

Different size of tympanic membranes and its functional and ecomorphological meaning in Crocidurinae and Soricinae (Lipotyphla: Soricidae)*

Wolfgang MAIER^{1,2}, Peter PILZ³ & Irina RUF^{2,4,5}

¹ Fachbereich Biologie, Institut für Evolutionsökologie, Universität Tübingen, Auf der Morgenstelle 28, D–72076 Tübingen, Germany

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

³ Lehrstuhl Tierphysiologie, Universität Tübingen, Auf der Morgenstelle 28, D–72076 Tübingen, Germany

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

⁵ corresponding author: irina.ruf@senckenberg.de

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Abstract. Adult skulls of *Crocidura russula* and *Sorex araneus* have been studied by μ CT and by histology. The virtual representations of these skulls in ventral view display the middle ear structures very clearly. It is evident that the ectotympanic rings, which frame the tympanic membrane, are significantly larger in *Crocidura* than in *Sorex*; simple measurements and calculations reveal that the tympanic area in the two chosen skulls is significantly larger in the former taxon than in the latter (4.3 mm² vs. 2.4 mm²). When a few more specimens from these two species as well as further taxa are added to the data set, a regression analysis shows that crocidurines have distinctly larger tympanic membranes than soricines – but there are a few exceptional species (*Suncus murinus* and *Anourosorex planipes*). Preliminary hypotheses concerning the meaning of these differences with regard to hearing performance (optimal range of frequencies) and ecomorphological adaptation (open or dense micro-habitat) are put forward. A histological cross section shows the anatomy of the ectotympanic and the tympanic membrane in *Sorex araneus*. It is hypothesized that the ectotympanic ring with the eardrum, which are loosely attached to the basicranium by a fibrous membrane, is not a primitive, but a derived character of soricids. The loss of a processus tympanicus could have facilitated the easy evolutionary change between ‘auditory adaptation zones’ – and perhaps explains the enormous number of soricid species.

Key words. *Crocidura russula*, *Sorex araneus*, ectotympanic ring, tympanic area, fibrous membrane, μ CT, regression analysis, ecomorphology, evolution

INTRODUCTION

Crocidura russula and *Sorex araneus* belong to two different subfamilies of the shrews (Soricidae). Both species are well represented in the European fauna. They are sympatric but not syntopic, i.e., the former species lives in more open, the latter in more dense and humid forest habitats (BAUMANN 1949, NIETHAMMER 1990). Formerly, the Soricidae was considered

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a member of the order Insectivora, but molecular cladistics of the last 25 years have clearly demonstrated that the Insectivora is not monophyletic and has to be abandoned as a taxon (cf. DOUADY & DOUZERY 2003, and many others). Only the Solenodontidae, Erinaceidae, Talpidae, and Soricidae remain as monophylum; although many authors call it Eulipotyphla, we stick to Lipotyphla as suggested by ASHER & HELGEN (2010). Lipotyphla are considered as basic branch of the Laurasiatheria, whereas the Tenrecoidea are placed within the Afrotheria. Most published cladograms consider the Erinaceidae to be the sister taxon of the Soricidae (DOUADY et al. 2002). With more than 350 species according to NOWAK (1999) or even more than 450 species according to WILSON & MITTERMEIER (2018), the shrews are one of the most speciose mammalian families. Most species are small, and *Suncus etruscus* is one of the smallest living mammals; however, their small size cannot be judged as real miniaturization according to the criteria of HANKEN & WAKE (1993). The soricids are distinguished by suppression of the complete first antemolar tooth generation (but molars are also members of the deciduous dentition). MAIER et al. (2022) have shown that the precumbent first permanent incisors are functionally linked with the double jaw joint that is shifted rostrally and is attached to the nasal capsule instead of the petrosal. These authors have also shown that the typical basicranial fontanella, which is homologous to the foramen lacerum medium, is a consequence of the forward shift of the jaw joint. The ring-like ectotympanic appears disconnected in the cleaned skull, but is in fact linked by a fibrous membrane with the basicranium and by other ligaments with the malleus (as shown in Fig. 2, see also VAN KAMPEN 1905, MACPHEE 1981).

