen (Figs 4, 25) and surrounds the **foramen opticum** completely (Fig. 4). The **nervus opticus** passes the bone in a slope from ventrolateral to dorsomedial direction.

In *Hemicentetes* the **ala orbitalis** is relatively small (Figs 4, 6). The regio ethmoidalis is not connected with the regio orbitotemporalis by a **commissura orbitonasalis** in the examined specimens (Fig. 4). However, it has to remain open whether this connection exists in younger specimens. The small gap between ala orbitalis and ethmoidal region as well as the shape of the ala orbitalis with the rostral border elongated towards the nasal capsule may indicate an earlier connection. Like the commissura orbitonasalis the **commissura orbitoparietalis** is absent in the examined specimens (Figs 4, 6). The **fenestra sphenoparietalis** is considerably larger than the **fissura orbitonasalis**, but the ala orbitalis is elongated also caudally, thus showing a triangular shape (Fig. 6). The caudal border of the lamina parietalis is slightly extended rostrally. However, in order to make final conclusions concerning the forming or reduction of the commissurae younger specimens had to be examined.

Caudally from the lamina trabecularis lies the **basisphenoid** (Figs 4, 5). The **processus tympanicus basisphenoidei** is strongly developed in *Hemicentetes*. It has the shape of a very flat plate orientated in mediodorsal to lateroventral direction (Fig. 21). In the 23

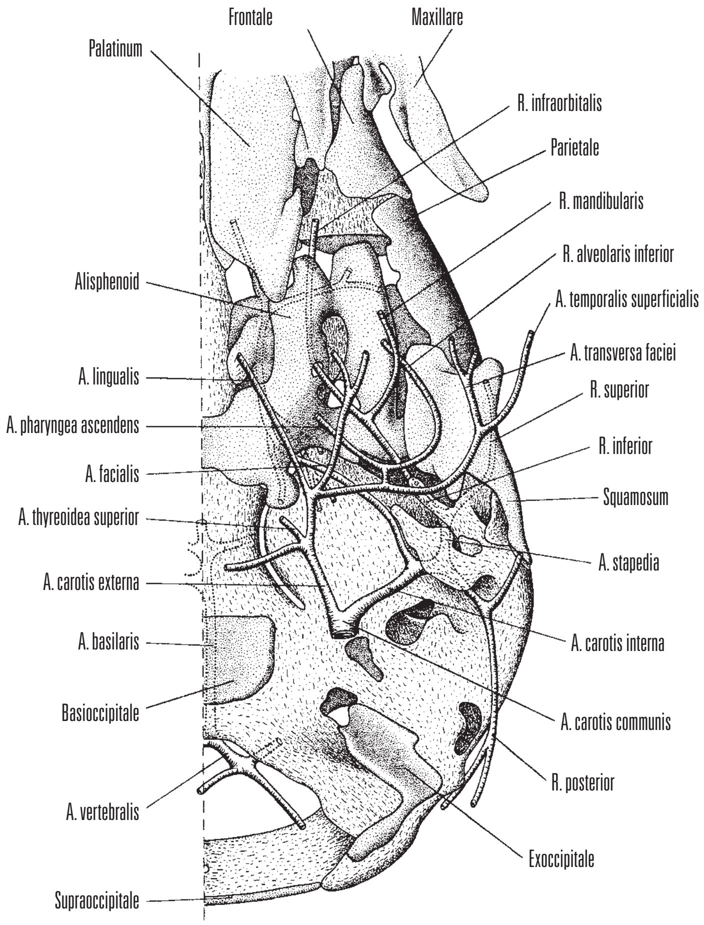

Fig. 9. *Potamogale velox*, embryo, head length 20 mm. Graphical reconstruction of the major arteries of left posterior part of the skull in ventral view. Dentary, tympanic bone, and Meckel's cartilage not drawn. Dashed: cartilage, dotted: bones.

mm specimen the process extends closely towards the medial area of the tympanic bone, but has not yet contact.

Laterally the basisphenoid continues into the **alisphenoid** (Figs 4, 5). This is, like all other elements of the orbitotemporal region in *Hemicentetes*, shortened in rostrocaudal direction. On the right side the caudal border shows a shallow **incisura ovalis** which is absent on the left side of the skull (Fig. 5). The oval foramen is still lacking in the 23 mm specimen, the mandibular nerve passes around the caudal border of the alisphenoid. The alisphenoid shows two openings. Rostral lies the **canalis alisphenoideus**, which is penetrated by the maxillary artery. Further caudal the maxillary nerve pierces the alisphenoid at the **foramen rotundum** (Figs 4, 5).

Within the Regio orbitotemporalis is also the **cavum epiptericum** located. The cavum epiptericum represents the space between the primary and secondary side wall of the braincase. In *Hemicentetes* a recess of the epipteric cavity is formed next to the caudal border of the nasal capsule (Fig. 25), which contains besides the **ganglion trigeminale** and parts of the **nervi oculomotorius**, **trochlearis**, **abducens** and **trigeminus** the **ganglion sphenopalatinum** as well as parts of the **nervus opticus**. The alisphenoid is located closely ventral of the nervi ophthalmicus and palatinus, the other nerves lie further dorsally. The optic nerve leaves the recessus of the cavum cranii through the foramen opticum.

The alisphenoid is connected with the otic capsule by the **commissura alicochlearis**, the basisphenoid further medial by the **commissura basicochlearis anterior** (Fig. 4). In between these two commissures is the **foramen caroticum** located, through which the internal carotid artery enters the epipteric cavity. The foramen caroticum is ventrally and medially enclosed by the alisphenoid and basisphenoid respectively, laterally and dorsally by the cartilage of the otic capsule. The **cartilago pterygoidea** is not visible in the graphical reconstruction, because it is already completely enclosed in bony material in the 14 mm specimen (Fig. 25). In the older embryos exists more cartilaginous tissue, but this is most probably secondary cartilage.

3. Regio otica

The regio otica includes the otic capsules, the part of the lamina parachordalis in between and the dorsally positioned parts of the side wall of the braincase and the skull roof. In *Hemicentetes* the lamina parachor-

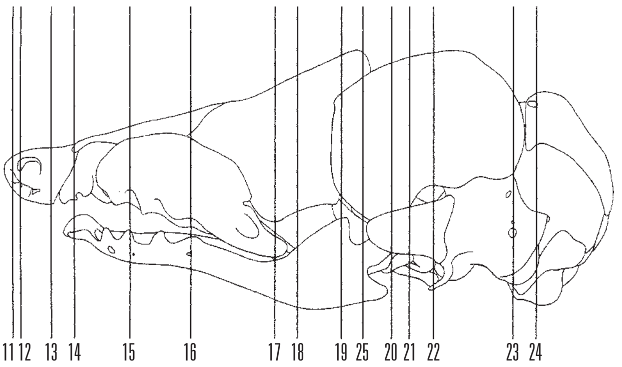

Fig. 10. *Hemicentetes semispinosus*, embryo, head length 14 mm, left lateral view (s. Fig. 7). Position of coronal sections given in Figs 11–25.

dalis is narrow rostrally and becomes wider caudally. The **chorda dorsalis** is not visible in this area. A small remainder is located in the tip of the dens axis.

In the examined specimen the otic capsules are completely chondrified, the **pars cochlearis** and the **pars canalicularis** are broadly connected (Fig. 4). The pars cochlearis is located in the ventral area of the cavum cranii. Different from the pars canalicularis it is not involved in the formation of the side wall of the braincaise. Rostrally the **capsula auditiva**, as already mentioned for the regio orbitotemporalis, is connected with the alisphenoid and basisphenoid by the commissurae alicochlearis and basicapsularis anterior respectively. The gap between the commissura basicapsularis anterior and the **commissura basicapsularis posterior** is formed by the **fissura basicochlearis**, which separates the pars cochlearis from the lamina basalis (Figs 4, 5). The fissura basicochlearis is elongated and positioned in rostromedial to caudodorsal direction. In the dorsal part of the broad commissura basicapsularis posterior is already a small ossification visible (Fig. 4).

Laterocaudally of the pars cochlearis lies the **fissura metotica** (Figs 4, 5). It is surrounded rostrally by the caudal border of the pars cochlearis, mediocaudal by the exoccipital and laterally by the pars canalicularis. In the rostrolateral area exists on the right side of the skull a connection between the fissura metotica and the **fenestra rotunda**, because the processus recessus is not yet fused with the pars canalicularis (Fig. 5).

The **commissura parietocapsularis** connects the pars canalicularis with the **lamina parietalis**. This structure has in *Hemicentetes* the shape of a slightly laterally curved cartilaginous plate of moderate height (Fig. 6). A **commissura exoccipitocapsularis** between pila occipitalis and pars canalicularis is absent. The **fissura exoccipitocapsularis** is in continuous connection with the **fissura supraoccipitalis** (=foramen jugulare spurium). The latter has in *Hemicentetes* an orientation from rostrodorsal to caudoventral direction (Fig. 6).

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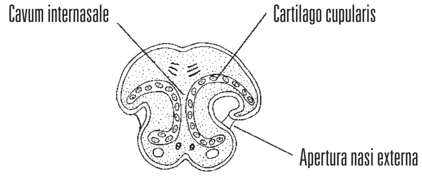

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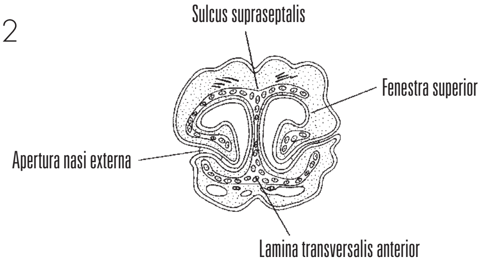

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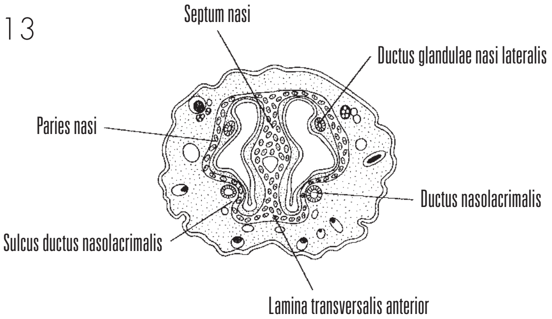

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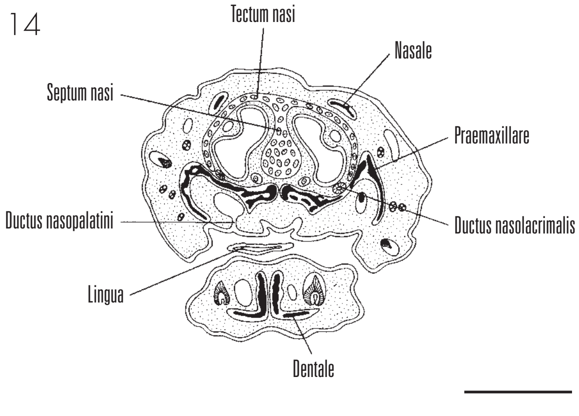

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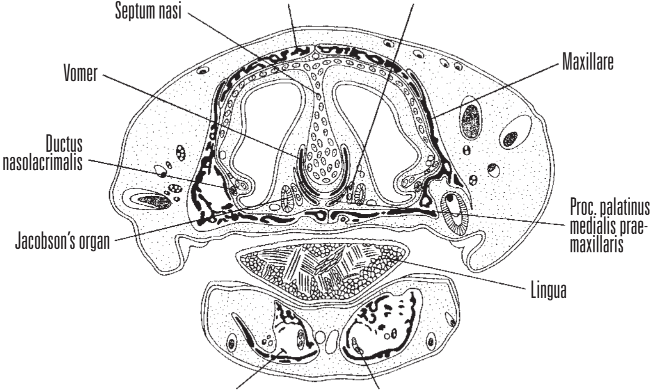

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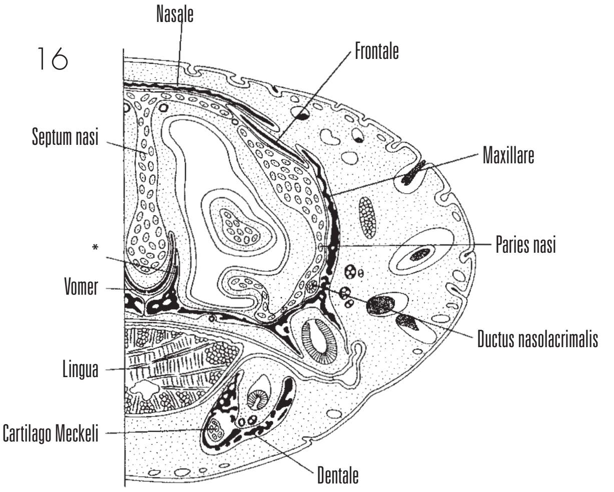

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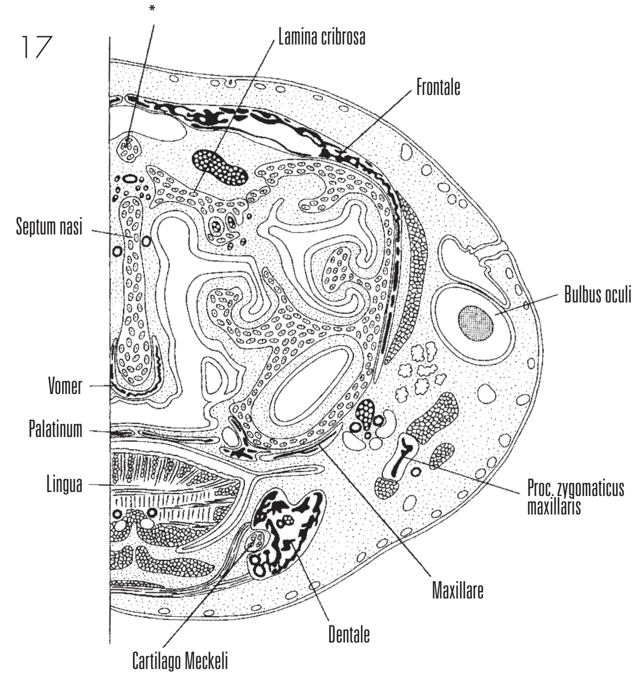

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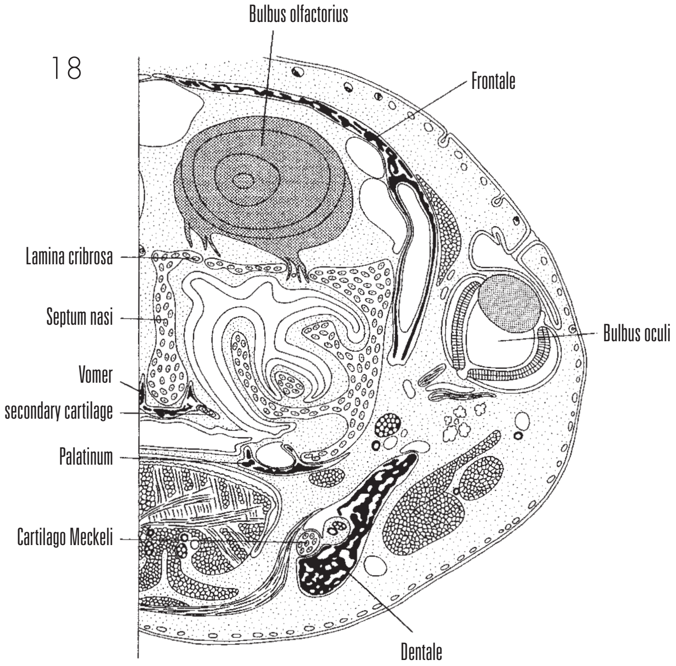

In the lateral area of the pars cochlearis, ventral of the ganglion geniculi and the facial nerve, originates a short, laterally directed process of the pars cochlearis (Figs 4, 22). The caudal part of the pars canalicularis is free, due to the connection of the fissura exoccipitocapsularis and the fissura supraoccipitocapsularis. A **processus opercularis** (Fischer 1901) is not visible in the examined specimens.

