

## Shield morphology of curly overhair in 22 genera of Soricidae (Insectivora, Mammalia)

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**Shield morphology of curly overhair in 22 genera of Soricidae (Insectivora, Mammalia).** - The structure of the shield of curly overhairs was studied in 22 genera of shrews, using scanning electron microscopy. The cross section of the shield is quadricconcave with two sides showing particular scale patterns or a relief which can be grouped into 4 morphological types: 1) a smooth type with, at most, shallow U-shaped notches; 2) a type with uniserial, V-shaped tiled notches; 3) a type with a groove and irregular notches; 4) a type with a deep ridged groove. *Myosorex*, which occupies a basal phyletic position, shows type 3. This type is therefore interpreted as an ancestral character state. It is found also in *Feroculus* and in some *Sylvisorex*. In the Crocidurinae, this type evolved into type 2 (*Scutisorex* and some Indomalayan *Crocidura*), and finally into type 1 (*Suncus* and most *Crocidura*). In the Soricinae, it evolved into type 4, which is common to all genera except *Megasorex* and *Notiosorex*. These two genera possess type 1 which is interpreted as being a synapomorphous character of these genera. The regression of the complex structure under dry climatic conditions supports the hypothesis that the function of the grooved form of hair is water repulsion.

**Key-words:** Soricidae - Shrews - Hair - Morphology - Function.

### INTRODUCTION

The fur of shrews (Soricidae) is made of three main hair types (Fig. 1): the guard hairs which are rather stiff, the curly overhairs which are segmented with an enlarged terminal shield and the underhairs which do not have a shield.

When considering morphology, the terminal shield of the curly overhairs, characterized by diverse complex structures, is the most interesting feature. Several

authors (MATHIAK 1938, WILLIAMS 1938, DAY 1966, APPELT 1973, DZIURDZIK 1973) have shown that the cross section of the shield is H-shaped in the genus *Sorex*. This profile is lacking in *Crocidura* (DZIURDZIK 1973).

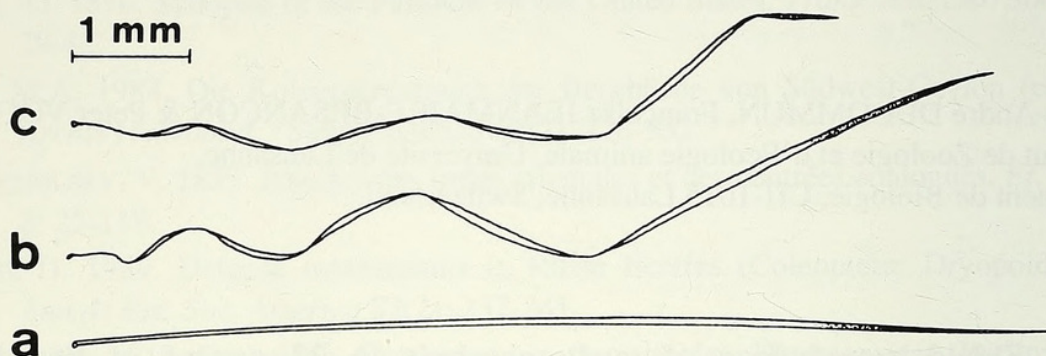


FIG. 1

Main hair types of shrews: a. guard hair, b. curly overhair, c. underhair.

An investigation using scanning electron microscopy by VOGEL & KÖPCHEN (1978) revealed that the H profile is due to two longitudinal grooves, containing a central ridge and inclined lamellae (Fig. 2, 3). This structure was confirmed for the genera *Blarina*, *Cryptotis*, *Neomys* and *Sorex*. It was interpreted as being a synapomorphy restricted to the subfamily Soricinae because it was not found in *Crocidura*, *Suncus* and *Sylvisorex*, members of the subfamily Crocidurinae. An

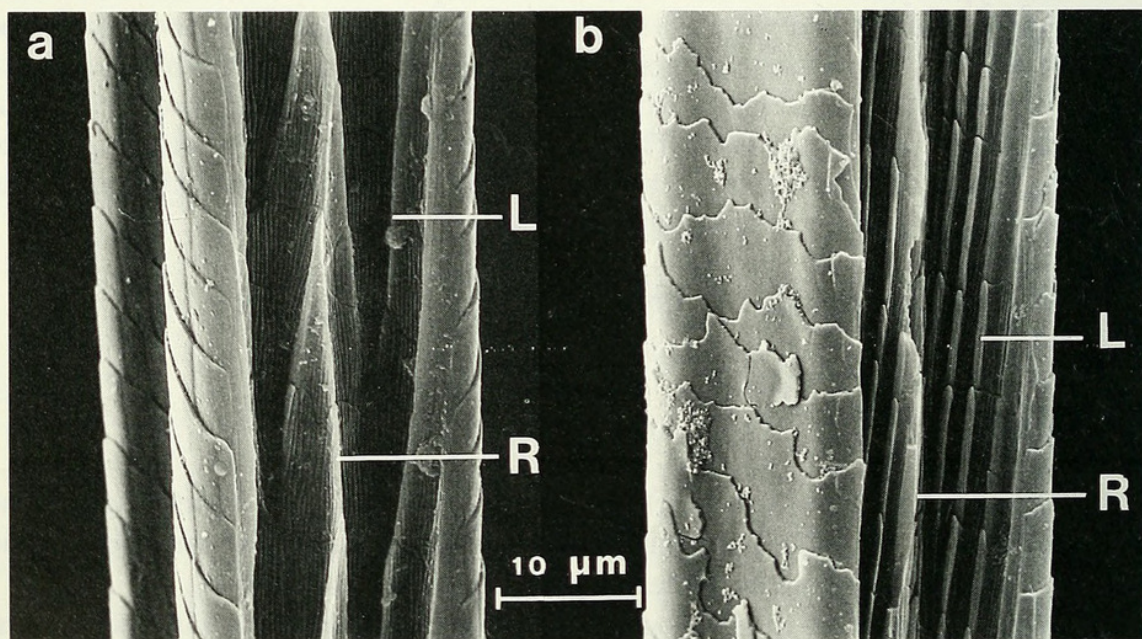


FIG. 2

SEM view of the terminal shield of a curly overhair with deep groove, central ridge (R) and oblique lamellae (L). a. *Sorex araneus*, b. *Neomys fodiens*.

examination of two other soricine shrews, *Chimarrogale* and *Nectogale*, confirmed this taxonomic interpretation (VOGEL & BESANÇON 1979).

However, a much wider investigation is necessary to assess whether the relationship between structure and taxonomy is consistent. With this in view, we have expanded our morphological investigation of the curly overhairs to 22 genera. Including our former findings, we present the results in the form of a catalogue with an illustration of the structure of curly overhairs for at least one member of each genus. Several photographs are presented in case of a considerable variability within a genus or a species, or when justified by phylogenetic considerations.

