



The orbitotemporal region and the mandibular joint in the skull of shrews (Soricidae, Mammalia)*

Wolfgang Maier^{1,2}, Adrian Tröscher³, Irina Ruf^{2,4}

1 *Fachbereich Biologie, Institut für Evolutionsökologie, Eberhard-Karls-Universität Tübingen, Auf der Morgenstelle 28, 72076 Tübingen, Germany*

2 *Abteilung Messelforschung und Mammalogie, Senckenberg Forschungsinstitut und Naturmuseum Frankfurt, Senckenberganlage 25, 60325 Frankfurt am Main, Germany*

3 *Fachbereich Geowissenschaften, Eberhard-Karls-Universität Tübingen, Hölderlinstraße 12, 72074 Tübingen, Germany*

4 *Institut für Geowissenschaften, Goethe-Universität Frankfurt am Main, Altenhöferallee 1, 60438 Frankfurt am Main, Germany*

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Corresponding author: Irina Ruf (irina.ruf@senckenberg.de)

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Abstract

Modern phylogenetics place the Soricidae (shrews) into the order Lipotyphla, which belongs to the relatively new superorder clade Laurasiatheria. Their most derived skull feature is the unusual position and shape of the jaw articulation: Whereas in all other mammals the glenoid region of the squamosum is more or less tightly attached to the otic capsule or petrosal, respectively, in the soricids it is attached to the nasal capsule. This new position of the jaw articulation becomes possible by the posterior extension of the nasal capsule and the rostral shift of the glenoid fossa. By the study of dated postnatal ontogenetic stages of *Crocidura russula* and *Sorex araneus*, we show that the glenoid part of the squamosal becomes fixed to the nasal capsule by the ossified alae orbitalis and temporalis. The ala orbitalis is displaced laterally by the expanded cupula nasi posterior; this posterior expansion is well documented by the lamina terminalis, which incorporates parts of the palatinum and alisphenoid. Both alae consist largely of ‘Zuwachsknochen’ (‘appositional bone’) and are then named orbitosphenoid and alisphenoid. By the forward move of the pars glenoidea and of the alisphenoid, the foramen lacerum medium (‘fenestra piriformis’) also expands rostrally. Functionally, the forward shift of the jaw joint helps to keep the incisal biting force high. Biomechanically the jaws can be considered as a tweezer, and the rostral position of the jaw joints makes the interorbital pillar and the shell-like walls of the facial skull a lever for the highly specialized incisal dentition.

Keywords

Crocidura russula, cupula nasi posterior, foramen lacerum medium, ontogeny, orbitosphenoid, *Sorex araneus*, squamoso-dental articulation

* Dedicated to the memory of Peter Vogel (1942–2015).

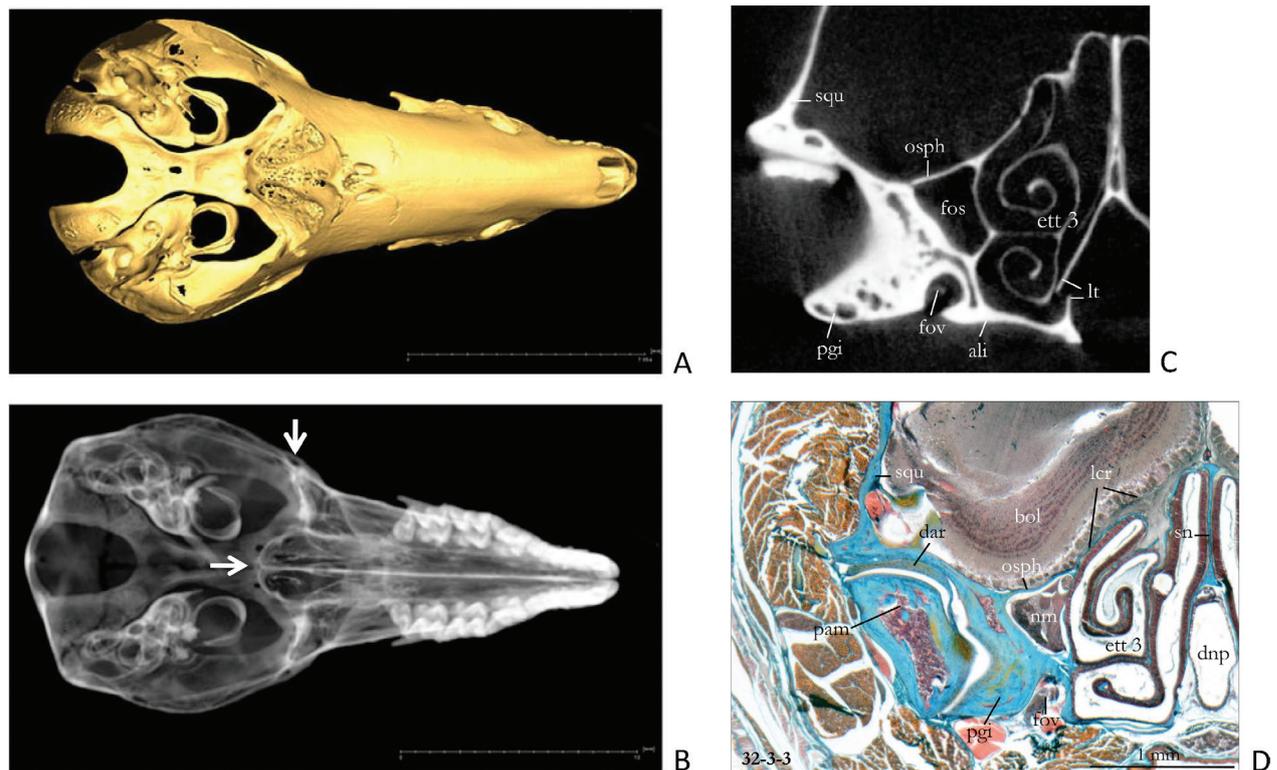


Figure 1. **A** Virtual picture of the skull of an adult specimen of *Sorex araneus* (SMF 82598). The roof of the braincase is removed to show the internal cranial base. **B** This semi-transparent figure (pseudo x-ray) of the same skull shows that the glenoid fossa (vertical arrow) appears to be attached to the posterior part of the nasal capsule. The recessus ethmoturbinalis and the posterior cupula of the nasal capsule reach back to the carotid foramina (horizontal arrow). **C** Virtual cross section (scan no. 1205, at about the level of the vertical arrow in C) showing the fixation of the glenoid portion of the squamosal to the lateral wall of the nasal capsule. The lamina terminalis is broken in this specimen. **D** Histological section of an adult specimen of *Sorex araneus* (Coll. W. Maier) at about the same plane as the μ CT scan. d1 32—3-3 means section series of neonate specimen: plate 32, row 3, and section 3. The fissura orbitalis superior is almost completely occupied by the ramus maxillaris of the trigeminal nerve and by the thin nervus opticus in its mediodorsal corner. The anterior notch of the foramen rotundum contains the ramus mandibularis of the trigeminal nerve. Note the pronounced dorsal protrusion of the posterior nasal capsule into the brain cavity and the peculiar structure of the jaw joint. The cross sections **C** and **D** are mirrored. Abbreviations: ali – alisphenoid, bol – bulbus olfactorius, dar – discus articularis, dnp – ductus nasopharyngeus, ett 3 – ethmoturbin 3, fos – fissura orbitalis superior, fov – foramen ovale, lcr – lamina cribrosa, lt – lamina terminalis, nm – nervus maxillaris, osph – orbitosphenoid, pam – processus articularis mandiblae, pgi – processus glenoideus inferior, sn – septum nasi, squ – squamosal.

Introduction

The morphology of the skull of Soricidae (shrews) is not well known. This is not too surprising, because the skulls are very small and are almost completely synostosed already in subadult stages. As will be demonstrated in this study, two distinctive features have been escaped notice so far: First, the progressive expansion of the posterior nasal capsule, which reaches the origin of the alae temporales; second, the rostral shift of the glenoid fossa and the mandibular joint. This results in the very peculiar position of the glenoid fossa of the squamosum to be attached at the sides of the nasal capsule (Fig. 1). In other mammals, the glenoid region of the squamosal is more or less closely attached to the petrosal (or parts of it such as the tegmen tympani) sometimes forming the compound os temporale (Mischknochen) as in Primates (Starck 1979).

From this unique feature arises the question whether the nasal capsule expanded actively, and second, whether the glenoid fossa moved progressively from the otic to the nasal region – or whether both structural complexes changed. The peculiar relationship of the glenoid facet on the squamosal with the nasal capsule needs further explanation, combined with the question about the functional meaning of these complicated modifications of the soricid skull.

Such morphological analyses can only be performed with the help of suitable ontogenetic stages. Fortunately, we have available dated sectional series of both *Sorex* and *Crocidura* of the first two postnatal weeks of development. We owe these sectional series to the late Peter Vogel, who had prepared them himself (Vogel 1973). This invaluable material was generously presented to the first author many years ago. As we will show, the shrews are quite immature at birth, and important processes of differentiation take place within the first two postnatal weeks.

Table 1. Material of Soricidae studied. Resolution is given as isotropic voxel size. Abbreviations: CRL – crown rump length, SMF – Mammal collection of the Senckenberg Forschungsinstitut und Naturmuseum Frankfurt.

Species	Collection	ID/ designation	Age/size	Histology	μCT scans				
				Staining	Voltage	Current	Timing	Projections	Resolution
<i>Crocidura russula</i>	P. Vogel	1d	neonatal/1 day	Azan					
<i>Crocidura russula</i>	P. Vogel	5d	5 days	Azan					
<i>Crocidura russula</i>	P. Vogel	7d	7 days	Azan, Ladewig					
<i>Crocidura russula</i>	P. Vogel	8d	8 days	Azan, Ladewig					
<i>Crocidura russula</i>	P. Vogel	15d	15 days	Azan					
<i>Crocidura russula</i>	W. Maier	No. 1	21 mm CRL	Azan					
<i>Crocidura russula</i>	W. Maier	No. 2	young adult	Azan					
<i>Crocidura russula</i>	W. Maier	No. 3	adult		145 kV	43 μA	708 ms	3500	0.00630 mm
<i>Crocidura russula</i>	SMF	95044	adult		90 kV	89 μA	1500 ms	1600	0.01147 mm
<i>Suncus etruscus</i>	SMF	26937	adult		90 kV	89 μA	1500 ms	1600	0.00794 mm
<i>Suncus murinus</i>	SMF	87406	adult		90 kV	89 μA	1500 ms	1600	0.01646 mm
<i>Myosorex varius</i>	SMF	55060	adult		90 kV	89 μA	1500 ms	1600	0.01259 mm
<i>Sorex araneus</i>	P. Vogel	1d	Neonatal/1 day	Azan, Ladewig					
<i>Sorex araneus</i>	P. Vogel	5d	5 days	Azan, Ladewig					
<i>Sorex araneus</i>	P. Vogel	10d	10 days	Azan					
<i>Sorex araneus</i>	P. Vogel	15d	15 days	Azan, Ladewig					
<i>Sorex araneus</i>	W. Maier	No. 4	adult	Azan					
<i>Sorex araneus</i>	SMF	82598	adult		90 kV	89 μA	1500 ms	1600	0.01148 mm
<i>Neomys fodiens</i>	SMF	68229	adult		90 kV	89 μA	1500 ms	1600	0.01259 mm
<i>Anourosorex squamipes</i>	SMF	48925	adult		90 kV	89 μA	1500 ms	1600	0.015126 mm

In the past, Parker (1885) studied two late fetal stages, a 10 to 12 days old postnatal stage, and an adult specimen of ‘*Sorex vulgaris*’ (= *Sorex araneus*). Late fetal stages of *Sorex araneus* based on serial sections were studied by DeBeer (1929). Very useful information on cranial anatomy of various soricids stem from Roux (1947) and Gaughran (1954). Masuda and Yohro (1994) analyzed the fetal skull of *Suncus murinus* by means of the staining and clearing technique. Vogel (1973) records several ossification sequences in postnatal stages of his soricids. More recently, Giere (2002) studied the orbitotemporal region of various ‘insectivores’, among them subadult and adult shrews; however, he did not systematically make use of ontogenetic stages.

While *Crocidura* is more derived in the reduction of the antemolar dentition, it seems to be somewhat more plesiomorphic in certain skull features. *Crocidura russula* has a pregnancy length of 30 days and *Sorex araneus* 20 days; therefore, *Crocidura* is born in a significantly more mature stage representing a derived pattern according to Vogel (1973), but we think it is the plesiomorphic one (see discussion). Therefore, in the following anatomical presentations, we always begin with the skull features of *Crocidura*.

Among the different components of the mammalian skull, the ear region has attracted by far the most interest. In recent years, with μCT technique available, the nasal region has won increasing importance (e.g., Van Valken-

burg et al. 2014; Ruf 2014; Ruf et al. 2015; Martinez et al. 2020). The orbitotemporal region is somewhat more problematical, because it consists of heterogeneous components and it overlaps with the other two regions. First of all, it is usually defined by the orbit and the size of the eyes, but this aspect is less relevant for soricids due to their greatly reduced eyeballs. The medial wall of the orbit has been considered informative in systematical regard (cf. Novacek 1980; Giere 2002). All of these parts of the head skeleton house important sense organs (smell, vision, hearing and equilibrium (cf. Demes 1981; Preuschoft 1989; Witzel 2020). Reduction of the eyes comprises a natural experiment which, we assume, may better illuminate the mechanical role of the orbitotemporal pillar (Maier 1993a; Ross 2001).

Material and Methods

We studied neonate to adult stages of *Sorex araneus* and *Crocidura russula* with histological serial sections and μCT scans; adult stages of further Soricidae were used for comparison. Details on the specimens, collections and scan parameters are presented in Table 1.

Histological serial sections of defined early postnatal age stages of *Sorex araneus* and *Crocidura russula* come

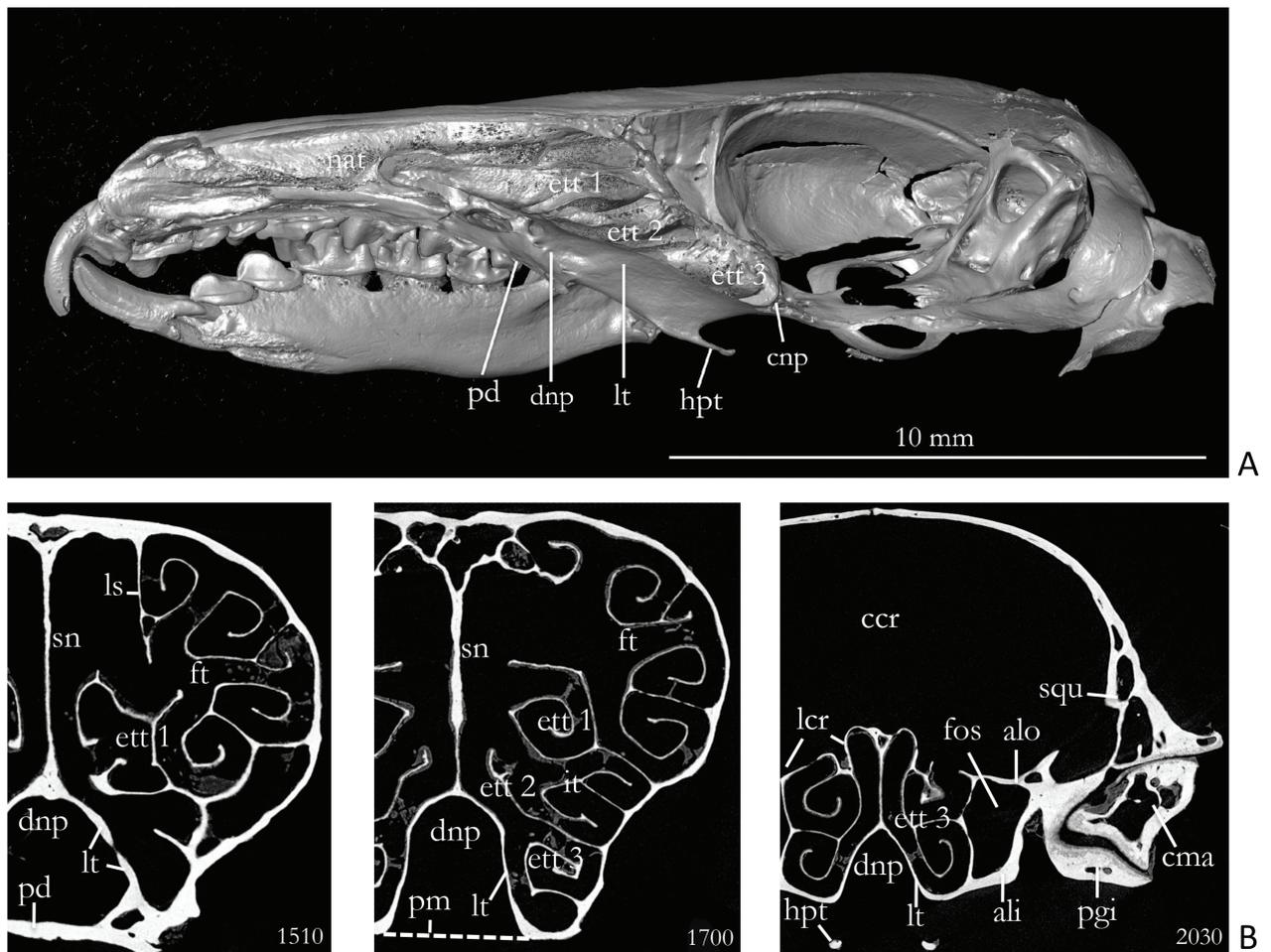


Figure 2. **A** Paramedian section of a skull of *Crocidura russula* (Coll. W. Maier). This figure shows the 3 ethmoturbinals filling the recessus ethmoturbinalis. The lamina terminalis is very elongated. **B** μ CT images of the same skull. – Cross section 1510 is near the anterior end of the lamina terminalis. – Section 1700 shows the lamina terminalis in about the middle of the nasopharyngeal duct, which is ventrally closed by the soft palate (stippled line). Cross-section 2030 shows the posterior part of the recessus ethmoturbinalis with the tips of the hamuli pterygoidei. The wall of the braincase and the snout may be interpreted as a strong shell (see discussion). Abbreviations: ali – alisphenoid, alo – ala orbitalis/orbitosphenoid, ccr – cavum cranii, cma – caput mandibulae, cnp – cupula nasi posterior, dnp – ductus nasopharyngeus, ett 1 – ethmoturbinal 1, ett 2 – ethmoturbinal 2, ett 3 – ethmoturbinal 3, fos – fissura orbitalis superior, ft – frontoturbinale, hpt – hamulus pterygoideus, lcr – lamina cribrosa, ls – lamina semicircularis, lt – lamina terminalis, nat – nasoturbinal, pd – palatum durum (secondary palate), pgi – processus glenoideus inferior, pm – palatum molle (velum palatinum), sn – septum nasi, squ – squamosus.

from the collection of the late Peter Vogel (Lausanne, Switzerland). They were prepared in the 1960s by P. Vogel for his dissertation under the supervision of Prof. Adolf Portmann at the University of Basel, Switzerland. We assume that the thickness of the sections is 10 μ m; the staining varies between ‘Azan’ and ‘Ladewig’. Histological serial sections of adult stages of *Sorex araneus* and *Crocidura russula* were prepared in the lab of the former Department of Zoology at the Eberhard-Karls-Universität Tübingen, Germany. All series comprise transversal sections except for a young adult specimen of *Crocidura russula* (Coll. W. Maier No. 2) that has been sectioned sagittally.

