

Morphology and adaptation of the auricle in Soricidae (Lipotyphla)

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Abstract. Shrews look rather similar at first sight, but a closer look reveals many different specializations according to different lifestyles. In this study, we took a closer look on the auricle of shrews. To reveal morphological adaptations, we analysed the inclination of the outer ear in relation to the nostril-eye-line, and its visibility. We could show that not only environmental cues have an influence on the shape of the outer ear, but there exist also differences at the subfamily level. We found a clear separation between Soricinae, Myosoricinae, and Crocidurinae concerning the visibility and the inclination of the auricle. Within the limits of a subfamily the auricle is modified due to behavioural and environmental constraints. Especially within Myosoricinae adaptations to a semi-fossorial life are well visible.

Key words. Soricidae, external ear, morphology, adaptation.

INTRODUCTION

Almost 455 extant species of shrews of the World (WILSON & MITTERMEIER 2018, ESSELSTYN et al. 2021) live in many different habitats, such as deserts, tropical rain forests and cold mountain streams. Although most species look quite similar at first sight, a closer look reveals differences in size, colour, and especially form (HUTTERER 1985). The tails of some species, for example, show special adaptations in relation to different lifestyles. In *Suncus megalura*, a scansorial shrew, the tail is extremely long and may support climbing (VOGEL 1974). *Sorex alpinus*, a scansorial species living and climbing in rocky high mountain regions, also has a relatively long tail, possibly for balancing in the habitat (HUTTERER 1982). The tails of some semiaquatic species (*Neomys fodiens*, *Chimarrogale* spp.) bear ventral keels of stiff hairs. *Nectogale elegans*, the species mostly adapted to a semi-aquatic lifestyle, even bears four keels, one on each side of the tail, and the ventral one splits into two at the end of the tail (HUTTERER & HÜRTER 1981, HUTTERER 1992). Semiaquatic forms also show a fringe of stiff hairs around their toes. These hairs support propulsion during swimming. This adaptation is also found in the psammophilic *Diplomesodon pulchellum*. Here, the hairs probably work like a snow-shoe as the species walks on the sandy ground (HUTTERER 1985). Differences exist also between the subfamilies Soricinae and Crocidurinae. As BURDA (1980) has shown, the auricle is mostly hidden in the pelage in Soricinae, whereas it is well visible and more sticking out in Crocidurinae. Besides for hearing, this may be related to different basal metabolic rates. Soricine shrews normally have higher basal metabolic rates and higher average body temperatures than crocidurine shrews. They also keep their body temperature at a more constant level (CHURCHFIELD 1990), while crocidurine

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shrews are able to use torpor, among other energetic strategies (GENOUD 1988). Soricinae mainly inhabit the cooler regions of the northern hemisphere, whereas Crocidurinae show their greatest diversity in warmer or even tropical regions, especially in Africa. The higher metabolic rate, the more constant body temperature and the hidden and hairy external ears might be an adaptation of the Soricinae to these cooler habitats, protecting the animals from heat loss. In Crocidurinae heat reduction might have been more important, and they reduced their metabolic rate. The less hairy and free-standing ears may also allow some cooling of the animal.

Form and position of the auricle also show differences between the species. While in some of the species the outer ear is large and has a positive inclination, it is tended backwards in other species. The outer ear is large in terrestrial and scansorial shrews and smaller and more reduced in semi-fossorial and semi-aquatic species. These forms often reduce the external ear, at least the upper parts, leading to a rearward position. This may serve to reduce resistance while digging or diving (HUTTERER 1985).

In this study, we concentrate on adaptations involving the auricle of shrews. Being mostly nocturnal animals with small eyes and poor vision, the acoustic sense, besides smell, is very important for shrews.

The vocalizations of shrews are still insufficiently known. Loud sounds of high frequency are known from a number of genera and species (KONSTANTINOV & MOVČAN 1985), such as *Crocidura* (HUTTERER & VOGEL 1977, HUTTERER & LÓPEZ-JURADO 1990, HUTTERER et al. 1992, SIMEONOVSKA-NIKOLOVA 2004), *Diplomesodon* (MOVČAN & ŠIBKOV 1982, KONSTANTINOV & MOVČAN 1985), *Neomys* (HUTTERER 1978, KÖHLER & WALLSCHLÄGER 1987, SHIBKOV et al. 2001, KÖHLER 2012), *Sorex* (HUTTERER 1976, 1982, MOVČAN & ŠIBKOV 1982, KÖHLER 1998, SANCHEZ et al. 2019), and *Suncus* (HUTTERER et al. 1979, SCHNEIDEROVÁ 2014). Some species even echolocate (GOULD et al. 1964, BUCHLER 1976, FORSMAN & MALMQUIST 1988) or use echo orientation (SIEMERS et al. 2009). Attempts to analyse the frequency of some calls in relation to the ear structure were not successful so far and should be repeated with a larger data set. This is also because vocalization studies on shrews are only present for species with developed auricles.