On the mediodorsally orientated surface of the capsula auditiva are several openings visible. The rostralmost is the **foramen faciale primarium**, through which the **nervus facialis** leaves the primary cavum cranii. Dorsally the foramen faciale primarium is restricted by the **commissura suprafacialis**, which connects the pars cochlearis and the vestibulum (Fig. 4). On the rostrolateral border of the pars cochlearis a short process is visible in the ventral area of the foramen faciale primarium (s. a.). Slightly further caudally are the **foramina acustica** located, through which the branches of the VIII. cranial nerve supply cochlea and vestibulum. The remaining openings and an elongated gap in the dorsomedial area of the canalis semicircularis posterior lie closely to the **ductus endolymphaticus**. Above the endolymphatic duct the cartilage has an irregular structure. In the 23 mm specimen the canalis semicircularis posterior ossifies first and is closed, apart from the **foramen endolymphaticum**. The endolymphatic duct lies within a canal which is separated from the canalis semicircularis posterior. The latter opens dorsally at the endolymphatic foramen, so that the endolymphatic duct lies within an ossified groove for a short distance.

Figs 11–18. *Hemicentetes semispinosus*, embryo, head length 14 mm. **11.** Coronal section at the tip of the rostrum (s. Fig. 10). Apertura nasi externa closed, cavum internasale narrow. Section 4/8 of the series. **12.** *Hemicentetes semispinosus*, embryo. Coronal section at the rostral area of the lamina transversalis anterior of the nasal capsule (s. Fig. 10). Section 6/4 of the series. **13.** *Hemicentetes semispinosus*, embryo. Coronal section in the area of zona anularis (s. Fig. 10). The ductus nasolacrimalis lies in the sulcus ductus nasolacrimalis, sulcus supraseptalis and sulcus ventralis nasi lack. Section 10/8 of the series. **14.** Coronal section at the premaxilla (s. Fig. 10). Septum nasi strongly thickened, dentary bones not fused. Section 15/4 of the series. **15.** Coronal section at the rostral area of the fenestra basalis (s. Fig. 10). Cartilago paraseptalis flat, septum nasi ventrally thickened, Meckel's cartilage with very small diameter. Section 23/8 of the series. **16.** Coronal section at the medial area of the fenestra basalis (s. Fig. 10). Section 33/8 of the series. *: sagital process of the maxilla. **17.** Coronal section at the rostral area of the lamina cribrosa (s. Fig. 10). Section 46/8 of the series. *: caudally directed process of the crista galli. **18.** Coronal section at the medial area of the lamina cribrosa (s. Fig. 10). Section 50/8 of the series. Scale = 1 mm.

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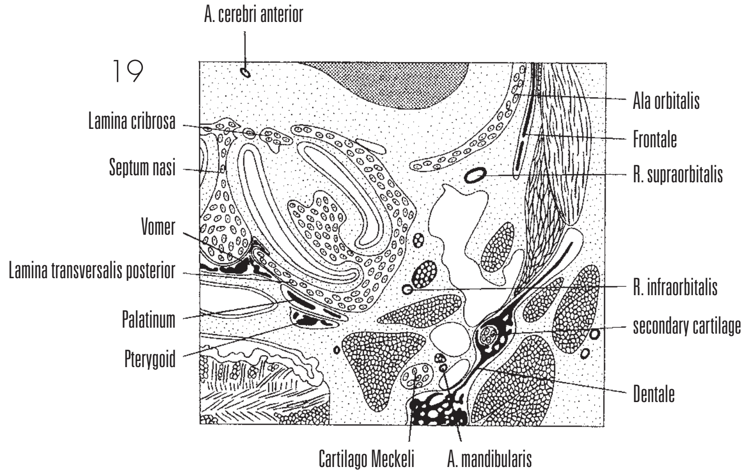

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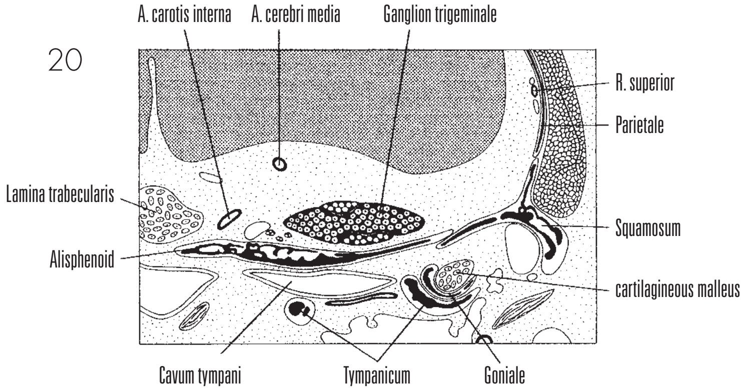

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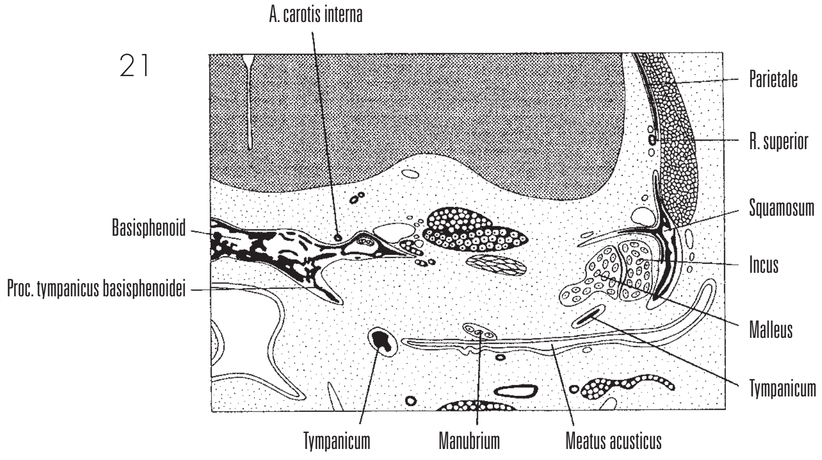

On the lateroventral surface lies the **fenestra ovalis**, which contains the footplate of the stapes. The **fenestra rotunda** is located medially and slightly caudally from the fenestra ovalis (Fig. 5). Within the fenestra rotunda the **membrana tympani secundaria** is stretched, which is slightly pulled towards the septum metacochleare, thus forming the relatively shallow **fossula fenestrae rotundae**. Between the fenestra ovalis and the fenestra rotunda lies the **promontorium**, which connects the laterocaudal border of the pars cochlearis with the rostral border of the pars canalicularis (Fig. 5). On the caudal border of the floor of the pars cochlearis originates the **processus recessus**, which forms on the right side of the skull a caudally and slightly laterally directed process (Fig. 5). Dorsal of the processus recessus lies the **aquaeductus cochleae**, which is penetrated by the **ductus perilymphaticus**. On the left side of the skull the processus recessus is already connected with the pars canalicularis, thus separating the fissura metotica and the fenestra rotunda completely (Fig. 5).

The **fossa subarcuata** is in *Hemicentetes* relatively large and irregularly shaped (Fig. 23). Medially lies a large opening which is covered in dorsal view from the medially sloped lamina parietalis. From lateral view two and three smaller openings respectively of

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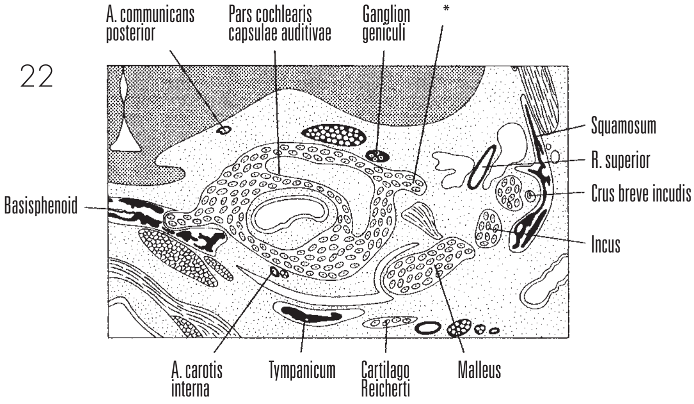

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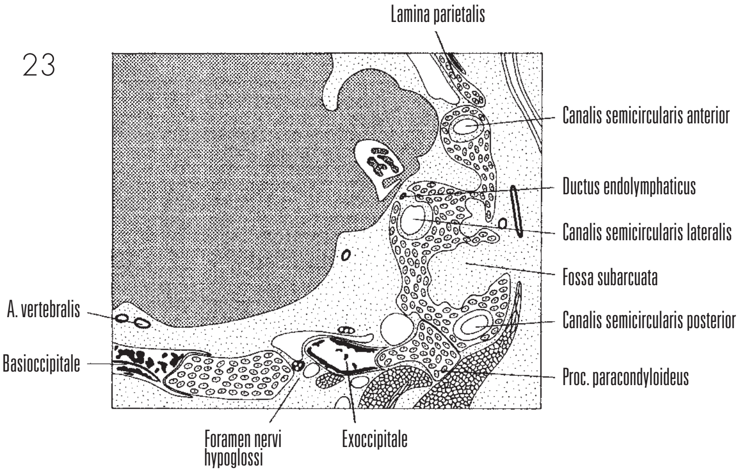

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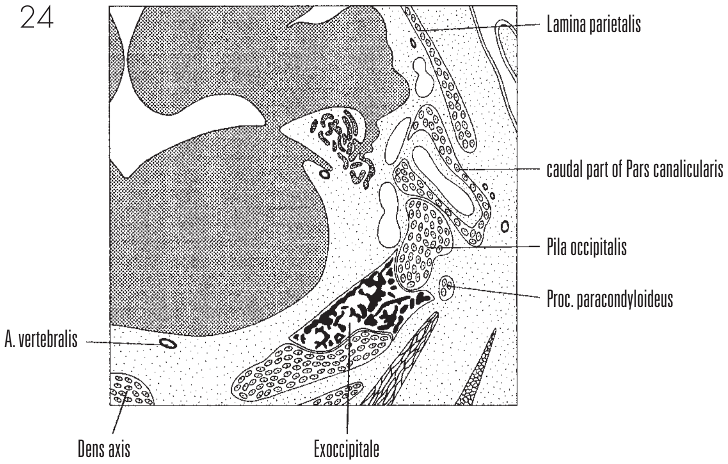

Figs 19–24. *Hemicentetes semispinosus*, embryo, head length 14 mm. **19.** Coronal section at the caudal area of the lamina cribrosa (s. Fig. 10). Lamina transversalis posterior fused with the vomer, septum nasi strongly thickened. Section 57/8 of the series. **20.** Coronal section at the rostral area of the cavum tympani (s. Fig. 10). Tympanic cavity dorsally limited by alisphenoid and squamosal. Section 66/4 of the series. **21.** Coronal section at the primary jaw joint (s. Fig. 10). Tympanic cavity dorsally open. Section 69/4 of the series. **22.** Coronal section at the pars cochlearis capsulae auditivae (s. Fig. 10). Arteria carotis interna in intermediate position between MICA and PICA type (see text for details). Section 72/4 of the series. *: lateral process of the pars cochlearis. **23.** Coronal section at the foramen nervi hypoglossi (s. Fig. 10). Fossa subarcuata irregularly shaped and laterally open, ductus endolymphaticus not covered. Section 85/4 of the series. **24.** Coronal section at the caudal area of the pars canalicularis capsulae auditivae (s. Fig. 10). Lamina parietalis partially covers pars canalicularis from lateral view. Section 89/4 of the series.

the fossa subarcuata are visible. The **flocculus cerebelli** is positioned in front of the medial opening. In the 23 mm specimen it has partly entered the grown fossa subarcuata.

On the lateral surface of the pars canalicularis mainly the **prominentia semicircularis lateralis** is clearly visible (Fig. 6). The **prominentia semicircularis anterior** is more pronounced on the medial surface than on the lateral surface. The relatively flat **prominentia semicircularis posterior** is only visible on the medial surface. On the rostrolateral border of the pars canalicularis lies a short, shallow **fossa incudis**. It is medially surrounded by the short **crista parotica** which merges caudally into Reichert's cartilage. The two latter structures together form the cartilaginous lateral wall of the tympanic cavity.

The **tegmen tympani** and the **processus tympanicus petrosi caudalis** are absent in *Hemicentetes*.

4. Regio occipitalis

The occipital region is formed by the caudal part of the lamina parachordalis, the pilae occipitales and the tectum posterius. In the 14 mm specimen the caudal part of the lamina parachordalis is already ossified as **basioccipital**. The replacement of cartilage by bone is not regular, thus the basioccipital seems to be considerably larger in ventral than in dorsal view (Figs 4, 5). The caudal part of the basioccipital is slightly involved in the formation of the **foramen magnum**, with two small processes on either side of the foramen.

Laterally the lamina parachordalis merges into the **pilae occipitales** (Fig. 6). On the rostral border of the pila occipitalis lies a very flat, rostroventrally directed process which partly covers the fissura occipitocapsularis (Figs 6, 7, 24). In the ventral area of the pila occipitalis a short, low **processus paracondyloideus** is visible (Figs 23, 24).

The **exoccipital** lies between the lamina parachordalis and the pilae occipitales. It is a rostrocaudally elongated bone which is strongly curved laterally in ventral view (Fig. 5). The dorsal surface is larger and approximately rectangular (Fig. 4). Between the exoccipital and the lamina parachordalis lies the **foramen nervi hypoglossi** (Fig. 5). The medial borders of the exoccipitals form partially the border of the foramen magnum.

Dorsally the pilae occipitales are connected by the tectum posterius. In the medial area this is surrounded by the **supraoccipital** (Fig. 4), but in the 14 mm specimen lasts a continuous cartilage bar inside. A precise delimitation of the supraoccipital is not possible, as it is continuously connected with the interparietals.

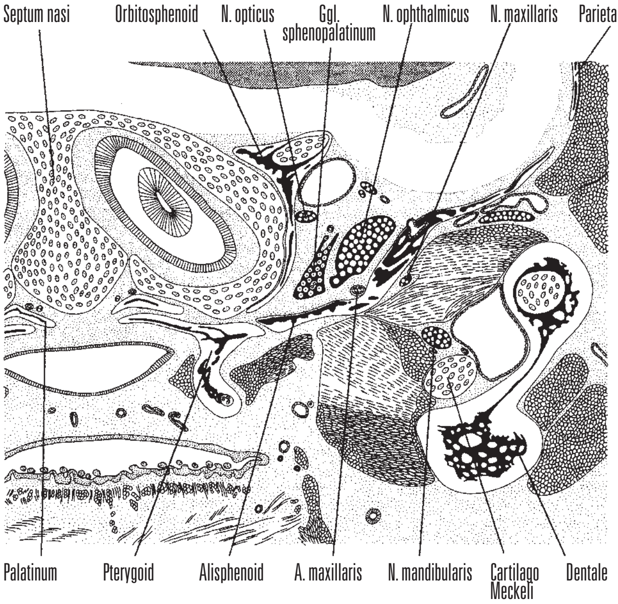

Fig. 25. *Hemicentetes semispinosus*, embryo, head length 14 mm. Coronal section at the ganglion sphenopalatinum (s. Fig. 10). Nervus opticus and ganglion sphenopalatinum lie inside a recessus of the cavum epiptericum which is bordered medially and in part dorsally by the orbitosphenoid and ventrally and laterally by the alisphenoid. Dorsally the recessus is not completely closed.