Mazerated skulls of adult sorcids were scanned with the μ CT scanner (Fraunhofer/ProConXray/Feinfocus) housed at the Senckenberg Forschungsinstitut und Naturmuseum Frankfurt, Frankfurt am Main, Germany. One wet specimen of *Crocidura russula* (Coll. W. Maier) with an articulated lower jaw was scanned with a Nikon XT

H 320 at the Senckenberg Centre for Human Evolution and Palaeoenvironment (HEP), Eberhard-Karls-Universität Tübingen, Germany. Based on the μ CT scans, virtual 3D models were automatically rendered and processed in Avizo 9.01 (Thermo Fisher Scientific FEI); the same software was used to produce pseudo X-ray images of the skulls based on the rendered 3D models.

Anatomy

Recessus ethmoturbinalis

Although the recessus ethmoturbinalis of the nasal cavity reaches far backward in sorcids, it contains only three ethmoturbinals and one interturbinal between ethmotur-

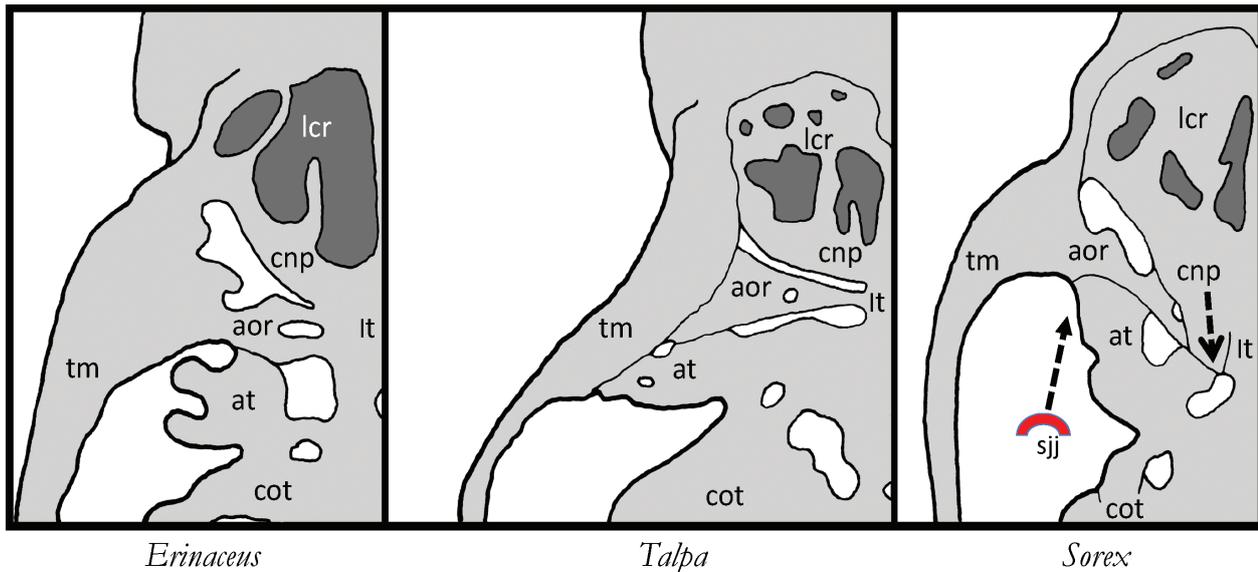


Figure 3. The endocranial base in three fetal Lipotyphla: *Erinaceus europaeus* (from Fawcett 1918), *Talpa europaea* (from Fischer 1901) and *Sorex araneus* (from DeBeer 1929). By the backward expansion of the posterior nasal capsule in *Sorex*, its ala orbitalis is largely separated from the trabecular plate of the central stem (remnants of this contact is described in the text). The tiny foramen opticum is medially framed by the lateral wall of the nasal capsule. In this fetus of *Sorex* the ‘anlage’ of the secondary jaw joint (sij) is still situated at some distance from the ala temporalis and the cupula nasi posterior; therefore, it cannot be primarily causal to the displacement of these structures. Abbreviations: aor – ala orbitalis, at – ala temporalis, cnp – cupula nasi posterior, cot – capsula otica, lcr – lamina cribrosa, lt – lamina trabecularis, sij – secondary jaw joint, tm – taenia marginalis.

binal 1 and 2 (Fig. 2); this number seems to be plesiomorphic for placental mammals (e.g., Ruf et al. 2015; Ruf 2014, 2020). The first ethmoturbinal is by far the largest, followed in size by ethmoturbinal 3; the second one is relatively simple and small. Obviously, the restrictions of the small absolute size of the recessus prevent an increase of turbinals which require a minimum of space for ventilation. Of course, there exists the question whether the nasal capsule actively expanded backwards, or whether it only changed its relationships with the adjacent structures (Figs 3, 4).

The base of the chondrocranium of three representatives of the Lipotyphla clearly elucidates the different proportions of the morphological and functional units of the skull (Fig. 3). The comparison of the cranial base of *Erinaceus*, *Talpa* and *Sorex* shows that in the first two taxa the ala orbitalis originates with one or two roots at the trabecular plate behind the nasal capsule; it then expands laterally at right angles to reach the taenia marginalis. In contrast, the ala orbitalis of the soricids seems to be detached from the trabecular plate and runs obliquely in rostralateral direction. However, we will show below that the ala has transitory contacts with the central stem in early postnatal life, but that this connection is covered by the cupula nasi posterior. Additional evidence for the progressive expansion of the posterior nasal pole comes from the lamina terminalis (see next chapter).

Lamina terminalis

The paramedian section of the skull of an adult *Crocodyrus russula* is shown in Fig. 2A. Very conspicuous is the

length of the lamina terminalis. The lamina terminalis is a neomorphic skeletal structure of mammals, which separates at least the posterior parts of the recessus ethmoturbinalis from the ductus nasopharyngeus. In monotremes it consists only of the lamina transversalis posterior (Kuhn 1971), but in therians it is commonly formed by a peculiar fusion of the cartilaginous lamina transversalis posterior of the nasal capsule and the transversal process of the vomer, i.e., it is a so-called ‘Mischknochen’ (Starck 1967, 1989; see also Ruf 2020). In most mammals it is relatively short and in some primates it may even be lost (Maier 1993a). Maier (2021: fig. 11-6 C) depicted a typical lamina terminalis in a juvenile of the marsupial *Mondelphis domestica*.

Due to the elongation of the pars posterior of the nasal capsule in soricids, the typical mammalian lamina terminalis is completed by additional components in a unique way: The typical therian composition between the lamina transversalis posterior and the crista lateralis of the vomer is only represented in its anteriormost part (Fig. 4A – b, c); it is then followed by a neomorphic cartilaginous bridge (Fig. 4A – d); thereafter, the lamina terminalis is formed by the processus ascendens of the palatine bone (Fig. 4A – e); this bone is underlain by the anterior process of the alisphenoid (Fig. 4A – f). The processus pterygoideus of the alisphenoid with its hamulus pterygoideus as a posterior appendix of the lamina terminalis, is no longer in direct contact with the nasal capsule (Fig. 4A – g). Finally, the posteriormost parts of the nasal capsule, i.e., the cupula nasi posterior and its lamina terminalis are completely formed by solid cartilage in the neonate (Fig. 4A – f, g; Fig. 4B). In later ontogenetic stages, the heterogeneous composition of the lamina terminalis is obscured

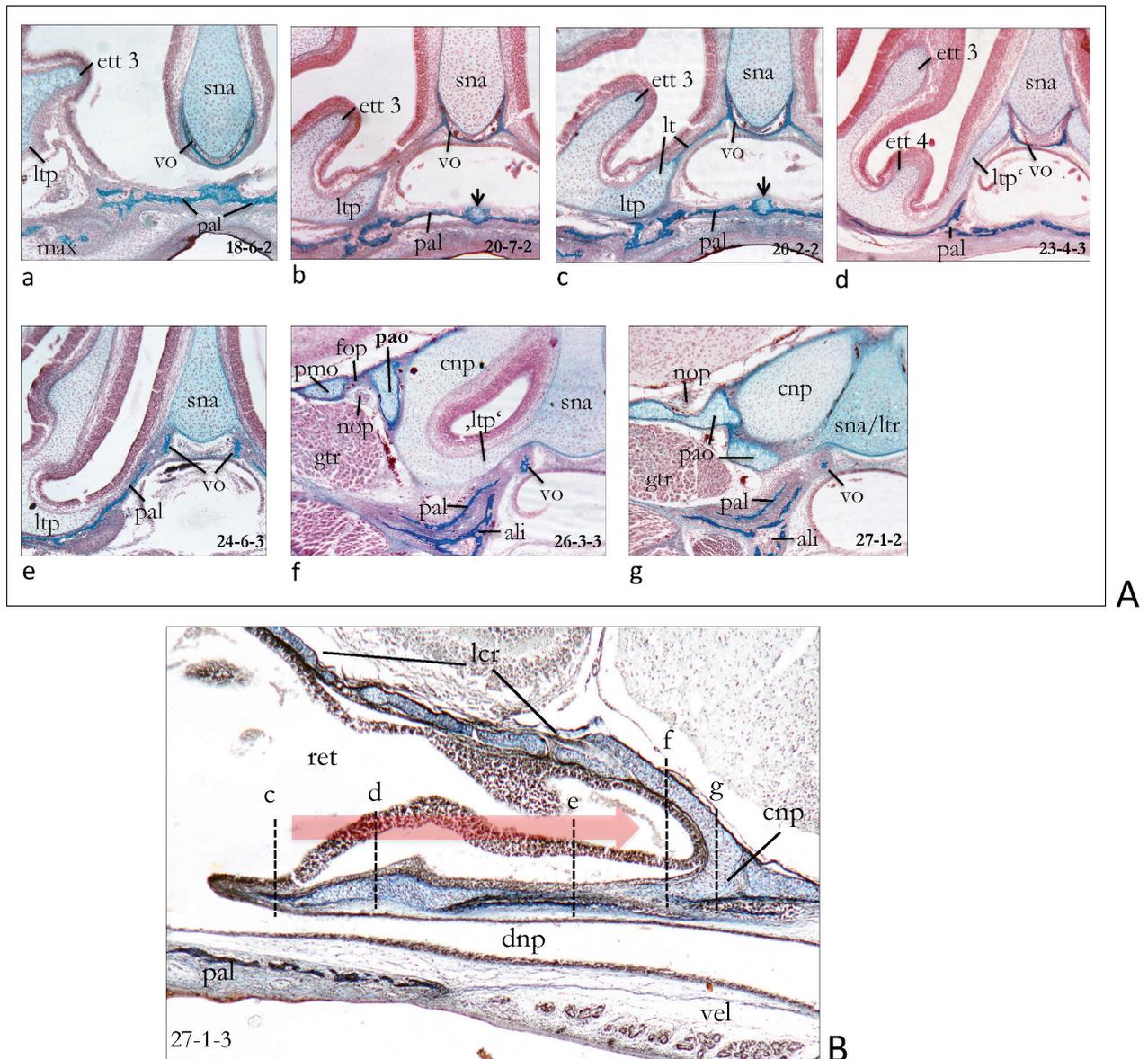


Figure 4. A Lamina terminalis in a neonate *Crocidura russula* (d1) with selected cross sections. **a** (section 18-6-2). Cross section slightly anterior to the lamina transversalis posterior (ltp). (The palate is pushed somewhat dorsally and therefore the internasal passage looks too narrow in **b** and **c**). **b** (section 20-7-2). Anterior end of the lamina transversalis posterior showing the heterogeneous origin of the lamina terminalis. Notice the secondary cartilage in the medial palatine suture (arrow). **c** (section 20-2-2). The complete lamina terminalis is a mixed bone ('Mischknochen') of enchondral bone from the nasal capsule and a lateral process of the dermal vomer. **d** (section 23-4-3). Behind the bony lamina terminalis there is a short gap which is closed by cartilage of the nasal capsule alone. **e** (section 24-6-3). Further behind this cartilaginous lamina is replaced by the ascending process of the palatine. **f** (section 26-3-3). Towards the cupula nasi posterior, the lamina transversalis posterior is again cartilaginous. The palatine is underlain by the alisphenoid. **g** (section 27-1-2). The ventral process of the pila praeoptica is bent around the ventral side of the posterior end of the massive cupula nasi posterior to reach its origin at the nasal septum. **B** Parasagittal section of a very young postnatal specimen of *Crocidura russula* (Coll. W. Maier, 21b) showing the recessus ethmoturbinalis and the lamina transversalis posterior. Letters c–f correspond approximately to the cross sections in **A**. Abbreviations: ali – alisphenoid, cnp – cupula nasi posterior, dnp – ductus nasopharyngeus, ett 3 – ethmoturbinal 3, fop – foramen opticum, gtr – ganglion trigemini, lcr – lamina cribrosa, lt – lamina terminalis, ltr – lamina trabecularis, ltp – lamina transversalis posterior, ltp' – medial transversal lamina, 'ltp' – terminal transversal lamina, max – maxillary, nop – nervus opticus, pal – palatinum, pao – pila praeoptica, fop – foramen opticum, pmo – pila metoptica, ret – recessus ethmoturbinalis, sna – septum nasi, vel – velum palatinum, vo – vomer.

by complete ossification and fusion of the heterogeneous elements. In the adult skull, all these components form a long and smooth bony plate providing the dorsolateral

walls of the relatively wide ductus nasopharyngeus (Fig. 2A, B).

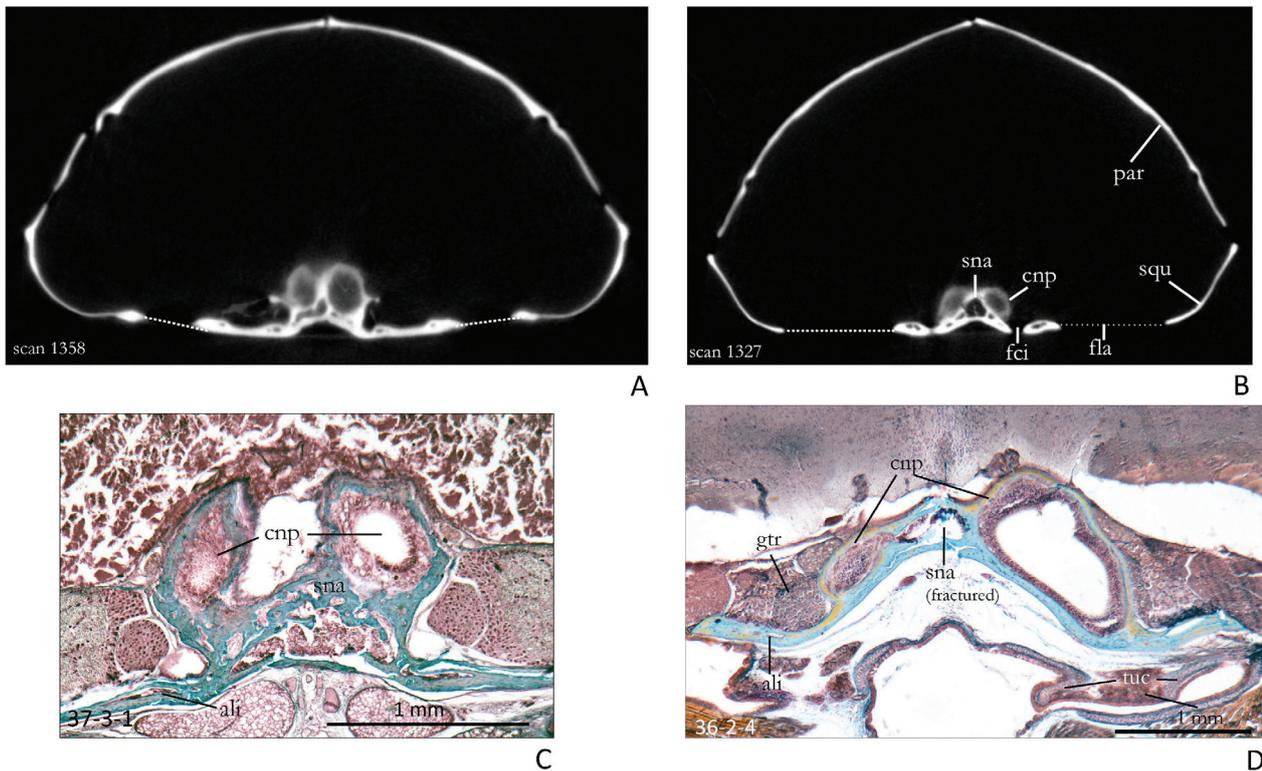


Figure 5. **A** μ CT scan at the level of the cupula nasi posterior in an adult specimen of *Crocidura russula* (SMF 95044, scan 1358). The septum between the cupulae is narrow. The brain cavity shows quite different proportions in the two taxa. **B** μ CT-scan of an adult specimen of *Sorex araneus* (SMF 82598, scan 1327). The septum between the cupulae is broad and triangular. The foramen caroticum internum and the anteriormost part of the foramen lacerum medium (stippled line) are also met; they reach further forward in *Sorex*. The squamosal is more narrow than in *Crocidura*. **C** Histological section of the cupula nasi posterior of an adult of *Crocidura russula* (Coll. W. Maier, section 37-3-1). The ossification of the cupula nasi posterior is still trabecular. **D** Histological section of an adult specimen of *Sorex araneus* (Coll. W. Maier, section 36-2-4). All bony elements are fused and transformed into lamellar bone. The posterior septum nasi is broad. The dorsal projection of the cupula nasi posterior of *Crocidura* is more pronounced than that of *Sorex*. Abbreviations: ali – alisphenoid, cnp – cupula nasi posterior, fci – foramen caroticum internum, fla – foramen lacerum medium, gtr – ganglion trigemini, par – parietal, sna – septum nasi (sphenethmoid), squ – squamosal, tuc – cartilago tubae auditivae.