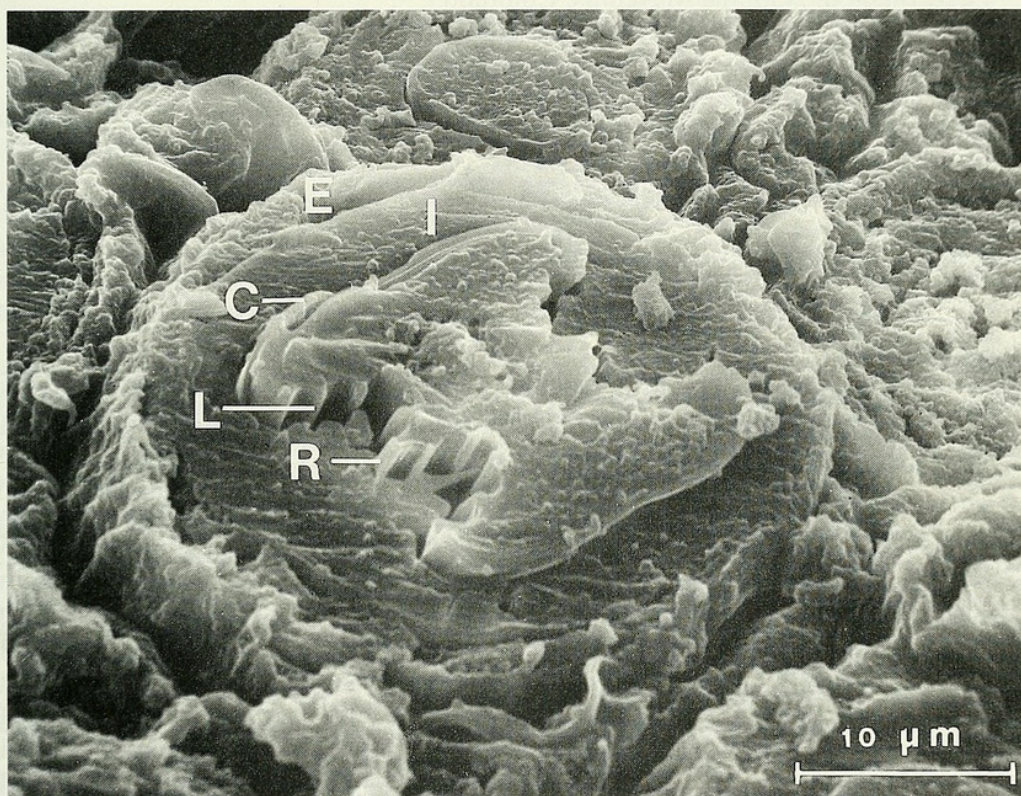


FIG. 3

SEM view of a horizontal skin section with growing hairs of a young (11 days) *Neomys fodiens*. Cross section of the shield of a curly overhair, which shows the H-profile with two grooves, the central ridges and the oblique lamellae. C: cuticle; E: external root sheet; I: internal root sheet; L: oblique lamellae; R: central ridge.

## MATERIAL AND METHODS

The curly overhairs of a total of 61 species of 22 genera were examined (Table 1). The samples were taken from the scapular region, washed and dehydrated in alcohol and then xylol. They were glued onto a support and metallized in gold. Observations with a scanning electron microscope (JEOL JSM-35) were carried out at 20 kV.

TABLE 1

List of shrews analyzed and structure of the shield, according to Fig. 9. (Abbreviations for structures: U: smooth; V: tiled notches; N: groove with irregular notches; W: groove with central ridge).

## Collections:

AMNH: The American Museum of Natural History, New York

BM(NH): British Museum (Natural History), London

CG: Muséum National d'Histoire Naturelle, Paris

CS: Collection Dr. F. Spitz, INRA, Toulouse

CSRS: Centre suisse de recherches scientifiques, CI

DNMC: Department of National Museums, Colombo

IMR: Institute for Medical Research, Kuala Lumpur

IZEA: Institut de Zoologie et d'Ecologie Animale, Lausanne

MHNG: Muséum d'Histoire Naturelle, Genève

MZL: Musée zoologique, Lausanne

NHMB: Naturhistorisches Museum, Basel

OFS: National Museum Bloemfontein, RSA

PSMII: Reference lost

ZFMK: Zoolog. Forschungsinstitut und Museum Alexander Koenig, Bonn

genus	species	coll.	number	country	structure
<b>Crocidurinae</b>					
<i>Crocidura</i>	<i>bottegi</i>	CSRS	925	Ivory Coast	U
	<i>cinderella</i>	CSRS	572	Ivory Coast	U
	<i>fuliginosa</i>	IMR	78173	Malaysia	V
		IMR	108152	Malaysia	V
		IMR	101545	Malaysia	V
		IMR	10242	Malaysia	V
		IMR	103710	Malaysia	V
		IMR	N-229	Malaysia	V
	<i>horsfieldii</i>			Sri Lanka	U
	<i>crosseii</i>	CSRS	751	Ivory Coast	U
	<i>lamottei</i>	CSRS	516	Ivory Coast	U
	<i>leucodon</i>	IZEA	86	Switzerland	U
	<i>lusitania</i>	CSRS	301	Niger	U
	<i>luna</i>	IZEA	2751		U
	<i>malayana</i>	BM(NH)	65.3754	Malaysia	N
	<i>miya</i>	BM(NH)		Sri Lanka	V
	<i>olivieri</i>	CSRS	6	Ivory Coast	U
	<i>o. giffardi</i>	CSRS	780	Ivory Coast	U
	<i>poensis</i>	CSRS	75	Ivory Coast	U
	<i>russula</i>	IZEA	76	Switzerland	U
		IZEA	2605	Switzerland	U
	<i>sicula</i>	IZEA	3893	Malta	U
	<i>suaveolens</i>	IZEA	1351	Greece	U
		IZEA	1242	Switzerland	U
	<i>theresae</i>	CSRS	167	Ivory Coast	U
	<i>wimmeri</i>	CSRS	385	Ivory Coast	U
	<i>zimmermanni</i>	IZEA	2058	Greece	U
<i>Diplomesodon</i>	<i>pulchellum</i>	IZEA	2211	Turkmenia	U
<i>Feroculus</i>	<i>feroculus</i>	BM(NH)	31.9.7.1.	Sri Lanka	N
		BM(NH)		Sri Lanka	N