One of the central topics of comparative anatomy and evolutionary biology of mammals is that most of the middle ear structures are derived from the lower jaw and primary jaw joint (theory of Reichert-Gaupp; GAUPP 1913). Modern palaeontology in particular has demonstrated the spectacular evolutionary translation from the lower jaw to the cranial base (KERMACK & MUSSET 1973, KERMAK et al. 1981, ALLIN 1975, TAKECHI & KURATANI 2010, MAIER & RUF 2016, LUO et al. 2016).

The morphological transition allows for the specific means of acquisition of airborne sound in synapsids, to which mammals belong (KEMP 2016). Airborne sound reaches the pinna and the external ear duct, which already increases the sound pressure at the tympanic membrane (eardrum) at certain frequencies. Of great importance for impedance matching is the tympanic membrane, which is framed by the ectotympanic bone. This ring-like bone is derived from the angulare of the lower jaw (ALLIN 1975). MAIER (1987) showed that in the postnatal ontogeny of *Monodelphis domestica* the mode of transition of the tympanic membrane from the lower jaw to the basicranium is repeated (MAIER 1987, 1990). The further transport of sound into the inner ear is not in the scope of the present paper (cf. FLEISCHER 1978, NEUWEILER 1993, HELDMAIER & NEUWEILER 2003).

FLEISCHER (1973), HEMILÄ et al. (1995), MASON (2001) and others have pointed out the importance of the tympanic membrane size to hearing in a large number of mammal species. ROSOWSKI (1992: fig. 29.6) has shown that best frequency of hearing is correlated inversely with the tympanic membrane area, i.e., that best frequencies decrease with the enlargement of the tympanic membrane. Here we study the ectotympanic ring and size of the tympanic membrane of the two sympatric shrew species *Crocidura russula* and *Sorex araneus* in comparison to further shrew species in order to elucidate potential adaptations to different ranges of hearing frequencies and ecologies.

It must be noted that BURDA (1979) already discussed the relationship of the tympanic membrane to body mass in a few soricid species. His simple regression lines (his fig. 7) show

a clear difference between the few measured crocidurine and soricine species – but he did not follow up the matter further. Although the feature was discovered independently, the present study may be considered as an elaboration of Hynek BURDA’s observations.

MATERIAL AND METHODS

Cleaned skulls of adult soricids listed in Table 1 mainly from the mammal collection of the Senckenberg Forschungsinstitut und Museum Frankfurt, Germany (SMF) were examined through μ CT scans. These were made with the μ CT scanner (Fraunhofer/ProConXray/Feinfocus) housed at Senckenberg Forschungsinstitut und Naturmuseum Frankfurt. The specimens were scanned with 90 kV, 89 μ A, 1500 ms exposure time and 1600 projections; resolution (isotropic voxel size) is 0.0079 mm in *Suncus etruscus* and ranges from 0.0115 mm to 0.0165 mm in all other studied species. One specimen of *Crocidura russula* (coll. W. MAIER) was scanned with a Nikon XT H 320 at the Senckenberg Centre for Human Evolution and Palaeoenvironment (HEP), Universität Tübingen, Germany. Scan parameters were 145 kV, 43 μ A, 708 ms exposure time, 3500 projections, 0.0063 mm voxel size.

The resulting μ CT volume data were processed with the 3D software VGStudio MAX 2.2 (Volume Graphics, Heidelberg, Germany) and Avizo 9.01 (Thermo Fisher Scientific FEI).

Measurements were performed in Avizo. Basal skull length (basion to prosthion) was taken with the linear measurement tool directly on the virtual 3D model of the μ CT data set (isosurface). Measurements of the inner circumferences of the ectotympanics of both sides were taken from segmented models of the bone by help of the Surface Path tool in Avizo. In *Sorex araneus* the ectotympanic does not form a closed ring and thus the resulting gap had to be measured with the linear measurement tool. Based on the mean inner circumference of the ectotympanic, the tympanic membrane area was calculated ($U=2\pi r$ and $F=\pi r^2$; U = inner circumference of ectotympanic, r = inner radius of ectotympanic, F = tympanic membrane area). However, we are aware that this is an approximation, because the tympanic membrane shape is much more complicated (FAY et al. 2006). Since all membrane areas are determined with the same methods, the data should be sufficient for comparison. We also do not know the relation between the pars flaccida and pars tensa of the tympanic membrane, but we assume that it is similar in all taxa.