Cupula nasi posterior

The cupula nasi posterior is defined as the posterior end of the nasal capsule (Voit 1909; Reinbach 1952a, b; Zeller 1983; Kuhn & Zeller 1987; Maier 1993a; Ruf 2020). Dorsally, the recessus ethmoturbinalis is mostly covered by the lamina cribrosa; only the posteriormost part consists of the solid lamina infracribrosa. Ventrally the cupula is separated from the ductus nasopharyngeus by the lamina terminalis (see above). Early in ontogeny, the cupula posterior consists of a more or less massive block of cartilage, which is in contact with several dermal bones of the posterior palate and of the sidewall of the skull (Maier 1993b, 2021). Eventually, all skeletal structures, including their ‘Zuwachsknochen’, fuse into one bone complex, which possesses a central position within the interorbital pillar (Fig. 5). The cupula nasi posterior of an adult *Sorex araneus* is shown in Fig. 5D; it consists of lamellar bone and it represents the ethmoid fused with the orbitosphenoid, the basisphenoid and the alisphenoid. The cupula of our *Crocidura* (Fig. 5C) consists of trabecular bone, because the animal was probably immature.

Figures 6 and 7 show the morphogenesis of the cupula nasi posterior in different ontogenetic stages. Both in

Crocidura russula and in *Sorex araneus* the cupula nasi posterior up to a postnatal age of about a week consists of solid cartilage, which is more or less closely connected with the posteriormost part of the nasal septum. This part of the septum nasi must have been the trabecular plate and interorbital septum in hypothetical forerunners, as is testified by the outgroups, i. e., the erinaceids and talpids (see Fig. 3). However ossified remnants of the pilae opticae are also incorporated into the skeletal block (Figs 8, 9). During the second week of postnatal development of both genera, the cupula nasi posterior becomes almost completely replaced by the ‘Zuwachsknochen’ (‘appositional’ bone, see below) of the orbitosphenoid, which originates within the perichondrium of the pila praeoptica or postoptica. We are not sure if endochondral ossifications of the cupula posterior contribute to the bony stage.

Ala orbitalis and orbitosphenoid

The ala orbitalis forms the posterior rim and the roof of the fissura orbitalis superior. The medial attachment of the ala orbitalis in soricids deserves special attention. In mammals the ala orbitalis is fixed to the dorsolateral

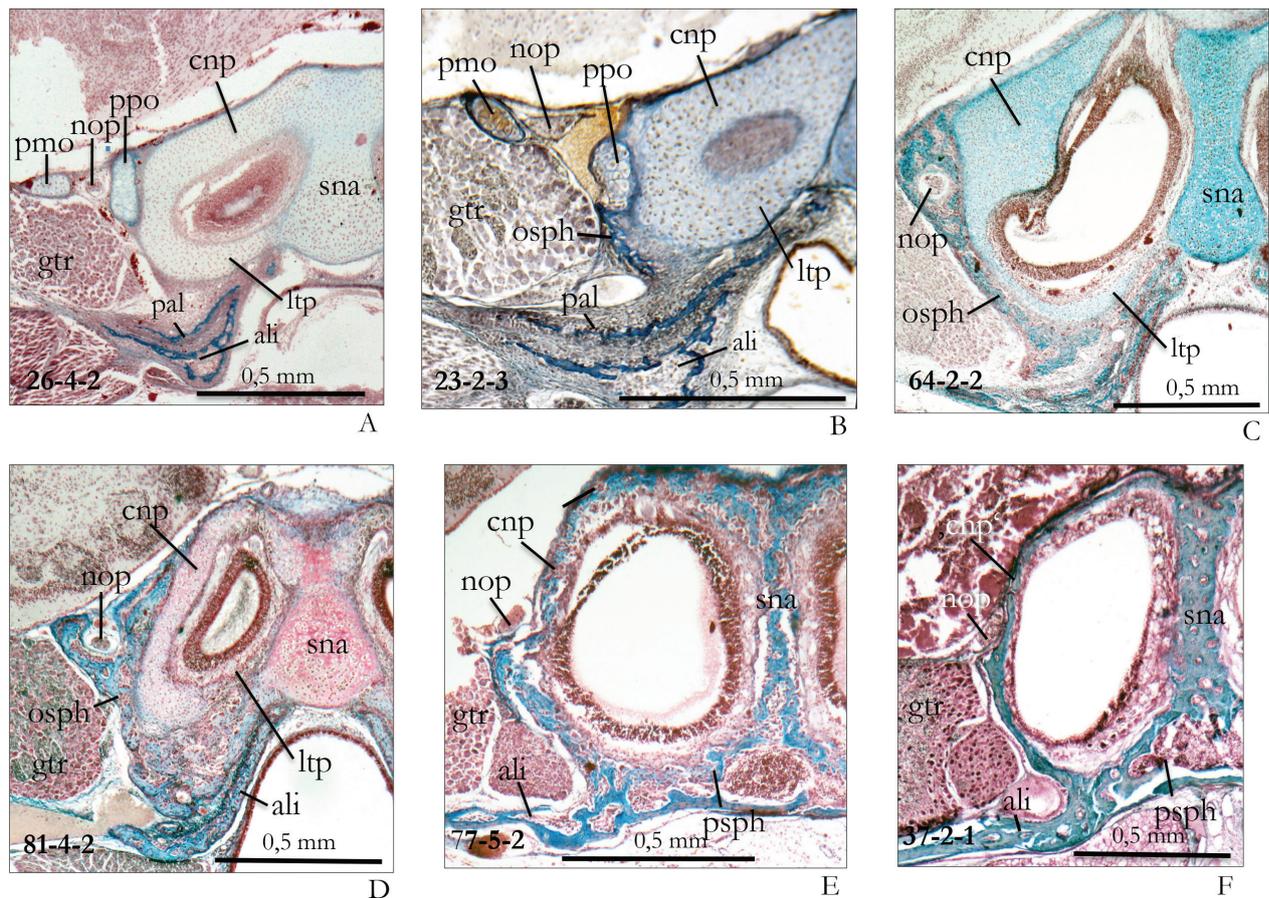


Figure 6. The cupula nasi posterior and orbitosphenoid in different ontogenetic stages of *Crocidura russula*. – **A** Neonate specimen (d1, section 26-1-2). The foramen opticum is shifted to the lateral side of the posterior nasal cupula. The large ganglion trigemini occupies almost completely the fissura orbitalis superior. **B** Young postnatal stage (Coll. W. Maier; section 23-2-3). The pila praeoptica forms ‘Zuwachsknochen’ (orbitosphenoid) at its ventral edge. The pila metoptica is partially ossified. **C** This specimen was 5 days old (d5, section 64-2-2). The expanded ‘Zuwachsknochen’ of the orbitosphenoid has enclosed the nervus opticus in a foramen opticum and spreads at the ventral side of the cupula nasi posterior. **D** This specimen was 8 days old (d8, section 81-4-2). The ‘Zuwachsknochen’ has almost completely enclosed the ventral parts of the cartilaginous cupula posterior. The cartilages of the cupula show first signs of reduction. The septum nasi begins to ossify endochondrally. **E** This specimen was 15 days old (d15, section 77-5-2). The cartilage has completely disappeared – probably resorbed. The narrow septum nasi is completely ossified and the orbitosphenoid ossification is fused with the alisphenoid. **F** This young adult still shows trabecular bone in the cupula nasi posterior, the nasal septum and the alisphenoid (cf. Fig. 5C). Abbreviations for Figs 6 and 7: ali – alisphenoid, cnp – cupula nasi posterior, fop – foramen opticum, gtr – ganglion trigemini, hpt – hamulus pterygoideus, ltp – lamina transversalis posterior, ltr – lamina trabecularis, nop – nervus opticus, osph – orbitosphenoid (‘Zuwachsknochen’), pal – palatinum, pmo – pila metoptica, ppo – pila praeoptica, ppt – processus pterygoideus, psph – praesphenoid, sna – septum nasi.

edge of the trabecular plate. Normally the attachments of the ala orbitalis lie behind the cupula nasi posterior (Parker 1885; Zeller 1987; Ruf et al. 2020). If there is an overlap with the pars posterior of the nasal capsule, as in *Oryctolagus* (Voit 1909), *Dasytus* (Reinbach 1952a, b), *Ptilocercus* (Ruf et al. 2015) and others, the cupula nasi posterior comes to lie below the pila praeoptica.

As shown in Figures 1 and 12, the ala orbitalis (and later the orbitosphenoid) of soricids is a slender bony plate that runs rostradorsally to reach the sidewall of the braincase. This special shape of the ala orbitalis is already seen in the chondrocranium of a fetal *Sorex araneus* (DeBeer 1929; see Fig. 3) and persists into the mature osteocranium (cf. Figs 1, 12, 18). Of particular interest is the medial contact of the ala orbitalis. Because of the caudal expansion of the

pars posterior of the nasal capsule, the pilae opticae are pushed laterally and seem to be detached from the central stem. However, in both *Sorex* and *Crocidura* the cartilaginous pila metoptica turns around the cupula posterior and maintains contact with the short trabecular plate; this contact is shortly after replaced by the ‘Zuwachsknochen’ of the orbitosphenoid. This early ontogenetic connexion may be considered as a phylogenetic retention. The structural details are different in both taxa (cf. Fig. 8), but it needs further study to decide whether the observed differences have systematic meaning or whether they are expression of natural variability. By the displacement of the rudimentary orbital pillars of the chondrocrania of soricids the tiny foramen opticum for the small tractus opticus appears to be often reduced to a small incisure. In juveniles the thin

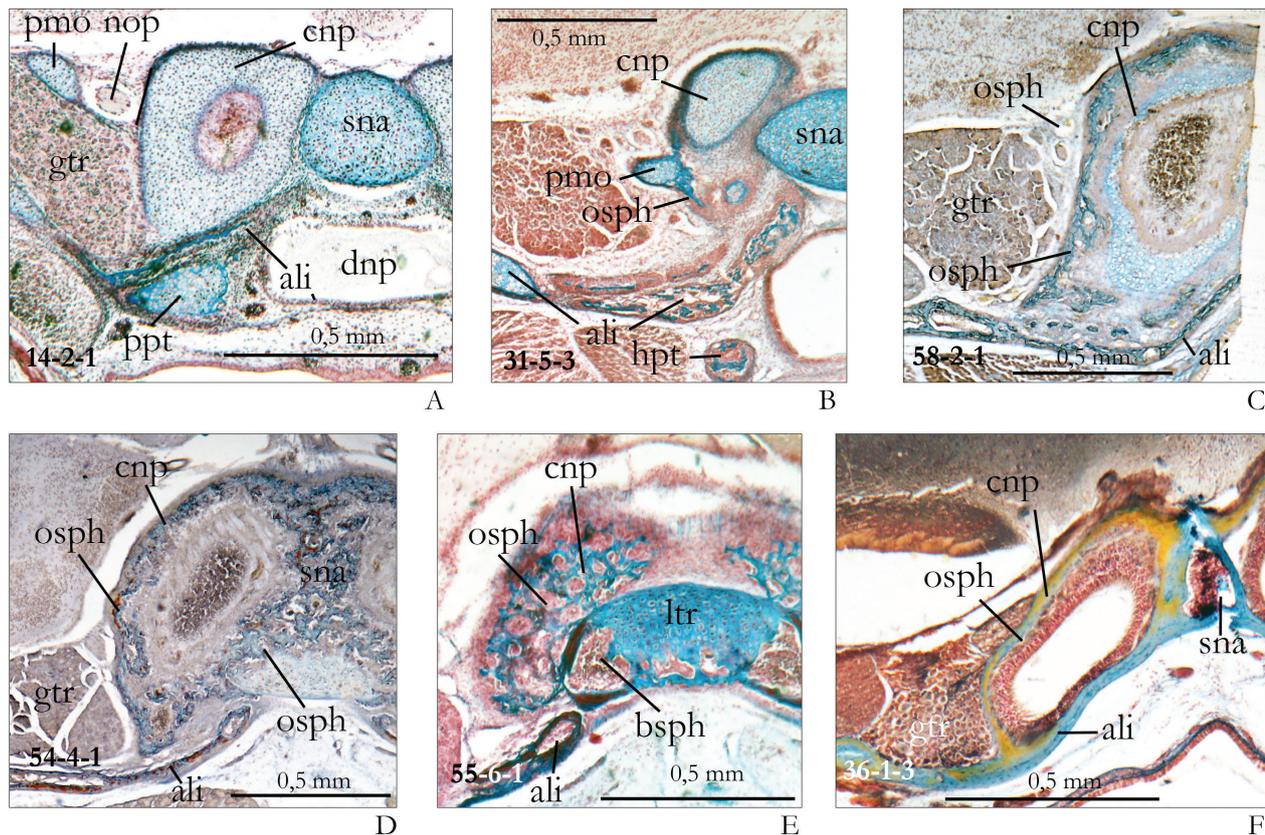


Figure 7. Posterior nasal cupula and orbitosphenoid in different ontogenetic stages of *Sorex araneus*. **A** (d1, section 14-2-1). In the neonate of *Sorex araneus* the cupula nasi posterior is still cartilaginous; the foramen opticum is framed by the pila metoptica only. The ganglion trigemini lies next to the cupula and is ventro-laterally supported by the ala temporalis. **B** (d5, section 31-5-3). The cupula nasi posterior and the pila metoptica of a *Sorex*-specimen of 5 days show the initial formation of ‘Zuwachsknochen’. **C** (d10, section 58-2-1). In this 10 days old specimen, the cartilaginous cupula nasi posterior is almost completely enclosed by Zuwachsknochen (orbitosphenoid) and the cartilage is in the process of resorption or endochondral ossification. **D** (d15, section 54-4-1). At this stage of 15 days, the cartilage of the cupula nasi posterior has completely disappeared and is replaced by Zuwachsknochen (orbitosphenoid). It is also fused with the bony nasal septum and with the cupula nasi of the other side. **E** (d15, section 55-6-1 of the same specimen) shows the very end of the bony cupula nasi. The edges of the trabecular plate are already ossified as basisphenoid. **F** (adult, section 36-1-3). In this adult specimen the cupula nasi posterior is formed by thin lamellar bone; it is fused with the bony septum nasi and the alisphenoid. Abbreviations: see Fig. 6, bsph – basisphenoid, dnp – ductus nasopharyngeus, nop – nervus opticus.

optical nerve becomes enclosed by the bone tissue of the orbitosphenoid (Figs 9, 10).

Starck (1979, 1989) stated that the pilae opticae are the places of origin of so-called ‘Zuwachsknochen’, but their first ossifications have different names: ala hypochiasmatica, ‘cartilago’ antorbitalis, orbitosphenoid, etc. The steps of differentiation of the ‘Zuwachsknochen’ in connection with the cupula nasi posterior are shown in Figures 6 and 7. Functionally, these secondary ossifications most likely mean that the origin of the ala orbitalis from the structures of the ‘central stem’ have become strengthened mechanically, and that mere endochondral ossification would not be sufficient.

In the neonate of *Crocidura* the cartilaginous ala orbitalis is laterally not yet tightly fixed to the rostral part of the squamosal (Fig. 9A). However, in the same specimen, the squamosal reaches a bit more forward, underlies the ala orbitalis and contacts the frontal bone; the squamosal has expanded ventromedially and meets the dorsal margin of the cartilaginous ala temporalis. The mandibular joint has already developed a single cleft, and the carti-

lage of the caput mandibulae begins to develop an internal process (Fig. 9C, D).