5. Visceral skeleton

Of the visceral skeleton only Meckel's cartilage, the structures involved in the formation of the primary jaw joint and Reichert's cartilage will be described here.

The resorption of **Meckel's cartilage** has already started in the 14 mm specimen (Fig. 15). The two cartilages touch each other medially, but are not fused. Whether this is the primary condition in *Hemicentetes* or due to resorption had to be clarified by examination of younger specimens.

The rostral half of Meckel's cartilage lies within the dentary ventral of the alveoles, apart from the rostralmost tip, which is positioned on the medial surface of the dentary (Figs 6, 16). Slightly caudal from the middle it leaves the dentary medially and runs caudal in a deep groove of this bone (Figs 17, 18), which grows increasingly shallow in caudal direction. In the caudal third it ascends gradually (Fig. 6). The rostralmost part of Meckel's cartilage is approximately circular in cross-section. The part inside the dentary is already mainly resorbed from lateral direction (Fig. 15), with the remains consisting of cartilage with large cells. After leaving the dentary Meckel's cartilage is ovally shaped in cross-section (Fig. 19).

The cartilaginously preformed part of the **malleus** is in the 14 mm specimen still in continuous connection with Meckel's cartilage (Figs 5, 6). The **manubri-**

um mallei is directed mediorostrally in ventral view (Fig. 5), in lateral view it points rostrally.

On the dorsal surface of the cartilaginous anlage of the **incus** is already a small, circular ossification visible (Fig. 4). The **crus breve incudis** lies in the very shallow fossa incudis. Within the primary jaw joint exists already a joint space (Fig. 21).

The **stapes** is in lateral view almost completely covered by the incus. It is still completely cartilaginous in the 14 mm specimen. The footplate is located in the fenestra ovalis of the pars cochlearis capsulae auditivae. The stapes is pierced by the stapedial artery.

Reichert's cartilage develops from a part of the hyoid visceral arch. In the 14 mm specimen it is connected with the pars canalicularis capsulae auditivae. In rostrocaudal direction Reichert's cartilage is flattened. In ventral view it runs from its origin at the pars canalicularis mediad (Fig. 5) before turning mediorostrally, where it grows broader. The rostromedial border is free; no connection with the **branchial arches** is visible in the examined specimens.

6. Dermal bones

The rostralmost dermal bone is the **premaxilla** (Figs 4, 5, 7). It encloses the rostral part of the nasal capsule from medial and ventral. Within the alveoles lie three anlagen of the upper incisors, with the Id3 in a very early stage of development. The joint alveolar compartment is not yet subdivided. A posterior wall towards the maxilla is missing, too. The **processus palatinus medialis** is strongly developed, it reaches as far caudal as the paraseptal cartilage. The caudal part is surrounded mediodorsally by the vomer, ventrally by the maxilla and laterally by the cartilago paraseptalis (Fig. 15).

Caudally the premaxilla is followed by the **maxilla** (Figs 4, 5, 7) which lies in its rostral part under the premaxilla. The maxilla contains the anlagen of the remaining teeth. The alveole of the Cd^1 is rostrally open, between the Cd^1 and Pd^1 as well as Pd^1 and Pd^2 a wall is visible. Pd^2 and Pd^3 have a joint alveolar comportment, which is open caudally.

Due to the strong enlargement of the nasal capsule the maxilla has a relatively large surface. Its dorsal edge is evenly convex. The **foramen infraorbitale** lies far caudally and has a relatively large diameter (Fig. 7). A **canalis infraorbitalis** is not formed, probably due to the caudal position of the foramen. At the caudal margin of the maxilla lies a narrow, moderately deep indentation, through which the nasolacrimal duct passes (Fig. 7). With its ventral face the maxilla builds a part of the secondary palate. In this part is a distinct groove for a small ramus infraorbitalis branch of the maxillary artery visible (Figs 5, 15, 16). Later in ontogeny this groove is closed ventrally. Caudally from the processus palatini of the premaxilla the maxilla forms a sagittal and dorsally pointed bony ridge, which is in close lateral contact with the vomer and reaches almost its heigth (Fig. 16).

On top of the maxilla and premaxilla lies the **nasal bone** (Fig. 4). It covers the larger part of the cartilaginous nasal capsule dorsally and a small part of the lateral surface. The two nasal bones are placed adjacent to each other with a slight overlap, in the caudal half they are fused. The ventral border of the nasal bone is positioned medially of the premaxilla and maxilla, the caudal border overlays the frontal bone. In the two older specimens lies a small piece of cartilage rostrally between nasal bones and maxilla, which shows no connection to one of the bones or the nasal capsule.

Nasal bones and maxilla are caudally followed by the **frontal** (Figs 4, 7). It is positioned laterally and dorsally of the caudal third of the nasal capsule. The caudal extension matches approximately that of the cupulae nasi posteriores, so that it covers little more than the bulbi olfactorii. In the area of the pars orbitalis the bone has an extremely large diameter and the bonal structure is interrupted by large venal plexus (Fig. 18). No **processus praeorbitalis** or **postorbitalis** are visible, only a slight flattening close to the eye (Fig. 18). The frontal is overlaid by all neighbouring bones.

Further caudally lies the **parietal**, which covers the middle part of the cavum cranii (Fig. 4). In lateral view it has an almost circular shape with an irregular margin ventro-caudally (Fig. 7). The medialmost point of the parietal lies shortly behind the centre, thus making the anterior fontanelle slightly larger than the posterior one.

The caudalmost placed dermal bone is the **interparietal** (Figs 4, 7). It has only in one small point contact with the parietal bone and its rostral extension matches approximately that of the foramen magnum. On the left side of the skull lies a small button-like piece of cartilage embedded in the bone close to the rostral border, which can not be found on the right side (Figs 4, 7). Rostrally the interparietal bones are separated, caudally they fuse with each other and with the supraoccipital bone. Due to the continuous connection the precise position of the borderlines is not visible, but the rostral separation and extension make an existence of interparietal bones very likely. For a proof younger stages should be investigated.

Ventrally the maxilla is followed by the **palatine** (Fig. 5). It shows a relatively low pars perpendicularis (Fig. 17) and no foramen sphenopalatinum in the 14 mm stadium. On the ventral surface of the palatine the groove for the ramus infraorbitalis of the maxillary artery continues from the maxilla, before this arterial branch passes inside between palatine and the caudal process of the maxilla. The **foramen palatinum** lies medial of the groove.

In the sagittal plain lies the unpaired **vomer** (Fig. 5). If it has a paired anlage had to be clarified by examination of younger states. The vomer covers the ventral margin of the nasal septum and participates with its caudal part in the building of the secondary palate. In *Hemicentetes* it is rostrally only slightly and caudally very shallow bifurcated. The short caudal parts are relatively far apart. In its rostral, bifurcated part the processus palatinus praemaxillaris lies very close to the vomer (Fig. 15). Slightly more caudally the processus palatinus lies only ventral of the vomer, laterally the latter touches the caudo-dorsal margin of the paraseptal cartilage. The two rostral processes of the vomer fuse medially in the same area where the palatine process and the paraseptal cartilage end and the sagittal, dorsal bone ridge of the maxilla begins. In the anterior part the vomer is U-shaped in cross-section (Figs 15, 16), the caudal third flattens increasingly (Figs 17, 18). In the 23 mm specimen the dorsal parts of the vomer as well as the sagittal bone crests of the maxilla are dorsally directed more towards each other and cover approximately four fifth of the thickened ventral margin of the nasal septum. The widest part of the vomer is laterally fused with the lamina transversalis posterior (Fig. 19). In this area small amounts of secondary cartilage can be found (Fig. 18). Approximately in the middle the vomer is pierced by a small vein.

Ventrally of the caudal parts of the vomer and the palatine lies the **pterygoid** (Fig. 5). It is a small dermal bone of approximately triangular shape which is fused with the alisphenoid in *Hemicentetes*. The **processus pterygoidei** is fused with the pterygoid bone.

Further caudally lies the **squamosal** on the lateral surface of the skull (Fig. 7). It participates with a small part in the secondary side wall of the braincase and in the secondary jaw joint. The joint space is about to be built in the 14 mm specimen. The ventral third of the squamosal is rostrally directed laterally and slightly ventrally. In this area lies a shallow, concave surface which is connected with the articular process of the dentary. This surface is pierced, slightly caudal of the joint area, by a small vein.

Medially and ventrally of the squamosal lies the horseshoe-shaped **tympanic bone** (Fig. 5). It lies approximately in a horizontal plane, with a slight inclination from rostral-dorsal to caudal-ventral (Fig. 6). The lateral border carries a ventral process which covers medially and laterally the gonial and Meckel's cartilage. Further rostral the process passes to the ventral side around gonial and Meckel's cartilage, thus lying in the ventrolateral area (Fig. 20).

Tympanic bone and squamosal play major roles in building the **cavum tympani**, which later houses the auditory ossicles. In the 14 mm specimen of *Hemicentetes* the roof of the tympanic cavity is still in part open. The squamosal builds in the anterior part the majority of the roof (Fig. 20). Further caudal it decreases and in the vicinity of the malleus-incus joint it only participates in the roof with a diminishing ridge (Figs 21, 22), which ends at the rostral margin of the pars canalicularis capsulae auditivae. The alisphenoid overlays the squamosal slightly in the rostral part (Fig. 20), further caudally it decreases towards the pars cochlearis quickly to less than one quarter, thus causing a wide opening of the roof in this area (Fig. 21). More posteriorly the roof is medially built by the pars cochlearis and its lateral process respectively (see above) and still further caudally also by the pars canalicularis, which also closes the roof laterally. Rostrally the tympanic cavity is open. The medial wall is formed rostrally by the processus tympanicus basisphenoidei, which has not yet reached the tympanic in the examined specimens (Fig. 21). Further caudally the medial wall is built by the pars cochlearis. The squamosal closes the cavum tympani laterally in the rostral area (Fig. 21), caudoventrally this is done by Reichert's cartilage. The caudal border of the eardrum is built by the Pars canalicularis, ventrally lie the tympanic and Reichert's cartilage (Fig. 5). A closed auditory bulla does not exist. In the 23 mm specimen the opening in the roof of the tympanic cavity has considerably decreased due to enlargement of alisphenoid and squamosal. Rostrally the alisphenoid extends laterally far enough to touch the parietal bone above the squamosal. As the caudal margin of the alisphenoid is curved rostrally a small opening remains in the middle part of the roof. Further caudally this opening is constricted medially by the pars cochlearis and its lateral process. Laterally and close to the pars cochlearis it is closed by the squamosal except for a narrow gap.

Within the tympanic cavity lies also the **gonial** (= prearticular), which later forms the **processus anterior** of the malleus. It is closely attached to the cartilaginous anlage of the malleus from medially, laterally and ventrally, but it is not yet fused with it (Figs 6, 20). Medially lies a small opening, through which the **chorda tympani** passes.

In the **dentary** (Figs 5, 6, 7) of the 14 mm specimen the anlagen of the teeth have not yet broken through. Both halves of the dentary lie close together rostrally, but are not fused. Meckel's cartilage is anteriorly already completely embedded in the dentary. The **canalis mandibulae** shows laterally three **foramina mentalia**. It has a continuous connection with the alveoles, which show only a slight constriction in the vicinity of the canine. Id_1, Id_2, Id_3 and Cd are still placed in a combined alveole with a relatively low border in the area of the incisives. The three premolars have already completely closed alveoles. In the caudal part the dentary is relatively low and shows secondary cartilage in the 14 mm specimen (Fig. 19). The secondary jaw joint lies approximately in the same level as the occlusion (Fig. 7). The **processus coronoideus** is relatively small and reaches hardly further dorsal than the jaw joint. Caudally it ends clearly anteriorly to the **processus articularis**. The **processus angularis** is strongly developed (Fig. 7).

The **lacrimal** is still missing completely in the 14 mm specimen. In the 23 mm specimen it is a very small bony plate positioned medially from the nasolacrimal duct. Anteriorly it is convex in medial direction and lies in close contact to the maxilla from inside with its dorsal and ventral margins, thus enclosing the ductus nasolacrimalis for a short part. After the nasolacrimal duct left through the caudal indentation of the maxilla it is closed by the lacrimal. As the lacrimal ends further rostrally than the maxilla a shallow groove remains visible. The rostral margin of the lacrimal is cartilaginous in the 23 mm specimen.

The **jugal** is not developed in *Hemicentetes*. The zygomatic arch is completely reduced except for a small caudal process of the maxilla and a small rostral process of the squamosal in the adult skull.

7. Cranial arteries

Described are here the larger arteries of the posterior part of the head (Fig. 8).

The **arteria carotis communis** bifurcates in ventral view below the pars cochlearis capsulae auditivae into the **arteria carotis interna** and the **arteria carotis externa**. The latter one immediately dispatches the **arteria thyreoidea superior**, which runs medially and ventrally towards the thyroid. Close to the rostral border of the pars cochlearis the external carotid artery gives rise to a branch which separates under the alisphenoid into the **arteria facialis** and the **arteria lingualis**. The arteria facialis runs in the beginning medially of the dentary and proceeds more posteriorly below its ventral margin in rostrodorsal direction. After the separation of the common root of arteria lingualis and arteria facialis from the external carotid artery the latter turns laterally and dispatches ventrally of the tympanic cavity in short succession the **arteria occipitalis** and the **arteria auricularis posterior**. These two arteries run laterally and caudally and fuse ventral of the connection between Reichert's cartilage and the pars canalicularis capsulae auditivae. The collective artery continues in caudal direction. At the bifurcation of the arteria auricularis posterior and the arteria carotis externa the latter also dispatches the **arteria pharyngea ascendens**, which runs medially and rostrally. Afterwards the external carotid artery continues for a short distance in lateral and rostral direction before it divides below the processus articularis of the dentary in quick succession into three branches. The first is the **arteria maxillaris** which runs between the processus articularis and Meckel's cartilage in medial and slightly rostral direction. Above Meckel's cartilage it also dispatches the **ramus mylohyoideus** and the **ramus mandibularis**, which runs lateral and dorsal of Meckel's cartilage rostrally. The arteria maxillaris proceeds in medial and slightly rostral direction and enters at the canalis alisphenoideus of the alisphenoid into the rostral recess of the cavum epiptericum. After passing through this it turns rostrally and continues laterally and slightly ventral of the nasal capsule. Shortly after dispatching the arteria maxillaris the external carotid artery bifurcates into the **arteria temporalis superfacialis** and the **arteria transversa faciei**. The latter divides quickly into its two final branches which proceed in rostral direction. The arteria temporalis superfacialis runs ventrally around the squamosal dorsally and caudally. The second branch of the arteria carotis communis is the arteria carotis interna. Its proximal part is short, before it bifurcates into the distal branch and the **arteria stapedia**. In the 14 mm specimen of *Hemicentetes* it does not divide in the typical way into the **ramus inferior** and the **ramus superior**, but shows no ramus inferior. In the 23 mm specimen two small branches are dispatched after passing through the stapes which continue in rostral direction. One runs above the lateral process of the pars cochlearis slightly medially before turning again in lateral direction and continues below the squamosal in rostral direction. The other branch proceeds below the lateral process medially towards the **musculus tensor tympani**.