Different species and genera show significant differences in size, form and position of the outer ear. In the present study we wanted to know whether these differences correlate with adaptations to different feeding and foraging strategies, like terrestrial, semi-fossorial, scansorial, or semi-aquatic lifestyles. Unfortunately, little is known about the life of most of the shrews, especially of rarer species.

MATERIAL AND METHODS

We compared 41 species and 15 genera (Table 1). Specimens with well-preserved auricles were taken from the collections of the Zoologisches Forschungsmuseum Alexander Koenig (ZFMK) and the Field Museum, Chicago (FMNH). The taxa *Sylvisorex* n. sp. 1 and 2 are not yet formally described. *Sylvisorex* n. sp. 1 is a small and slender long-tailed new species from the Yoko Forest, D. R. Congo. *Sylvisorex* n. sp. 2, also from Yoko Forest, is a species related to *Sylvisorex ollula* (VAN DE PERRE et al. 2019). *Nectogale elegans*, the species most adapted to a semiaquatic lifestyle among shrews, has completely reduced auricles and therefore was not included in this study.

To measure the angle of inclination of the auricle, lateral sketches of the head were drawn with the help of a Olympus SZX12 binocular with drawing mirror, showing the position of the ear, eye and nostrils. Then two lines, one connecting the eye and the nostril (nostril-eye line) and another one connecting the upper and lower beginning of the external ear (ear line), were drawn. The angle of inclination was taken as the value between the ear line and the line vertical to the nostril-eye line at the point of intersection of

Table 1. Angles of inclination and visibility category for the species studied; AI – angle of inclination; VC – visibility category

species	AI	VC	species	AI	VC
<i>Blarina brevicauda</i>	-52°	0	<i>Sorex shinto</i>	-54°	2
<i>Congosorex phillipsorum</i>	-27°	1	<i>Sorex vagrans</i>	-69°	1
<i>Crocidura arabica</i>	-8°	3	<i>Soriculus caudatus</i>	-50°	1
<i>Crocidura attenuata</i>	-17°	3	<i>Suncus aequatorius</i>	-31.5°	3
<i>Crocidura bottegi</i>	6°	3	<i>Suncus etruscus</i>	-6°	3
<i>Crocidura leucodon</i>	-20°	3	<i>Suncus megalura</i>	14°	3
<i>Crocidura viaria</i>	-18°	3	<i>Suncus murinus</i>	5°	3
<i>Cryptotis osgoodi</i>	-28°	1	<i>Surdisorex polulus</i>	-85°	0
<i>Diplomesodon pulchellum</i>	-5°	3	<i>Sylvisorex akaibe</i>	-39°	3
<i>Myosorex okuensis</i>	-38.5°	1	<i>Sylvisorex camerunensis</i>	-10°	3
<i>Neomys milleri</i>	-37°	1	<i>Sylvisorex granti</i>	-34°	3
<i>Neomys fodiens</i>	-61°	1	<i>Sylvisorex howelli</i>	-21°	3
<i>Paracrocidura maxima</i>	-16°	3	<i>Sylvisorex johnstoni</i>	-26°	3
<i>Ruwenzorisorex suncooides</i>	8°	3	<i>Sylvisorex konganensis</i>	10°	3
<i>Scutisorex somereni</i>	-22°	3	<i>Sylvisorex lunaris</i>	-24°	3
<i>Sorex alpinus</i>	-56.5°	2	<i>Sylvisorex morio</i>	-32°	3
<i>Sorex cf. araneus</i>	-60°	1	<i>Sylvisorex n. sp. 1</i>	-12°	3
<i>Sorex hoyi</i>	-45.5°	2	<i>Sylvisorex n. sp. 2</i>	0°	3
<i>Sorex minutus</i>	-60.4°	2	<i>Sylvisorex ollula</i>	-11°	3
<i>Sorex palustris</i>	-50°	1	<i>Sylvisorex vulcanorum</i>	-47°	3
<i>Sorex raddei</i>	-55°	1			

the nostril-eye line and the ear line (Fig. 1). In case that the upper part of the auricle is well developed, the value would be positive. If reduced to some extent, the value gets negative. For *Blarina brevicauda*, *Crocidura bottegi* and *Neomys fodiens* the sketches were taken from HUTTERER (1985) and for *Sylvisorex*