Table 1. The phylogenetic systematics of the specimens studied in the present paper are shown in the simplified cladogram on the left side (modified from DUBEY et al. 2007). Grey circles indicate plesiomorphic, the black one apomorphic conditions concerning tympanic membrane area. The basicranial measurements and the calculated areas of the tympanic membranes are listed on the right. The two specimens presented at the beginning of the present paper are listed as numbers 1 and 8 (bold letters). Crocidurinae: species (1) – (7); Soricinae: species (8) – (13)

	Taxon	Basal length (mm)	Tympanic membrane (mm ²)
	(1)Crocidura russula (SMF 95044)	18,2	4,3
	(2) <i>Crocidura russula</i> (SMF 26732)	17,3	3,4
	(3) <i>Crocidura russula</i> (Coll. WM 1)	17,9	3,8
	(4) <i>Suncus mertensi</i> (SMF 18868)	17,9	4,0
	(5) <i>Suncus murinus</i> (SMF 87406)	27,2	5,1
	(6) <i>Suncus etruscus</i> (SMF 26937)	11,4	1,7
	(7) <i>Myosorex varius</i> (SMF 55060)	18,5	3,3
	(8)Sorex araneus (SMF 82598)	16,8	2,4
	(9) <i>Sorex araneus</i> (SMF 48211)	16,6	2,3
	(10) <i>Sorex araneus</i> (SMF 95029)	16,3	2,4
	(11) <i>Sorex minutus</i> (SMF 77205)	13,3	1,7
	(12) <i>Neomys fodiens</i> (SMF 68229)	17,9	2,4
	(13) <i>Anourosorex squamipes</i> (SMF 48925)	21,0	4,5

These data are completed by histological serial sections (embedding in paraffin, 15 μ , staining Azan-Domagk) of adult specimens of *Crocidura russula* and *Sorex araneus* (Histological Collection W. MAIER at the Institut für Evolution und Ökologie of the Universität Tübingen, Germany). In terms of soricid phylogeny we follow DUBEY et al. (2007) in that *Myosorex varius* is assigned to the subfamily Crocidurinae.

In order to quantify the observed differences in the studied species a common regression of tympanic membrane area on basal skull length was calculated. For each subfamily (Crocidurinae, Soricinae, for species see Table 1) the difference between the tympanic membrane area and this regression line (i.e., the distance on the y-axis) was determined and significance was tested (Mann-Whitney U-test). All statistical calculations were run in Excel and SAS JMP.

RESULTS AND DISCUSSION

Crocidura russula vs. *Sorex araneus*

Fig. 1 demonstrates that the ectotympanic ring and hence the area of the tympanic membrane are significantly larger in this specimen of *Crocidura russula* than in that of *Sorex araneus* (see also Table 1). In this *Crocidura* specimen the area was measured and calculated as 4.3 mm², in