The stapedial artery runs in a slight rostrally convex bow laterally, where it dispatches the **ramus posterior**. This vessel bifurcates into one branch which proceeds below the pars canalicularis medially and caudally and another one which runs around it in caudal and dorsal direction. The latter branch bifurcates lateral of the pars canalicularis into one artery which proceeds caudally and one which divides further close to the fissura occipitocapsularis, which is also pierced by one small branch. After dispatching the ramus posterior the stapedial artery proceeds in lateral and slightly rostral direction. It passes through the stapes and leaves the tympanic cavity through the still wide opening between the lateral process of the pars cochlearis and the squamosal (Fig. 22). Lateral of the brain it proceeds rostrally close to the squamosal and the parietal (Figs 20, 21) and dispatches a small artery to the outside through the opening between squamosal and parietal. Further rostral it runs medially below the rostral border of the ala orbitalis and divides into several branches in the medial area of the of the fissura orbitonasalis. First it dispatches the **ramus temporalis** which proceeds below the ventral border of the frontal bone in lateral direction. Two more branches run rostrally in the lateral part on the tectum nasi. The last artery continues medially across the caudal part of the lamina cribrosa where it passes through one of the openings close to the nasal septum inside of the nasal capsule. There it proceeds approximately in the middle of the septum in rostral direction.

The distal branch of the stapedial artery passes through the carotic foramen inside the skull where it fuses with the **arteria communicans posterior** to build the **arteria cerebri anterior** which proceeds ventrally in the medial area of the brain in rostral direction. It enters the nasal capsule at the lamina cribrosa and continues in the angle between the septum and the tectum nasi. The arteria communicans posterior links the arteria carotis interna with the **arteria basilaris**. The latter represents the fusion of the left and the right **arteria vertebralis** which in *Hemicentetes* takes place above the basioccipital. Therefore and because of the early subdivision the arteria basilaris is very short. The subdivision also happens above the basioccipital and the branches turn in a right angle laterally. In the same place the **arteria cerebri posterior** is dispatched which is connected by way of the arteria communicans posterior with the arteria cerebri media as a branch of the internal carotid artery.

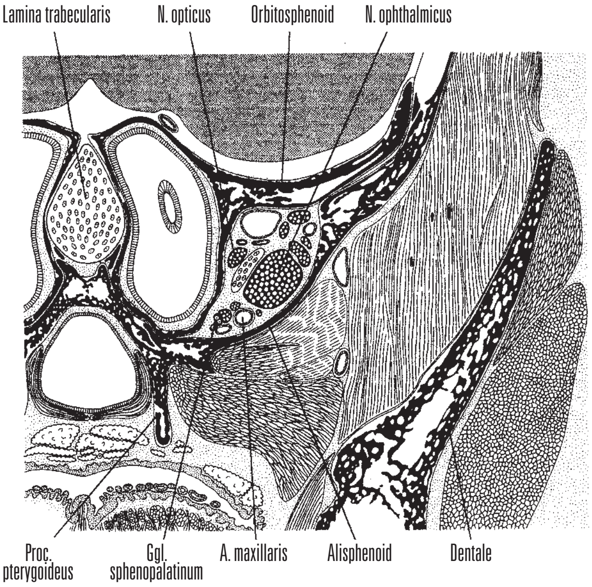

Fig. 26. *Tenrec ecaudatus*, embryo, head length 48 mm. Coronal section at the ganglion sphenopalatinum. Nervus opticus and ganglion sphenopalatinum lie inside a recessus of the cavum epiptericum which is bordered dorsally and medially by the orbitosphenoid and ventrally and laterally by the alisphenoid.

Comparative part and discussion

1. Regio ethmoidalis

The nasal region is in *Hemicentetes* much stronger developed than in *Potamogale*. The length of the nasal capsule relative to the length of the skull is in adult *Erinaceus* and *Talpa* 62 %, in *Sorex* and *Crocidura* 67 % (WÖHRMANN-REPENNING 1975; WÖHRMANN-REPENNING & MEINEL 1977), in the embryos of *Potamogale* 56 %, in *Tenrec* 63 %, and in *Hemicentetes* 71 %. Although the relative size of the nasal capsule allows no direct proof of olfactory abilities it is very likely that a correlation exists between the relatively short nasal capsule and the semiaquatic way of living in *Potamogale*. In contrast *Hemicentetes* has the relatively longest nasal capsule and is most likely extremely macrosmatic (see below). The probability of different olfactory abilities is also supported by the fact that in *Potamogale* despite the otherwise strongly developed brain the olfactory bulb is the smallest of all examined 'Lipotyphla' (STEPHAN 1967). *Tenrec* and *Setifer* have considerably enlarged olfactory bulbs which is supposed to be the derived character state by NOVACEK (1986).

The **fenestra internasalis** (Tab. 1) is absent in *Hemicentetes*, *Setifer*, *Potamogale*, *Eremitalpa*, and *Suncus* (ROUX 1947). In *Talpa* (FISCHER 1901) and *Erinaceus* (SPURGAT 1896) exists an opening in the rostral part of the nasal septum closed with connective tissue, which is considered here to be the derived character state. In *Potamogale* the **cupula nasi anterior** is less clearly separated from the rest of the nasal capsule than in *Hemicentetes*. According to GAUPP (1904) the cartilaginous tip of the nose was built in order to achieve a higher mobility. In *Hemicentetes* the extreme narrow nasal region (HOFER 1982) and the expected high mobility due to the shape of the Cupula nasi form a very suitable tool for searching the leaf litter and the upper soil layer (EISENBERG & GOULD 1970). In *Potamogale* in contrast the anterior part of the skull is rather widened and more compactly built due to the semiaquatic way of life. The **cartilagines cupulares** stand in *Potamogale* relatively far apart and fuse further caudally than in *Hemicentetes* and also in *Neomys* (MAIER 2002), *Suncus* (ROUX 1947), and *Sorex* (DE BEER 1929, MAIER 2002) exists a clearly visible **cavum internasale** (Tab. 1) which is probably the derived character state. *Setifer* (ROUX 1947), *Solenodon* (MENZEL 1979), and *Erinaceus* (FAWCETT 1918) show a state of the cavum internasale intermediate to that of *Potamogale*

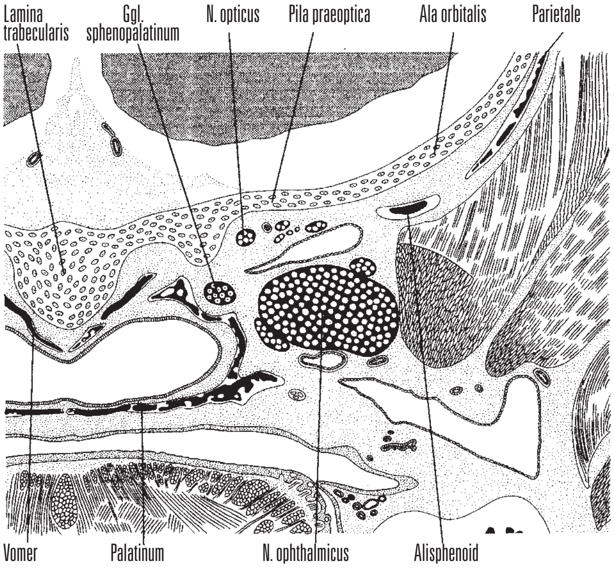

Fig. 27. *Potamogale velox*, embryo, head length 25 mm. Coronal section at the ganglion sphenopalatinum. Nervus opticus and ganglion sphenopalatinum lie lateral and ventral of the palatine and alisphenoid bones. A recessus of the cavum epiptericum is not formed.

and *Hemicentetes*. In *Talpa* (Fischer 1901) and even stronger in *Eremitalpa* (Roux 1947) the cavum internasale is, like in *Hemicentetes*, reduced.

Opposite to the relatively flat lamina transversalis anterior in *Hemicentetes Potamogale* shows a deep **sulcus ventralis nasi** (Tab. 1) which extends as far as the ventral margin of the septum. *Suncus* (Roux 1947), *Sorex* (de Beer 1929), the adult *Erinaceus* (Wiegand 1980), and *Solenodon* (Menzel 1979) also have caudally a very deep sulcus ventralis nasi. The relatively shallow form of the sulcus ventralis nasi in *Setifer* (Roux 1947), *Tenrec* (Leimgruber 1939), and *Eremitalpa* (Roux 1947) represents probably the primitive character state of the Eutheria.

The **processus cupularis**, **processus lateralis ventralis** and **processus alaris superior** (Tab. 1) in *Tenrec* (Leimgruber 1939) and *Setifer* (Roux 1947) show the same characteristics as those described for *Hemicentetes*. In *Potamogale* they are considerably larger and more complicated shaped (Behrens 1998; Asher 2001) and thus closer to the primitive state. In *Eremitalpa* the processes develop relatively late in ontogeny and remain small except for the processus cupularis (Roux 1947). *Suncus* (Roux 1947), *Neomys*, and *Sorex* (Maier 2002) have considerably larger processes than the Tenrecinae. In *Talpa* (Fischer 1901) they are strongly reduced. *Erinaceus* (Fawcett 1918) and *Hemiechinus* (Youssef 1971) show an intermediate character state of the processus cupularis, lateralis ventralis and alaris superior. These two species also have an additional **processus transversus** in the lateral area of the lamina transversalis anterior, which is lacking in all other investigated species (Tab. 1). The **commissura alicupularis** could not be found in the examined specimens of *Potamogale*, but as they develop very late in *Hemicentetes* no comparative statement is possible.

The cartilagines cupularis are rostrally closed in *Potamogale* in contrast to *Hemicentetes*, where the **fenestra narina** opens mainly in lateral and slightly dorsal direction. *Potamogale* has a **fenestra superior** (Tab. 1), but it lies clearly above the aperture of the ductus glandulae nasi lateralis into the vestibulum nasi. In *Tenrec* (Leimgruber 1939), *Setifer*, *Suncus, Eremitalpa* (Roux 1947), *Neomys*, *Sorex* (Maier 2002), *Hemiechinus* (Youssef 1971), and *Solenodon* (Menzel 1979) occurs a fenestra superior which lies in the latter clearly below the aperture of the ductus glandulae nasi lateralis. *Erinaceus* (Fawcett 1918) and *Talpa* (Fischer 1901) also have openings above the fenestra narina, but, different from the previously mentioned genera, they lie clearly more dorsally and are smaller and more rounded which makes the homologisation difficult. In *Erinaceus* the opening called “foramen dorsale” by Fawcett (1918) lies also very far rostral. Michelsson (1922) neither showed it in his figures nor mentioned it in his description. In the adult skull Wiegand (1980) pictured them in the form described for the other examined species. In the very young *Erinaceus* embryo no fenestra superior is visible.

The **tectum nasi** of *Potamogale* shows a strongly developed **sulcus supraseptalis** (Tab. 1) which is only in its rostralmost part flattened, in contrast to *Hemicentetes*, *Tenrec* (Leimgruber 1939), and *Setifer* (Roux 1947). *Eremitalpa* has a wide, deep sulcus supraseptalis. In *Suncus* (Roux 1947), *Neomys*, *Sorex* (Maier 2002), and *Talpa* (Fischer 1901) the sulcus supraseptalis is strongly developed rostrally but flattens increasingly in caudal direction. The primitive character state is probably a rather flat shape which has developed in *Potamogale* and the Tenrecidae in different directions. In the 20 mm specimen of *Potamogale* two openings closely behind one another can be found on the tectum, the 25 mm specimen shows only a single opening which is pierced, as in *Hemicentetes*, by a branch of the arteria cerebri anterior.

A **foramen epiphaniale** (Tab. 1) can be found neither in *Potamogale* nor in *Hemicentetes*. It is also lacking in *Tenrec* (Leimgruber 1939), *Suncus* (Roux 1947), *Sorex* (de Beer 1929, Maier 2002), *Neomys* (Maier 2002), and *Hemiechinus* (Youssef 1971), but Roux (1947) described it for *Setifer* and *Eremitalpa*. Fawcett (1918) described a foramen epiphaniale in *Talpa* which lies far caudal while Fischer (1901) mentiond none. In *Erinaceus* the epiphanial foramen is absent according to Fawcett (1918). Also Michelsson (1922) neither described this foramen for *Erinaceus* nor showed it in his figures, but he mentioned a foramen cribroethmoidale. The existence of the epiphanial foramen is considered to be the plesiomorphy of the Mammalia (ZELLER 1989), but in the examined species it had been frequently and probably independently reduced.

At the caudal margin of the tectum the nasal septum continues in *Potamogale* in a short **crista galli** (Tab. 1), which ends caudally with a short process. *Hemicentetes, Tenrec* (LEIMGRUBER 1939), *Suncus* (ROUX 1947), and *Sorex* (DE BEER 1929) have a short, flat crista galli. In *Setifer* it is extremely weakly developed, in *Talpa* (FISCHER, 1901) and *Eremitalpa* (ROUX 1947) relatively strong. It is absent in *Hemiechinus* (YOUSSEF 1971). A small or missing crista galli is supposed to be a primitive character state in the Mammalia (NOVACEK 1986).

In the species examined so far the **spina mesethmoidalis** is lacking, which is the derived character state (Tab. 1).

The **lamina cribrosa** (Tab. 1) is in *Potamogale* less inclined than in *Hemicentetes*, *Tenrec* (LEIMGRUBER 1939), and *Suncus* (ROUX 1947). A steep angle of the lamina cribrosa is considered to be the primitive character state of the Mammalia (ROUX 1947; GAUPP 1905b). In *Potamogale* the lamina cribrosa shows a considerably smaller number of **foramina olfactoria** than in *Hemicentetes* (Tab. 1), which are additionally spread over a smaller area. The primitive state in the Mammalia is here supposed to be a high number of olfactory foramina, which had been reduced in *Potamogale*. In *Hemicentetes* the number had possibly been secondarily increased.

The **cupula nasi posterior** and the adjacent base of the skull are less clearly separated in *Potamogale* than in *Hemicentetes*. Lamina cribrosa and cupula nasi posterior (Tab. 1) are caudally considerably more narrow in *Potamogale* and *Suncus* (ROUX 1947) than in *Hemicentetes, Tenrec* (LEIMGRUBER 1939), *Eremitalpa* (ROUX 1947), *Talpa* (FISCHER 1901), and *Erinaceus* (FAWCETT 1918), who retained the primitive character state.

Due to the deep sulcus ventralis nasi no typical **lamina transversalis anterior** is developed in *Potamogale*. For the same reason there is no real **zona anularis**, because in this area exists no completely closed cartilaginous ring. One apomorphy of Potamogalinae is the reduction of the **ductus nasolacrimalis** and the coherent absence of the **sulcus ductus nasolacrimalis** (BEHRENS 1998; ASHER 2001; GIERE *et al.* 2001; Tab. 1). The character state in *Setifer* matches basically that found in *Hemicentetes*, but in *Setifer* the nasolacrimal duct passes through a separate **foramen praetransversale** (= foramen pretransversarium, YOUSSEF 1971) inside the nasal capsule (Tab. 1). Such a foramen would be formed in *Hemicentetes* by a fusion of the processus lateralis ventralis with the rostral margin of the paries nasi. The presence of a foramen praetransversale is here considered to represent a derived character. The course of the nasolacrimal duct in *Sorex* (DE BEER 1929), *Erinaceus* (FAWCETT 1918), and *Hemiechinus* (YOUSSEF 1971) matches that found in *Setifer*. In *Hemiechinus* (YOUSSEF 1971) the sulcus ductus nasolacrimalis is reduced. *Suncus* (ROUX 1947) has a completely closed zona anularis. The lateral sulcus ductus nasolacrimalis is lacking, because the nasolacrimal duct runs in *Suncus* in this area inside of the nasal capsule. Further rostral lies ventral of the fenestra nasi superior another opening called ”deficiency in zona annularis for exit of ductus nasolacrimalis” by ROUX (1947). Through it leaves the nasolacrimal duct the nasal capsule and returns further rostrally through the foramen praetransversale. This opening lies between the ”deficiency in zona annularis for exit of ductus nasolacrimalis” and the fenestra narina. In *Eremitalpa* the nasolacrimal duct runs in relatively young embryos lateral of the nasal capsule in a deep sulcus ductus nasolacrimalis which closes completely forming a canal later in ontogeny.