In the 7 days old-specimen of *Crocidura*, the anterior rim of the ala orbitalis is already transformed by Zuwachsknochen into orbitosphenoid, and this bone is partially fused with the inner side of the squamosal (Fig. 10A). The squamosal in front of the glenoid fossa is also tightly fused with the frontal. Ventrally, the squamosal almost reaches the ascending process of the palatine. More posteriorly the ala orbitalis and its orbitosphenoid ossification are detached from the squamosal, whose ventral process gains contact with the anterior process of the alisphenoid (Fig. 10B). It is only after the firm attachment of the squamosal and the alisphenoid is realized, when the jaw joint becomes visible. In the 8 day-old specimen, the largely ossified ala orbitalis only contacts the squamosal in front of the jaw joint (Fig. 10C). At day 15 (Fig. 10E), the skeletal elements are more or less completely fused to a bony massa glenoidea underlying the fossa glenoidea of the mandibular joint and combine it with the ethmoid of the nasal capsule.

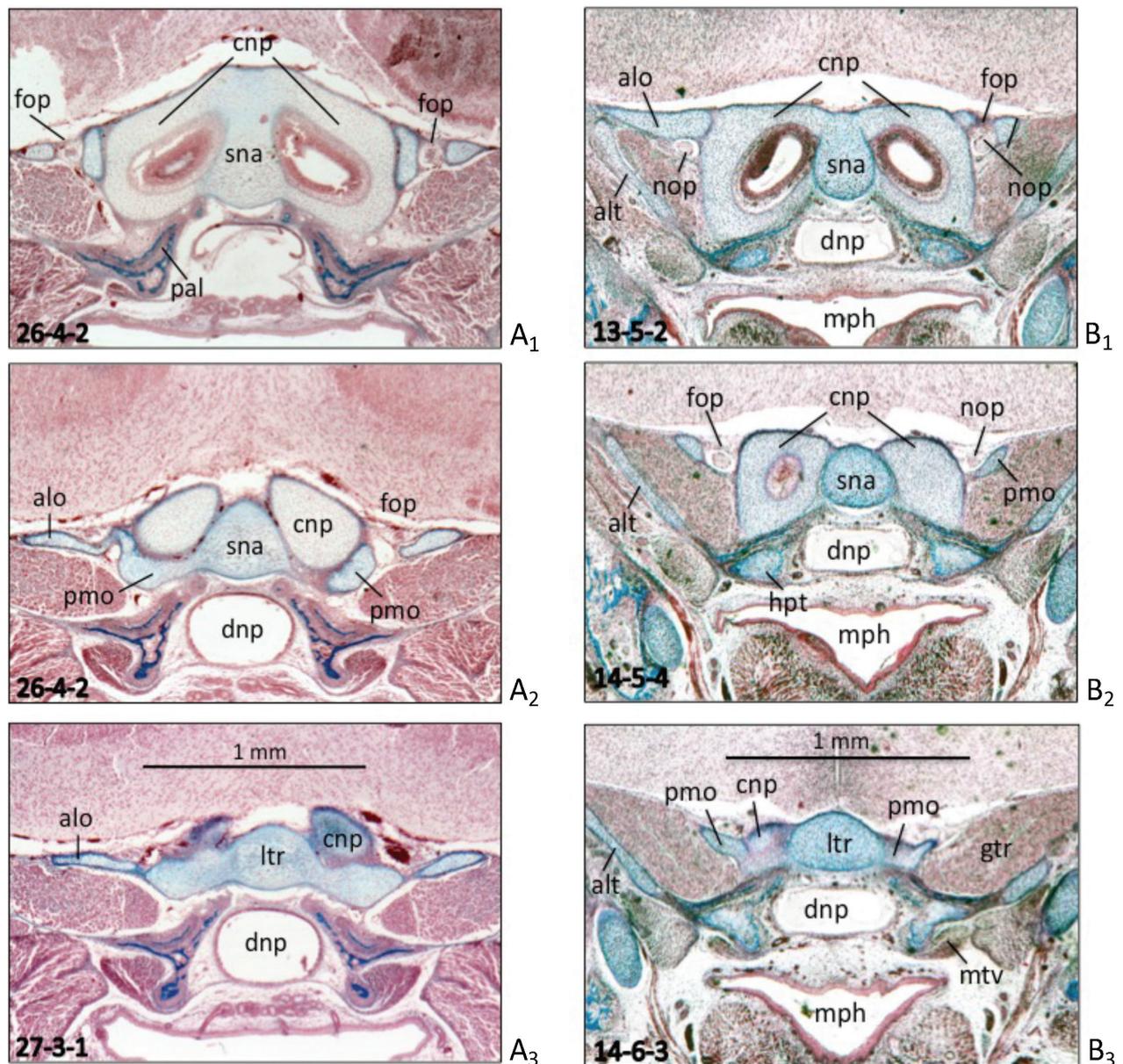


Figure 8. Posterior end of the nasal capsule and its topographic relations with the cartilages of the pila metoptica and the lamina trabecularis in neonates of *Crocidura russula* (A₁–A₃) and *Sorex araneus* (B₁–B₃). The proportions of the cupula and its relations with the ala orbitalis are somewhat different in the two taxa. In *Crocidura* the cupula nasi posterior comes to lie completely at the dorsal side of the pila metoptica, whereas in *Sorex* the tip of the cupula is enclosed by the pila metoptica. Abbreviations: alo – ala orbitalis, ali – alisphenoid, alt – ala temporalis, cnp – cupula nasi posterior, dnp – ductus nasopharyngeus, fop – foramen opticum, gtr – ganglion trigemini, htp – hamulus pterygoideus, ltr – lamina trabecularis, mph – mesopharynx, mtv – musculus tensor veli palatini, nop – nervus opticus, pal – palatinum, pmo – pila metoptica, sna – septum nasi.

In *Sorex araneus*, with its distinctly shorter gestation length, the squamosum of the neonate ends anteriorly at the level of the cupula nasi posterior, and it does just reach the ala orbitalis (Fig. 11A). The anterior process of the ala temporalis is in touch with the underside of the ala orbitalis. The anlage of the jaw joint lies posterior to the cupula, and it is still quite undifferentiated; no medial process or articular cleft is yet developed. On day 5, the squamosum has reached the ala orbitalis at the level of ethmoturbinal 3, but the two skeletal elements are not closely connected (Fig. 11B). The jaw joint, which is now distinctly more differentiated, lies at the level of the cupula nasi posterior (Fig. 11B). Except for the pila metoptica, where ‘Zu-

wachsknochen’ begins to spread, the ala orbitalis is still cartilaginous. At day 10 the ala orbitalis is almost completely transformed by ‘Zuwachsknochen’ into the orbitosphenoid; the ala temporalis is completely transformed into the wing of the alisphenoid, and both are closely connected with the expanded squamosal, which is beginning to differentiate a fossa glenoidalis (Fig. 11C, D).

Alisphenoid

The inspection of dorsal views of pseudo-X-rays of the skulls of *Crocidura* and *Sorex* reveals that in the latter

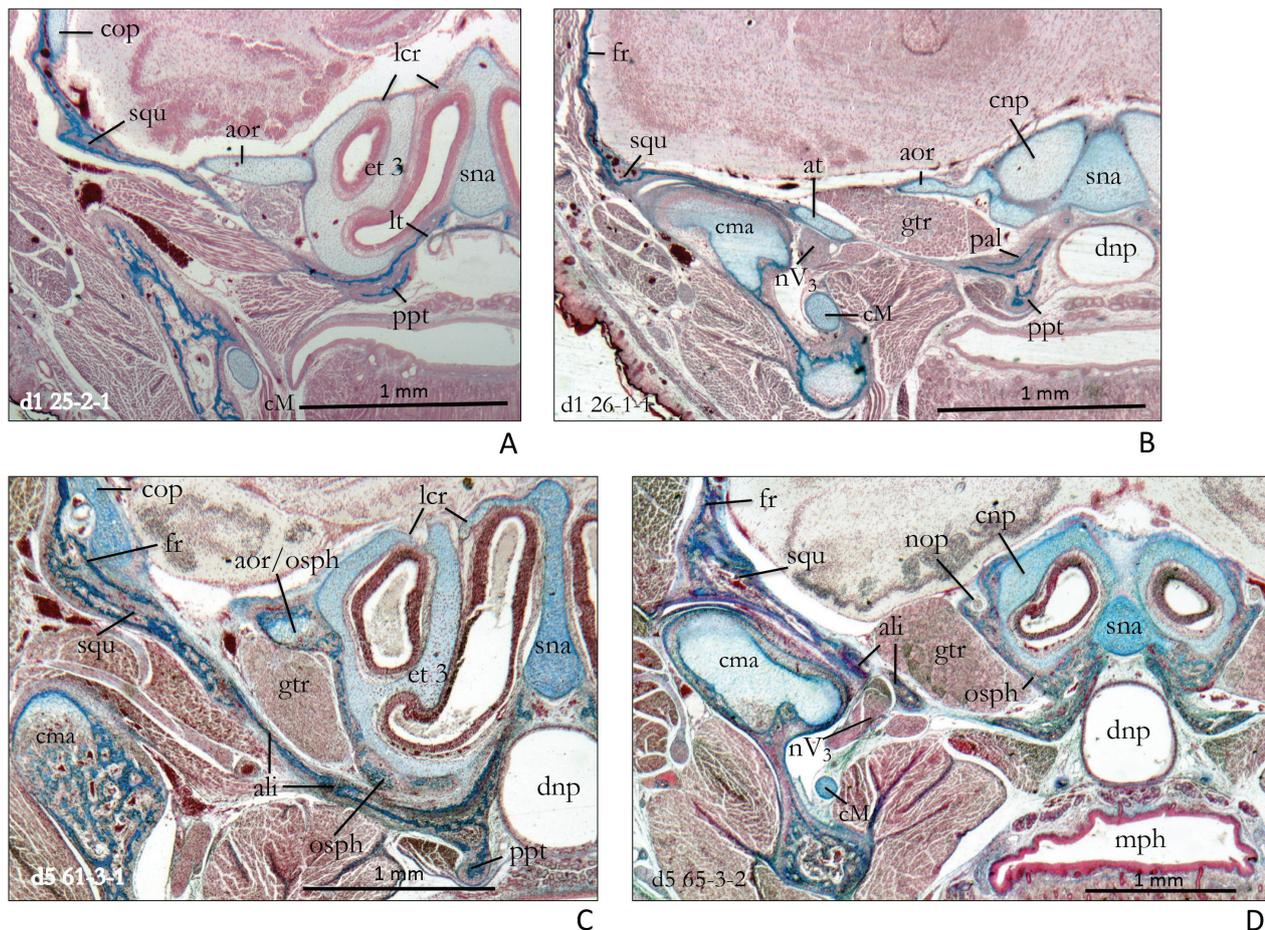


Figure 9. Ala orbitalis and squamosum in a neonate (above) and a five days old specimen (below) of *Crocidura russula*. **A** In section d1 25-2-1 the cartilaginous ala orbitalis has only feeble contact with the rostral end of the squamosum. **B** Section d1 26-1-1 shows that at the level of the initially differentiated jaw joint the squamosum is in contact with the ala temporalis. The proximal edge of the ala orbitalis is connected with the trabecular plate by the rudimentary pila metoptica. **C** At d5 61-3-1 the ala orbitalis is ossified in its distal and proximal parts, and the pila metoptica is partly developed into an expanded orbitosphenoid by ‘Zuwachsknochen’. **D** In section d5 65-3-2 the bony orbitosphenoid has almost completely enclosed the cartilaginous cupula nasi posterior. The genoid region of the squamosum is closely connected with the alisphenoid. The lateral and posterior part of the alisphenoid is pierced by the foramen ovale for the ramus mandibularis of the nervus trigeminus. Abbreviations: ali – alisphenoid, aor – ala orbitalis, at – ala temporalis, cM – cartilago Meckeli, cma – caput mandibulae, cnp – cupula nasi posterior, cop – commissura orbitoparietalis, dnp – ductus nasopharyngeus, et 3 – ethmoturbinal 3, fr – frontale, gtr – ganglion trigemini, lcr – lamina cribrosa, lt – lamina terminalis, mph – mesopharynx, nop – nervus opticus, nV₃ – nervus mandibularis, osph – orbitosphenoid, ppt – processus pterygoideus, sna – septum nasi, squ – squamosum.

species the jaw articulation is shifted slightly more rostrally than in *Crocidura*; therefore, the alisphenoid can hardly be recognized in dorsal view (Fig. 12). In *Crocidura* the alisphenoid originates more caudally and is hardly covered by the ala orbitalis. The alae temporales are also inclined somewhat differently in the two taxa, i.e., it is oriented more transversely in *Crocidura*. In *Crocidura russula* the fossa glenoidalis is only directly supported by the alisphenoid, and the orbitosphenoid contacts the anterior process of the squamosum before the jaw joint. In *Sorex araneus* the jaw joint has moved a little more rostrally, and the glenoid part of the squamosum is medially in contact with both the alisphenoid and the orbitosphenoid. Because of the rostral shift of the alisphenoid, the foramen lacerum medium of *Sorex* reaches distinctly more forward than in *Crocidura* (Fig. 12). A short comparative presentation of the inner cranial base and the al-

isphenoid is given below in the context of the foramen lacerum medium (Fig. 18).

In the early postnatal stages of both *Crocidura* and *Sorex* the lamina ascendens of the ala temporalis is still cartilaginous, whereas the proximal part, which probably represents the processus alaris, consists of bone. The periphery of the ala temporalis is in its periphery enlarged by the ‘Zuwachsknochen’ of the alisphenoid. The ventral process pterygoideus, which provides the hypomochlion (hamulus) for the m. tensor tympani, is bony from the beginning. Later on, its tip is partly transformed into secondary cartilage. At the posterior margin of the ala temporalis exists a conspicuous incisure for the ramus mandibularis trigemini (V₃); it is later transformed into the foramen ovale. After the endochondral ossification of the ala temporalis and its fusion with the ‘Zuwachsknochen’, the whole bone is by convention named alisphenoid.

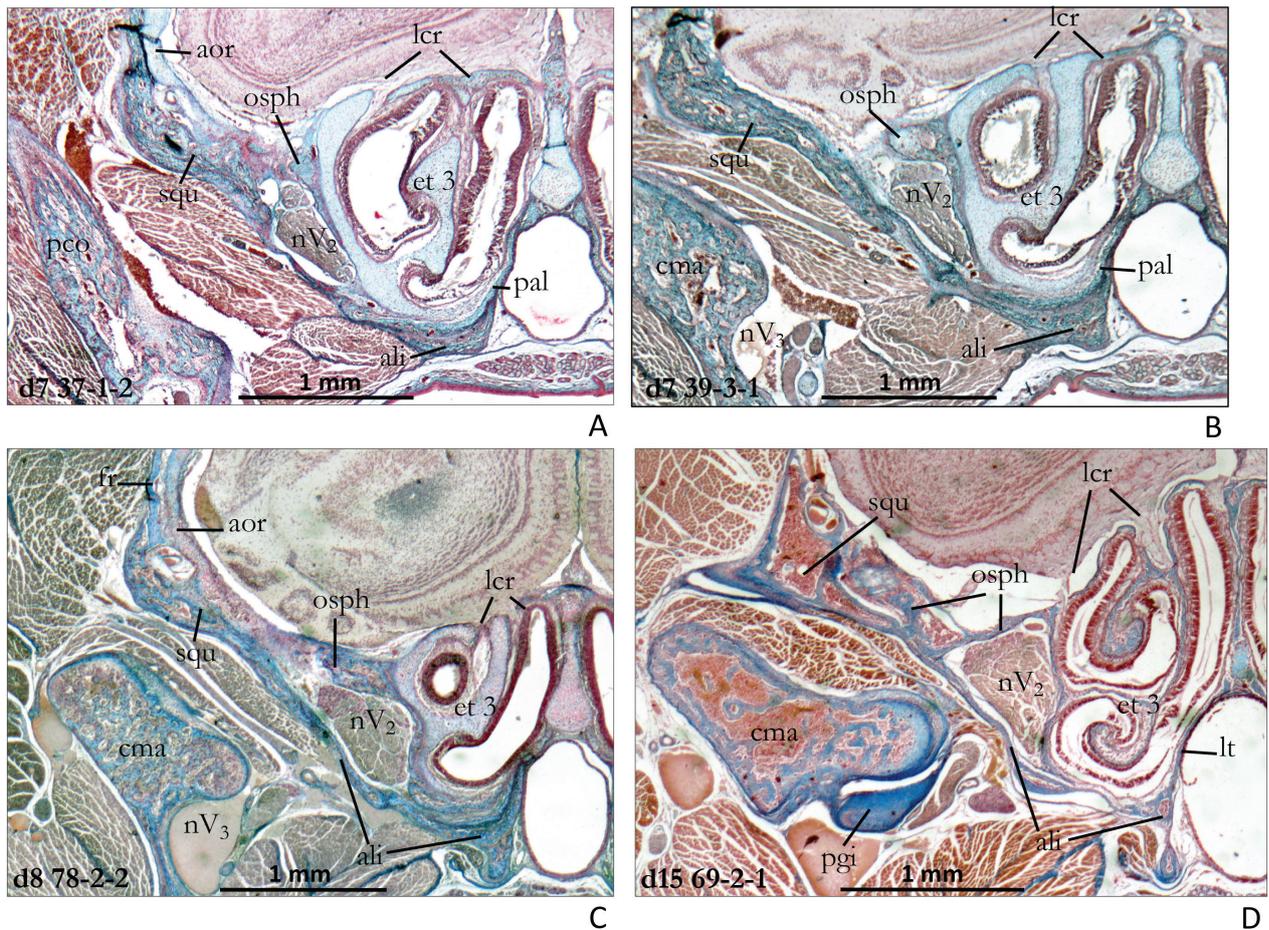


Figure 10. Orbitosphenoid, squamosum and alisphenoid in postnatal days 7–15 of *Crocidura russula*. **A** In section d7 37-1-2 the ‘Zuwachsknochen’ of the orbitosphenoid begins to contact the squamosum. **B** In section d7 39-3-1 the orbitosphenoid underlies the squamosum only rostral to the glenoidal region, i.e. the mechanical support for the joint is only indirect. **C** In section d8 78-2-2 the support of the squamosum is provided by the anterior process of the alisphenoid only. **D** In section d15 69-2-1 the pars glemoidea of the squamosum is connected with the nasal capsule (ethmoid) by the orbitosphenoid and the alisphenoid. Abbreviations: see Fig. 9, nV2 – nervus maxillaris, pal – palatinum, pco – processus coronoideus, pgi – processus glemoideus inferior.