genus	species	coll.	number	country	structure
<i>Myosorex</i>	<i>cafer</i>	IZEA	1588	South Africa	N
	<i>eisentrauti</i>	ZFMK	69.382	Cameron	N
	<i>varius</i>	MHNG		South Africa	N
		IZEA	1431	South Africa	N
<i>Paracrocidura</i>	<i>schoutedeni</i>	ZFMK	61.76	Cameron	U
		ZFMK	61.768	Cameron	U
<i>Scutisorex</i>	<i>somereni</i>	NHMB	L 14386	Congo	U-N
		NHMB	LR 14387	Congo	U-N
		IZEA	1586	Congo	U-N
<i>Solisorex</i>	<i>pearsoni</i>	MZL		Sri Lanka	U
<i>Suncus</i>	<i>etruscus</i>	CSRS	1233	France	U
	<i>malayanus</i>	BM(NH)	73.658	Malaysia	U
	<i>murinus</i>	IZEA	2	Singapor	U
		IZEA	10	Singapor	U
	<i>varilla</i>	OFS		South Africa	U
<i>Sylvisorex</i>	<i>lunaris</i>	ZFMK	68.526	Congo	V
	<i>megalura</i>	CSRS	1233	Ivory Coast	U
	<i>morio</i>	ZFMK	61.746	Cameron	V
<b>Soricinae</b>					
<b>Blarinini</b>					
<i>Blarina</i>	<i>brevicauda</i>	MHNG	1163.53	Canada	W
<i>Cryptotis</i>	<i>thomasi</i>	MHNG	849.18	Ecuador	W
<b>Neomyini</b>					
<i>Anourosorex</i>	<i>squamipes</i>	CG		Assam	W
<i>Chimarrogale</i>	<i>hantu</i>	IMR	75277	Malaysia	W
		IMR	85189	Malaysia	W
		IZEA		Japan	W
<i>Megasorex</i>	<i>platycephala</i>	IZEA		Japan	W
<i>Nectogale</i>	<i>gigas</i>	AMNH	212190	Mexico	U
	<i>elegans</i>	AMNH	115572	China	W
		CG	1896-527	China	W
<i>Neomys</i>	<i>anomalus</i>	IZEA	71	Switzerland	W
	<i>fodiens</i>	IZEA	433	Switzerland	W
<i>Notiosorex</i>	<i>crawfordi</i>	IZEA	1649	Arizona, USA	U
<i>Soriculus</i>	<i>hypsibius</i>	ZFMK	50.186	China	W
	<i>leucops</i>	CG		Nepal	W
	<i>nigrescens</i>	CG		Nepal	W
<b>Soricini</b>					
<i>Blarinella</i>	<i>quadraticauda</i>	BM(NH)	112156	China	W
		BM(NH)	112159	China	W
<i>Microsorex</i>	<i>hoyi</i>	BM(NH)	7773917	Canada	N
		BM(NH)	7773919	Canada	N
<i>Sorex</i>	<i>alpinus</i>	IZEA	160	Switzerland	W
	<i>araneus</i>	IZEA	X 778	Switzerland	W
		IZEA	152	Switzerland	W
		IZEA	30	Switzerland	W
		IZEA	25	Switzerland	W
	<i>bendirii</i>	PSMII	14441	USA	W
	<i>caecutiens</i>	IZEA	X 1007	Finland	W
	<i>cinereus</i>	MHNG	1162.7	Canada	W
	<i>coronatus</i>	IZEA	27	Switzerland	W
		IZEA	146	Switzerland	W
		IZEA	153	Switzerland	W

genus	species	coll.	number	country	structure
	<i>granarius</i>	IZEA	633	Spain	W
	<i>isodon</i>	IZEA	X 916	Finland	W
	<i>minutus</i>	IZEA	157	Switzerland	W
	<i>palustris</i>	PSMII	10640	USA	W
	<i>samniticus</i>	IZEA	866	Italy	W
<b>Soricidae</b>	<i>Insertae Sedis</i>				
<i>Podihik</i>	<i>kura</i>	DNMC	183 A	Sri Lanka	U

A comparison between hairs from different body parts showed only differences in size, but not in structure. For species represented by several individuals, no important qualitative differences were observed at the individual level. Differences between species of the same genus were often scanty, but sometimes more important. These differences, mostly of a quantitative nature, may be used in certain cases to discriminate between sympatric species of a local fauna as KELLER (1978) established for some shrews from Switzerland and TEERINK (1991) for European mammals.

Our systematic classification is mainly based on REPENNING (1967), especially concerning the subfamilies and tribes. The interpretation of this author has been confirmed by JAMMOT (1983). Some important phylogenetic problems have been discussed by GEORGE (1984) and MADDALENA (1990) on a biochemical basis. Nomenclature is generally based on HUTTERER & *al.* (1982), except for *Crocidura* spp. from Malaysia (RUEDI & *al.* 1990) and *C. olivieri* (MADDALENA 1990). For *Soriculus* spp., revised by HOFFMANN (1985), we followed CORBET & HILL (1992).

## RESULTS

### HAIR STRUCTURES OF THE TAXA EXAMINED

Within a taxonomic unit (e.g. subfamily or tribe), the genera are mentioned in alphabetic order.

#### Subfamily **Crocidurinae**

*Crocidura* (19 species examined): The two structured sides of the terminal shield are generally smooth, often with one row of shallow, U-shaped notches which do not appear in a cross section. This pattern is found in all European species, illustrated by *C. suaveolens* and *C. zimmermanni* (Fig. 4) and also in the African branch, illustrated by *C. bottegi*, *C. cinderella*, *C. giffardi*, *C. luna*, *C. olivieri* and *C. poensis* (Fig. 4).

*C. fuliginosa* (Fig. 5): A groove is formed by a line of rather deep, V-shaped, slightly tiled notches.

*C. malayana* (Fig. 5): The shield has a clear groove which is formed by a double or triple row of elongated notches, forming spaced oblique lamellae.

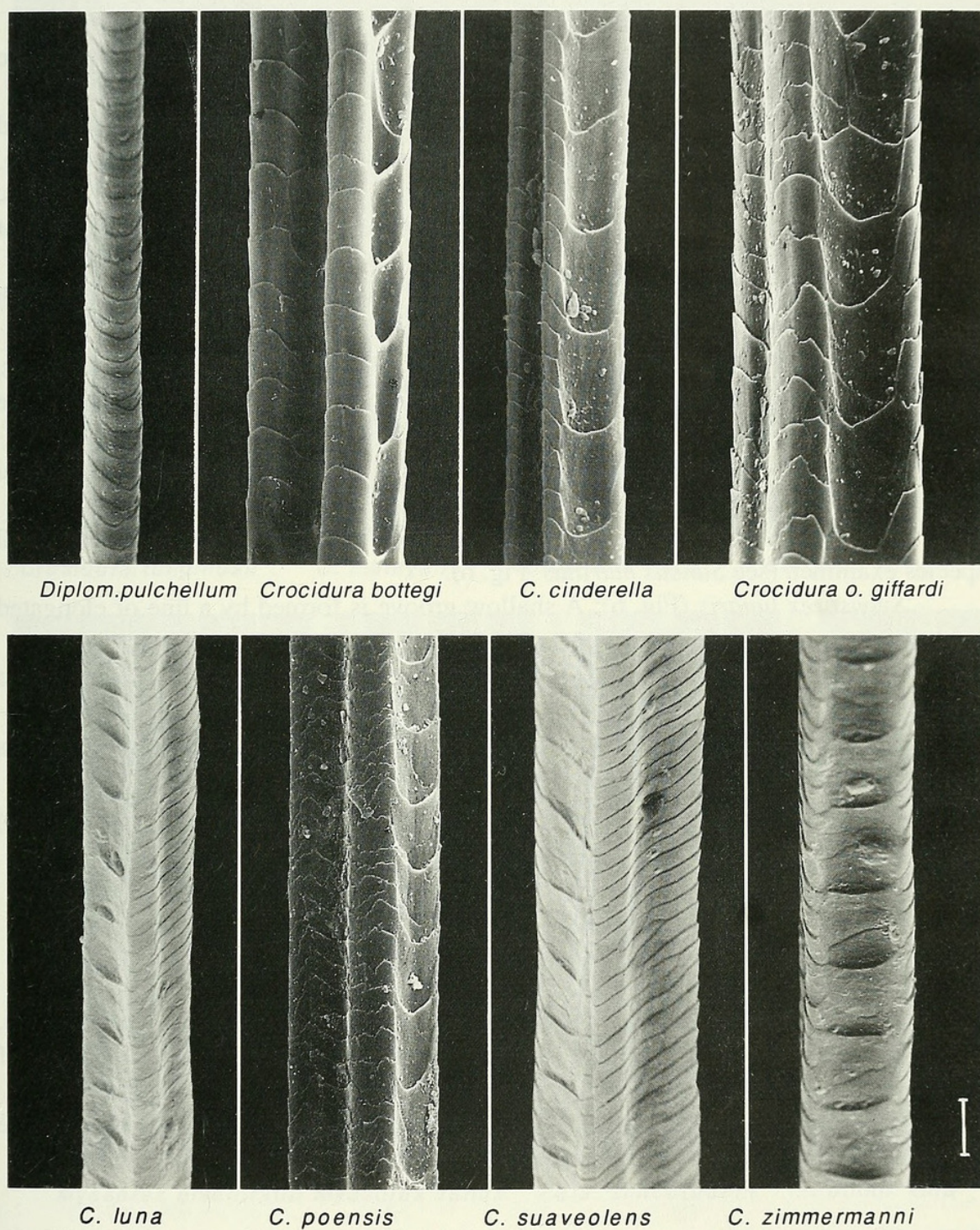


FIG. 4

SEM view of the shield of curly overhairs: Crocidurinae (*Diplomesodon*, African line of *Crocidura* (*C. bottegi* to *C. poensis*) and Palearctic species (*C. suaveolens* and *C. zimmemanni*). Scale is 10  $\mu$ m long.