The **cartilago palatina** (Tab. 1) is represented in the 25 mm specimen of *Potamogale* by a flat cartilaginous disc. *Hemicentetes*, *Setifer*, and *Echinops* (ROUX 1947) also have a palatine cartilage which is built late in the ontogeny of the latter two. According to LEIMGRUBER (1939) the cartilago palatina is absent in *Tenrec* as well as in *Eremitalpa* (ROUX 1947). In *Suncus* (ROUX 1947), *Sorex* (DE BEER 1929; ÄRNBÄCK-CHRISTIE-LINDE 1907, 1914), and *Crocidura* (ÄRNBÄCK-CHRISTIE-LINDE 1914) the palatine cartilage is probably strongly reduced and forms a small process of the cartilago ductus nasopalatini. The existence of the palatine cartilage is supposed to be plesiomorphic for the Mammalia (ZELLER 1989, but see SÁNCHEZ-VILLAGRA 2001 for plesiomorphic condition in Marsupialia).

In *Potamogale* the **cartilago ductus nasopalatini** (Tab. 1) is fused with the rostroventral margin of the paraseptal cartilage (BEHRENS 1998). The presence of the cartilago ductus nasopalatini is a plesiomorphic character of the Eutheria (ZELLER 1989, but see SÁNCHEZ-VILLAGRA 2001 for plesiomorphic condition in Marsupialia). ÄRNBÄCK-CHRISTIE-LINDE (1914) assumes that the cartilago ductus nasopalatini (=sickle-shaped cartilage) has developed from the paraseptal cartilage, which would also explain the frequently found fusion of both cartilages as a primitive character state. For *Setifer* and *Echinops* ROUX (1947) described the lack of a cartilago ductus nasopalatini, according to LEIMGRUBER (1939) it exists in *Tenrec*. It is developed late in ontogeny in *Eremitalpa* (ROUX 1947). In *Suncus* (ROUX 1947), *Sorex* (DE BEER 1929; ÄRNBÄCK-CHRISTIE-LINDE 1907, 1914) and *Crocidura* (ÄRNBÄCK-CHRISTIE-LINDE 1914) as well as in *Talpa* (FISCHER 1901) the cartilago ductus nasopalatini is fused with

Tab. 1. Characters and possible character states used in the phylogenetic analyses. “0” represents the primitive, “1” the derived character state.

1. *fenestra internasalis*: **(0)** absent; **(1)** present.
2. *cavum internasale*: **(0)** small; **(1)** large.
3. *sulcus ventrali nasi*: **(0)** shallow; **(1)** deep.
4. *processus cupularis, lateralis ventralis, alaris superior*: **(0)** large; **(1)** intermediate; **(2)** small.
5. *processus transversus*: **(0)** absent; **(1)** present.
6. *fenestra superior*: **(0)** absent; **(1)** present.
7. *sulcus supraseptalis*: **(0)** intermediate; **(1)** shallow; **(2)** deep.
8. *foramen epiphaniale*: **(0)** present; **(1)** absent.
9. *crista galli*: **(0)** lacking/small; **(1)** larger.
10. *spina mesethmoidalis*: **(0)** present; **(1)** absent.
11. *lamina cribrosa*: **(0)** steep; **(1)** flat.
12. *number of foramina olfactoria*: **(0)** high; **(1)** low.
13. *cupula nasi posterior*: **(0)** wide; **(1)** narrow.
14. *ductus nasolacrimalis*: **(0)** present; **(1)** absent.
15. *sulcus ductus nasolacrimalis*: **(0)** present; **(1)** reduced; **(2)** absent.
16. *foramen praetransversale*: **(0)** absent; **(1)** present.
17. *cartilago palatina*: **(0)** present; **(1)** absent.
18. *cartilago ductus nasopalatini*: **(0)** present; **(1)** absent.
19. *cartilago paraseptalis*: **(0)** long; **(1)** short.
20. *cartilago paraseptalis and lamina transversalis anterior*: **(0)** fused; **(1)** separated.
21. *fibula reuniens*: **(0)** present; **(1)** absent.
22. *cartilago paraseptalis posterior*: **(0)** present; **(1)** absent.

23. *septum interorbitale*: **(0)** absent; **(1)** present.
24. *ala orbitalis*: **(0)** larger than ala temporalis; **(1)** smaller than ala temporalis.
25. *comissura orbitonasalis*: **(0)** present; **(1)** absent.
26. *comissura orbitoparietalis*: **(0)** present; **(1)** absent.
27. *processus tympanicus basisphenoidei*: **(0)** present; **(1)** absent.
28. *canalis alisphenoideus*: **(0)** absent; **(1)** present.
29. *foramen ovale*: **(0)** absent; **(1)** present.
30. *foramen rotundum*: **(0)** absent; **(1)** present.
31. *processus tympanicus alisphenoidei*: **(0)** absent; **(1)** present.
32. *recess of the cavum epiptericum*: **(0)** absent; **(1)** intermediate; **(2)** present.

33. *fissura basicapsularis*: **(0)** absent; **(1)** present.
34. *fossula fenestrae rotundae*: **(0)** absent; **(1)** present.
35. *processus tympanicus petrosi caudalis*: **(0)** absent; **(1)** present.
36. *lamina parietalis*: **(0)** intermediate; **(1)** high; **(2)** low.
37. *fissura occipitocapsularis*: **(0)** continouos; **(1)** interrupted.
38. *processus opercularis Fischer*: **(0)** present; **(1)** absent.
39. *lateral process of pars cochlearis*: **(0)** absent; **(1)** present.
40. *foramen endolymphaticum*: **(0)** medially covered; **(1)** medially not covered.
41. *fossa subarcuata*: **(0)** without lateral openings; **(1)** with lateral openings.
42. *tegmen tympani*: **(0)** present; **(1)** absent.

43. *processus paracondyloideus*: **(0)** weakly developed; **(1)** strongly developed.
44. *processus opercularis Fawcett*: **(0)** absent; **(1)** small; **(2)** present.
45. *tectum posterius*: **(0)** wide; **(1)** intermediate; **(2)** narrow.

46. *cartilago Meckeli*: **(0)** rostrally fused; **(1)** rostrally separated.
47. *orbicular apophysis*: **(0)** absent; **(1)** present.
48. *musculus tensor tympani*: **(0)** present; **(1)** absent.

49. *premaxillaries*: **(0)** separated; **(1)** fused.
50. *sagittal process of maxilla*: **(0)** absent; **(1)** present.
51. *processus zygomaticus of maxilla*: **(0)** strongly developed; **(1)** weakly developed.

Tab. 1. Continuation.

52. *foramen infraorbitale*: **(0)** wide; **(1)** narrow.
53. *crista sagittalis*: **(0)** absent; **(1)** present.
54. *interparietal and supraoccipital*: **(0)** separated; **(1)** fused.
55. *palatine bones*: **(0)** separated; **(1)** fused.
56. *„postpalatine torus“*: **(0)** absent; **(1)** present.
57. *vomer and lamina transversalis posterior*: **(0)** separated; **(1)** fused.
58. *pterygoid and alisphenoid*: **(0)** separated; **(1)** fused.
59. *processus zygomaticus of squamosal*: **(0)** strongly developed; **(1)** weakly developed.
60. *„epitympanic wing“ of squamosal*: **(0)** lacking or small; **(1)** large.
61. *tympanic*: **(0)** horseshoe-shaped; **(1)** different shape.
62. *ventral face of cavum tympani*: **(0)** mainly membraneous; **(1)** other structures involved.
63. *dentary*: **(0)** with mobile symphysis; **(1)** without mobile symphysis.
64. *secondary cartilage in dentary*: **(0)** present; **(1)** absent.
65. *lacrimal bone*: **(0)** pierced by ductus lacrimalis; **(1)** not pierced by ductus nasolacrimalis.
66. *jugal*: **(0)** present; **(1)** absent.

67. *stapedial artery*: **(0)** without bony canal; **(1)** with bony canal.
68. *arteria carotis externa*: **(0)** takes not over parts of the stapedial artery; **(1)** takes over parts of the stapedial artery.
69. *stapedial artery*: **(0)** takes not over parts of the arteria carotis externa; **(1)** takes over parts of the arteria carotis externa.
70. *arteria carotis interna*: **(0)** PICA type; **(1)** MICA type.

the rostroventral margin of the paraseptal cartilage. In *Hemiechinus* (Youssef 1971) the cartilago ductus nasopalatini develops late in ontogeny. It can also be found in the adult *Erinaceus* (Wiegand 1980).

The **Cartilago papillae palatini** is absent besides in *Hemicentetes, Tenrec*, and *Potamogale* also in *Suncus* (Roux 1947) and *Hemiechinus* (Youssef 1971). Ärnbäck-Christie-Linde (1907) described for adult *Sorex* a very small ‘Papillarknorpel’ which is not mentioned in the other examined Lipotyphla. The Cartilago papillae palatini is considered to be a plesiomorphic character of the Mammalia (Zeller 1989). Probably it develops late in the ontogeny, so it might have been too early in the examined specimens.

In *Potamogale* the **cartilago paraseptalis anterior** (Tab. 1) is considerably stronger developed than in *Hemicentetes*. It reaches almost across the whole fenestra basalis and below the lamina cribrosa. Its caudal border slightly overlaps the likewise stronger developed **Jacobson’s organ**. The plesiomorphic character state of the Mammalia is a continuous cartilago paraseptalis communis, although it had been frequently reduced (Gaupp 1910; Weber 1927). In the species examined so far no cartilago paraseptalis communis occurs. In *Setifer*, *Suncus* (Roux 1947), *Talpa* (Fischer 1901), *Erinaceus* (Fawcett 1918), and *Hemiechinus* (Youssef 1971) the cartilago paraseptalis anterior reaches caudally approximately half of the length of the fenestra basalis thus displaying an intermediate state between *Hemicentetes* and *Potamogale*. In *Eremitalpa* the paraseptal cartilage has approximately one third of the length of the fenestra basalis, but it ends further rostral than Jacobson’s organ.

Like in *Hemicentetes* the **fibula reuniens** is absent also in *Potamogale* (Tab. 1). Roux (1947) found it in *Echinops*, but not in *Setifer* and *Eremitalpa*. For a very short period a fibula reuniens can be found in *Suncus* (Roux 1947), which is completely reduced soon after its emergence. In its place a dense layer of connective tissue can be found. The fibula reuniens was also described for *Sorex* (de Beer 1929) and *Crocidura* (Ärnbäck-Christie-Linde 1914). *Erinaceus* (Wiegand 1980) and *Solenodon* (Menzel 1979) have as adults an almost complete fibula reuniens, in *Hemiechinus* (Youssef 1971) it is lacking in the examined specimens. The fibula reuniens is a plesiomorphic character of the Mammalia (Zeller 1989, Sánchez-Villagra 2001). In the Lipotyphla the fibula reuniens can develop and disappear in very different times during the ontogeny (Roux 1947). In order to provide a definitive statement, particularly concerning the lack of a fibula reuniens, more or less complete series of ontogenetic stages needed to be examined.

The paraseptal cartilage is, like in *Hemicentetes* (own observation), *Echinops*, and *Setifer* (Asher 2001), in the 20 mm specimen of *Potamogale* not fused with the lamina transversalis anterior (Tab. 1). In the 25 mm specimen in contrast exists a connection by way of a short, vertically positioned cartilaginous plate, and Asher (2001) figured a broad fusion in his specimen. In *Setifer* (Roux 1947), *Geogale*, *Microgale*, *Tenrec* (Asher 2001), *Chrysochloris* (Broom 1916), *Talpa* (Fischer 1901), *Erinaceus* (Fawcett 1918; Asher 2001), and *Hemiechinus* (Youssef 1971), the cartilago paraseptalis anterior is connected by a narrow cartilaginous bridge with the lamina transversalis anterior. Roux (1947) described for *Suncus* that the cartilago paraseptalis anterior develops from an own centre of cartilage and at the beginning is only ”blastematously continous” with the lamina transversalis anterior. Later exists a continuous connection between both structures which is still later again reduced. In the adult *Solenodon* the paraseptal cartilage is also separated from the lamina transversalis anterior (Menzel 1979). A separate centre of cartilaginisation of the cartilago paraseptalis was also described by Roux (1947) for *Erinaceus, Sorex*, *Crocidura*, and *Eremitalpa*. A separation of the cartilago paraseptalis anterior from the lamina transversalis anterior was within the Eutheria so far only known from *Felis* and *Mustela* (Stadtmüller 1936).

According to Roux (1947) *Setifer* shows besides the cartilago paraseptalis anterior also a **cartilago paraseptalis posterior** (Tab. 1) which is a small, rostrally directed process of the lamina transversalis posterior. In the examined specimens of *Hemicentetes* and *Potamogale* no such process is visible, but in all specimens the lamina transversalis posterior is already connected with the vomer. It is not impossible that a small cartilago paraseptalis posterior occurs in younger stages. It can also be found in *Eremitalpa* (Roux 1947). For *Suncus* Roux (1947) described a cartilago paraseptalis posterior which has the form of a caudally directed process that is fused with the lamina transversalis posterior. The cartilago paraseptalis posterior has no separate centre of cartilaginisation but develops from the lamina transversalis posterior. For *Sorex* de Beer (1929) described a cartilago paraseptalis posterior which is only connected by a narrow cartilaginous bridge with the lamina transversalis posterior.

2. Regio orbitotemporalis

In correlation with the reduction of the nasal capsule the orbitotemporal region is stronger developed in *Potamogale*. It takes approximately 18 % of the total length of the skull in contrast to about 7 % in *Hemicentetes*.

The **septum interorbitale** (Tab. 1) is lacking besides in *Hemicentetes* also in *Potamogale*, *Talpa* (Noordenbos 1905), *Erinaceus*, and *Hemiechinus* (Youssef 1971). Haines (1950) considered it to be absent in all Insectivora. Gaupp (1904, 1910) interpreted the interorbital septum as a plesiomorphic character of the Mammalia. According to Gaupp (1910) it becomes included into the nasal capsule when this is caudally enlarged. For *Tenrec* Leimgruber (1939) described an existing septum interorbitale.

In the 20 mm specimen of *Potamogale* the building of the **orbitosphenoid** has not yet started. The 25 mm specimen shows two centres of ossification, one lateral of the cupula nasi posterior, the other one close to the rostral border of the optic foramen.

The **ala orbitalis** (Tab. 1) is also in *Potamogale* relatively small, but it reaches further dorsal than in *Hemicentetes*. In *Hemicentetes, Setifer* (Roux 1947), *Potamogale*, and *Suncus* (Roux 1947) the ala orbitalis is very small, in *Talpa* (Fischer 1901), *Erinaceus* (Fawcett 1918; Michelsson 1922), and *Hemiechinus* (Youssef 1971) considerably larger. *Eremitalpa* (Roux 1947) shows an intermediate size. The plesiomorphic character state of the Eutheria is probably a large ala orbitalis.