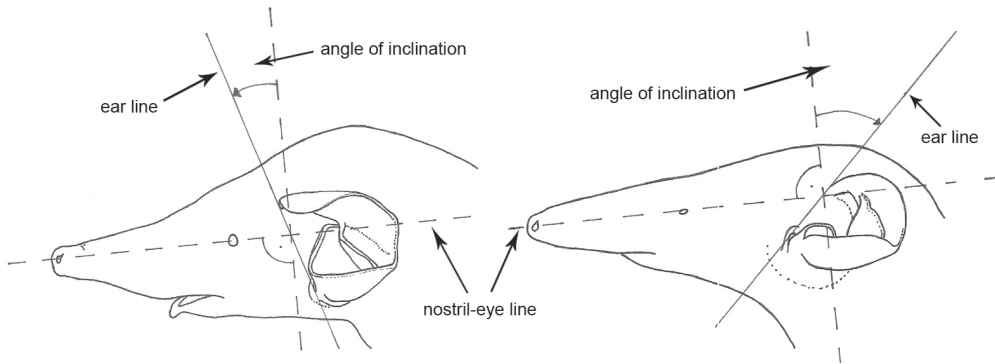


Fig. 1. Schemes showing the measurement of ear inclination. *Suncus megalura* (left) with positive and *Sorex hoyi* (right) with negative value.

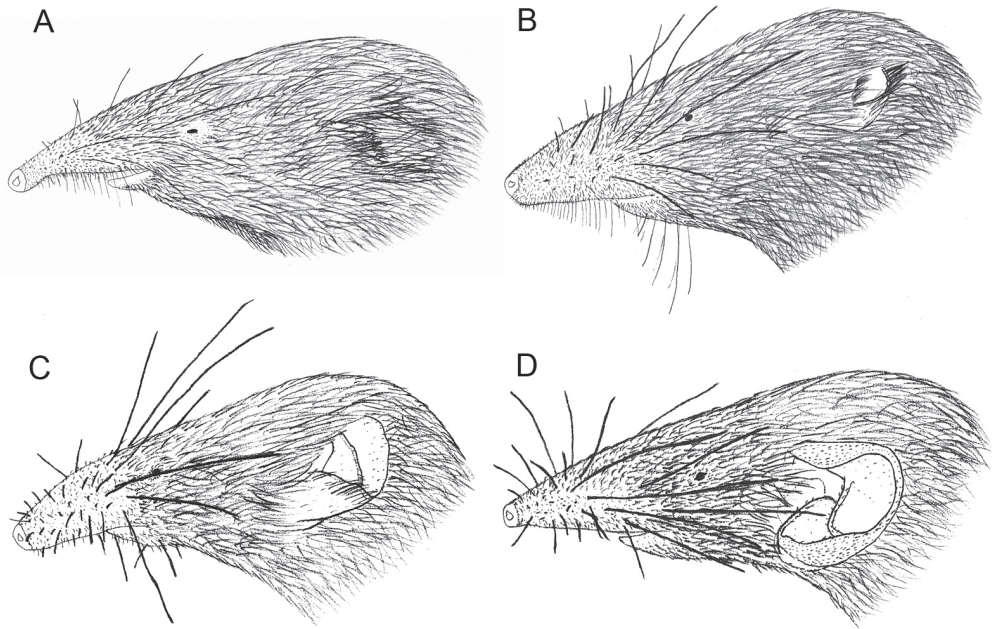


Fig. 2. Sketches showing the different visibility of the outer ear. A – *Surdisorex polulus* (VC0); B – *Neomys milleri* (VC1); C – *Sorex hoyi* (VC2); D – *Sylvisorex johnstoni* (VC3).

konganensis from RAY & HUTTERER (1996). For *Diplomesodon pulchellum* the value was taken from a picture of a living animal which was kindly made available to us by K. RUDLOFF. In most cases, one specimen was measured per species (Figs. 4–7). Measuring the angles from the final sketches was more accurate than measuring three-dimensional ears under the binocular.

To compare the visibility of the external ear, the species were grouped into four categories: 0= external ear completely hidden in the pelage, not visible; 1= external ear visible $\leq 33\%$, 2= external ear visible $\leq 66\%$, 3= external ear visible $\leq 100\%$ (Fig. 2, Table 1).

Background of the soricid auricle morphology

The soricid auricle is unique among mammals in its special form. Its appearance therefore can be regarded as an autapomorphy of the Soricidae. The auricle of shrews has two distinct pockets on its surface, which is unique. This was already stated by MOHR (1952), but found little attention since then. We wish to bring this special soricid character back to mind and to review the development of the soricid auricle. The external ear, in contrary to the middle or inner ear, unfortunately is not well studied (except for the human and chiropteran ear). Few works provide a general comparison on the mammalian auricle (BOAS 1912, MOHR 1952, BROWN 1971, BURDA 1980). According to the work that has been done on the auricle, there is also no clear nomenclature for the different anatomical structures, except for the human auricle. The most complete and detailed study on the mammalian auricle is that of BOAS (1912). He compared the cartilaginous structures of the mammalian auricles through all mammalian families and invented a clear nomenclature. BURDA (1980) also worked on the cartilage of soricid auricles, following BOAS' nomencla-

ture for the cartilaginous structures. For the soft structures in the natural ear configuration, he used terms analogous to the current nomenclature used for human or chiropteran auricles.