*C. miya* (Fig. 5): The shield has a groove which is formed by deep, elongated not tiled notches.

*Diplomesodon pulchellum* (Fig. 4): The hairs are very thin with a shield of the smooth type, that has a rather round cross section.

*Feroculus feroculus* (Fig. 5): A very deep groove is formed by elongated notches with the superimposition of about 4 notches, forming oblique closed lamellae.

*Myosorex eisentrauti* (Fig. 5): A deep groove is formed by elongated notches, which do not form a central ridge. *M. cafer* and *Myosorex varius* (Fig. 5) have hairs of similar structures.

*Paracrociodura schoutedeni* (Fig. 5): The shield is of the smooth type with shallow notches, as in most species of the genus *Crociodura*.

*Scutisorex somereni* (Fig. 6). This species has extremely long and thick hairs. The shield has in general a line of deep notches of highly variable form. Double notches or deep holes (not U-shaped) are frequent.

*Solisorex pearsoni* (Fig. 6): Hairs are of the smooth type with only superficial notches, length shorter than width.

*Suncus*: A smooth shield and a line of superficial notches were present in all species examined (see *Suncus murinus* Fig. 6).

*Sylvisorex lunaris* (Fig. 6): A shallow groove is formed by a line of elongated but not superimposed notches.

*S. morio* (Fig. 6): A deeper groove is formed by the superimposition of two notches.

*S. megalura* (Fig. 6): A smooth shield has a shallow, widely spaced notches as in many *Crociodura*.

## Subfamily **Soricinae**

### Tribe **Blarinini**

*Blarina brevicauda* (Fig. 7): The shield has a deep groove with a central ridge, resulting from two rows of parallel V-shaped notches. There is a superimposition of often two rather short notches.

*Cryptotis thomasi* (Fig. 7): The hairs are as in *Blarina*, but irregularities are frequent, e.g. 3 parallel rows of notches are found instead of 2.

### Tribe **Neomyini**

*Anourosorex squamipes* (Fig. 7): A deep narrow groove has a central ridge. Irregularities are frequent (1 or 3 rows of notches instead of 2).

*Chimarrogale platycephala* (Fig. 7): The shield is very enlarged. There is a deep groove with a central ridge. Notches are elongated with 4 to 6 superimposed units, leading to strong oblique lamellae. *C. hantu* is similar to *C. platycephala*.

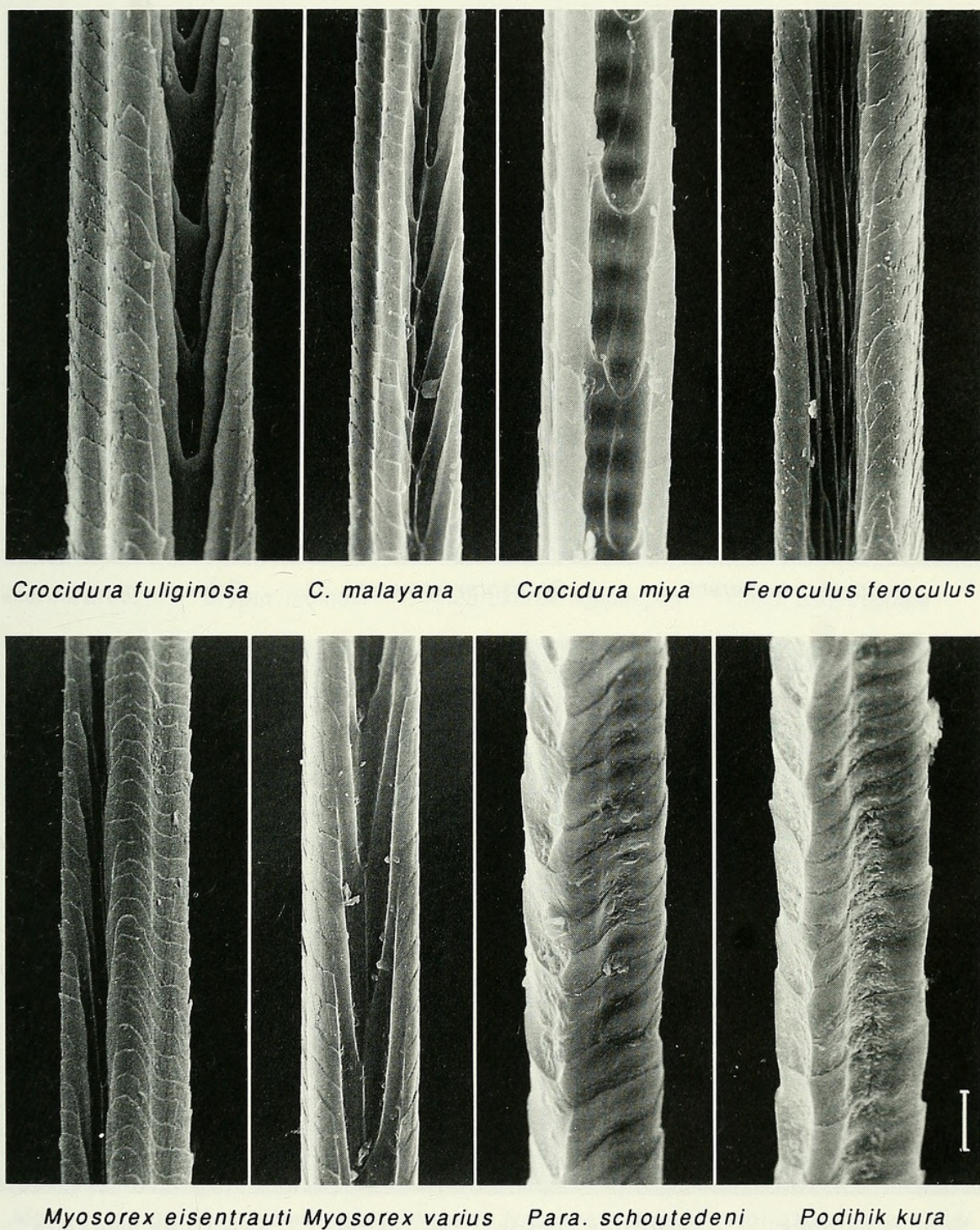


FIG. 5

SEM view of the shield of curly overhairs: Crocidurinae (*Crocidura* of the Oriental region, *Feroculus*, *Myosorex*, *Paracrocidura* and *Podihik*). Scale is 10  $\mu\text{m}$  long.