In *Potamogale* occurs a **commissura orbitonasalis**, but the **commissura orbitoparietalis** is lacking (Tab. 1). Like in *Hemicentetes* there is a large distance between the ala orbitalis and the lamina parietalis, but the dorsal margins of both structures are pointed towards each other in both genera. The possible occurrence of the commissura orbitonasalis and the commissura orbitoparietalis in *Hemicentetes* in earlier stages during the ontogeny is supported by the fact that in a very young *Tenrec* embryo (Leimgruber 1937) and in *Setifer* (Roux 1947) both commissurae exist. *Suncus* (Roux 1947) shows a wide commissura orbitonasalis, but the commissura orbitotemporalis is absent in all specimens examined by Roux. *Sorex* (de Beer 1929), *Erinaceus* (Fawcett 1918; Michelsson 1922), *Talpa* (Fischer 1901), *Hemiechinus* (Youssef 1971), and *Eremitalpa* (Roux 1947) possess a commissura orbitonasalis as well as a commissura orbitoparietalis. Originally both commissurae were present in the Mammalia (Gaupp 1905b). Statements concerning the lack of the commissurae orbitonasalis and orbitoparietalis respectively should be generally treated with caution, particulary if not complete series of ontogenetical stages could be examined. In *Tupaia* for example the commissura orbitoparietalis is only present for one day during the ontogeny (Zeller 1983, 1987).

The **basisphenoid** carries in *Potamogale* a **processus tympanicus basisphenoidei** (Tab. 1) which is in both specimens considerably more compactly built than in *Hemicentetes*, where it has rather the shape of a flat plate. This shape is also shown in *Tenrec*, *Setifer*, and *Echinops* (Roux 1947). In *Talpa* the processus tympanicus basisphenoidei participates in the building of the bulla tympanica (van der Klaauw 1929; McDowell 1958). *Eremitalpa* (Roux 1947) and *Chrysochloris* (Cooper 1928) also have a strongly developed processus tympanicus basisphenoidei. The process is absent in the soricids and *Solenodon* (MacPhee 1981), according to Segall (1970) is occurs in all genera except for *Sorex* and *Solenodon*. The processus tympanicus basisphenoidei represents a derived character which was assumed to be an autapomorphy of the Lipotyphla by Weber (1928).

The **alisphenoid** is in *Potamogale* like in *Hemicentetes* continuously connected with the basisphenoid. As in *Hemicentetes* also *Potamogale* has a **canalis alisphenoideus** and a **foramen rotundum**, the **foramen ovale** is not shown by any of the examined specimens of both genera (Tab. 1). For the adult skull of *Potamogale* Guth *et al*. (1959) described a foramen ovale. The lack of the foramen ovale was considered to be a plesiomorphic character state of the Mammalia by Gaupp (1904). Grassé (1955) assumed the absence of the alisphenoid canal as common character state of the Tenrecidae and Chrysochloridae, but it could be observed in all examined specimens of *Hemicentetes* and Mivart (1871) also described an alisphenoid canal for *Hemicentetes*. According to Weber (1928) all Lipotyphla except for the chrysochlorids have a canalis alisphenoideus.

The Foramen rotundum develops generally late in the ontogeny and is formed by different structures. The lack of the foramen ovale, foramen rotundum and canalis alisphenoideus was considered to be the plesiomorphic character state of the Mammalia (Zeller 1989). *Eremitalpa* (Roux 1947) shows besides the processus tympanicus basisphenoidei also a **processus tympanicus alisphenoidei** (Tab. 1). Both structures participate in the building of the bulla tympanica. The alisphenoid in *Eremitalpa* has no openings (Roux 1947). In *Suncus* (Roux 1947) the fusion of the alisphenoid with the basisphenoid occurs after birth. The alisphenoid forms in *Suncus* a processus tympanicus alisphenoidei which is involved with a small part in the medial wall of the tympanic cavity. The processus tympanicus alisphenoidei is lacking in the examined specimens of *Hemicentetes, Tenrec*, and *Potamogale*.

The recess of the **cavum epiptericum** (Kuhn & Zeller 1987), which occurs besides in *Hemicentetes* also in *Tenrec* (Fig. 26), can also be found in comparable, but not as enlarged form in soricids (Tab. 1). *Talpa* and *Erinaceus* do not show this kind of recess. In *Potamogale* the epipteric cavity can also be found in the shape typical for Theria (Fig. 27), which means parts of the cranial nerves III to VII as well as the ganglion trigeminale lie inside, nervus opticus and ganglion sphenopalatinum outside the cavum epiptericum (Gaupp 1902). Caudally follows, like in all Theria, the **cavum supracochleare**, which contains the ganglion geniculi (Voit 1909).

3. Regio otica

In the ear region the differences between *Potamogale* and *Hemicentetes* are less pronounced than in the two anterior regions. **Pars cochlearis** and **pars canalicularis** of the **capsula auditiva** are broadly fused in all examined specimens of *Hemicentetes* and *Potamogale*. A connection to the alisphenoid is made by the **commissura alicochlearis**, to the basisphenoid by the **commissura basicapsularis anterior**. Between both lies the **foramen caroticum** which is less inclined in *Potamogale* than in *Hemicentetes* and thus visible in dorsal and ventral view respectively (Behrens 1998). The commissura basicapsularis anterior is followed by the laterally curved, narrow **fissura basicapsularis** (Tab. 1), whose caudal border is formed by the **commissura basicapsularis posterior**. *Setifer* (Roux 1947) shows anatomic relationships like those in *Hemicentetes*. In the *Tenrec* described by Leimgruber (1939) the fissura basicapsularis is split by a broad connection between basal plate and otic capsule which was called ”anterior chordo-cochlear commissure” by Roux (1947) in *Suncus*. In the latter genus the fissura basicapsularis is completely closed temporarily during early craniogenesis. Later the commissura basicapsularis anterior is resorbed, thus the fissura basicapsularis anterior and the foramen caroticum fuse (Roux 1947). In *Eremitalpa* the fissura basicapsularis is undivided; the commissura alicochlearis is lacking (Roux 1947). The fissura basicapsularis is completely absent in *Sorex* (de Beer 1929), *Crocidura* (Levi 1909), *Erinaceus* (Fawcett 1918), and *Hemiechinus* (Youssef 1971), while *Talpa* has a broad and short fissura basicapsularis (Fischer 1901). As plesiomorphic character of the Mammalia the lack of the fissura basicapsularis was suggested (Zeller 1989). Differences between the other examined species are probably caused by repeated independent development.

The **fissura metotica** is already completely separated from the **fenestra rotunda** in the 20 mm specimen of *Potamogale*. The fusion of the processus recessus with the pars canalicularis was considered to be a plesiomorphic character of the Theria (de Beer 1937). The **membrana tympani secundaria** forms in *Hemicentetes* and *Tenrec* a **fossula fenestrae rotundae** (Tab. 1). In *Micropotamogale* it is spread in the fenestra rotunda, which was assumed to be the plesiomorphic character state in the Mammalia (Zeller 1985). *Potamogale* also has a fossula fenestrae rotundae, but here the membrana tympani secundaria is caudally split in the older specimen. The horizontal part is attached to the promontorium and the lateral margin of the septum metacochleare and obturates the foramen perilymphaticum. The vertical part connects the medial margin of the septum metacochleare with the processus recessus and forms the borderline of the apertura medialis of the recessus scalae tympani.

Laterally and slightly caudal of the fenestra rotunda *Potamogale* shows the strongly developed **processus tympanicus petrosi caudalis** (Tab. 1), which is absent in *Setifer, Eremitalpa* (Roux 1947), and *Hemiechinus* (Youssef 1971). In *Hemicentetes* it is in the 23 mm specimen visible as a short, low process lateral of the fenestra rotunda, likewise in *Tenrec*. Leimgruber (1939) described in the younger embryo examined by him the lack of a processus tympanicus petrosi caudalis. This leads to the conclusion that this process is developed relatively late during ontogeny in the Tenrecidae. In the adult skulls of *Limnogale, Nesogale*, and *Geogale* it is clearly developed (McDowell 1958). In *Suncus* it has the shape of a flat and in medial direction pointed plate, which forms a small bulla in the adult skull (Roux 1947). The occurrence of the processus tympanicus petrosi caudalis was supposed to be a derived character of the Mammalia (Zeller 1989).

The **commissura parietocapsularis** connects the Capsula auditiva with the **lamina parietalis** (Tab. 1). The latter is strongly developed in *Potamogale* and roofs in its highest point approximately one third of the cavum cranii laterally in the 20 mm specimen. In the 25 mm specimen the laminae parietales are still enlarged and touch each other medially with their caudal margins. In *Eremitalpa* the lamina parietalis is strongly reduced. Its function is taken over by an "antero-laterally directed wing of supra-occipital cartilage" (Roux 1947). The relatively low lamina parietalis in *Hemicentetes, Tenrec* (Leimgruber 1939), *Setifer*, *Suncus* (Roux 1947), *Talpa* (Fischer 1901; Fawcett 1918), and *Erinaceus* (Fawcett 1918; Michelsson 1922) represents the plesiomorphic character state for the Eutheria.

In *Potamogale* the pars canalicularis ends like in *Hemicentetes* caudally free, that means it has a continuous **fissura occipitocapsularis** (Tab. 1). Different from *Hemicentetes Potamogale* has in front of the elongated split-like opening a second, smaller one which is also pierced by a small vein.

The terms fissura occipitocapsularis and foramen jugulare spurium are used ambiguously in the literature. Zeller (1983) distinguished a fissura exoccipitocapsularis and a fissura supraoccipitocapsularis, the latter being identical with the foramen jugulare spurium. Generally a small vein passes through this opening. Probably this foramen corresponds to the fissura occipitocapsularis superior of Fawcett (1918). Yet for *Tenrec* Leimgruber (1939) described the existence of a fissura occipitocapsularis superior as well as the lack of the foramen jugulare spurium. According to the position the mentioned opening might be the fissura exoccipitocapsularis (sensu Zeller 1983). *Suncus* has according to Roux (1947) a foramen jugulare spurium as well as a fissura occipitocapsularis superior. For *Erinaceus* (Fawcett 1918) only a fissura occipitocapsularis superior is described. In *Eremitalpa* (Roux 1947) and *Hemiechinus* (Youssef 1971) the undivided fissura occipitocapsularis is rostrally open. Summarising it can be said that within the studied species the connection between the caudal border of the pars canalicularis and the occipital area is relatively weakly developed and variable.

Like in *Hemicentetes* and *Tenrec* (Leimgruber 1939) the **processus opercularis** (Fischer 1901; Tab. 1) is absent in *Potamogale*. It can be found in *Eremitalpa* (Roux 1947), *Suncus* (Roux 1947), *Sorex* (de Beer 1937), and *Talpa* (Fischer 1901). In *Erinaceus* (Fawcett 1918; Michelsson 1922) and *Hemiechinus* (Youssef 1971) it is lacking as well as in „vielen anderen Säugern" ["many other mammals"] (Stadtmüller 1936). As it develops in *Eremitalpa* relatively late in the ontogeny Roux (1947) assumed that it is not yet developed in most described mammal chondrocrania and therefore considered to be lacking. Roux continued concerning the processus opercularis: „It appears to be devoid of any phylogenetic significance, having developed, as it seems, to afford protection for the lateral jugular vein" (Roux 1947). According to Zeller (1989) the processus opercularis is a plesiomorphic trait of the Mammalia.

Another similarity between *Potamogale* and *Hemicentetes* is the existence of a lateral process of the pars cochlearis (Tab. 1) in the ventral area of the **foramen faciale primarium**. It is shorter in rostro-caudal direction in *Potamogale*, but reaches, particularly in the 25 mm specimen, considerably further laterally. In the most pronounced part it lies clearly above the medial process of the squamosal. Both genera also show an elongated split in the area of the canalis semicircularis posterior above the **ductus endolymphaticus**. This area is also in the 25 mm specimen of *Potamogale* still completely cartilaginous and widely open. In the adult skull of *Potamogale*, like in *Hemicentetes*, can a bony plate in the area of the **foramen endolymphaticus** be found (Tab. 1), which covers the true opening.

The **fossa subarcuata** is in *Potamogale* more regularly shaped than in *Hemicentetes*. Lateral openings are not visible (Tab. 1). The **flocculus cerebelli** has still a small gap towards the fossa subarcuata. In *Tenrec* (Leimgruber 1939) and *Suncus* (Roux 1947) lateral openings of the fossa subarcuata are also absent, but they can be found in *Setifer* (Roux 1947). The occurrence of lateral openings is a derived character. In *Eremitalpa* the fossa subarcuata is strongly reduced.

A **tegmen tympani** (= processus perioticus superior) is lacking in the younger specimen of *Potamogale* as well as in *Hemicentetes*, *Tenrec* (Leimgruber 1939) and *Setifer* (Roux 1947; Tab. 1). The older specimen of *Potamogale* has a very small tegmen tympani. In *Suncus* (Roux 1947), *Sorex* (de Beer 1929), *Erinaceus* (Fawcett 1918), *Hemiechinus* (Youssef 1971), *Talpa* (Fischer 1901), and *Eremitalpa* it is also visible, in the latter it is relatively large (Roux 1947). Within the Lipotyphla the tegmen tympani is generally very weakly developed (MacPhee 1981). This character state was considered to be plesiomorphic for the Eutheria (ZELLER, 1986).

4. Regio occipitalis

The occipital areas of *Hemicentetes* and *Potamogale* show only minor differences. **Basioccipital** and **exoccipital** are very similar in shape and position. The **foramen nervi hypoglossi** is slightly larger in *Potamogale*.

Lateral of the exoccipital *Potamogale* has a ventral-lateral-caudal directed **processus paracondyloideus** (Tab. 1), whose origin lies approximately below the caudal border of the pars canalicularis capsulae auditivae. In the examined specimens of *Hemicentetes* and *Tenrec* the processus paracondyloideus is very weakly developed. In the adult skull of *Hemicentetes* (MIVART 1871) and *Tenrec* the processus paroccipitalis is relatively large. According to ROUX (1947) the processus paracondyloideus can also be found in *Setifer, Suncus*, and *Sorex*, but it is absent in *Chrysochloris*. *Eremitalpa* (ROUX 1947), *Sorex* (DE BEER 1929), and *Talpa* (FISCHER 1901) have a small processus paracondyloideus, while it is strongly developed in *Hemiechinus* (YOUSSEF 1971). According to ZELLER (1989) the weak development is the plesiomorphic character for the Mammalia, in contrast considered NOVACEK (1986) the strongly developed processus paracondyloideus as primitive. Within the investigated species both character states can be found.

The shape of the **pilae occipitales** corresponds in *Potamogale* to that of *Hemicentetes*. At the rostral border of the pila occipitalis lies in *Setifer*, *Echinops*, and *Eremitalpa* a rostrally and slightly ventrally directed „anterior prolongation of supraoccipital“ (ROUX 1947, = **processus opercularis** FAWCETT 1917), which covers the foramen jugulare spurium from dorsal (Tab. 1). In *Hemicentetes* and *Potamogale* this character can be found rudimentarily. It is lacking in *Talpa* (FISCHER 1901) and *Erinaceus* (FAWCETT 1918).

In *Potamogale* and *Tenrec* (LEIMGRUBER 1939) the **tectum posterius** (Tab. 1) is considerably wider than in *Hemicentetes*. It covers the **foramen magnum** in its caudal third, while in *Hemicentetes* it only forms a narrow caudal crest.

5. Visceral skeleton

With respect to the visceral skeleton no basic differences exist between *Potamogale* and *Hemicentetes*. **Meckel's cartilage** runs in an almost identical course, only shows *Potamogale* in both specimens a rostral fusion, while in *Hemicentetes* they are already in the 14 mm specimen clearly separated (Tab. 1). In the relatively young *Tenrec* embryo described by LEIMGRUBER (1939) the rostral contact is also only made by connective tissue. The separation of Meckel's cartilages is here considered to be the derived character state.