Fig. 3 shows the auricle of a shrew, describing the different anatomical structures of the soricid auricle. The distinct soricid pockets are labelled as I+II. The nomenclature of the pincal structures follows BURDA (1980), names in brackets refer to the internal cartilaginous structures as defined by BOAS (1912). Pocket I is formed by a very strong posteron 6 (P6) and posteron 7 (P7). P6, normally orientated longitudinally, turns transversal in soricids (BOAS 1912). The relative size of pocket I differs among the different species of shrews. Pocket II is homologous to the plica principalis, a structure normally located more anteriorly on the ear surface. In shrews, it is located posteriorly, maybe through an enlargement of the anterior parts of the auricle (BOAS 1912). It is not related to the bursa, a pocket-like structure found on the posterior margin of many carnivores. The tragus, formed by the posteron 4 (P4) and extremely strong developed in most bats (Chiroptera), is relatively small in soricids, only forming a bulge around the opening of the auditory canal. These two pockets are present in all shrews, except those that have secondarily reduced the external ear due to environmental adaptations (e.g. *Nectogale elegans*). The function of the two soricid ear pockets is not clearly known.

RESULTS

Morphological study

Most of the species studied show negative angles of inclination, but the overall range of values is very broad, reaching from -85° in *Surdisorex polulus* to $+14^\circ$ in *Suncus megalura* (Table 1, Fig. 4). Both *Crocidura* and *Sorex* group in distinct low-range clusters, whereas *Sylvisorex*

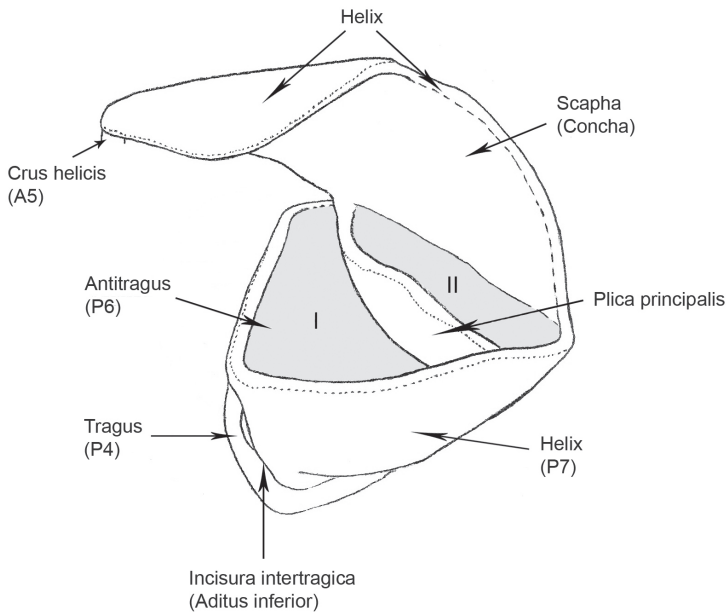


Fig. 3. Auricle of a shrew: A5 – Anteron 5; P4, 6, 7 – Posteron 4, 6, 7 (see text for further information).