Squamosum

It is well known that the secondary jaw articulation of mammals evolved during the Jurassic between the squamosal and the processus articularis of the dentary (Gaupp 1913; Allin 1975). The primary articulation between the quadrate and the articular became the incudo-malleolar joint. (Takechi and Kuratani 2010; Maier and Ruf 2016). Kermack et al. (1981) have shown that both joints existed together in the fossil *Morganucodon*. The squamosal bone originally is part of the primary skull roof, but with its new function as socket of the secondary jaw articulation it developed an internal process which later participated with its squama in the formation of the new orbitotemporal sidewall of therian mammals. Other components of the secondary sidewall are deep processes of the frontal and the parietal bones (Maier 1987, 1993b). The posterior part of the zygomatic arch (zygomatic process) represents the old part of the primary roof of the skull. Otherwise the old roof disappears by the extension of the fenestra temporalis, i.e. it survives as fascia temporalis. The new squama comes to lie underneath the temporal muscle at the level of the epipterygoid or alisphenoid.

The squama of the squamosum of soricids is low and stretched rostrocaudally; rostrally it is fused with the frontal in front of the mandibular jaw, but the exact line of contact cannot be identified. The squamosal reaches a little higher in *Crocidura* than in *Sorex* (Figs 5, 13). In the fetus of *Sorex araneus* described by DeBeer (1929), the squamosal has not reached the frontal yet; the head of the mandible and the anterior tip of the dentary are still quite apart (double arrow in Fig. 13A).

The glenoid fossa is positioned at the transition between the primary and secondary parts of the squamosum. Gegenbaur (1892) called the ‘Gelenkgrube’ cavitas glenoidalis or fossa articularis; the modern nomina anatomica term is fossa mandibularis (Feneis 1974); Starck (1979) speaks of ‘Kiefergelenkspfanne’; McDowell (1958) and Dötsch (1982) used ‘glenoid fossa’. This glenoidal part of the squamosum normally is in close but variable connection with the petrosal bone. In primates these two bones even fuse (together with the ectotympanicum and the tympanohyal) to form the temporal bone (‘Mischknochen’ of Starck 1979). The mammalian glenoid fossa is situated anterior to the meatus acusticus externus; very often both structures are separated by a

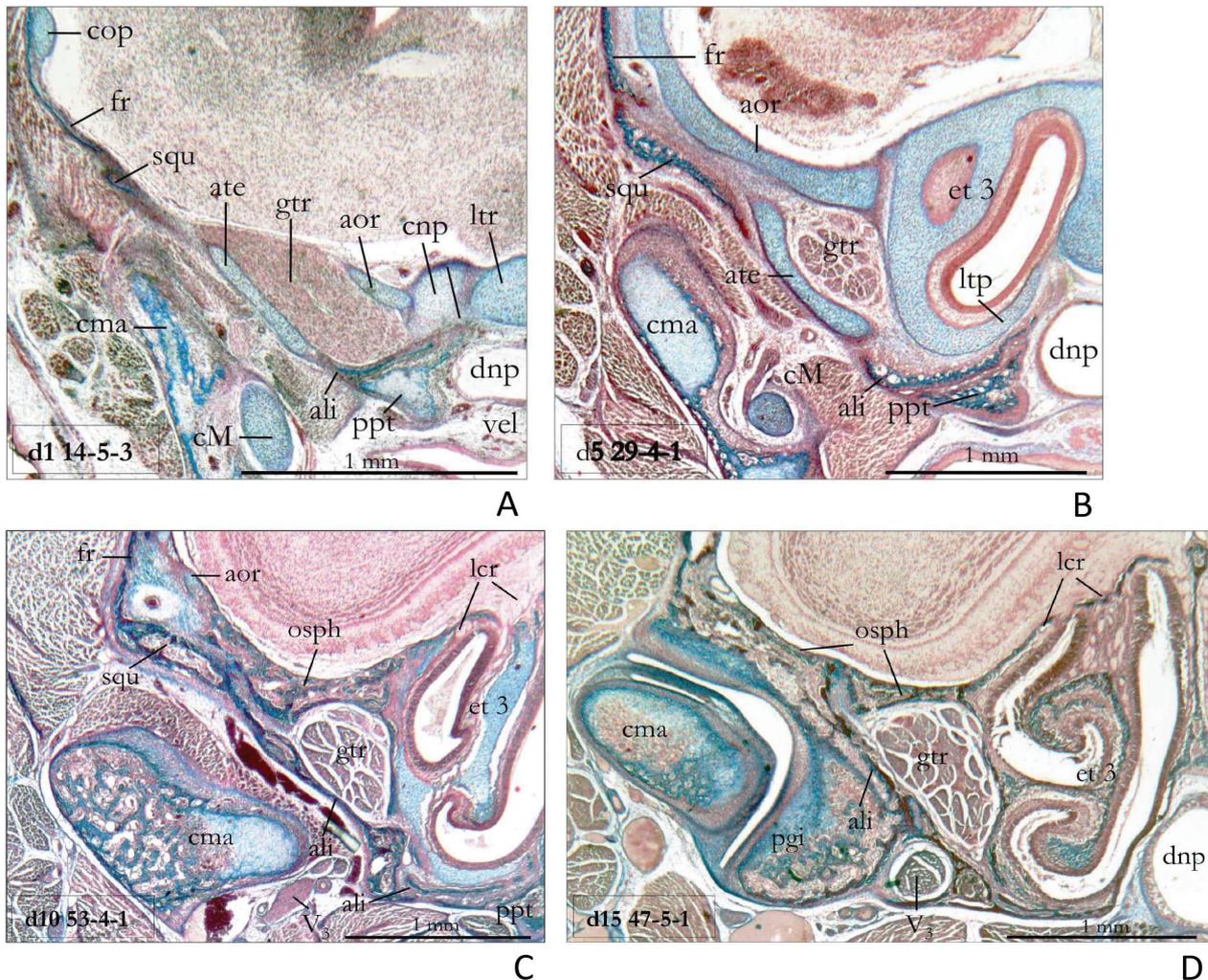


Figure 11. Ala orbitalis, ala temporalis and jaw joint in different postnatal stages of *Sorex araneus*. **A** Section d1 14-5-3 shows that the anterior tip of the squamosal does not yet contact the ala orbitalis in the neonate. The anlage of the jaw joint is very immature, and it is still situated at the level of the cupula nasi posterior. **B** At day 5 (section d5 29-4-1), the squamosal and the ‘anlage’ of the jaw joint have reached the ala orbitalis and both are already positioned at the level of ethmoturbinal 3. However, frontal bone, ala orbitalis, ala temporalis and squamosal are not yet closely connected. **C** At day 10 (section d10 53-4-1), the orbitosphenoid and the alisphenoid are providing solid supports for the squamosum. **D** At day 15 (section d15, 47-5-1) we already see similar structural proportions as in the adult (cf. Fig. 1 D). The foramen ovale for the mandibular branch of the trigeminus nerve is situated directly behind the fully developed processus glemoideus inferior. Abbreviations: see Fig. 9, ate – ala temporalis, ltp – lamina transversalis posterior, ltr – lamina trabecularis, pgi – processus glemoideus inferior, V3 – nervus mandibularis, vel – velum palatinum.

more or less prominent processus postglenoideus of the squamosum. Regularly, a thick vena postglenoidea leaves the braincase between the glenoidal fossa and the meatus acusticus externus.

Fossa glenoidalis and processus glenoides inferior

The fossa glenoida is the concave counterpart of the caput mandibulae. It is well known that the squamoso-dentary joint of soricids is very complicated (Dötsch 1982). In fact, it shows two compartments which stand at about right angles to each other. The processus articularis of the lower jaw is a dermal bone, but its proximal end is very often transformed into more or less extensive secondary cartilage. The complicated relief of the fossa glenoidalis

in soricids has been studied repeatedly by functional anatomists (Fearnhead et al. 1955; Dötsch 1982).

Ontogenetically, the dorsal part of the joint is beginning to develop in the neonate of *Crocidura russula*; the articular cleft already exists, but the squamosum has not yet developed secondary cartilage. The discus articularis is not yet detached from the articular head of the mandible (Fig. 14A). After five postnatal days, an epithelial lamina is growing ventrally, and the squamosal has begun to produce a processus glemoideus inferior (Fig. 14B). After ten days, the ventral chamber of the jaw articulation and the processus glemoideus inferior are already well developed (Fig. 14C). After fifteen postnatal days the joint has almost reached the adult proportions (Fig. 14D).

In the neonate *Sorex araneus* the jaw is less well developed, i.e., it is more altricial (Fig. 15A). The processus glemoideus inferior, which is prominent in *Sorex*,

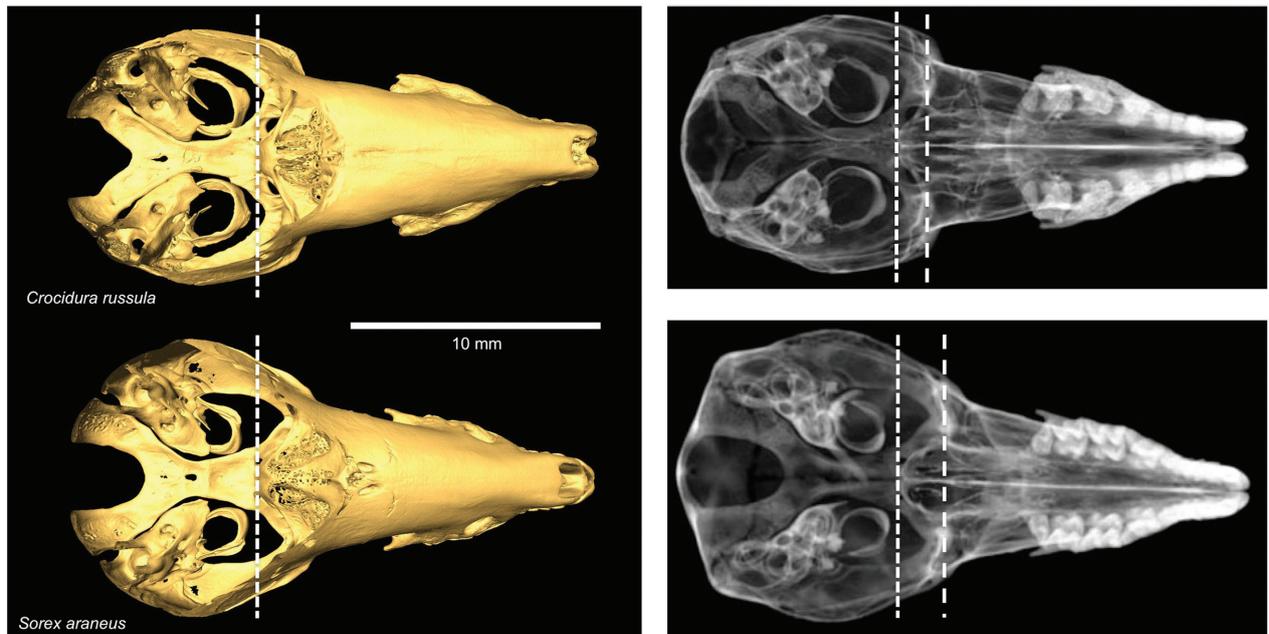


Figure 12. Dorsal view and ‘pseudo X-rays’ of the same specimens of *Crocidura russula* (SMF 95044) and *Sorex araneus* (SMF 82598). In both specimens, the cupula nasi posterior is exactly in the same position in comparison with the basicranial length (stippled line). However, the jaw joint of *Sorex* lies somewhat more rostrally than that of *Crocidura* (anterior dashed lines in the pseudo-X-rays). In *Crocidura*, the alisphenoid originates more caudally at the basisphenoid, and its wing is less inclined and is more exposed in dorsal perspective. In *Sorex* the foramen lacerum medium extends more rostrally.

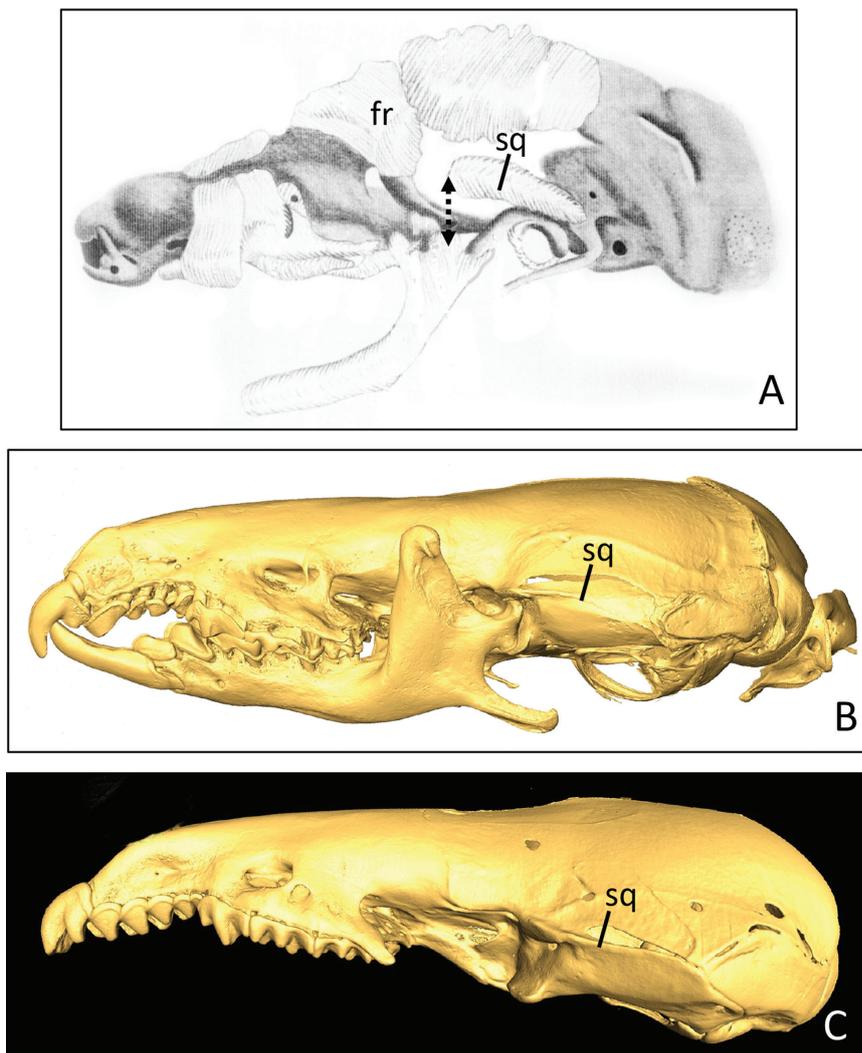


Figure 13. Lateral view of the skulls of soricids. **A** Chondrocranium of a fetal stage (11 mm) of *Sorex araneus* (reversed) (modified from DeBeer 1929). The squamosal (sq) has not yet reached the frontal bone (fr); the elements of the jaw articulation, fossa glenoidalis and caput mandibulae, are quite apart, but have begun to differentiate as a joint (cf. fig. 19–21 in DeBeer 1929). **B** Skull of *Crocidura russula* (Coll. W. Maier) with lower jaw in situ. The suture with the parietal bone is visible, but rostrally the squamosum is tightly fused with the frontale. **C** Skull of *Sorex araneus* (SMF 82598). Note the enormous size of the processus glenoideus inferior (see below). Abbreviations: fr – frontale, sq – squamosum.