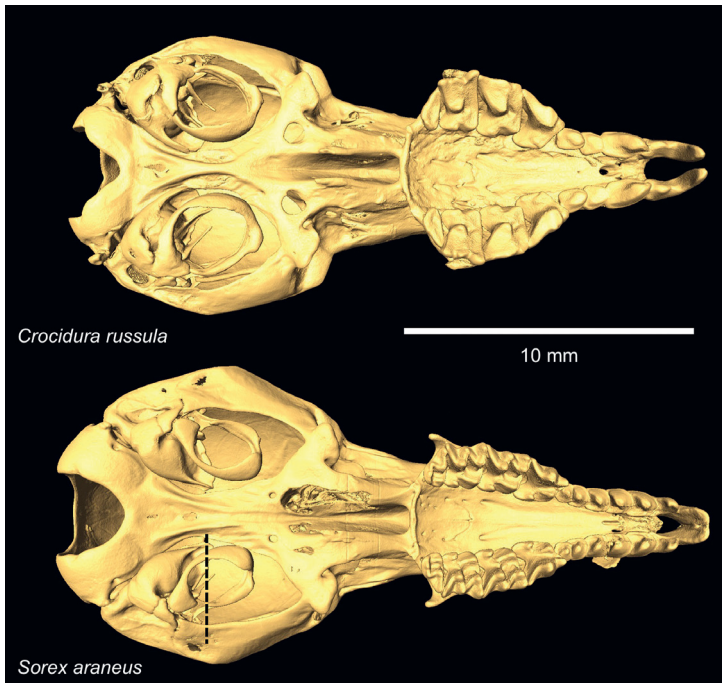


Fig. 1. Ventral view of the skull of *Crocidura russula* (SMF 95044) and *Sorex araneus* (SMF 82598). Both skulls were reconstructed from complete μ CT scans and they are presented in identical magnification. It is clearly evident that the area of the presumptive tympanic membrane inside the ring-like ectotympanic is significantly larger in *Crocidura russula* than in *Sorex araneus*. The stippled line indicates the section plane of Fig. 2.

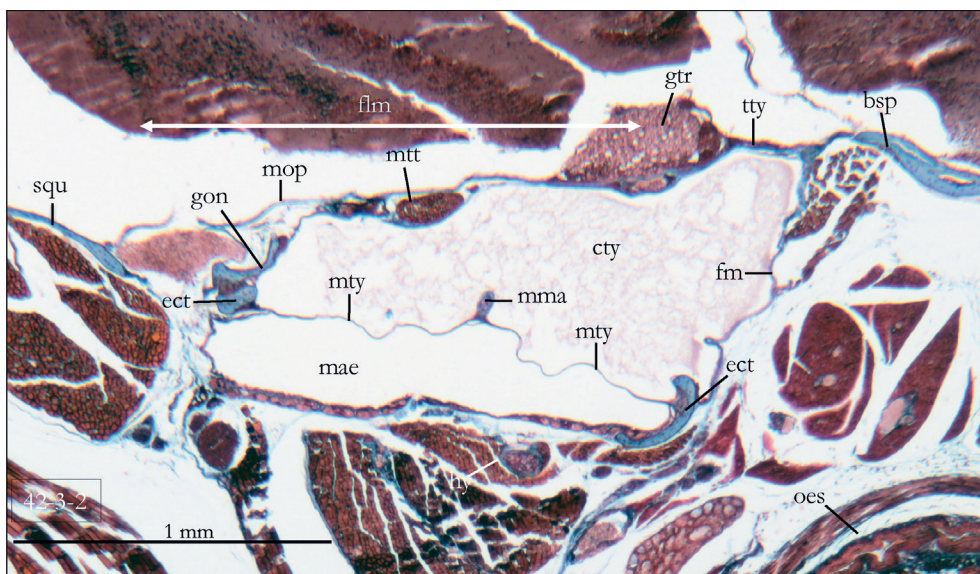


Fig. 2. The histological cross section (no. 42-3-2) of the middle ear of an adult *Sorex araneus* shows the connections of the ectotympanic and of the tympanic membrane. The wide fontanella at the cranial basis (foramen lacerum medium) is closed by the membrana obturatoria posterior. Abbreviations: bsp – basisphenoid, cty – cavum tympani, ect – ectotympanicum, flm – foramen lacerum medium, fm – fibrous membrane, gon – goniale (praearticulare), gtr – ganglion trigeminale, mae – meatus acusticus externus, mma – manubrium mallei, mop – membrana obturatoria posterior, mtt – musculus tensor tympani, mty – membrana tympani, oes – oesophagus, squ – squamosum, tty – tegmen tympani.

Sorex as 2.4 mm². That means that it is about 80% larger in the former – or the other way round, in *Sorex* it is only 56% of the area in *Crocidura*. Although the other two *Crocidura* specimens show absolute smaller tympanic areas than specimen SMF 95044, the observed pattern in size difference is still valid as their skulls are also smaller (Table 1).