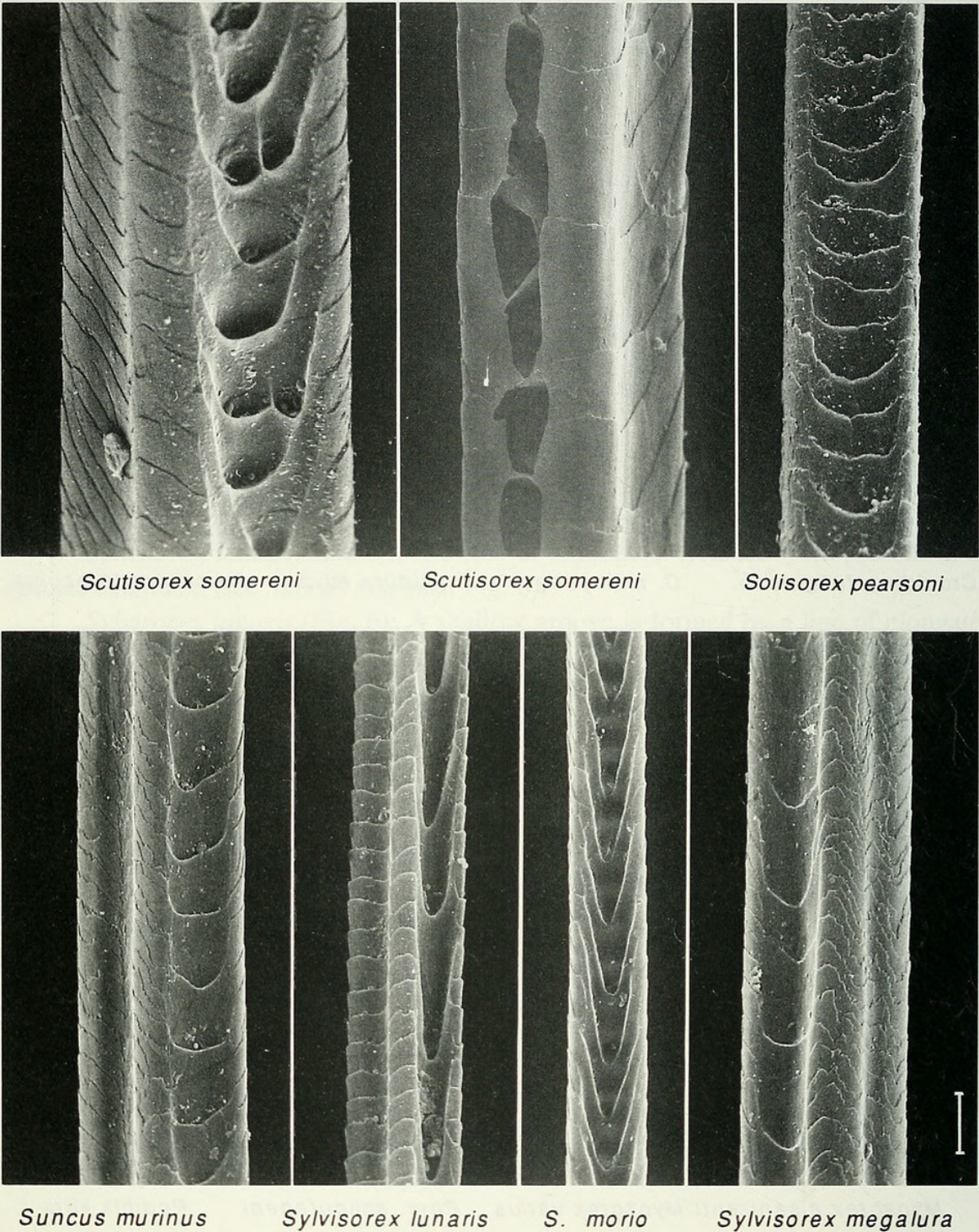


FIG. 6

SEM view of the shield of curly overhairs: Crocidurinae (*Scutisorex*, *Solisorex*, *Suncus* and *Sylvisorex*). Scale is 10 µm long.

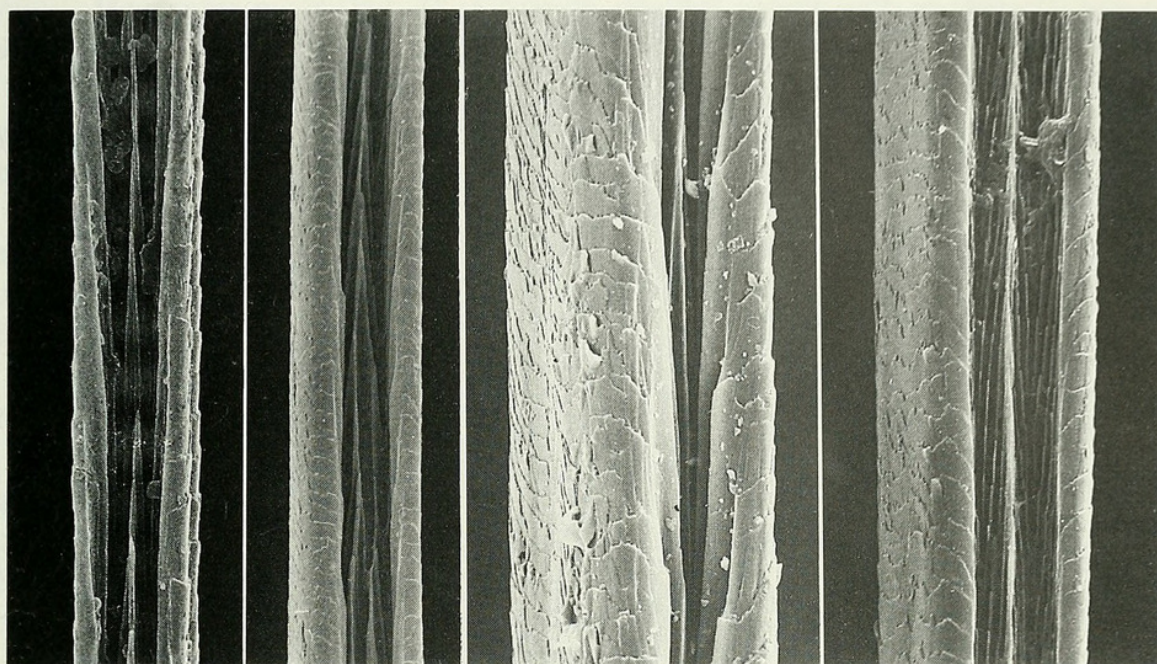
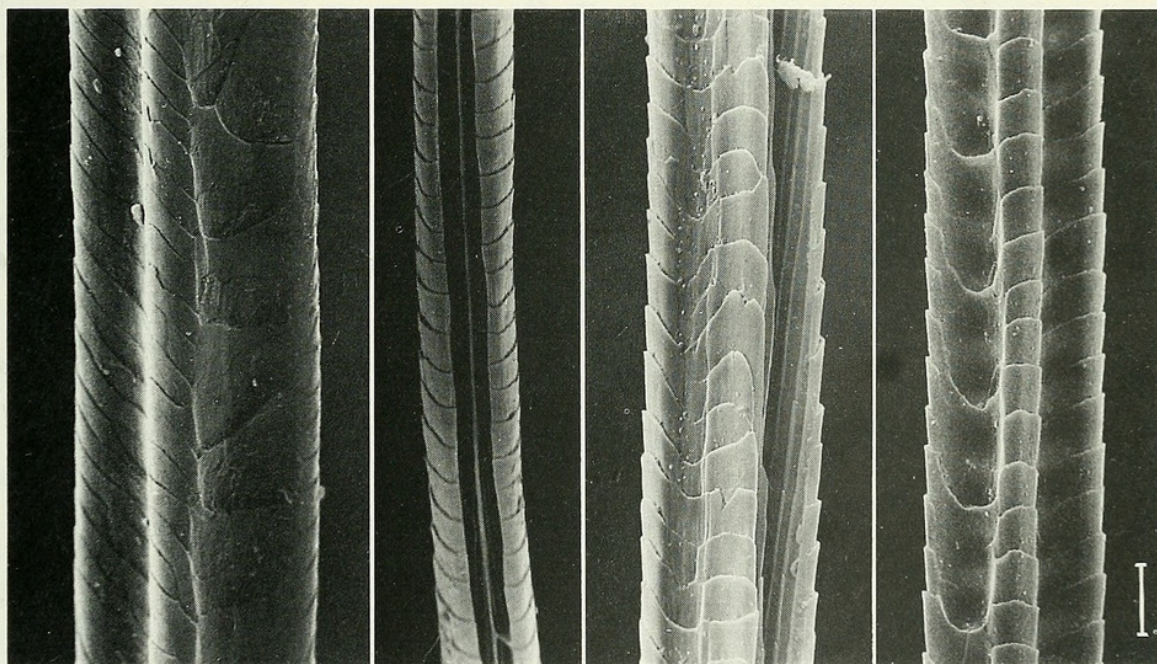
*Blarina brev.**Crypto. thomasi**Anourosorex squamipes**Chim. platycephala**Megasorex gigas**Nectogale elegans**Neomys fodiens**Notiosorex crawfordi*