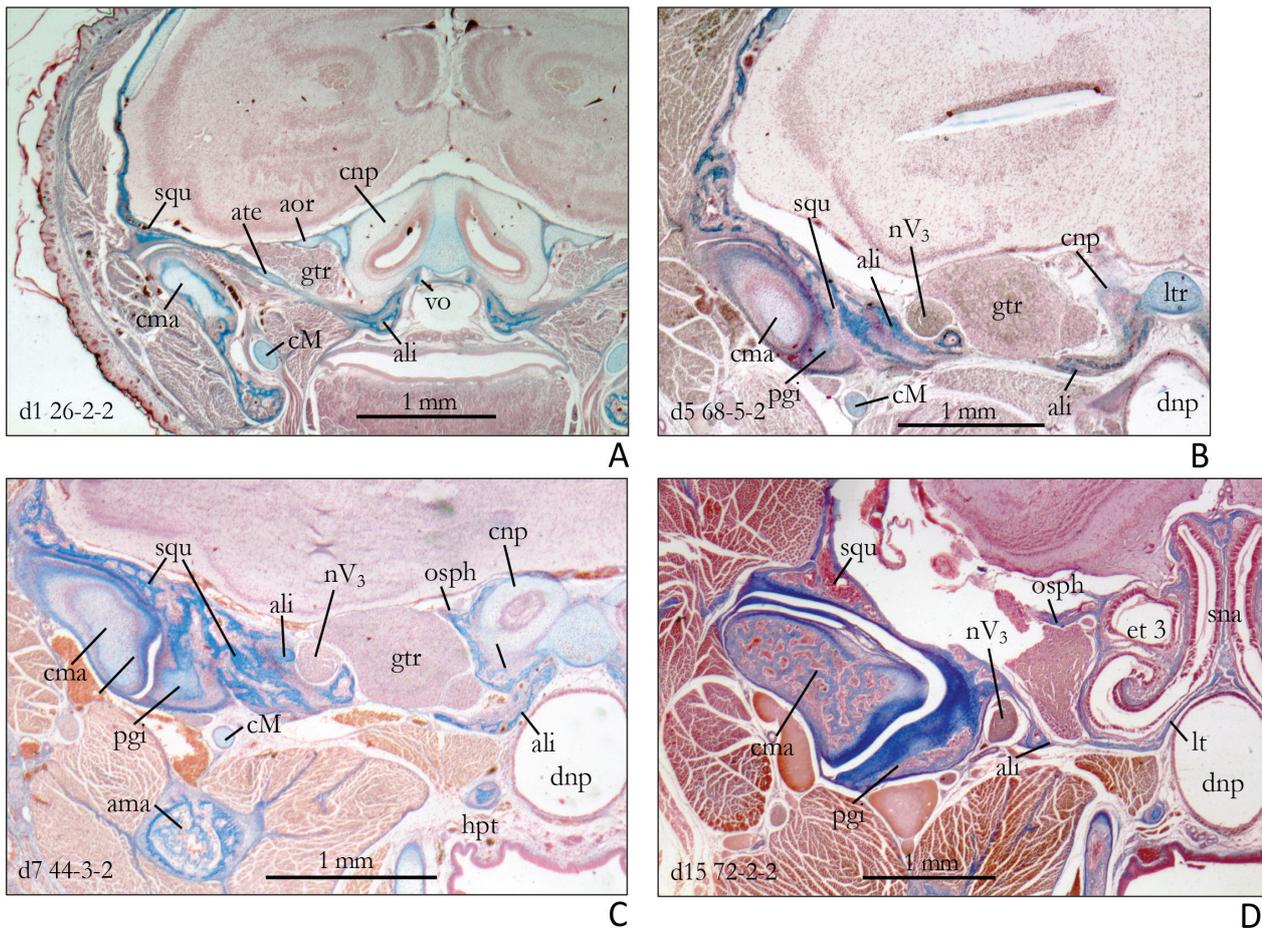


Figure 14. **A** Histological cross section of the squamoso-dental jaw articulation in a neonate *Crocidura russula*. **B** At postnatal day 5 the mandibular jaw is beginning to differentiate its lower chamber. **C** After 10 days, the secondary lower compartment of the jaw is already well differentiated; the processus glenoideus inferior shows secondary cartilage at its tip. **D** After 15 postnatal days of development, the mandibular jaw of *Crocidura russula* is approaching the proportions of the adult (cf. Fig. 17 A). Abbreviations: ali – alisphenoid, ama – angulus mandibulae, aor – ala orbitalis, ate – ala temporalis, cM – cartilago Meckeli, cma – caput mandibulae, cnp – cupula nasi posterior, dnp – ductus nasopharyngeus, et 3 – ethmoturbinal 3, gtr – ganglion trigemini, hpt – hamulus pterygoideus, lt – lamina terminalis, ltr – lamina trabecularis, nV₃ – nervus mandibularis, osph – orbitosphenoid, pgi – processus glenoideus inferior, sna – septum nasi, squ – squamosum, vo – vomer.

develops as secondary cartilage from the free end of the squamosum (Fig. 15B, C); this prominence later ossifies endochondrally (Fig. 15D). The mandibular jaws of *Crocidura russula* and *Sorex araneus* do not only differ in proportions in the adults (Fig. 16), but show differences in their morphogenesis. This may be not too surprising considering the short gestation of *Sorex araneus* (Vogel 1973).

Foramen lacerum medium

In all soricid skulls there exists a wide opening at the skull basis that extends from about the jaw articulation to the tegmen tympani at the middle ear region. Its posterior parts are hidden underneath the middle ear structures. With the histological serial sections at hand, we can identify this opening as foramen lacerum medium (sensu Starck 1979). A closer look on the internal cranial base reveals that in *Crocidura* its anterior margin ends at the level of the cupula nasi posterior, whereas it projects

further forward in *Sorex*. This difference is a side-effect of the different position of the jaw joints and of the alisphenoid (Fig. 12). A comparison of a broader sample of soricid skulls prepared by μ CT shows that the size of the foramen lacerum medium varies considerably, but its rostral extension is defined by the position of the alisphenoid (Figs 17, 18).

The foramen is closed by a tough membrane which is homologous to the posterior sphenobuturate membrane (Maier 1987; Maier et al., in the press). Medially this membrane is attached to the tegmen tympani, laterally it is fixed at the lower end of the squamosum. At its dorsal side is closely apposed to the underside of the trigeminal ganglion, i.e., it forms the ventral wall of the cavum epiptericum. At its ventral side, the sheath of the musculus tensor tympani is fixed to the membrane. Whether this membrane has a specific functional meaning, or whether it simply replaces the more 'expensive' bone tissue of the posterior part of the alisphenoid remains an open question.

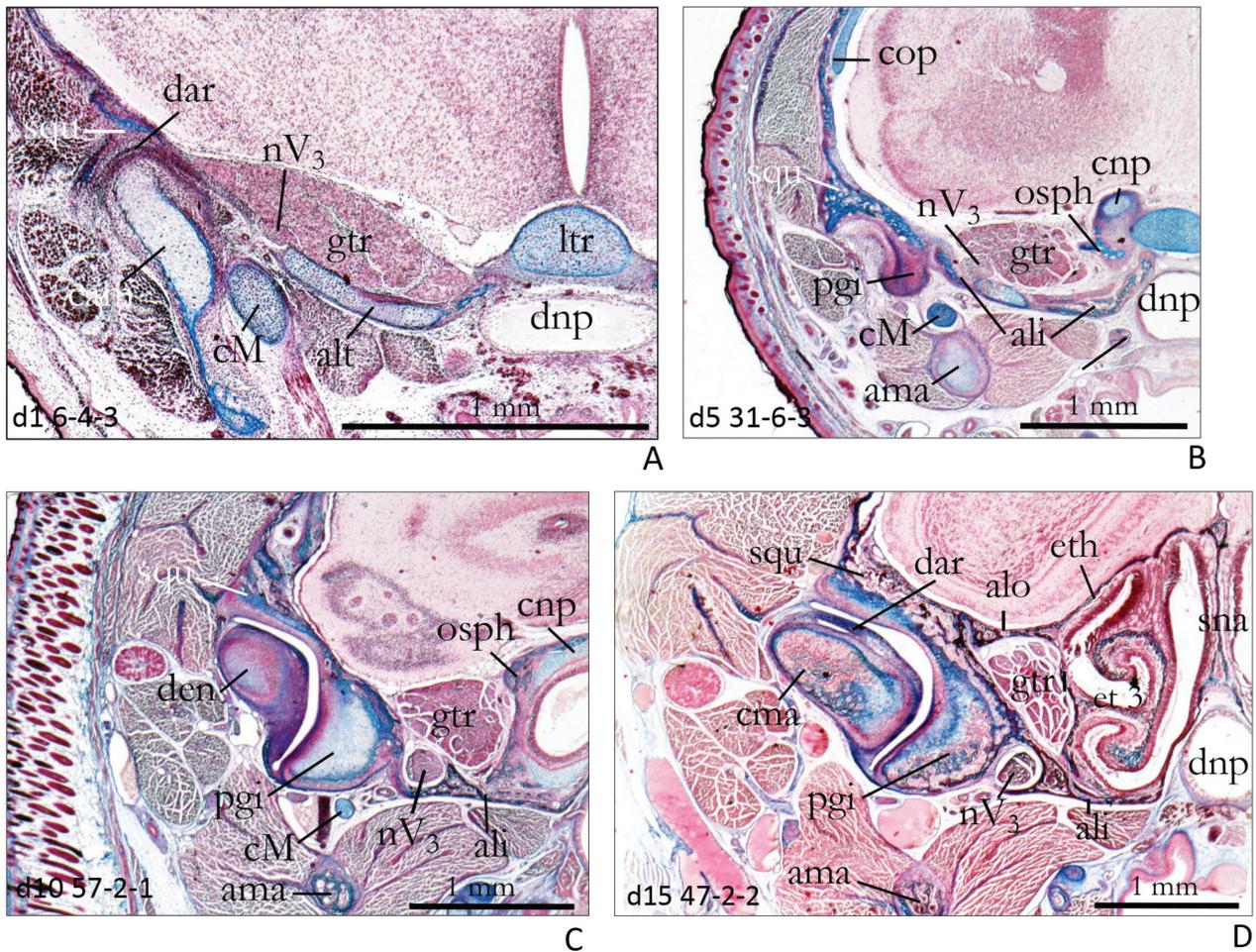


Figure 15. Histological cross sections showing the differentiation of the jaw joint of *Sorex araneus*. **A** In the newborn (d1 6-4-3) the skeletal elements of the joint are in great proximity, but their histogenesis is not much advanced. **B** At day 5 (d5 31-6-3) the processus glenoideus inferior is represented by a blastema at the lower end of the squamosum. **C** At day 10 (d10 57-2-1) the dorsal chamber of the mandibular joint has grown ventrally and meets the processus glenoideus inferior of the squamosum, which consists entirely of secondary cartilage. **D** At day 15 (d15 47-2-2), the processus glenoideus inferior is almost completely ossified endochondrally from its ventromedial side. A discus articularis is separated off in the upper compartment only. Abbreviations: see Fig. 14, alt – ala temporalis, alo – ala orbitalis, cam – caput mandibulae, cop – commissura orbitoparietalis, dar – discus articularis, den – dentary, eth – ethmoid.

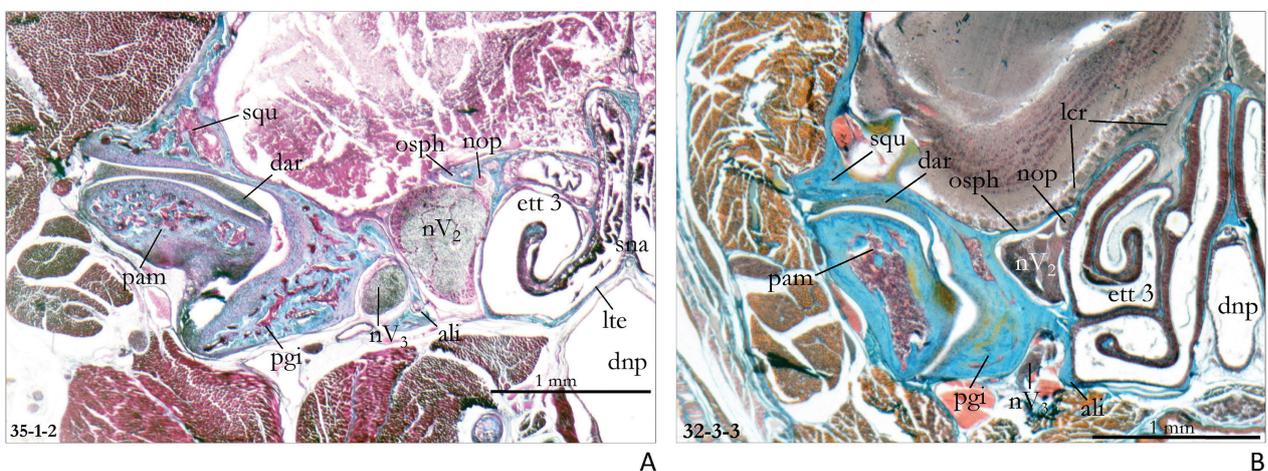


Figure 16. Comparison of histological cross sections of the jaw joints of adult specimens of *Crocidura russula* (A) and *Sorex araneus* (B). In the former it lies more laterally than in the latter. Abbreviations: see Fig. 14, dar – discus articularis, ett 3 – ethmoidal 3, lcr – lamina cribrosa, lte – lamina terminalis, nop – nervus opticus, pam – processus articularis mandibulae.

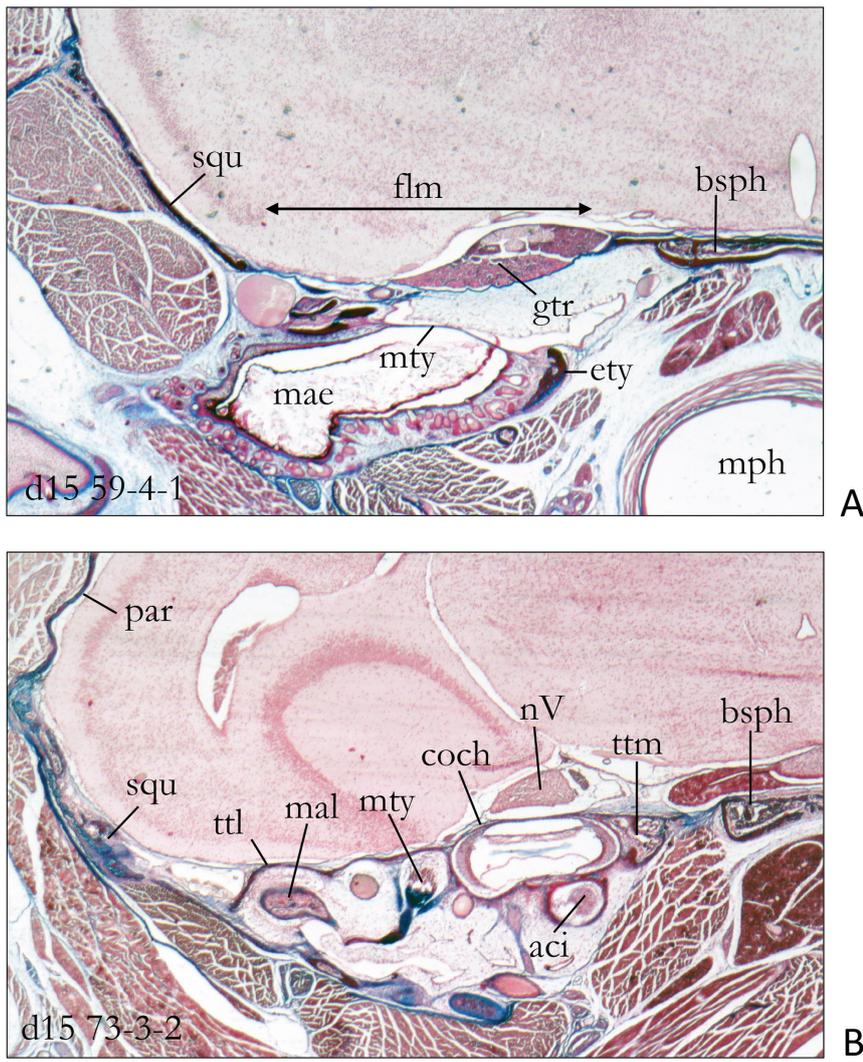


Figure 17. Histological cross sections of the posterior end of the foramen lacerum medium in a two weeks old specimen of *Sorex araneus*. **A** In this cross section the foramen lacerum medium spans between the basisphenoid and the squamosum; it is closed by the posterior sphenobulate membrane. On the dorsal side of the membrane lies closely attached the trigeminal ganglion, i.e. it represents the wall of the cavum epiptericum. Below the membrane we see the rostral parts of the tympanic cavity with the ectotympanic and the tympanic membrane. **B** More posteriorly the roof of the tympanic cavity is tegmen tympani and the cochlea. Abbreviations: aci – arteria carotis interna, bsph – basisphenoid, coch – cochlea, ety – ectotympanicum, flm – foramen lacerum medium, gtr – ganglion trigemini, mae – meatus acusticus externus, mal – malleus, mph – mesopharynx, mty – membrana tympani, mty – membrana tympani, nV – nervus trigeminus, par – parietale, squ – squamosum, ttl – tegmen tympani laterale, ttm – tegmen tympani mediale.

Figure 18 shows the inner cranial base of a few taxa of the Crocidurinae and the Soricinae. These examples demonstrate that the size of the foramen lacerum medium appears to primarily depend on the position of the alisphenoid. The extreme size dimensions of the opening are found between the two soricine taxa *Anourosorex squamipes* and *Sorex araneus*.

Discussion

The present study is not comparative in a strict sense, because meaningful comparisons have to begin with at least three taxa, whose phylogenetic systematic position is defined as precisely as possible. However, our two taxa *Crocidura russula* and *Sorex araneus* can at least be attributed to the two well established subfamilies of the Soricinae, the Crocidurinae and Soricinae, which are probably separated since the Eocene (Douady and Douzery 2003). More elaborate comparisons have not been possible at present, because serial sections of defined postnatal age have only been available from the two common shrews just men-

tioned. μ CT scans of adult skulls of a few other soricids (*Suncus*, *Myosorex*, *Anourosorex*, *Neomys*) have been prepared for comparison of a few osteological features of adults. Hence, this study is only meant as an initial foray into the skull morphology of extant soricids and a basis for future studies of soricid craniology and systematics. Nevertheless, a simplified cladogram should help to understand the systematic outlines of this study (Fig. 19).