FLEISCHER (1973) measured the diameter of the ‘Trommelfelling’ in *Crocidura russula* as 1.9 mm, and that of *Suncus etruscus* as 1.2 mm; assuming a circular membrane, that means that the area of the tympanic membrane of his *Crocidura russula* is 2.8 mm² and for *Suncus etruscus* 1.14 mm². BURDA et al. (1992) reported a tympanic area of 2.0 mm² for *Sorex araneus*. HEMILÄ et al. (1995) stated 1.92 mm² for the eardrum of *Sorex araneus*. MASON (2001) provided data from quite a number of soricid taxa (*Sorex*, *Neomys*, *Blarina*, *Cryptotis*, *Crocidura*, *Suncus*) regarding the body mass and the pars tensa area; the measurements of the eardrum area fit quite well with our data recorded in Table 1.

According to studies in other mammalian taxa (ROSOWSKI 1992, WEBSTER & PLASSMANN 1992, BURDA et al. 1992), the difference observed in the two soricid species means that the best frequency of hearing should be somewhat lower in *Crocidura russula*. The few audiograms published by KONSTANTINOV et al. (1987) of several species of *Sorex* and one crocidurine

(*Diplomesodon*) seem to show a tendency toward lower frequency hearing in the latter taxon. However, much more investigation is necessary to confirm these hypotheses.

Lower frequency hearing is typical for orientation in more open environmental structures, whereas higher frequencies are useful in dense undergrowth (NEUWEILER 1984, SIEMERS & SCHNITZLER 2004, SIEMERS et al. 2009). Ecomorphologically, this difference could mean that the greater white-toothed shrew *Crocidura russula* is adapted to a microhabitat that is somewhat more open than that of the common shrew *Sorex araneus*. This assumption seems to be in accordance with the published data. BAUMANN (1949), who largely relied on LÖHRL (1938), stated that *Sorex araneus* mostly lives in burrows of mice and moles, and prefers dense forest floors, hedges and swamps; in contrast, *Crocidura russula* prefers more open habitats such as gardens, stone walls, garden houses, fields etc. HAUSSER et al. (1990) confirmed this for *Sorex araneus* and GENOUD & HUTTERER (1990) for *Crocidura russula*.

It is also likely that the species-specific hearing is correlated with vocalization in social communication and in orientation. It is well known that shrews are fairly ‘noisy’, although they are solitary animals. KONSTANTINOV et al. (1987: 233) wrote: “Most of the acoustical signals [...] are a sequence of pulses with clearly expressed maximums in shrews at 8.5–27.4 kHz”. Of course, the type of vocalization largely depends on the circumstances, but in *Diplomesodon* the first harmonics tend to range at the lower frequencies. SIEMERS et al. (2009: 595) studied the relationship of call rates with substrate density and suggested an ‘echo orientation hypothesis’ meaning that “they may use call reverberations for simple close-range spatial orientation”. ZSEBÖK et al. (2015) analyzed call parameters in six species of soricids: in their fig. 5 the mean frequency of the two crocidurine species *Crocidura russula* and *Crocidura leucodon* appears to lie significantly below that of the soricines. These authors discuss at length various methods of identifying different species by call analysis.

In the histological cross section of the middle ear of an adult *Sorex araneus* (Fig. 2), the ectotympanic bone (and the membrana tympani) is fixed to the medial tegmen tympani by the fibrous membrane; laterally it is connected with the goniale (= praearticulare) and the processus anterior of the malleus. At the posterior end of the bulla there is a small remnant of the processus tympanicus; it supports the broad end of the medial leg of the ectotympanic (Fig. 1). The roof of the tympanic cavity is largely formed by the membrana obturatoria posterior, which is defined as the lateral wall of the cavum epiptericum behind the ala temporalis (MAIER 1987). Most authors now call this large fontanella the ‘foramen piriforme’, but this new term of McDOWELL (1958) did not consider the aspect of homology of this ‘Nervenöffnung zweiter Ordnung’ of GAUPP (1911). The homology of the ‘foramen piriforme’ as an enlarged foramen lacerum medium is discussed in MAIER et al. (2022).

Crocidurinae versus Soricinae

In order to evaluate how representative the presented data of the two species *Crocidura russula* and *Sorex araneus* are, we have studied a few more soricid taxa (see Table 1 and Fig. 3). The systematic relationships of these few taxa can also be seen in the simplified cladogram. We attempted to consider at least one representative of the major phylogenetic branches (*Suncus*, *Myosorex*, *Neomys*, *Anourosorex*).