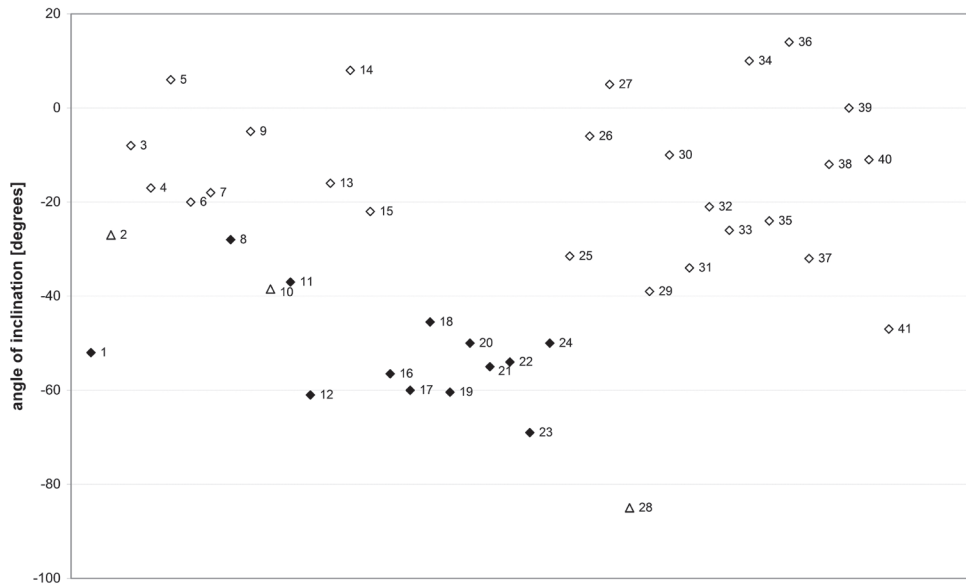


Fig. 4. Angles of inclination, symbols showing membership to subfamily: full rhomb = Soricinae, open rhomb = Crocidurinae, open triangle = Myosoricinae. 1 – *Blarina brevicauda*, 2 – *Congosorex philippisorum*, 3 – *Crocidura arabica*, 4 – *Crocidura attenuata*, 5 – *Crocidura bottegi*, 6 – *Crocidura leucodon*, 7 – *Crocidura viaria*, 8 – *Cryptotis osgoodi*, 9 – *Diplomesodon pulchellum*, 10 – *Myosorex okuensis*, 11 – *Neomys milleri*, 12 – *Neomys fodiens*, 13 – *Paracrocidura maxima*, 14 – *Ruwenzorisorex suncoides*, 15 – *Scutisorex somereni*, 16 – *Sorex alpinus*, 17 – *Sorex cf. araneus*, 18 – *Sorex hoyi*, 19 – *Sorex minutus*, 20 – *Sorex palustris*, 21 – *Sorex raddei*, 22 – *Sorex shinto*, 23 – *Sorex vagrans*, 24 – *Soriculus caudatus*, 25 – *Suncus aequatorius*, 26 – *Suncus etruscus*, 27 – *Suncus murinus*, 28 – *Surdisorex polulus*, 29 – *Sylvisorex akaibe*, 30 – *Sylvisorex camerunensis*, 31 – *Sylvisorex granti*, 32 – *Sylvisorex howelli*, 33 – *Sylvisorex johnstoni*, 34 – *Sylvisorex konganensis*, 35 – *Sylvisorex lunaris*, 36 – *Suncus megalura*, 37 – *Sylvisorex morio*, 38 – *Sylvisorex n. sp. 1*, 39 – *Sylvisorex n. sp. 2*, 40 – *Sylvisorex ollula*, 41 – *Sylvisorex vulcanorum*.

shows a relatively broad range (Fig. 4). According to the subfamilial status, there exists a weak separation between them. Almost all species above -40° of inclination belong to crocidurines, while almost all species below this value are soricine shrews (Fig. 5). The linear line-up of values also shows that there are no distinct clusters indicating different lifestyles. If the variation is only caused by environmental factors, different lifestyles should group in distinct clusters.

Concerning the visibility of the external ear to the observer, the species were grouped in four categories, as explained above. The comparison of the visibility categories shows that there is a weak correlation between less conspicuous external ears and negative inclination values, proving our theory that the form of the outer ear and the state of reduction might be due to adaptive processes (Fig. 6). But again there is no clear cut between the categories with an overlap especially for the angles ranging from -20° to -50° .

If we look at the different subfamilies of shrews separately, the differences get clearer (Fig. 7). While Soricinae mostly show very negative values, Crocidurinae mostly have higher inclina-

tion values, with only a relatively small area of overlap. Myosoricinae more or less resemble Soricinae, with *Surdisorex* reaching the most negative value measured. The mean values of the subfamilies, however, are clearly distinct (Soricinae = -52.18° , Myosoricinae = -50.17° , Crocidurinae = -14.26°).

Similar results exist for the visibility category in relation to the subfamily status. All Crocidurinae are placed in category 3. Soricinae are grouped in categories 0, 1 and 2, and Myosoricinae in category 0 and 1.

DISCUSSION

The inclination value in general does not provide direct information on the adaptation of species to different lifestyles, as there is no clustering of different foraging types in the results. Nevertheless, the strength of the reduction of the outer ear can be used to predict the lifestyle of