The phylogenetic systematics of mammals has experienced some dramatic changes during the last 25 years (Douady et al. 2002). One of the major insights was the invalidity of the old category Insectivora (Wagner 1855), which had already been suspected to be a waste basket. The Tenrecidae, Chrysochloridae, and Macroscelididae are now considered to be a member of the Afrotheria, and the remaining soricids, talpids, erinaceids and solenodontids are united in a monophylum Lipotyphla (Asher and Helgen 2010). The relationship of the Soricinae to either the Erinaceidae or the Talpidae is also disputed in the literature. Most cladistic studies based on molecular data favour erinaceids as sistergroup of shrews (Liu et al. 2001; Douady et al. 2002; Dubey et al. 2007, 2008; Bininda-Emonds et al. 2007; O’Leary et al. 2013) to name but a few. Especially *Hylomys* and *Uropsilus* need

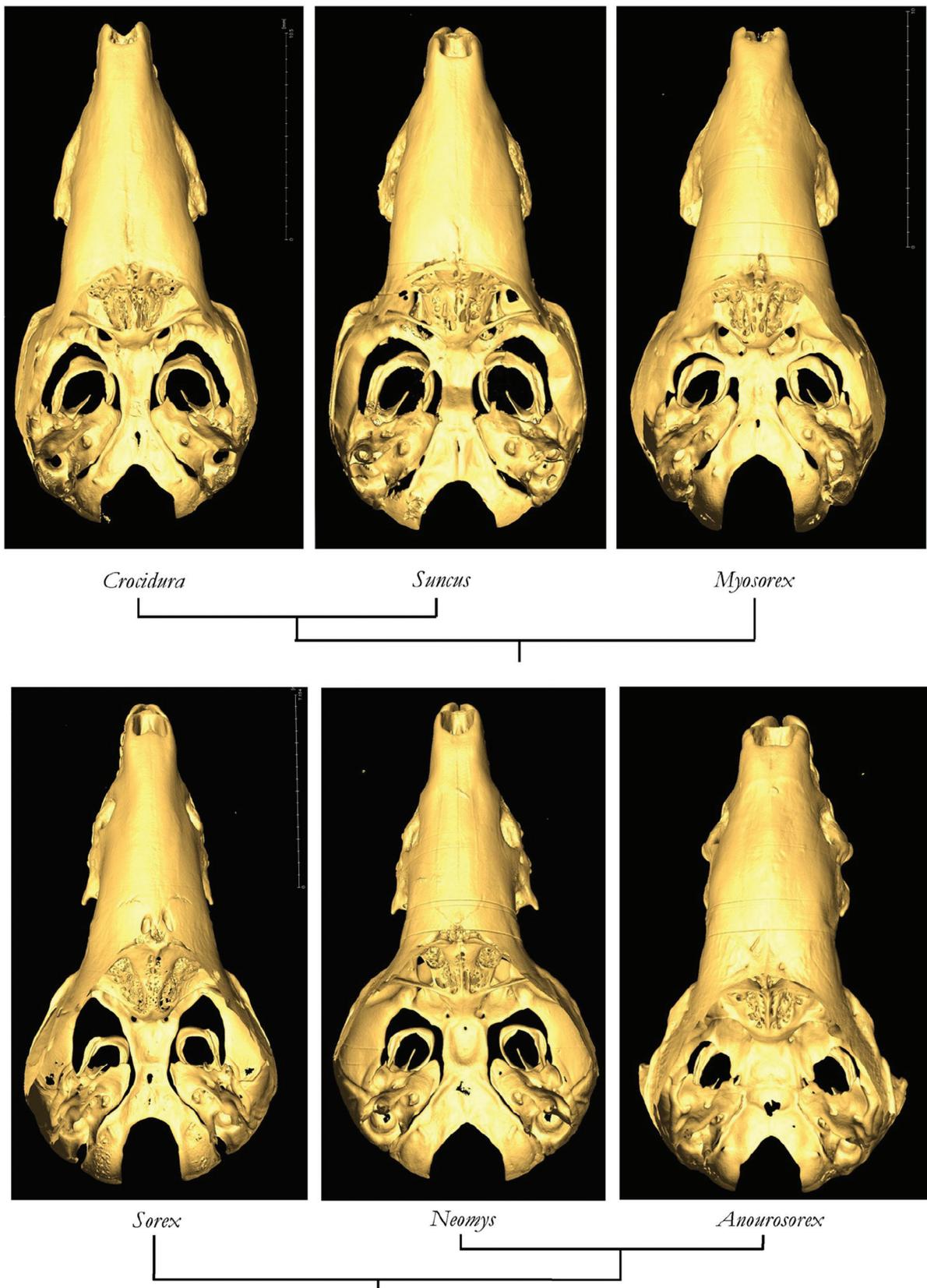


Figure 18. Inner cranial base in some soricid taxa whose phylogenetic-systematic position is shown in Fig. 19. All skulls are brought to about the same size. **A** Crocidurinae (*Myosorex varius* SMF 55060, *Suncus etruscus* SMF 26937, *Crocidura russula* SMF 95044). In *Myosorex varius* the alisphenoid is almost completely exposed dorsally, and consequently the foramen lacerum medium is relatively small. In *Suncus etruscus* and *Crocidura russula*, the position of the alisphenoid and the size of the foramen lacerum medium are intermediate. The large *Suncus murinus* is quite different. **B** Soricinae (*Anourosorex squamipes* SMF 48925, *Neomys fodiens* SMF 68229, *Sorex araneus* SMF 82598). *Anourosorex squamipes* has a very broad alisphenoid and a very small foramen lacerum medium, *Neomys fodiens* is intermediate, and in *Sorex araneus* the alisphenoid almost disappears underneath the orbitosphenoid and the foramen consequently reaches far forward.

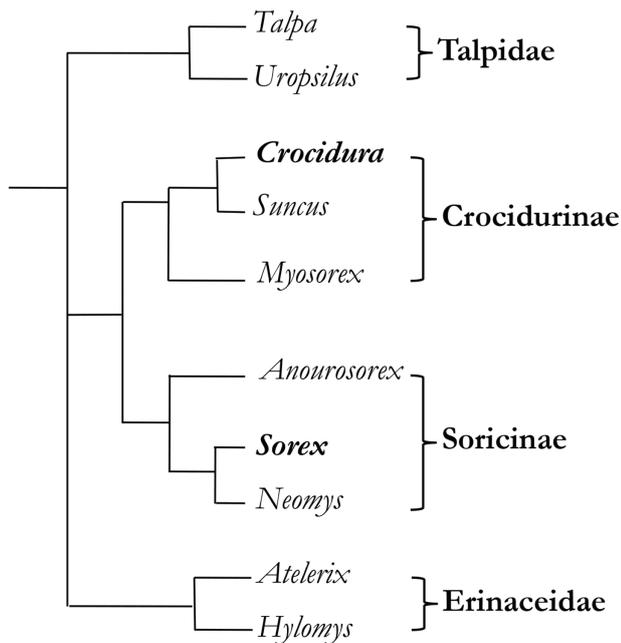


Figure 19. Simplified cladogram of the Lipotyphla and Soricidae underlying this study. The relationship of the Soricidae to either the Talpidae or the Erinaceidae is still disputed in the literature (simplified from Dubey et al. 2007; *Myosorex* is ranged only at the generic level).

further study before morphology can contribute to the open systematic problems.

What is even more relevant for our study is the place of the Lipotyphla within the mammalian tree. Already the first published phylogenetic trees based on molecular data showed that the Lipotyphla are not a basal offshoot of eutherian mammals, but that they nest within the superorder Laurasiatheria – or are their sistergroup; more basal branches of the Placentalia are either the Xenarthra or the Afrotheria (e.g., Springer 1997; Stanhope et al. 1998; Mouchaty 1999; Madsen et al. 2001; van Dijk et al. 2001). These early studies have been essentially confirmed by all later publications. Contrary to the older studies based on morphology alone, which considered ‘insectivorans’ as models for basal eutherian mammals, the new phylogenetic data rather suggest that an ‘Insectivora-type’ of mammals evolved several times convergently. Of course, this conclusion does not preclude that they may resemble in some way an archaic adaptation-type (‘Lebensform-Typus’) (Weber 1904; Simpson 1945; Thenius 1979; Starck 1995). This adaptation-type can be characterized as small carnivore searching its animal food in the litter and undergrowth of forests and bushes. Among marsupials, tiny shrew-like species occur several times both in the Neotropic and Australian realms (Nowak 1999).

The most striking peculiarity of the cranial base is the different proportioning of some of its skeletal elements. Figure 3 shows schematic dorsal views of chondrocrania of three lipotyphlans. They clearly demonstrate that in *Sorex* the posterior part of the nasal capsule has expanded caudally. This progressive growth is most clearly shown by its relationships with the ala orbitalis: The narrow ala orbitalis is inclined rostrally before it is fused

with the taenia marginalis, which represents the primary sidewall of the braincase in the chondrocranium. This secondary expansion of the cupula nasi posterior almost completely pushes aside the roots of the ala orbitalis from the trabecular plate or septum nasi respectively. The cupula nasi posterior lies slightly above the level of the ala orbitalis. In the adult skull, the cupula nasi posterior projects into the cranial cavity, and it is medially fused with the sphenethmoid. This connection is somewhat different in *Crocidura* and *Sorex* (Figs 5, 8).

The morphology of the ala orbitalis of soricids is only properly understood when the early postnatal stages are considered. At this developmental period, the original cartilaginous structures are largely covered and replaced by ‘Zuwachsknochen’, which originates at the roots of the ala orbitalis (Figs 6, 7). Endochondral ossifications of the ala orbitalis are of minor importance and fuse with the ‘Zuwachsknochen’. Therefore, the orbitosphenoid of the juvenile and adult skulls consists mainly of ‘Zuwachsknochen’. There exist minor differences in the mode of ossification between *Crocidura* and *Sorex* (see Fig. 8).

Because it reaches so far posteriorly, the roots of the alisphenoid appear to originate from the lower end of the cupula nasi posterior in the juvenile and adult skull. The transitory connection of the pila metoptica with the trabecular plate may be considered as an example of ‘recapitulation’, but within the first postnatal days the ‘Zuwachsknochen’ of the ala orbitalis fuses indistinguishingly with the remnants of the cupula nasi posterior. Generally, the origin of the ala orbitalis by two slender pilae probably has to be considered as a weak point of the biomechanical construction of the posterior facial skull, and therefore it seems plausible to assume that mechanical strengthening by ‘Zuwachsknochen’ begins in all mammals right at these pilae.

The progressive elongation of the pars posterior of the nasal capsule is also testified by the secondary elongation of the lamina terminalis. This horizontal septum, which separates the posterior recessus ethmoturbinalis from the nasopharyngeal duct, usually consists of the lamina transversalis posterior of the nasal capsule and the horizontal process of the vomer (Ruf et al. 2015, 2020; Ruf 2020). However, in soricids the lamina terminalis additionally includes the lamina transversalis posterior, the vomer, the ascending lamina of the palatine and the complete floor of the cupula nasi posterior. In the adult osteocranium, the heterogeneous components of the lamina terminalis fuse early into a thin and smooth bony plate, which forms an oblique roof and sidewall of the nasopharyngeal duct (cf. Fig. 2). This air passage of soricids is certainly adapted to high airstream velocities connected with the breathing frequencies up to 120 per minute (Flindt 2000).

The squamosum is relatively narrow dorsoventrally but stretched rostrocaudally. Near its anterior end it forms the fossa glenoidea with its prominent processus glenoidius inferior. The Nomina Anatomica officially uses fossa mandibularis, but Gegenbaur (1892), McDowell (1958) and Dötsch (1982) use cavitas or fossa glenoidea, and we adopt this term. The connections of the anterior end of the squamosum do not become clear in juveniles and adults,

because the sutures are all fused. In the fetus of *Sorex araneus*, as shown by the plate reconstructions of DeBeer (1929), the slender squamosum does not yet reach the orbital process of the frontal bone, and the contact with the mandibular head does not yet exist either; however, his cross-sections (DeBeer 1929: figs 19-21) show that the differentiation of the secondary jaw articulation has already begun. In adult skulls of both *Crocidura* and *Sorex*, the dorsal suture with the parietal is retained, showing that in *Crocidura* the squamosum appears to be somewhat broader than in *Sorex* (cf. Fig. 5).

The functional meaning of the forward-inclination of the alae orbitalis and temporalis becomes clear when their relations with the glenoid region of the squamosum are considered. The rostral end of this membrane bone is tightly fused with other bone structures, namely the frontal, the orbitosphenoid and the alisphenoid. These close contacts are necessary, because this part of the squamosum is differentiated as 'glenoid complex', which is destined to withstand the pressure forces caused by the condyle of the mandible (Fearnhead et al. 1955). As shown in Figure 1, the glenoid fossa is fixed to the sidewall of the nasal capsule (lamina antorbitalis) and the nasal floor by means of two bony bars. The study of the early postnatal stages clearly proves, that the upper bar is the orbitosphenoid and the lower the alisphenoid. Both are tightly fused with the inner side of the squamosal, and thereby provide oblique pillars that can transmit pressure forces produced by the jaw muscles to the nasal capsule, the central stem or basisphenoid respectively.

The complicated fossa glenoidea has been carefully described by Fearnhead et al. (1955), Dötsch (1982) and others. From these studies we know that the articular fossa of the soricids has in fact two more or less separate compartments. The study of the morphogenesis of the joint clearly shows that the upper compartment develops first, and that the ventral joint cavity follows later (see Figs 15, 16). Only the upper joint develops a discus articularis. These morphogenetic observations are clearly in favour of the hypothesis to consider the upper compartment as the primary one, i.e., that it is homologous to the joint in the other mammals. The membrane bones squamosum and dentale develop secondary cartilage, which is functionally necessary in any diarthrotic joint.

For the lower compartment the squamosal develops a prominent process as counterbalance for the inferior condyle. Dötsch (1982) named this process simply 'margo inferior' of the glenoid fossa, but by its peculiar morphogenesis and its functional importance for jaw mechanics, this structure deserves a name of its own, and we therefore call it 'processus glenoideus inferior', but we do not rule out that it may be homologous with the 'postglenoid capitular facet' of McDowell (1958: fig. 8). It obviously resists muscle forces pulling the mandible backwards and can guide it ventrally and rostrally. There exist differences in the modes of development of the processus between *Crocidura* and *Sorex* suggesting some degree of convergence.

Dötsch (1982) carefully described the movements of the mandibular head within the glenoid fossa, but she did

not single out its extreme position at the occlusion of the leading edges of the procumbent first incisors. This rostral biting point is obviously reached when the mandible is shifted forward and downward. Figure 20 suggests that this movement is guided by the oblique dorsal plane of the processus glenoideus inferior. By this downward movement of the lower jaw, the articulation of the molars is unlocked. This assumed functional relationship between the secondary development of the lower compartment of the squamoso-dentary jaw joint (with its processus glenoideus inferior) and the specialized and apomorphic incisal biting, suggests that there exists a correlation between these two neomorphic features – a case of co-evolution of two heterogeneous structural units. In ontogeny, the differentiation of the jaw joint takes place prior to tooth eruption (Figs 15, 16). Whereas the joints have already reached maturity by postnatal day 15, tooth eruption begins in *Crocidura russula* just at this time, and in *Sorex araneus* only at day 22 or 23 (Vogel 1973). The function of the incisal bite seems to depend on the finished mandibular joint. Prior to biting, the mandibular jaw functions in suckling. The validity of this hypothesis may be tested by the fossil record. Heterosoricids from the Oligocene and Miocene already possess procumbent lower incisors and an elongated and oblique mandibular facet (Rabeder 1998). In *Trimylus* the dentary facets are widely divergent, whereas in *Domina* they are much more continuous (Asher 2005: fig. 5.3).

Figure 20 shows that the temporomandibular joint of soricids is shifted forward by at least 10 % of skull length, i.e., somewhat more than 2 mm in the two studied species. In other mammals the jaw joint is normally located directly adjacent to the meatus acusticus externus, i.e., anterolateral to the middle ear, but in the soricids it is shifted to the posterior part of the orbitotemporal fossa. Only cross sections show that the joint thereby comes to lie at the side of the expanded posterior nasal capsule (cf. Fig. 1). Our ontogenetic analysis shows that the connection of the glenoid region of the squamosal with the nasal capsule is therefore provided by the orbitosphenoid and alisphenoid. It was also shown above, that the final stages of this shift only take place in the first two postnatal weeks, and it was also demonstrated that the shift proceeds a little further in *Sorex* than in *Crocidura* (see also Fig. 12). Because we have no data available from the mass of the adductor muscles, we have made no efforts to calculate absolute measures of incisal bite force (Carraway and Verts 1994).