The cartilaginous anlagen of **malleus**, **incus** and **stapes** also show no conspicuous differences. An orbicular apophysis of the malleus, as described by FLEISCHER (1973, 1978) for soricids and SEGALL (1970) for *Setifer, Echinops, Oryzoryctes, Potamogale, Echinosorex*, and *Hylomys* was not visible in the examined specimens (Tab. 1). The orbicular apophysis is also absent in *Erinaceus, Hemiechinus*, and *Talpa* (SEGALL 1970). BURDA et al. (1992) considered the auditory ossicles of the tenrecs to be unspecialised. In most of the other species they also show a relatively primitive state, except for subterraneous forms like the Talpidae (WILKIE 1925; STROGANOV 1945) and Chrysochloridae (SEGALL 1970).

The **musculus tensor tympani** can be found in *Potamogale* as well as in *Hemicentetes*, *Tenrec*, *Cryptotis*, and *Erinaceus* (HENSON 1961; Tab. 1). It is missing in *Talpa* (WEBSTER 1966), *Scalopus* (HENSON 1961), and *Chrysochloris* (ZELLER 1986) which is here assumed to represent the derived character state.

Paauw's cartilage is absent in all insectivores (SHUTE 1956).

Reichert's cartilage is in *Potamogale* insignificantly wider and lies slightly further rostral than in *Hemicentetes*.

6. Dermal bones

The **premaxilla** of *Potamogale* shows no major differences from that of *Hemicentetes*. The **processus palatinum medialis** ends clearly in front of the paraseptal catilage, because it is considerably longer in *Potamogale*. With its dorsal border it covers slightly more of the ventral margin of the nasal septum, which might be due to its less pronounced ventral swelling. Like in *Hemicentetes* the premaxillas of *Potamogale* are not fused with each other (Tab. 1). Generally the separation of bones by a clear suture was considered as the primitive character state (WEBER 1928). In *Suncus* (ROUX 1947) the premaxillas fuse medially late in ontogeny. The premaxillas of *Eremitalpa* are fused medially as well as with the maxilla and nasal bones (ROUX 1947).

The dimension of the lateral face of the **maxilla** in *Potamogale* corresponds approximately to that in

Hemicentetes. Additionally it shows the same sagittally positioned bone crest lateral of the vomer (Tab. 1). Different from *Hemicentetes*, where the plate initiates immediately behind the caudal borders of processus palatinum medialis, paraseptal cartilage and Jacobson's organ and thus has close contact to the lateral faces of the vomer, in *Potamogale* lie between vomer and maxillary process additionally the paraseptal cartilage and Jacobson's organ. The latter is therefore surrounded medially and ventrally by the paraseptal cartilage and laterally by the maxillary process (BEHRENS 1998). This bony crest is a derived character which occurs also, though weaker developed, in *Suncus*.

The **processus zygomaticus** of the maxilla is in *Potamogale* stronger developed than in *Hemicentetes* (Tab. 1). In caudal direction it reaches in *Potamogale* behind the eye, in *Hemicentetes* it ends already below the rostral half of the eye. *Tenrec* (LEIMGRUBER 1939) and *Setifer* (ROUX 1947) show an intermediate development, *Sorex* (DE BEER 1929) a very weak one. *Eremitalpa* has a closed zygomatic arch (see below). The maxilla bones are fused medially as well as with the premaxilla, nasal, frontal, lacrimal, and palatine bones (ROUX 1947).

In *Potamogale* the **foramen infraorbitale** (Tab. 1) lies approximately in the same position as in *Hemicentetes*. Its even larger diameter is most likely caused by the semiaqatic lifestyle of this species (Sánchez-Villagra & Asher 2002). Due to the elongation of the processus zygomaticus in caudal direction in *Potamogale* a short **canalis infraorbitalis** is formed. NOVACEK (1986) described a short, wide infraorbital canal for the Tenrecomorpha and Soricoidae and an also short, but narrower tube for the Erinaceomorpha. In the same paper the author considered a long canalis infraorbitalis as primitive character state. The relatively wide diameter of the canalis infraorbitalis in the majority of the studied species is most probably a primitive character state related to the strongly developed enervation of the vibrissae.

The **nasal bones** of *Hemicentetes* and *Potamogale* show almost no differences. In the latter they fuse already far rostrally; in the 20 mm specimen only the first quarter is unconnected, in the 14 mm specimen of *Hemicentetes* approximately the anterior half. In *Setifer*, *Suncus*, and *Eremitalpa* occurs also a median fusion (ROUX 1947). A free piece of cartilage between nasal bone and maxilla can not be found in *Potamogale*.

The lateral face of the **frontal** shows in *Potamogale* a shallow but visible impression on a level with the eye. The **processus praeorbitalis** and **postorbitalis** are lacking like in *Hemicentetes*. In *Eremitalpa* the frontal bones are medially fused (ROUX 1947).

Between the **parietal bones** of *Hemicentetes* and *Potamogale* no conspicuous differences can be found. In the adult *Tenrec* a very pronounced **crista sagittalis** is formed, which is absent in all other examined species except for *Solenodon* (Tab. 1). The crista sagittalis is a derived character in large species which enlarges the area of origin of the musculus temporalis (STARCK 1995).

The **interparietal** is still missing in the 20 mm specimen of *Potamogale*, but it is visible in the 25 mm embryo. It is clearly separated from the supraoccipital bone (Tab. 1). In the *Tenrec* examined by LEIMGRUBER (1939) a strongly developed interparietal bone clearly separated from the supraoccipital bone can be seen. In *Setifer* and *Suncus* (ROUX 1947) the interparietal bone fuses shortly after its origin with the supraoccipital bone. *Eremitalpa* has most probably an unpaired interparietal bone (ROUX 1947).

The **palatine** (Tab. 1) of *Potamogale* differs from that of *Hemicentetes* by the part which is medially in contact being considerably longer than the parts showing in lateral direction. In *Hemicentetes* the first part takes only one third of the total length. Additionally *Potamogale* shows in the caudo-ventral area a laterally directed process which is lacking in *Hemicentetes*. The **pars perpendicularis** is much stronger developed in *Potamogale* than in *Hemicentetes*. In *Suncus* and *Eremitalpa* the palatine bones fuse medially (ROUX 1947). For the adult skulls of the Erinaceomorpha and Soricoidae NOVACEK (1986) described a bulging swelling of the caudal margin of the palatine („**postpalatine torus**"; Tab. 1). The weak or lacking development of this structure in the „Tenrecomorpha" was considered to be primitive by Novacek. For a fossil *Geogale* BUTLER & HOPWOOD (1957) described the presence of a comparable swelling.

Different from the in cross-section U-shaped **vomer** of *Hemicentetes*, where the ventral margin is semicircularly bent, the vomer of *Potamogale* shows a rather square cross-section with a very slightly convex ventral part and two vertical plates lateral of the nasal septum, particularly in the caudal area. Additionally it is less flattened in the caudal part. Like in *Hemicentetes* the vomer fuses in *Potamogale* with the lamina transversalis posterior (Tab. 1). This is a derived character state which also occurs in *Suncus*. In the respective area secondary cartilage can be found.

The **pterygoid** of *Potamogale* shows in ventral view a quadrangular shape in contrast to the rather triangular outline in *Hemicentetes*. In the 20 mm specimen it is still separated from the alisphenoid, in the 25 mm specimen they are already fused (Tab. 1). In *Setifer* the pterygoid bone fuses with the alisphenoid and the basisphenoid, in *Suncus* with the alisphenoid. The pterygoid bone of *Eremitalpa* remains separated (ROUX 1947). The **processus pterygoidei** is in both specimens of *Potamogale* fused with the pterygoid bone but can still be identified.

The **squamosal** differs in *Potamogale* and *Hemicentetes* by the occurrence of a short, rostro-laterally directed zygomatic process in *Potamogale* which is lacking in *Hemicentetes*, *Tenrec* (LEIMGRUBER 1939), *Setifer*, and *Suncus* (ROUX 1947; Tab. 1). In the adult skull of *Hemicentetes* it is weakly developed. A small zygomatic process can be found in *Sorex* (DE BEER 1929) and *Eremitalpa* (ROUX 1947). In the tenrecs, otter shrews, and golden moles the flat process of the squamosal which is involved in building the roof of the tympanic cavity („**epitympanic wing**", Tab. 1) is enlarged (GREGORY 1910; VAN DER KLAAUW 1931; MACPHEE 1981). An opening in the articular area which is passed by a vein can not be found in *Potamogale*. In *Eremitalpa* the squamosal participates in the lateral and ventral surrounding of the bulla tympanica (ROUX 1947).

Between the **tympanic** of *Potamogale* and that of *Hemicentetes* only slight differences can be observed (Tab. 1). In *Suncus* the tympanic bears in its rostral half a small, rostrally directed process (ROUX 1947). The laterally open horseshoe-shape and the almost horizontal position are plesiomorphic characters of the Mammalia (WEBER 1927; VAN DER KLAAUW 1931; NOVACEK 1980; ZELLER 1986). In *Setifer* the tympanic is steeper inclined (SEGALL 1970). The soricids have a closed ring (WEBER 1927). The contact between tympanic and other parts of the skull is in the examined specimens of *Hemicentetes* and *Potamogale* exclusively formed by connective tissue, but according to PRESLEY (1978) it is generally closer in insectivores, which is considered to be the derived character state (PRESLEY 1978).

The structures participating in building the **cavum tympani** are much alike in *Potamogale* and *Hemicentetes*, differences existing mainly in the relative proportions. In both genera the tympanic cavity is rostrally open. The roof is formed by the alisphenoid, squamosal and the pars cochlearis capsulae auditivae or its rostro-lateral process (see above), with the dorsal opening having only the shape of a narrow, slant split in the 25 mm specimen of *Potamogale*. In contrast the 23 mm specimen of *Hemicentetes* has still a considerably larger opening. In the Oryzoryctinae exists dorsally a larger aperture than in the Potamogalinae (GUTH et al. 1959). In the Chrysochloridae the squamosal also participates in building the roof (BROOM 1916; COOPER 1928; KEEN & GROBBELAAR 1941). A roof that is wide open and only covered by the membrana sphenoobturatoria between petrosal bone, squamosal, alisphenoid, and basisphenoid was supposed to be the primitive character state within the Mammalia (MACPHEE 1981; BUTLER 1988; WIBLE & MARTIN 1993). Laterally the cavum tympani is closed by a short, low crista parotica, Reichert's cartilage and the squamosal in *Potamogale*. The participation of the squamosal in the lateral wall was considered to be the primitive character state for the Mammalia (NOVACEK 1986). In the medial part lies the processus tympanicus basisphenoidei which is shorter and stronger developed in *Potamogale* compared to the narrow bony plate in *Hemicentetes* (s. regio orbitotemporalis). Reichert's cartilage and the tympanic bone form the incomplete floor (Tab. 1). In *Potamogale* as well as in *Limnogale, Nesogale*, and *Geogale* participates from caudal direction additionally the processus tympanicus petrosi caudalis, which is absent in *Hemicentetes, Tenrec, Echinops*, and the Erinaceidae (NOVACEK 1977). In *Talpa* the squamosal indirectly takes part in building the roof of the tympanic cavity by forming a small process at which the membrana sphenoobturatoria inserts (FISCHER 1901). The primitive character of the Mammalia was supposed to be a cavum tympani ventrally mainly closed membranously, in which also the tympanic bone and small processes of the alisphenoid and the petrosal bone participate (NOVACEK 1977, 1993; CARTMILL & MACPHEE 1980; MACPHEE 1981; BUTLER 1988; MOORE 1981). This character state can be found in the Soricidae and Solenodontidae (NOVACEK 1993).

The **goniale** has in the examined specimens of *Potamogale* and *Hemicentetes* only contact with Meckel's cartilage. In the soricids and *Echinops* the gonial is fused with the tympanic (FLEISCHER 1973).

The **dentary** is in *Potamogale* rostrally not fused (Tab. 1). This flexible symphysis occurs in all Insectivora (ORON & CROMPTON 1985) and was assumed to be a plesiomorphic character of the Mammalia. The caudal third of the dentary is in *Potamogale* dorsally steeper angled than in *Hemicentetes*, thus the secondary jaw joint lies slightly above the occlusal level. The **processus coronoideus** shows no difference between both genera. The joint surface of the **processus articularis** is in *Potamogale* flatter than in *Hemicentetes*. Additionally more secondary cartilage can be observed in this area (Tab. 1). In *Sorex* (DE BEER 1929) and *Talpa* (FISCHER 1901) occurs also secondary cartilage in the dentary, but not in *Erinaceus* (FAWCETT 1918). The **processus angularis** is shaped similarly in both genera examined, but in *Potamogale* also in this area secondary cartilage can be found.

Even in the 25 mm specimen of *Potamogale* the **lacrimal** is not visible, like in the *Tenrec* described by LEIMGRUBER (1939) and the *Setifer* described by ROUX (1947). MULLER (1934) could also not find a lacrimal in an adult skull of *Potamogale*, but mentioned its occurrence in the Tenrecinae. According to Sánchez-Villagra and Asher (2002) lacrimal and nasolacrimal duct are absent in all semiaquatic tenrecids. The character state in *Echinops* (ROUX 1947) corresponds to that in *Hemicentetes*. In *Suncus* (ROUX 1947) and *Sorex* (DE BEER 1929) the lacrimal is relatively strongly developed and pierced by the nasolacrimal duct (Tab. 1). It fuses with the maxilla in *Suncus* and with the maxilla and frontal in *Eremitalpa* (Roux 1947). The ductus nasolacrimalis runs in this species between maxilla and lacrimal. An opening for the nasolacrimal duct within the lacrimal was supposed to be the primitive character state (Muller 1934). In *Chrysochloris* and *Talpa* the lacrimal is according to Muller (1934) in most cases absent, in the Oryzoryctinae always. However, the findings from the adult skull have to be treated with caution, because Muller (1934) mentioned the lacking also for the soricids while Roux (1947) and de Beer (1929) described well developed lacrimal bones in embryos (see above). According to Broom (1916) *Chrysochloris* has a very small lacrimal.

The **jugal** (Tab. 1) is absent besides in *Hemicentetes* also in *Potamogale, Tenrec* (Leimgruber 1939), and *Suncus* (Roux 1947, see below). It occurs in *Erinaceus* (Fawcett 1918), though reduced compared to the primitive character state (Muller 1934). According to McKenna (1975) the talpids and chrysochlorids do not have a jugal, but Fischer (1901) found an anlage composed of several bony parts in *Talpa*, Hogben (1919) mentioned its occurrence in the Chrysochloridae. De Beer (1929) described for *Sorex* a small jugal which has neither contact with the maxilla nor with the squamosal. In *Sorex* and *Neomys* also a small remainder of the jugal can be found (McDowell 1958). According to Roux (1947) most Lipotyphla have two separate centres of ossification which fuse early in ontogeny. One forms the zygomatic process, the other one the rest of the maxilla, the first one possibly being the jugal. However, in *Homo* two centres of ossification can be found in spite of the existing jugal, one of them lying within the Processus zygomaticus (McDowell 1958). See also Asher (2005) for discussion of the jugal bone in insectivoran-grade placental mammals.

7. Cranial arteries

Concerning the cranial arteries some remarkable differences between *Hemicentetes* (Fig. 8) and *Potamogale* (Fig. 9) can be found.