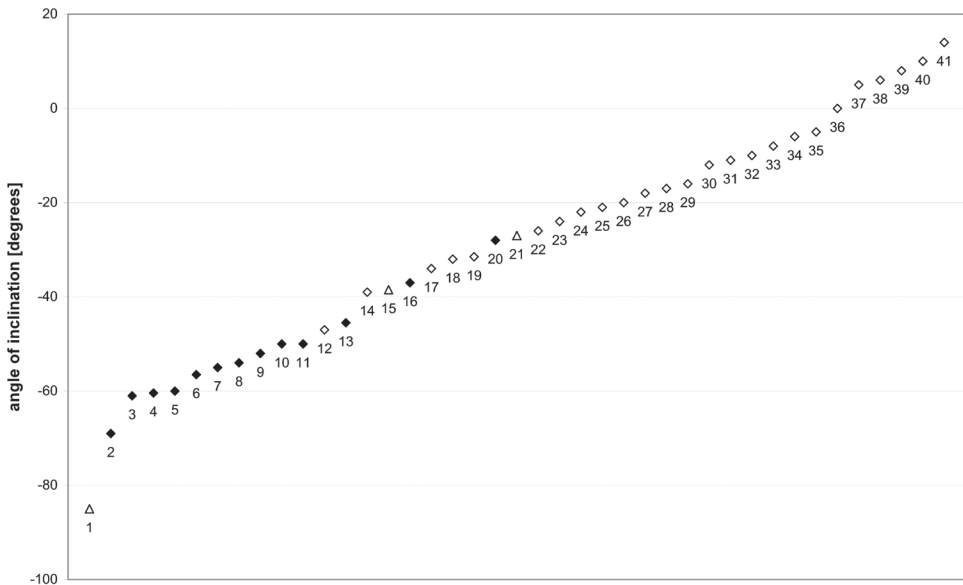


Fig. 5. Angles of inclination, from lowest to highest value, symbols for subfamily as in Fig. 4. 1 – *Surdisorex polulus*, 2 – *Sorex vagrans*, 3 – *Neomys fodiens*, 4 – *Sorex minutus*, 5 – *Sorex cf. araneus*, 6 – *Sorex alpinus*, 7 – *Sorex raddei*, 8 – *Sorex shinto*, 9 – *Blarina brevicauda*, 10 – *Sorex palustris*, 11 – *Episoriculus caudatus*, 12 – *Sylvisorex vulcanorum*, 13 – *Sorex hoyi*, 14 – *Sylvisorex akaibeii*, 15 – *Myosorex okuensis*, 16 – *Neomys milleri*, 17 – *Sylvisorex granti*, 18 – *Sylvisorex morio*, 19 – *Suncus aequatorius*, 20 – *Cryptotis osgoodi*, 21 – *Congosorex phillipsorum*, 22 – *Sylvisorex johnstoni*, 23 – *Sylvisorex lunaris*, 24 – *Scutisorex somereni*, 25 – *Sylvisorex howelli*, 26 – *Crocidura leucodon*, 27 – *Crocidura viaria*, 28 – *Crocidura attenuata*, 29 – *Paracrocidura maxima*, 30 – *Sylvisorex n. sp. 1*, 31 – *Sylvisorex ollula*, 32 – *Sylvisorex camerunensis*, 33 – *Crocidura arabica*, 34 – *Suncus etruscus*, 35 – *Diplomesodon pulchellum*, 36 – *Sylvisorex n. sp. 2*, 37 – *Suncus murinus*, 38 – *Crocidura bottegi*, 39 – *Ruwenzorisorex suncoides*, 40 – *Sylvisorex konganensis*, 41 – *Suncus megalura*.

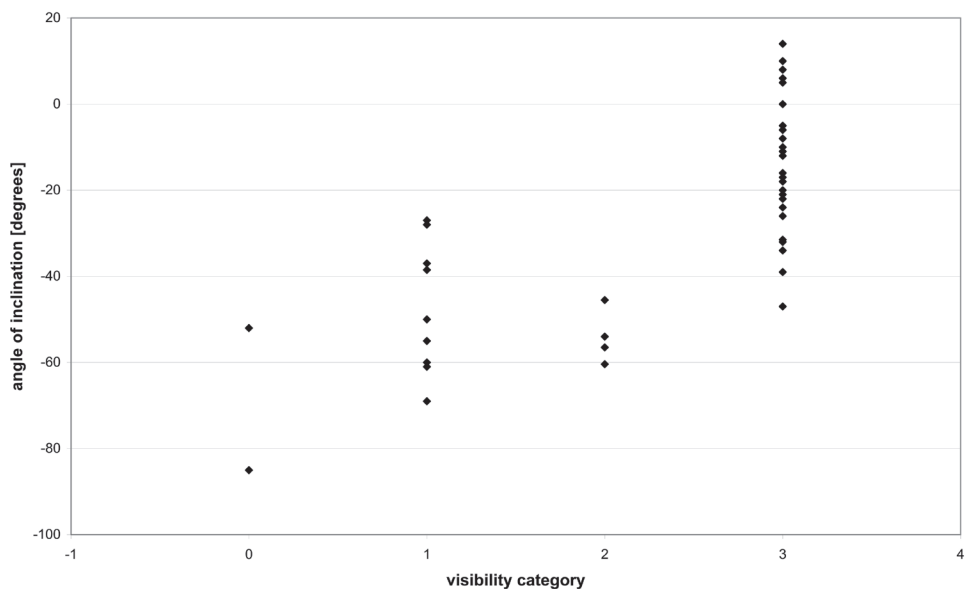


Fig. 6. Visibility category of the external ear in relation to the inclination value.

species within subfamily levels. We could show that there is a clear difference in the morphology of the subfamilies of shrews. As proposed by BURDA (1980), who analysed five soricine and one crocidurine species, our results on 41 species (13 soricine, 25 crocidurine, 3 myosoricine) suggest that the ear of soricines is hairy, less conspicuous and nearly completely hidden in the fur, whereas the ear of crocidurines is much less hairy and well visible.