This unique shift of the jaw is also reflected by the peculiar elongated shape of the squamosum, and by the elongated foramen lacerum medium (see asterisk in Fig. 20 B). The name of this foramen is contentious in the literature. Our ontogenetic approach has shown that this foramen is posteriorly bound by the tegmen tympani and rostrally by the alisphenoid, and that it is therefore homologous with the foramen lacerum medium. The foramen lacerum medium is defined as the gap between the alisphenoid and the ear capsule or petrosium (Starck 1979, p. 361). According to Gaupp (1911) the foramen lacerum medium is a secondary cranial exit ('Nervenöffnung

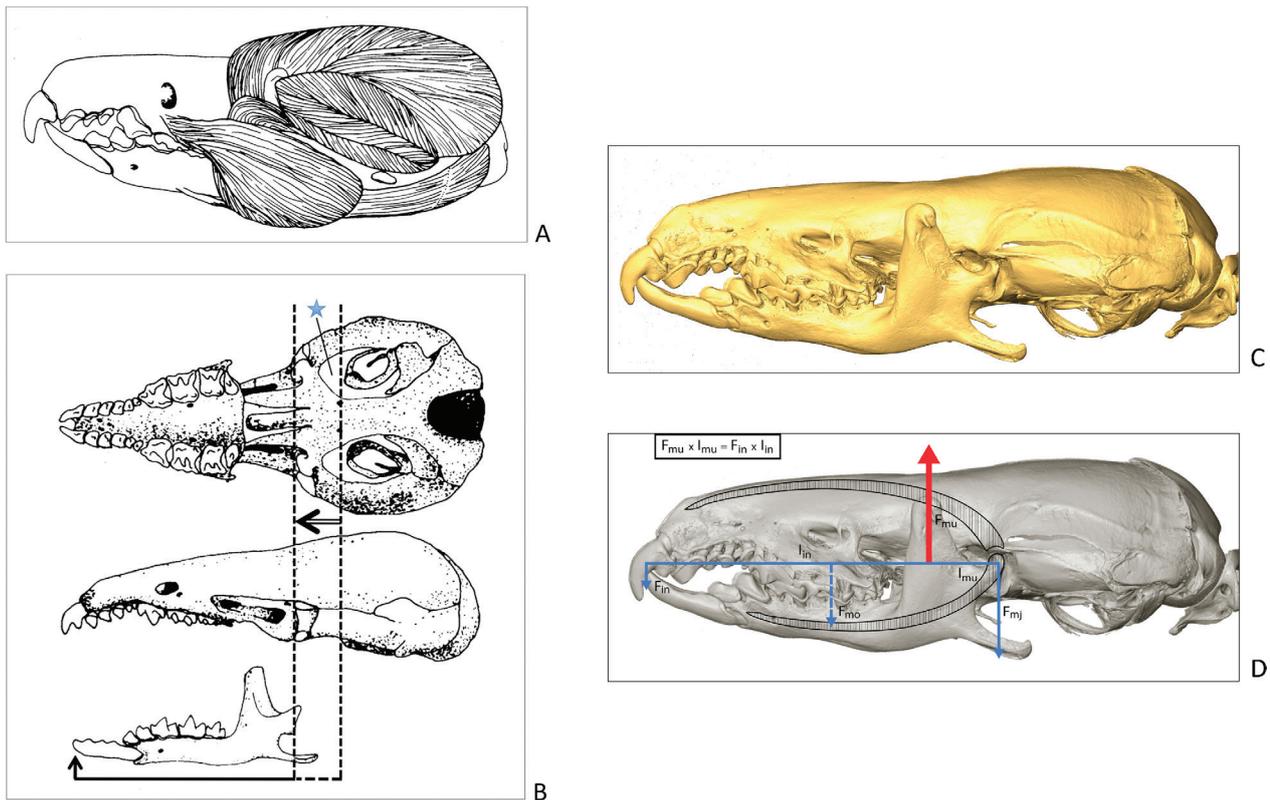


Figure 20. **A** Complex adductor muscles in *Suncus murinus* (after Dötsch 1983). **B** Ventral and lateral view of a skull and mandible of *Sorex araneus* (after Dötsch 1982). The arrow shows the positional shift of the jaw joint by about 2,2 mm. The solid beam represents the shortened loadlever (– 18 %) for the anteriormost biting point, by which the prominence of the incisors is compensated for. The jaw articulation is detached from the periotic ossification – a unique feature in mammals. The wide fenestra at the cranial base (blue asterisk) is interpreted as foramen lacerum medium (sensu Starck 1979). **C** Lateral view of a skull of *Crocidura russula* (Coll. W. Maier no. 3, virtual reconstruction of a μ CT scan) with the molars in maximal occlusion. For the occlusion of the edge of the incisors, the mandible must be lowered at the secondary jaw joint. **D** The same specimen of *Crocidura* with a simplified drawing of the basic mechanic vectors and trajectories of the upper and lower jaws: Black colour – upper and lower jaws conceived as a pair of tweezers; blue colour – biting forces at the first incisors (K_{in}) and at the molars (K_{mo}) and jaw load K_{mj} . Red colour (F_{mu}) – estimated resultant of vertical adductor muscle forces with muscle-lever (L_{mu}). All partial forces were calculated in relation to $F_{mu} = 1$.

zweiter Ordnung’) for the mandibular branch of the nervus trigeminus (V_3). The foramen lacerum medium must not be mistaken for the foramen prooticum or foramen sphenoparietale, which lies at a deeper level and means the primary opening between the pila antotica and the capsula otica of the chondrocranium (“Nervenöffnung erster Ordnung”, Gaupp 1911; Kuhn and Zeller 1987). The nervus mandibularis (V_3) may be enclosed by an incisura or foramen ovale at the posterior margin of the alisphenoid. The textbook of Gray (1858) mentioned a foramen lacerum medium; Gegenbaur (1892) used foramen lacerum anterius. Versluys (1927) and Stadtmüller (1936) named the ‘prootische Spalte’ also foramen lacerum anterius. Gregory (1910) had named the relatively large opening in *Solenodon paradoxus* (his fig. 18) “f.l.m.” (i.e., foramen lacerum medium). Maier (1987) used the term fissura sphenopetrosa. The nomenclature of this skull opening was confused by McDowell (1958), who named the opening ‘fenestra pyriforme’ without acknowledging or discussing the problems of terminological priority or homology. Nevertheless, most authors subsequently have used this new term since then (MacPhee 1981; Novacek 1993; Wible 2008; Wible and Shelley 2020).

In neonate sorcids the foramen lacerum medium is still fairly narrow, and it is mediorostrally framed by the cartilage of the ala temporalis. In postnatal day 5, the gap has become distinctly wider, but is still partly bordered anteriorly by the cartilaginous ala temporalis. In the adult skull of *Crocidura* and *Sorex* this foramen of the basicranium is very wide, and it is closed by a membrane, which extends from the ventral side of the inner tegmen tympani to the free ventral edge of the squamosal (Maier et al. in press). Anteriorly it is attached to the ala temporalis or, later, to the alisphenoid; posteriorly it is attached to the anterior rim of the tegmen tympani and the tip of the pars cochlearis of the petrosal. Therefore, it is homologous to the posterior sphenobutrate membrane (Maier 1987). The mandibular branch of the trigeminal nerve becomes enclosed by the alisphenoid, forming the foramen ovale.

We assume that the wide foramen lacerum medium is causally connected with the rostral shift of the mandibular joint. Its size can best be interpreted as saving of bone tissue of the alisphenoid, i.e. it is a feature of economization. Therefore, *Anourosorex*, which has a broad alisphenoid, possesses a small foramen lacerum medium (see

Fig. 19 and McDowell 1958: fig. 38D) and *Sorex araneus* an excessively large one (McDowell 1958: figs 12, 19). In other taxa with a conspicuous foramen lacerum medium (*Solenodon*, *Microgale*; cf. MacPhee 1981: fig. 57), the size of the foramen lacerum is defined by the posterior margin of the alisphenoid. In the soricids its posterior margin is also defined by the tiny pars cochlearis of soricids (Ekdale 2013, 2015), which is partly compensated for by the expanded tegmen tympani.

Burda (1979), who did not use histology and microscopic anatomy, misinterpreted the dorsal membrane of the tympanic cavity: "Its dorsal wall is formed by the dura mater separating the tympanic cavity from the brain" (p. 8). He may not have been aware of the existence of the cavum epiptericum and its main contents, the huge trigeminal ganglion, which lies between the tympanic cavity and the brain cavity - at least in its medial part. Primarily, the alisphenoid and the sphenobasale membrane constitute the lateral wall of the cavum epiptericum (Maier 1987). Because of the expansion of the brain, this lateral wall is in the adult pushed into a horizontal position below the trigeminal ganglion. However, in its lateral part, the membrane may indeed include a bit of the dura mater of the brain cavity. Krapp and Niethammer (1990) characterized the big opening in the basicranium of soricids as follows: „Bei den Spitzmäusen dagegen ist der Schädelboden über dem Ectotympanicum membranös begrenzt und nicht von den Knochen Squamosum und Perioticum wie bei Igel und Maulwürfen“ (p.16). („In shrews, the floor of the basicranium above the ectotympanic is membranous and not from the squamosal and periotic bones as in hedgehogs and moles“; transl. WM). In terms of functional morphology, this expanded foramen lacerum medium may be analogous to the maxillary-palatine vacuities found in many small mammals.

Functionally, the rostral shift of the mandibular joint most probably is correlated with the acquisition of the procumbent first incisors, which put the anterior biting point forward. The upper and lower jaw can be conceived as a tweezer, where the upper arm consists of the interorbital pillar and the shell-like wall of the facial skeleton. The biting force at the incisors (F_{in}) produced by the adductor muscles, depends on the length of the load lever (l_{in}) of the mandible (Fig. 20D) – and is therefore increased by a shortening of the jaw length. The same holds true, of course, for the biting force at the molars. The functionally less important unicuspid antemolar teeth, which do not occlude, could become easily reduced to various degrees in different taxa of shrews; this part of the tooth rows may be considered as an initial diastema. The homology of these teeth is difficult to determine, because the ante-molar milk deciduous dentition is reduced prior to eruption completely (Ärnäck-Christie-Linde 1912; Kindahl 1959; Dannelid 1998; Yamanaka et al. 2010).

This unique loss of a complete dental generation – molars, which belong to the first tooth generation, excepted - to us is the strongest proof of miniaturization of the whole family Soricidae (see below). That the similarity of the front dentition of rodents and soricids is analogous, is simply proven by the fact that the incisors of the Glires

belong to the first dental generation (Luckett 1985), and that of the shrews to the second. The zygomatic arch has become mechanically unimportant and was reduced. The pressure forces acting on the glenoid facets are therefore completely transferred by the bony trajectories of the interorbital pillar and the solid walls of the snout, which seems to have the characteristics of a mechanical shell (Figs 2, 12, 18, 21). The anterior end of the skull, where the upper incisors are implanted, became fortified by fusion of the maxillaries and premaxillaries mainly. We therefore hypothesize that the complicated mandibular jaw joint and mandibular apparatus is highly determined by the special requirements of the incisal and molar biting respectively. The 'incisal complex' will be studied in a separate paper (Maier, in prep.).

It is an open question whether soricids should be considered as an example of miniaturization, i.e., a product of evolution toward extremely small body size (Hanken and Wake 1993). Recently Polilov (2016) has shown examples of extreme miniaturization in insects, but Hanken and Wake (1993) have pointed out that vertebrates never became so small, that dramatic effects in their body organization resulted. *Suncus etruscus* is known as one of the smallest living mammals, and therefore it is likely that the whole family is miniaturized at specific mammalian conditions. We find a considerable span of body size between *Suncus etruscus* and *Suncus murinus*, but with no significant change in skull morphology; most soricid species range in the size category of *Crocidura* and *Sorex* (Fig. 21). However, the strongest argument of size reduction of the group as a whole is to us the suppression of the complete premolar dentition (Kindahl 1959). Therefore, soricids can be characterized as very small predators which have highly specialized their first incisors, jaw joint and jaw muscles. They have almost completely lost their eyesight, and rely instead on olfactory and tactile senses. It is an unsettled problem, whether soricids make use of their acoustic and vibration senses (Siemers et al. 2009; Zaytseva et al. 2015; Zsebök et al. 2015, Maier et al. in press). At present, it seems most appropriate, to define shrews as tiny insectivorous and carnivorous eutherian mammals, which search for their prey on microhabitats of forest and shrub floors as well as in superficial burrows dug by moles and rodents.

The scales in our histological figures indicate that almost all structures of the soricid skulls treated here measure only a few millimeters - even in adult animals. This means, that we are dealing with a mesoscopic size dimension (Maier 2021). This size category is situated between the microscopic and macroscopic approach, and it is difficult to handle technically. Therefore, morphological problems of this sort have been neglected in the past. However, modern μ CT technique will help to solve some of the methodical problems at least as far as the osseous skeleton of adult mammals is concerned. Fetal and juvenile age stages will have to be studied by means of 'microtome histology' also in the future (Bargmann 1956).

Vogel (1973) concluded from his ontogenetic studies that *Sorex* has a more 'primitive' ontogeny than *Crocidu-*

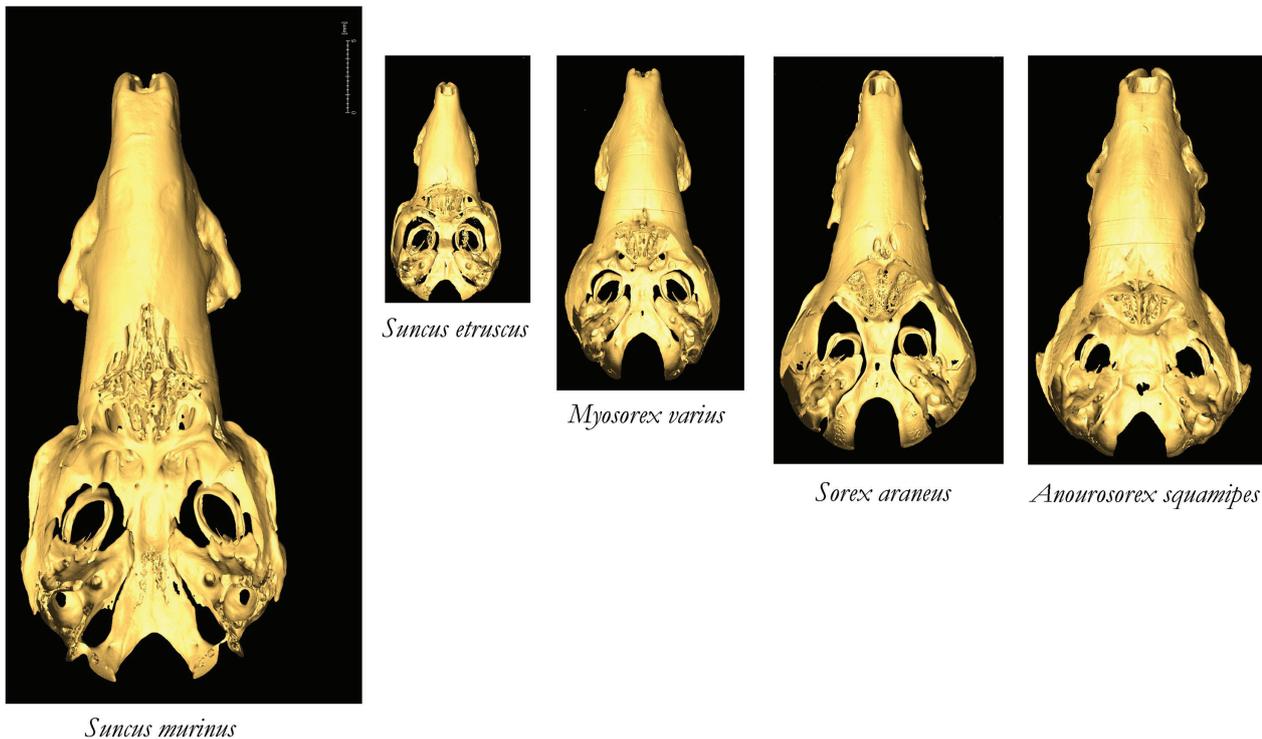


Figure 21. Skull size range of extant Soricidae as represented by *Suncus murinus* SMF 87406, *Suncus etruscus* SMF 26937, *Myosorex varius* SMF 55060, *Sorex araneus* SMF 82598 and *Anourosorex squamipes* SMF 48925. *Suncus etruscus* is the smallest living mammal. At this level of miniaturization, the skulls are relatively similar. All species are depicted in identical magnification (scale in *Suncus murinus* is 5 mm).

ra. According to him, this difference is not only expressed by a much shorter gestation length, i.e., 20 vs. 30 days, but also by a different speed of development. He named *Sorex* a ‘primitiver Nesthocker’ (“primitive and remaining in natal group”) and *Crocidura* an ‘evolierter Nesthocker’ (“evolved and remaining in natal group”). He even stated: “Die Geburtsreife von *Sorex* und *Neomys* liegt dem Geburtszustand der Marsupialier wesentlich näher als demjenigen der zur Zeit bekannten Eutheriennesthocker“ (p. 1314). (“The maturity of neonates of *Sorex* and *Neomys* is closer to that of marsupials than to any other known eutherians”; transl. by WM). At that time the understanding of mammalian phylogeny was quite undeveloped, and evolutionary constraints were not considered to be important factors. Because lipotyphlans are now generally associated with the superorder Laurasiatheria, it is very unlikely that they represent a morphotype from the lowermost base of placental mammals – and shrews are even the most specialized and derived members of the extant lipotyphlans. Contrary to Vogel (1973) we consider *Sorex* to be somewhat more derived than *Crocidura* in several features, but the problem of character polarity is not finally settled. Such questions of polarity are difficult to solve, and the answer normally depends on a reliable cladogram and on the reconstruction of the grundplan of different ancestral stages as well as on well-defined outgroup comparisons (Hennig 1982). Later on, Peter Vogel became very active in phylogenetic systematics based on molecular data (Dubey et al. 2007, 2008), but to our knowledge he did not revise his primary ontogenetic model of shrews.

Conclusion

The skull of shrews is not well studied, because it is too small for macroscopic and too big for microscopic investigations, i.e., it represents a ‘mesoscopic’ type of biological organization. μ CT technique helps a lot to solve this problem, at least as far as bony structures are concerned. However, traditional ‘microtome histology’ will remain essential at least for the study of earlier ontogenetic stages and for the study of soft tissue structures.

The present study has shown that soricids are not only highly specialized in their dentition (complete loss of their anterior milk dentition; procumbent first incisors with highly effective biting edge) but also in their double mandibular joint. We postulate that the rostral shift of the glenoid fossa compensates for the prominence of the procumbent incisors, and that the lower extension of the jaw joint co-evolved with the specialized incisal bite. As a result of this shift, the glenoid part of the squamosum became largely detached from the otic or petrosal and instead attached to the nasal capsule by means of the orbitosphenoid and the alisphenoid. As a by-product of the rostral move of the glenoid fossa and of the alisphenoid, the soricid foramen lacerum medium increased in size and was covered by the posterior sphenobuturate membrane.

Because in soricids most skull elements fuse within the first 2–3 weeks of postnatal life, as many as possible ontogenetic stages are necessary to identify and homologize skeletal elements of the head skeleton – comparative anatomy necessarily has to become comparative ontog-

eny (Vergleichende Entwicklungsgeschichte). Moreover, it is mandatory for comparisons that the objects of study are defined within a suitable phylogenetic-systematical framework, and hypotheses on functional adaptations are necessary to understand evolutionary transformations. The present study barely reaches these methodological standards. Future research should widen the number of soricid taxa in order to better understand the existing differences. The 'key innovation' appears to be incisal biting, which explains both the permanent dentition as well as the jaw apparatus. Of course, the comparative ontogenetic study of other lipotyphlans, for example *Uropsilus* and *Hylomys*, is necessary to better understand soricids.

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