In Fig. 4 a common regression was calculated between the logarithms of the basicranial length (basion-prosthion) and the tympanic membrane area. The difference of the tympanic membrane area to this regression line was determined. If all data points were included in the analysis, there

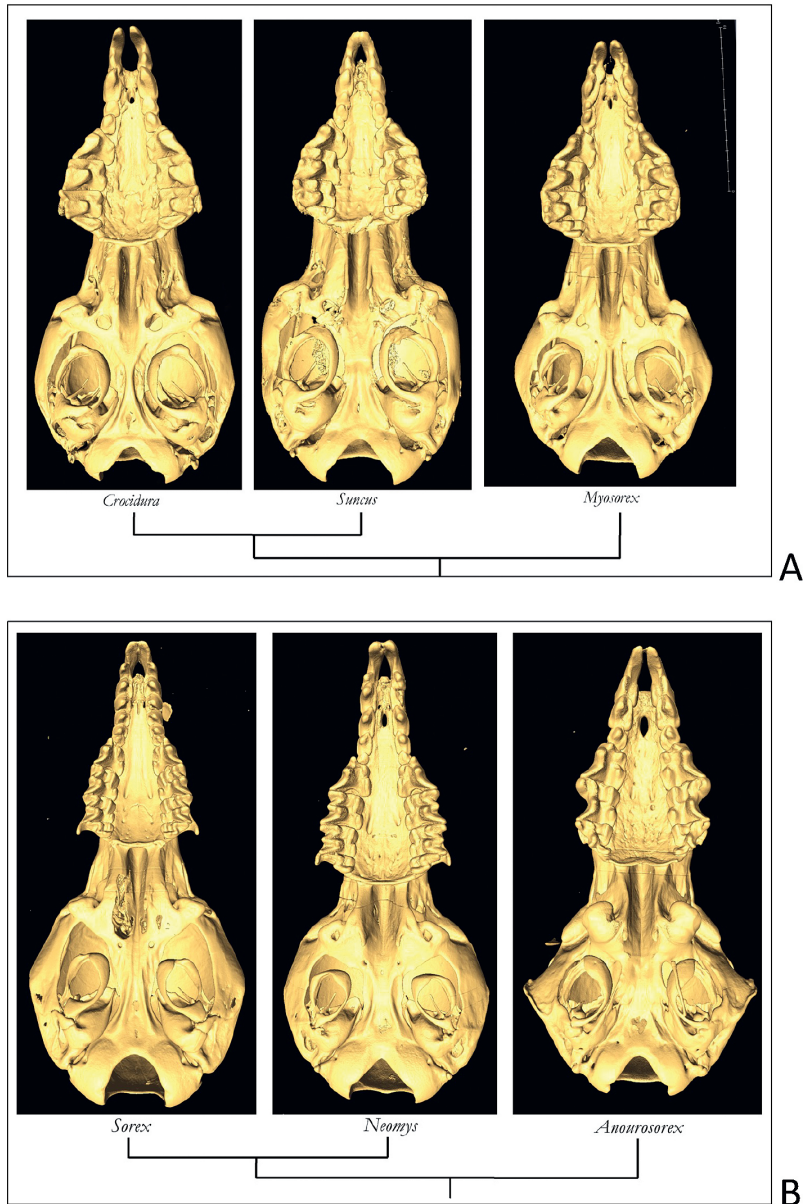


Fig. 3. Ventral views of crocidurine (A) and soricine (B) skulls. These figures are all reconstructed from μ CT scanned specimens, i.e., they are in fact virtual views. All are brought to about the same size. It is obvious that the tympanic rings are larger in the crocidurines; in their skulls the foramen lacerum medium is almost obscured by the tympanic area; due to the postulated secondary reduction of the ectotympanic ring, it is more exposed in the soricines – except *Anourosorex* (see text).