FIG. 7

SEM view of the shield of curly overhairs: Soricinae (Blarinini: *Blarina*, *Cryptotis*; Neomyini: *Anourosorex*, *Chimarrogale*, *Megasorex*, *Nectogale*, *Neomys* and *Notiosorex*). Scale is 10  $\mu$ m long.

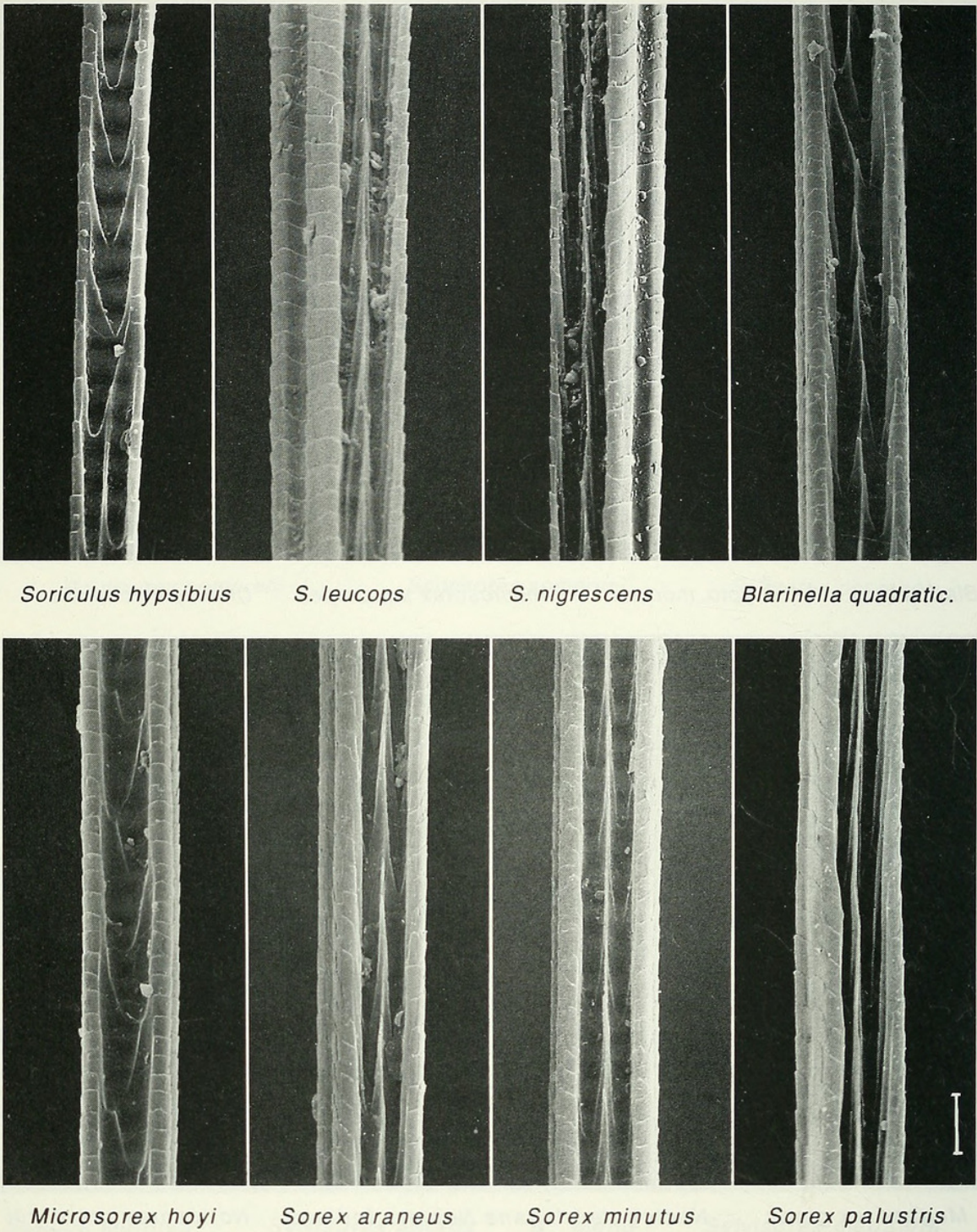


FIG. 8

SEM view of the shield of curly overhairs: Soricinae (Neomyini: *Soriculus*; Soricini: *Blarinella*, *Microsorex* and *Sorex*). Scale is 10  $\mu$ m long.

*Megasorex gigas* (Fig. 7): A smooth shield is visible with an uniserial line of superficial notches, similar to structures of *Crocidura*.

*Nectogale elegans* (Fig. 7): The shield is very thin. It has a deep, narrow groove with a central ridge. The superimposition of 3 to 4 elongated notches forms closed lamellae.

*Neomys fodiens* (Fig. 7): The shield is rather strong with a deep groove and a central ridge; notches are elongated, with the superimposition of 3 to 4 units forming closed oblique lamellae. *N. anomalus* shows only a superimposition of 1 to 3 notches, the oblique lamellae are therefore less closed.

*Notiosorex crawfordi* (Fig. 7): The shield is smooth like in *Megasorex*, but the notches are slightly deeper.

*Soriculus* (*Soriculus*) *nigrescens* (Fig. 8): The shield has, as in *Sorex*, a deep groove with a central ridge. *S. (Episoriculus) leucops* (Fig. 8): The deep groove with a central ridge shows 2 to 3 superimposed notches, forming lamellae closer than in *Sorex*. *S. (Chodsigoa) hypsibius* (Fig. 8): The groove is broad and shows one or two rows of notches either not superimposed or weakly superimposed.

### Tribe Soricini

*Blarinella quadricaudata* (Fig. 8): The hairs have a deep groove with a central ridge as in *Blarina*, but with some irregularities.

*Microsorex hoyi* (Fig. 8): The groove is formed by two rows of rather well spaced notches (only partial superimposition) without the formation of a central ridge.