S o r i c i n a e

In our analyses, all Soricinae had relatively negative inclination values (-28° to -69°), with their external ear mostly covered by fur. The low range of inclination values within the genus *Sorex* indicates that the inclination is not only due to environmental adaptations, but to some extent may be phylogenetically determined.

While most of the *Sorex* species seem to be terrestrial, two of the studied species are known for different lifestyles. *Sorex alpinus*, living in rocky alpine regions, is known to climb very well over rocks and through rocky slits. The other species, *Sorex palustris*, is known to be semiaquatic. Contrary to *Neomys fodiens*, it does not have a hairy keel on its tail, showing less adaptation to a semiaquatic life. Its only remarkable adaptation is the fringe of long hairs around its feet, just as in *Neomys* (HUTTERER & HÜRTER 1981). In relation to our theory we would expect that *Sorex alpinus* shows a relatively high inclination value. *Sorex palustris*, being semiaquatic should have a more negative value, maybe the most negative of all *Sorex* species studied. But this is not the case. The value for *Sorex palustris* is less negative than that of *Sorex alpinus*, showing

less reduction of the outer ear. The most negative value for *Sorex* found in our study is that for *Sorex vagrans*, a terrestrial species. Especially within the genus *Sorex*, the inclination seems to be more dependent on phylogenetic constraints than on adaptations to different lifestyles.

In *Neomys*, however, the adaptive value of its lifestyle is obvious. *Neomys fodiens* has a longer tail and a longer ventral keel of stiff hairs than *Neomys anomalus*. It is also a better diver than its congener (MENDES-SOARES & RYCHLIK 2009). Our results support its advanced semiaquatic lifestyle. The inclination of the auricle in *Neomys fodiens* is more negative than in *Neomys anomalus*, indicating an advanced reduction of the upper ear part. In semiaquatic shrews, this reduction is thought to reduce water resistance while diving for prey.

Cryptotis osgoodi has the highest inclination value of all Soricinae (-28°), although showing body features typically for semi-fossorial shrews, like an auricle covered by long hair on the margins of the ear pockets and elongated claws on front and hind feet. Thus, we should expect a more negative inclination value due to the reduction of resistance while digging. In *Cryptotis osgoodi* the relatively positive inclination is compensated by a stronger reduction of the ear. In its upper parts, the external ear is nearly completely reduced, only forming very shallow pockets. In this case, a reduction of resistance may not be achieved through a negative inclination alone, but more through a reduction of the auricle.

In *Blarina brevicauda*, a semi-fossorial shrew, the external ear is small and completely hidden in the fur. It also shows a relatively negative inclination. All these factors can be regarded as adaptations to its lifestyle. Like in Myosoricinae, these results are strengthened by the animal's short tail and elongated claws, also indicating a fossorial life.

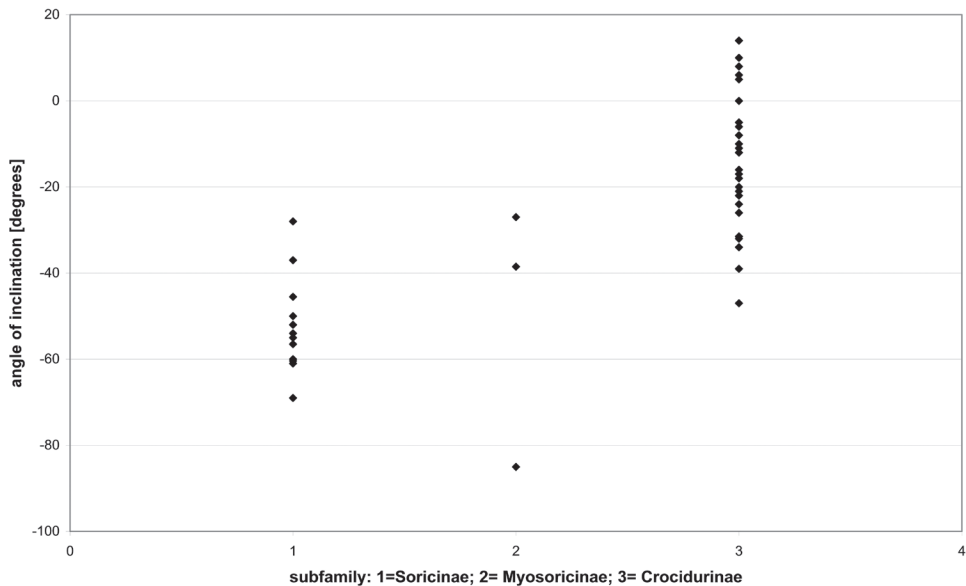


Fig. 7. Angle of inclination in relation to subfamily.

With -50° , the inclination value for *Episoriculus caudatus* ranges near the average for the Soricidae, indicating a more or less terrestrial lifestyle. This is supported by small claws and a relatively long tail that are not typical for semi-fossorial shrews.