was a significant group effect (Mann-Whitney U-test, $\text{Chi}^2(1)=5.22$, $p=0.022$). In Crocidurinae (blue colour) in all but one case the tympanic membrane area was at or above the common regression line. In the Soricinae (orange colour) the tympanic membrane area was in all but one case below the common regression line. In this calculation three specimens of *Crocidura russula* and three specimens of *Sorex araneus* were included. Since these measurements were statistically not independent, we also calculated the U-test using mean values for each of these two species. In this case, the group difference was no longer significant (Mann-Whitney U-test, $\text{Chi}^2(1)=2.94$, $p=0.086$); however, it still showed a statistical trend. If the difference of log tympanic membrane area from the common regression line was calculated for the 3+3 specimens of *Crocidura russula* versus *Sorex araneus*, the difference was significant (Mann-Whitney U-test, $\text{Chi}^2(1)=3.86$, $p=0.0495$).

When the regression is run with linear measurements, in Crocidurinae the mean difference between the average of the tympanic membrane area and the common regression line was $+0.32 \text{ mm}^2$. In the Soricinae the mean difference is slightly greater taking a value of -0.37 mm^2 . In sum, the area difference between the two taxa groups is therefore 0.70 mm^2 . This difference is significant (t-test): $t(11)=2.57$, $p=0.026$.

It is obvious that the blue regression line of the Crocidurinae is pulled down a little by the outlier *Suncus murinus* (5), the giant musk shrew; however, it is known that interspecific re-

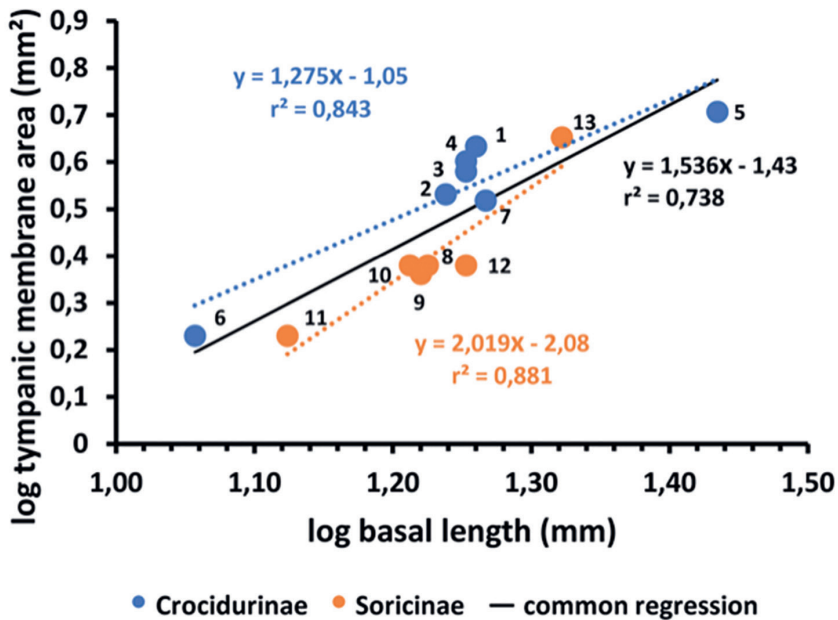


Fig. 4. Diagram of the regression analysis of our logarithmized skull measurements (basal skull length) and calculations (tympanic membrane area) of the specimens listed in Table 1. The plot numbers are identical with those of the species list in Table 1.