The **arteria carotis communis** bifurcates in *Potamogale* slightly further caudally than in *Hemicentetes* into the **arteria carotis interna** and the **arteria carotis externa**. The latter dispatches like in *Hemicentetes* firstly the **arteria thyreoidea superior**. Slightly further rostral the **arteria lingualis** and the **arteria facialis** branch off in the examined specimen almost in the same position; a joint root like in *Hemicentetes* is not visible. However, Asher (2001) found in his specimen a clear distance between the origins of the two arteries, comparable rather to *Hemicentetes*. After dispatching both branches the external carotid artery turns laterally. Below the rostral border of the pars cochlearis capsulae auditivae the **arteria pharyngea ascendens** and the **ramus alveolaris inferior** branch off with a short common root. The external carotid artery runs in a curve further laterally and rostrally. Below the squamosal it divides into the **arteria transversa faciei**, which bifurcates slightly further rostrally into its two major branches and the **arteria temporalis superficialis**.

The internal carotid artery runs in *Potamogale* undividedly across the major part of the pars cochlearis in lateral direction. The common root of the proximal and distal parts of the internal carotid artery is relatively long, with the first turning rostro-medially, the latter continues in lateral direction. After dispatching the **ramus posterior** latero-caudally the distal part pierces the stapes as **arteria stapedia** in rostral direction. Immediately after passing the stapes it bifurcates into the **ramus superior** and the **ramus inferior**. The ramus superior runs like in *Hemicentetes* between the pars cochlearis and the squamosal into the cavum cranii where it continues in rostral direction. The ramus inferior turns medially and rostrally below the alisphenoid. It dispatches slightly further lateral and caudal of the foramen rotundum the **ramus mandibularis** which runs lateral of Meckel's cartilage into the dentary. At the canalis alisphenoideus the ramus inferior enters the cavum epiptericum and continues rostrally below the nasal capsule. The proximal part of the arteria carotis interna runs below the pars cochlearis medially and rostrally before entering the cranial cavity through the foramen caroticum.

The two **arteriae vertebrales** fuse below the rostral border of the foramen magnum into the **arteria basilaris**. The latter is approximately three times as long as in *Hemicentetes* before it divides further. The fusion with the proximal part of the arteria carotis interna takes place, like in *Hemicentetes*, slightly medially and rostrally of the foramen caroticum.

Altogether shows *Potamogale* no conspicuous differences from the the character state supposed to be plesiomorphic for the Mammalia (Wible 1984, 1987; Wible & Zeller 1994). Generally the Lipotyphla are considered to be highly conservative with respect to the cranial arteries (Cartmill & MacPhee 1980). Still under discussion is the question whether the passing of the ramus inferior of the stapedial artery through the canalis alisphenoideus and its course inside the cavum epipterricum is a derived character (de Beer 1926; Wible 1987) or the course ventral of the alisphenoid (Novacek 1980), as described by Roux (1947) for *Suncus*.

A bony tube for the stapedial artery in the area of the stapes, as can be frequently seen in the Talpidae and Chrysochloridae, does not occur in *Hemicen-*

Tab. 2. Data matrix for different groups of insectivorous mammals (see Tab. 1. for characters). “?” represents missing data in this group, “/” an intermediate character state and “+”shows that more than one character state is present in the group.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Tenrecinae	0	0	0	2	0	1	1	/	0	1	0	0	0	0	0	/	/	/	1	+	/	/
Potamogalinae	0	1	1	0	0	1	2	1	0	1	1	1	1	1	2	0	0	0	0	+	1	1
Chrysochloridae	0	0	0	2	0	1	2	0	1	1	0	?	0	0	0	0	1	0	1	0	1	0
Soricidae	0	1	1	0	0	1	0	1	0	1	0	?	1	0	2	1	?	0	1	+	0	0
Talpidae	1	0	0	2	0	1	0	/	1	1	?	?	0	0	0	0	?	0	1	0	1	?
Erinaceidae	1	0	1	1	1	/	1	1	0	1	?	?	0	0	1	1	?	0	1	0	/	?
Solenodontidae	?	0	1	2	0	1	1	?	?	?	?	?	?	0	0	0	?	?	?	1	0	?

	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
Tenrecinae	/	1	/	/	1	/	0	1	0	2	1	1	/	0	0	1	1	1	/	1
Potamogalinae	0	1	1	0	1	1	/	1	0	0	1	/	1	1	1	1	1	1	0	+
Chrysochloridae	?	0	0	0	1	0	0	0	1	?	1	?	0	2	0	0	?	?	0	0
Soricidae	?	1	0	/	/	1	?	1	1	1	0	?	1	0	1	0	1	1	0	0
Talpidae	0	0	0	0	1	?	?	?	?	0	1	0	?	0	0	0	?	?	0	0
Erinaceidae	0	0	0	0	1	?	?	?	?	0	0	?	0	0	0	1	?	?	0	0
Solenodontidae	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

	43	44	45	46	47	48
Tenrecinae	+	/	/	1	/	0
Potamogalinae	1	1	0	0	/	0
Chrysochloridae	0	2	2	?	?	1
Soricidae	0	2	?	?	1	0
Talpidae	0	0	1	?	0	1
Erinaceidae	1	0	1	?	0	0
Solenodontidae	?	?	?	?	?	?

	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70
Tenrecinae	0	1	1	0	/	/	0	0	1	1	1	1	0	1	0	0	1	1	0	/	0	1
Potamogalinae	0	1	0	0	0	0	0	0	1	1	0	1	0	1	0	0	1	1	0	0	0	0
Chrysochloridae	1	?	0	?	0	1	1	?	?	0	0	1	?	1	?	?	1	1	1	0	0	0
Soricidae	1	1	1	0	0	1	1	1	1	1	/	0	1	0	?	0	0	1	0	0	0	?
Talpidae	1	1	0	0	0	1	1	1	?	?	?	0	?	1	?	0	1	0	1	0	1	?
Erinaceidae	0	?	0	1	0	?	0	1	?	?	1	?	?	1	?	1	?	0	0	0	0	0
Solenodontidae	0	?	1	?	1	?	1	?	?	?	0	?	?	0	?	0	?	?	0	?	0	?

tetes, Tenrec, and *Potamogale* (Tab. 1). The lack of this canal represents the plesiomorphic character state of the Eutheria (Wible 1984). The stapedial artery is generally well developed in the Lipotyphla, often stronger than the external carotid artery (Tandler 1899; du Boulay & Verity 1973). In *Talpa* parts of the external carotid artery are taken over by the stapedial artery (Tandler 1899; Sicher 1912; Bugge 1974; Tab. 1). The opposite is the case in *Hemicentetes* and *Tenrec* (own observations; Asher 2001); here the ramus mandibularis and the ramus infraorbitalis of the stapedial artery are absorbed by the external carotid artery (Tab. 1). Bugge (1974) referred to this as the most derived character state within the Insectivora. In the examined specimens of *Potamogale* as well as in *Echinops* (Bugge 1972, 1974; Asher 2001), *Setifer* (Roux 1947), *Geogale*, *Microgale*, *Micropotamogale*, (Asher 2001) and the Chrysochloridae (Roux 1947; Bugge 1972, 1974) occurs the character state plesiomorphic for the Mammalia.

Some interest has also been attracted by the position of the internal carotid artery ventral of the pars cochlearis capsulae auditivae (Tab. 1). Presley (1979) distinguished a medial course (MICA) and one below or lateral of the promontorium (PICA). Lipotyphla are generally assumed to show the PICA type (Presley 1979; Novacek et al. 1983). However, in *Hemicentetes* the course of the internal carotid artery presents at least an intermediate state. Possibly the artery shifts later in the ontogeny from this ‘indifferent’ position (Novacek 1980), but even in the oldest embryo the internal carotid artery has the same course like the reconstructed one. A comparable course is taken by the arteria carotis interna of *Geogale*, *Microgale*, and *Tenrec* according to the figures given in Asher (2001). In *Potamogale* the PICA type is already visible in the

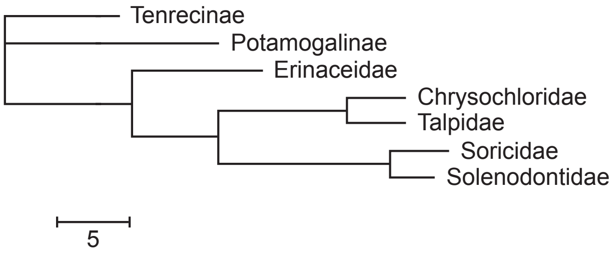

Fig. 28. Shortest parsimony tree calculated with 70 unordered, equally weighted characters without defined outgroup. Tree length = 83, consistency index = 0.7711 (0.6415 excluding uninformative characters), homoplasy index = 0.2289 (0.3585 excluding uninformative characters), retention index = 0.4722, rescaled consitency index = 0.3641.

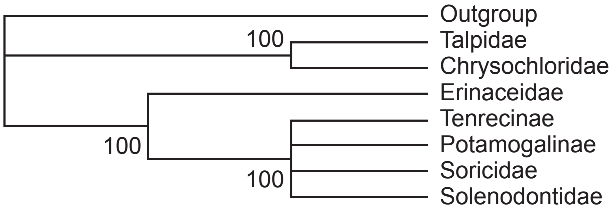

Fig. 29. Strict consensus tree from four shortest parsimony trees calculated with 70 unordered, equally weighted characters with outgroup showing all characters in the assumed plesiomorphic character state.

youngest specimen examined as well as in *Micropotamogale* (Asher 2001).

Presley (1979) considered the MICA type as plesiomorphic for the Mammalia. However, according to Wible (1980) the PICA type has been developed early within the Eutheria and Butler (1988) assumed it to be the primitive character state.

Phylogenetic analyses

Altogether 70 characters were recorded for *Hemicentetes* and *Potamogale* and supplemented with data from other insectivorous mammals (Tab. 1). The resulting character matrix is given in Table 2.

In the first analysis all characters were equally weighted, unordered, and no assumptions concerning the evolutionary direction was made. 13 characters were constant, 28 parsimony-uninformative and 29 parsimony-informative. The exhaustive search produced one shortest tree which required 83 steps (Fig. 28). For the second analysis an outgroup was defined which carried in all characters the assumed plesiomorphic state coded with '0' and the analysis repeated as above. In this case 7 characters were constant, 26 parsimony-uninformative and 37 parsimony-informative and the search resulted in 4 shortest trees with 100 steps. Figure 29 shows the strict consensus of the four trees. In both cases the bootstrap analyses with 10000 replicates found only a group consisting of moles and golden moles in more than 50 % of the trees. The monophyly of the Tenrecidae is not contradicted and some evidence for a closer relationship of shrews and *Solenodon* was also found by Asher *et al.* (2002) as well as for a group consisting of all three taxa, as found in the analysis including the hypothetical outgroup (Fig. 29).

In 26 cases more than one character state was found within one group, mostly differing between species, in some cases the character states changed with age. For these cases it would be desirable to examine more species and to reconstruct 'grundmuster' in order to define primitive character states for agreed monophyletic groups, e.g. families. Problems with characters which change during ontogeny could only be solved with more developmental stages and a precise definition like 'always absent' or 'absent in late/early stages'.

Conclusions and summary

In the ethmoid region some striking differences between *Hemicentetes* and *Potamogale* can be found, but the majority of them are most probably due to the extremely divergent way of life. In *Hemicentetes* the nasal area is narrow and elongated; at the same time it is enlarged in caudal direction, thus providing space for the olfactory epithelium of this strongly macrosmatic species. The other examined forms of the tenrecs show the same tendency, though never as pronounced as in *Hemicentetes*. In *Potamogale* the original character state had been derived in the opposite direction by reducing the regio ethmoidalis in correlation with the semiaquatic way of life. The basic differences between both species consist in the relative length of the nasal capsule as compared with the total length of the skull, in the shape and size of the processes of the cupula nasi anterior, the formation of the zona anularis and the ductus nasolacrimalis, and the completeness of the solum nasi.

Besides the differences some similarities of *Potamogale* and *Hemicentetes* can also be found. One is the opening in the tectum nasi which is pierced by a small artery, which has not been described in other Lipotyphla. Caution has to be taken in order to exclude confusion with the foramen epiphaniale. Additionally both *Hemicentetes* and *Potamogale* have an isolated cartilago palatina which is lacking in the other investigated specimens, but this is a symplesiomorphy. In both species the paraseptal cartilage is separated from the lamina transversalis anterior in early stages. However, this character has to be treated with caution because both structures fuse later in the ontogeny at least in *Potamogale*. In very young embryos of the other species only an indirect connection can be seen due to the existence of two separated centres of chondrification which makes a separation relatively easy. Finally the size and shape of the paraseptal cartilage differs considerably in both species, being extremely reduced in *Hemicentetes* while in *Potamogale* it has the largest caudal elongation of all investigated species.

In the orbitotemporal region like in the ethmoidal region considerable differences between *Hemicentetes* and *Potamogale* exist, most of them correlated with the modification of the nasal capsule. Due to the caudal enlargement of the latter occurs in *Hemicentetes* a recess of the cavum epiptericum which can also be found, although to a smaller extent, in soricids. *Potamogale* shows in this respect the primitive character state.

Differences in the otic region between *Hemicentetes* and *Potamogale* on one hand and the other studied species on the other exist basically in details. The processus tympanicus petrosi caudalis is in *Potamogale* considerably stronger developed than in *Hemicentetes*. In this character *Potamogale* shows similarities with some Oryzoryctinae. The lamina parietalis extends further dorsally in *Potamogale* than in all other examined specimens. The fossula fenestrae rotundae had probably been independently developed, which is supported by the different shape as well as by its lacking in *Micropotamogale*.

The occipital region as well as the visceral skeleton are generally very conservative, thus observed similarities are mainly based on plesiomorphies. The orbicular apophysis occurs also in other groups.

In the dermal bones of *Hemicentetes* and *Potamogale* generally few conspicuous differences can be found. The interparietal is formed considerably later in *Potamogale* than in *Hemicentetes* and remains separated from the supraoccipital for some time. All shared deviations from the original state, e. g. the reduction of the jugal and the participation of the squamosal in the roof of the tympanic cavity, occur also in other species.

The course of the cranial arteries differs considerably between *Potamogale* and *Hemicentetes*. *Potamogale* displays very conserved features, while *Hemicentetes* shows a strongly derived state. Similarities between *Hemicentetes* and *Potamogale* in the examined area are exclusively based on symplesiomorphies.

In the summarising view of the characters examined here no unambiguous synapomorphies of *Hemicentetes* and *Potamogale* could be found. Similarities turned either out to be symplesiomorphies and/or occurred in a comparable form also in other species. For the future functional causes for similarities, as observed in golden moles and moles, should be analyzed, and it would be desirable to investigate less specialized oryzoryctine tenrecs and the semiaquatic tenrec *Limnogale* in order to further evaluate morphological differences and similarities within the members of the Tenrecomorpha. More detailed examinations of golden moles, elephant shrews, and solenodons would help to understand character evolution of the chondrocranium in insectivoran grade mammals.

Acknowledgements

The authors wish to thank the Max Planck Institute for Brain Research in Frankfurt, Germany, the Hubrecht Laboratory, Utrecht, Netherlands, and D. Starck for providing the valuable material. K. Rehbinder, Johannes-Gutenberg-Universität, Mainz, made the drawings of the present paper and J. Zeller prepared the serial sections and helped with the photographical work. Graphical reconstructions and drawings of his *Potamogale* models were kindly provided by H. Behrens prior to finishing his thesis. A. Edelmann helped with the organisatory details that were necessary to perform the work presented here. Finally we are grateful to Peter Giere and an anonymous reviewer for helpful comments on earlier drafts of the manuscript.

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