Summing up, clear indications for anatomical adaptations to different foraging strategies can be found in the Soricinae.

Myosoricinae

Within Myosoricinae, there is a clear tendency for a progressive adaptation to a semi-fossorial lifestyle from *Congosorex* to *Surdisorex*. *Congosorex phillipsorum* shows the least negative inclination value, low reduction of the external ear and a relatively good visibility of the auricle. *Myosorex okuensis* more or less resembles *Congosorex* in the visibility and reduction of the external ear, but has a more negative angle of inclination. *Surdisorex polulus* shows the most reduced auricle of all species studied here, resulting in the lowest inclination value measured (-85°). Due to the strong reduction of the auricle, it is also completely hidden in the mole-like pelage. These results, indicating the increasing adaptation to a semi-fossorial life, are also supported by other characters. The front claws of these species get continuously longer from *Congosorex* to *Surdisorex*, whereas the tail gets shorter and the fur even more dense and mole-like (HUTTERER et al. 2002). The general adaptation of the whole subfamily to a semi-fossorial life results in a clear morphological difference to its sister taxon Crocidurinae. While the latter have large conspicuous outer ears, the Myosoricinae more resemble Soricinae in the reduced visibility of the outer ear, having hidden and smaller outer ears. In Myosoricinae the reduction of the auricle clearly shows an adaptation to a semi-fossorial lifestyle.

Crocidurinae

Almost all Crocidurinae show higher inclination values than in Soricinae. Within Crocidurinae there are the only species which reach positive inclination values. And all Crocidurinae are grouped in visibility category 3, meaning that the auricle is (almost) completely visible. This might be due to their phylogeographical origin and to physiological aspects, as mentioned above. But, within this subfamily, and especially within the different genera, there exists evidence for anatomical adaptations of the auricle due to different foraging modes.

Diplomesodon pulchellum is a psammophilic shrew, living in sandy desert habitats. It has a fringe of hairs around its feet working as a kind of snow-shoe, convergent to semiaquatic shrews. The external ear is well visible with little negative inclination (-5°). The species inhabits warm regions, and its visible ear probably works as a heat exchange surface. There is no need to save heat by hiding the auricle in the fur. *Diplomesodon pulchellum* hunts its prey on the surface of open sandy dunes. The main auditory stimuli therefore reach the animal horizontally, as shown by the nearly vertical ear inclination, as presumed for terrestrial shrews.

The genus *Crocidura*, similar to *Sorex*, shows a relatively small range of values (-20° to 6°), at least for the species studied. Because all *Crocidura* species are terrestrial, the narrow range is not unexpected.

Similar results are also found within the genus *Suncus*. *S. etruscus* and *S. murinus* are terrestrial. Their inclination values (*S. etruscus* = -6° , *S. murinus* = 5°) range within our assumption. *Suncus megalura* is known to be scansorial. It also shows the highest inclination value of all species studied here (14°). The positive inclination value therefore fits with its lifestyle. For *Suncus aequatorius*, little is known about its lifestyle. But compared to its congeners, its incli-

nation value of -31.5° is very low. This might indicate a semi-fossorial or at least less terrestrial lifestyle for *S. aequatorius*.

For *Ruwenzorisorex suncoides*, *Paracrocidura maxima* and *Scutisorex somereni* the results also support our theory. They are all considered to be terrestrial or foraging in leaf litter, but not fossorial, although unfortunately little is known on their biology. But again, their inclination values are moderate, comparable to those of *Crocidura*, indicating the proposed terrestrial lifestyle.

The widest overall range of inclination values is found within *Sylvisorex*. They reach from 10° in *Sylvisorex konganensis* to -47° in *Sylvisorex vulcanorum*. For most of the species, the substrate utilisation is poorly known. *Sylvisorex konganensis* (10°) may also be more or less scansorial, according to its inclination value. *Sylvisorex akaibei*, *S. granti*, *S. morio*, and *S. vulcanorum* show low inclination values (-32° to -47°) for crocidurine shrews, indicating possibly a semi-fossorial lifestyle. But they miss other typical features such as elongated claws. These species therefore might forage within the leaf litter or ground vegetation. The remaining species of this genus range within the values indicating a terrestrial life, correlating with presumptions for these species.

To sum up, there is a separation between the subfamilies of shrews according to the visibility and the inclination of the auricle, especially between Soricinae and Crocidurinae. Within subfamilies, we could find a clear relation between foraging type and inclination of the outer ear. The proposed adaptive value of the foraging type of a species on the appearance of the auricle therefore can be proven within its phylogenetic (subfamily) limits. In the future, a possible relation between the morphology of the auricle and the vocalizations of shrews should be studied, particularly in genera with fully or highly reduced auricles, as in *Nectogale* and *Surdisorex*.

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

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