*Sorex*: All of the 11 species examined show deep grooves with a central ridge, as illustrated for *S. araneus*, *S. minutus* and *S. palustris* (Fig. 8). In general there is a superimposition of 2 rather elongated notches.

### Soricidae, Incertae Sedis

*Podihik kura* (Fig. 5): This species has a smooth shield with one row of superficial notches as in *Crocidura* and *Suncus*.

### STRUCTURAL TYPES

Total preparations of curly overhairs, observed by light microscopy show an enlarged lanceolate terminal segment, a picture also suggested by the term "shield". This analogy is inappropriate because the cross section has a quadricconcave form (Fig. 3). Two opposed facets are always smooth. The only structure of these facets is the cuticular pattern. According to the definitions of TEERINK (1991), the scales are of the transversal type, ordered in a regular wave pattern with distant to near margins. The two other facets are in some cases also smooth, but with a rather streaked scale pattern. In most cases they are ornamented with a particular relief. This can be formed from a uniserial line of notches to a deep longitudinal groove resulting in a H-shaped

cross section. In an arbitrary fashion we define 4 types (Fig. 9) which are not always clearly separated:

- A smooth type, with sometimes shallow, weakly superimposed U-shaped notches.
- A type with strongly tiled, often V-shaped notches, forming a groove in some cases.
- A type with a deep groove, formed by strongly tiled notches or several rows of irregular notches.
- A type with a deep groove and a central ridge, formed by a double line of deep notches, separated by oblique lamellae.

The recapitulation in Table 1 shows that the classification is rarely problematic, even if some intermediate types may be observed. If occasionally the shield shows a less complex structure, then it is often a smaller segment of atypical hairs of an intermediate form ("Grannen-Wollhaar"). However, some species show a more pronounced variability (e.g. *Scutisorex*) and therefore they do not well fit in our classification. In such a case, we take into account the most frequent form.

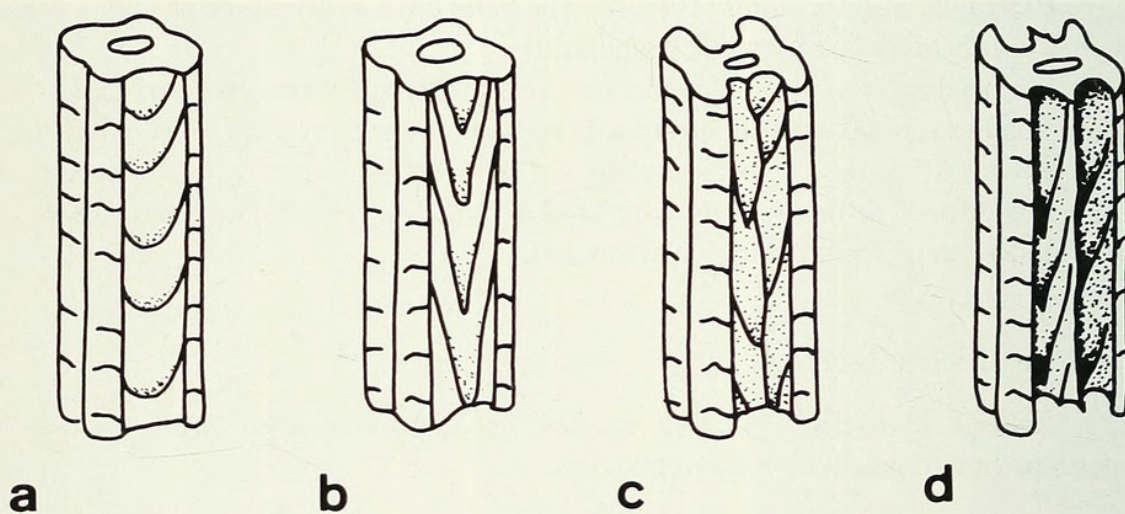


FIG. 9

Schematic presentation of the main morphological shield structures: a. smooth type with possibly shallow U-shaped notches; b. tiled deep V-shaped notches; c. groove with irregular notches; d. groove with central ridge and oblique lamellae.

## DISCUSSION

### HAIR NOMENCLATURE

A comparison of different publications shows that the denomination of the major hair types is highly variable. This is certainly due to the fact that the number of clear recognizable morphological types differ between mammalian orders. In rodents,

TRAPP (1980) distinguished 4 types. Concerning shrews, most authors distinguish 3 major types, but use quite different terms for their designation (Table 2). Moreover, some intermediate forms exist, e.g. BIEBER & EICK (1974) found "Grannen-Wollhaare" in *Sorex araneus* and DEBROT & *al.* (1982), DANNELID (1986) and TEERINK (1991) mentioned guard hairs with the typical shield structures of curly overhairs. These examples demonstrate an important plasticity in hair formation.

TABLE 2

Terms used for the three major hair types in shrews

reference	type 1	type 2	type 3
TOLDT (1935)	Leithaar	Grannenhaar	Wollhaar
MATTHIAK (1938)	guard hair	intermediate hair	furhair
WILLIAMS (1938)	heavy overhair	curly overhair	furhair
DANNELID (1986)	lead hair	awl hair	zigzag
SAGARA (1986)	straight guard hair	awn	furhair
TEERINK (1991)	overhair GH0	overhair GH2	underhair
this work	guard hair	curly overhair	underhair

## FUNCTIONAL INTERPRETATIONS

Each of the three main categories of hairs in the fur of shrews is mainly responsible for a particular function. The fine underhairs are responsible for thermic insulation. The guard hairs, which project over the fur, present a sensitive tactile component. Inbetween lie the terminal shields of the curly overhairs with the main function of surface protection. With their segmented base they contribute also to thermic insulation. The protection they give may be threefold, against mechanical stress, against wind, and certainly against water. The functional interpretation of the shield structures, particularly developed in some shrews, has been a subject of discussion for several years.

## WATER REPELLENT HYPOTHESIS

APPELT (1973) was the first to state that the strongly H-shaped profile of the terminal shield in the water shrew permits the retention of an air layer in the fur to prevent wetting while it is submerged. This intuitive hypothesis was supported by the observation of HUTTERER & HÜRTER (1981). They compared shrews of increasing semiaquatic foraging behaviour, including *Sorex* (*S. bendirii*, *S. palustris*), *Neomys*, *Chimarrogale* and the most specialized *Nectogale*, and found a correlation with increasing groove complexity. VOGEL (1991) confirmed experimentally that in diving water shrews the fur's surface remains dry and that this small shrew is able to maintain a high body temperature even in icy water. Finally, KÖHLER (1991) demonstrated that only the triboelectrically charged fur of *Neomys* is water repellent.

From the descriptive study presented here, one new fact may contribute to this discussion: in *Megasorex* and *Notiosorex*, two genera of Soricinae, the H-shaped profile is completely lacking. These shrews invaded the hot and dry environment in southern North America with subdesertic conditions, a quite unique habitat for soricine shrews. In the Palaearctic and Palaeotropical region, this habitat is always occupied by crocidurine shrews. In this environment, water repellent structures are of limited importance. Therefore, we interpret the disappearance of the H-shaped profile in these soricine genera as a regression due to a released selective pressure.

### *Adaptation to desert environment*

The Turkestan desert shrew *Diplomesodon pulchellum* is the only shrew with obvious adaptations for living in a sandy habitat. The palm and digits of hands and feet are fringed on both sides with rather long, stiff, elastic hairs. The increasing surface area of the paws gives the animal support on loose sand (WALKER, 1975). The fur is particularly soft and fine, due to hairs of a smaller diameter and a shield of a rather circular cross section (Fig. 4). Some desert rodents, *Microdipodops* and *Dipodomys* (HOMAN & GENOWAYS 1978) and *Jaculus* (P.V. pers. obs.) have the same soft fur which possibly has a higher coefficient of thermic insulation.