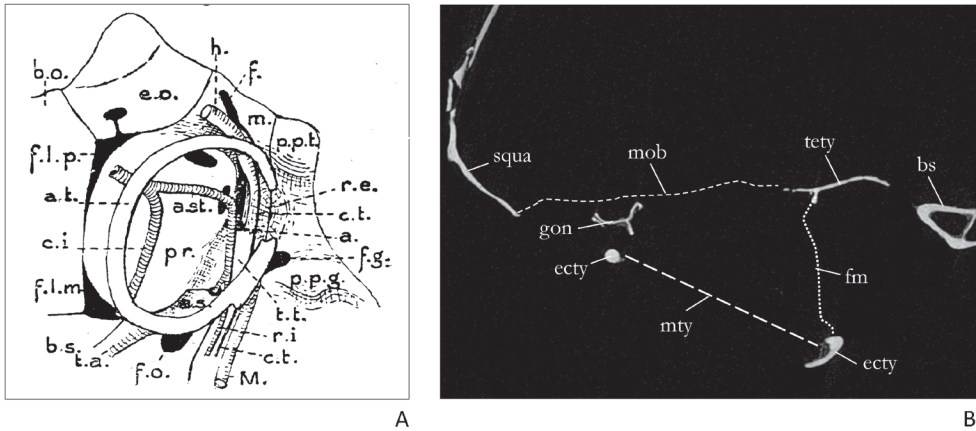


Fig. 5. A – Semi-schematic drawing of the therian middle ear region. This figure of VAN KAMPEN (1905) shows a late fetal stage, in which the ectotympanic is expressed as a simple ring of bone (a.t. – annulus tympanicus; the other abbreviations should be checked at the original source). B – This scan of an adult skull of *Crocidura russula* (coll. WM; image no. 2600) shows a cross section of the ectotympanic ring (ecty) mainly fixed by the reconstructed fibrous membrane (fm). The tympanic membrane (mty) is also reconstructed, as is the sphenobturate membrane (mob) closing the foramen lacerum medium. Other abbreviations: bs – basisphenoid, gon – goniale, squa – squamosum, tety – tegmen tympani. Not to scale.

gressions generally show a reduced inclination. The orange line of the Soricinae is pulled up by the Sichuan mole shrew *Anourosorex planipes* (13). We assume that this taxon represents a plesiomorphic state, which is also confirmed by further cranial structures like a plesiomorphic alisphenoid (see cladogram in Table 1 and MAIER et al. 2022). As judged from its larger eardrum, we conclude from the distribution of this character (see Table 1) that the Crocidurinae in general are plesiomorphic, i.e., they represent the inferred groundplan of the Soricidae. Consequently, Soricinae with their smaller tympanic membranes are considered as derived. In line with our ecomorphological arguments we also infer that both in hearing and in vocalization the crocidurines and *Anourosorex* use somewhat lower frequencies than *Sorex* and *Neomys*.

Evolutionary biology – a new scenario

We present here some hypotheses concerning the peculiar structure of the soricid middle ear in general. There seems to be a broad consensus that the middle ear of shrews with their exposed and only loosely attached ectotympanic rings is primitive for mammals (cf. Fig. 5B); this assumption may have been stimulated by the schematic drawing of VAN KAMPEN (1905, see Fig. 5A). However, we find such a configuration neither in marsupials nor in other basal eutherian mammals (VAN KAMPEN 1905, MCDOWELL 1958, MACPHEE 1981, MAIER 1989). Moreover, modern molecular phylogenetics unequivocally show that lipotyphlans are not basal eutherians, but that they are associated with the Laurasiatheria (STANHOPE et al. 1998, and many others). Of special interest is the fact that in both the Erinaceidae and Talpidae, which are considered with

good evidence to be the sister groups of the Soricidae, the ectotympanic ring is fixed more or less firmly to a stout processus tympanicus of the petrosal (VAN KAMPEN 1905). In *Solenodon paradoxus* the ectotympanic also lies free (WIBLE 2008).

We hypothesize that the loose ectotympanic of soricids, which is attached almost completely to the perioticum not by a processus tympanicus but by a fibrous membrane, is a derived feature. Our observations on relatively few, but fairly representative species of the Soricidae, indicate that the size of the tympanic membrane appears to be quite variable, probably in adaptation to varying ecomorphological conditions of their niches – and this variety may be facilitated morphogenetically by the relatively loose ligamentous attachment of the ectotympanic ring at the basicranium. The ectotympanic ring seems to be able to change its size easily and can thereby switch into neighbouring ‘auditory adaptive zones’ (cf. SIMPSON 1951); these adaptation zones are primarily identical with the crocidurines and the soricines. We speculate that this adaptability of the hearing system could be the crucial factor behind the enormous evolutionary success (450 species, WILSON & MITTERMEIER 2018) of these small insectivorous mammals when compared with moles (54 species, WILSON & MITTERMEIER 2018) and hedgehogs (26 species, WILSON & MITTERMEIER 2018). Of course, much further ecological, developmental and other physiological research is needed to test this hypothesis.

A c k n o w l e d g e m e n t s

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