### *Hair structure in Scutisorex*

The Armored shrew *Scutisorex* is an African giant shrew with a long fur. The well developed shield shows often modifications (Fig. 6) for which no plausible explanation is yet available. This big shrew is well known for other enigmatic structures, namely vertebrae with lateral and ventral interlocking spines and ten instead of five lumbar vertebrae, a condition unrecorded for any other mammal (HEIM DE BALSAC & LAMOTTE 1957, AHMED & KLIMA 1978).

### PHYLOGENETIC INTERPRETATION

According to the first publications (DZIURDZIK 1973; VOGEL & KÖPCHEN 1978), two principal types of hair shields were described for the two subfamilies: the smooth type of the Crocidurinae and the type with two deep, centrally ridged grooves of the Soricinae. Information from the strongly enlarged sample presented here shows that the situation is far more complex. On the one hand, two "exceptions" appear in the Soricinae: *Megasorex* and *Notiosorex*, which are characterised by the smooth hair type. On the other hand, new structural intermediate types were found within both subfamilies. The interpretation of the evolution of these structures are to be carried out in the light of the phylogeny of the Soricidae.

In order to determine the primitive hair type, two approaches are possible. The first deals with looking for a plesiomorphic type in an outgroup close to the Soricinae.

Therefore we analysed the hair of Talpidae (*Talpa europaea* and *Scalopus aquaticus*) and of Echinossoricinae (*Hylomys* sp.). In these taxa, the curly overhair is of the smooth type. But the shield has a round or oblong cross section (sensu TEERINK 1991), completely different from the quadriconcave cross section in shrews. A comparison is therefore not possible. Moreover, the smooth type in shrews is to be found in highly evolved taxa with reduced dentition (genus *Crocidura*). It is rather improbable that a plesiomorphic structure has been conserved.

A second approach entails the examination of primitive shrew taxa. *Myosorex* holds a very basic position within the Crocidurinae because it is the only recent shrew in which a fourth lower antemolar remains. According to REUMER (1987), who considers morphological features, it may even be possible that *Myosorex* is a survivor of the extinct subfamily Crocidosoricinae. Based on a biochemical comparison, MADDALENA & BRONNER (1992) confirm the distant position of *Myosorex*. Interpreted in this context, the hairs characterized by a deep groove without a ridge could well present the primitive type. Thus, the structures found in the other taxa have to be interpreted in the light of this hypothesis.

Within the Crocidurinae, the type with the deep groove exists in different genera and different continents, a fact in favour of a plesiomorphic interpretation. In *Feroculus* and *Crocidura miya*, both endemic to Sri Lanka, the H-shaped profile of the cross section was first shown by AMERASINGHE (1986). In the Malayan region, *Crocidura malyana* has conserved the same type with multiple notches, whereas *C. fuliginosa* shows the type of the strongly tiled, V-shaped notches, interpreted as a modification of the former type. In Africa, *Sylvisorex lunaris*, *Sylvisorex morio* and *Scutisorex somereni* show the same type.

The smooth type was found in *Sylvisorex megalura*, in all the species studied of the genus *Suncus* and in most species of the genus *Crocidura*, even in *C. luna*, which is, according to biochemical results, a particular primitive form (MADDALENA 1990). *Crocidura oliveri giffardi*, formerly known under the name of *Praesorex goliath*, is a giant shrew from Africa. It was separated in a particular genus for its size and long coarse fur. However, the hair structure is of the normal smooth type. The same holds true for *Paracrocidura schoutedeni*. The Turkestan Desert shrew, *Diplomesodon pulchellum*, has also curly overhairs of the smooth type. From skull morphology, loss of an upper antemolar and the fine fur, *Diplomesodon* seems to occupy a special position. However, biochemical results (MADDALENA 1990) showed that this shrew is an offshoot from the genus *Crocidura*.

In the Soricinae, the type with the deep groove and the central ridge is widely distributed in all three tribes: the Blarinini with *Cryptotis* and *Blarina*, the Neomyini with *Anourosorex*, *Chimarrogale*, *Neomys*, *Nectogale* and some species of the genus *Soriculus* and the Soricini with *Blarinella* and *Sorex*. If this structure is really an adaptation to improve the fur against wetting, then it is quite plausible that this structure is lacking in *Megasorex* and *Notiosorex*, which both live in semidesert conditions. The systematic status of *Megasorex* is a matter of much current discussion. Originally placed in the genus *Notiosorex*, it was separated by HIBBARD (1950), followed by REPENNING (1967), ARMSTRONG & JONES (1972 a, b) and

HUTTERER & *al.* (1982). According to GEORGE (1984), the two taxa are separated by a great genetic distance and seem to have a common root with *Neomys*. The identity of the hair structure of *Megasorex* and *Notiosorex*, which is different from all other Soricinae, may be interpreted as synapomorphy, attesting a common origin.

The hair type with a deep ridgeless groove, corresponding to our hypothetical plesiomorphic state, is found in only two soricine species, *Microsorex hoyi* and *Soriculus hypsibius*. According to the biochemical data of GEORGE (1984), *Microsorex*, which is considered as a subgenus of *Sorex* by DIERSING (1980), is clearly a branch within an American group of the genus *Sorex* and therefore certainly not a primitive taxon. Concerning *Soriculus hypsibius*, the situation is similar. The congeneric *Soriculus* (*Episoriculus*) *leucops* and *S.* (*Soriculus*) *nigrescens*, both subgenera with an upper dental formula of 1-5-3 (REPENNING 1967) have the typical soricine hair structure. *Soriculus* (*Chodsigoa*) *hypsibius* with a reduced upper dental formula of 1-4-3 is certainly a more specialized, derived form. This leads to the conclusion, that the hairs with deep ridgeless grooves in the Soricini are not conserved ancestral characters, but secondary simplifications.

*Podihik kura* is a particular case of controversial taxonomical interpretations. DERANIYAGALA (1958) described red teeth and mentioned a probable close relationship with *Soriculus* (Soricinae). For zoogeographical reasons, REPENNING (1967) had doubts about this interpretation, all the more that meanwhile the red colour of the teeth disappeared. Hill (in WALKER 1975) had the opportunity to study the paratype and stated that the specimen may be a misidentified *Suncus etruscus* with which they share the same tooth formula. The hair shield is of the smooth type, the typical structure in *Suncus* and several *Crocidura*. After combining evidence from the tooth formula and hair structures, we can confirm that *Podihik* is a junior synonym of *Suncus*.

#### FUNCTIONAL PLASTICITY VERSUS PHYLOGENETIC CONSTRAINTS

Hairs are complex protective structures. Like other morphological features, they have an important adaptative value, but possibilities for new adaptations may be constrained by the phylogenetic history. Therefore, analyses entirely limited on functional aspects do not permit to understand the complex situation. An example may illustrate this fact. Working with West African rodents, one may wonder about the function of harsh spiny fur of several murids living in completely different ecological conditions: the rock dwelling *Acomys* of semi-deserts, the digging *Uranomys* of savannas and *Lophuromys* of tropical rain forest. Recently, based on molar structures (DENYS & MICHAUD 1992) and DNA hybridization (CHEVET & *al.* 1993), it was shown that the three genera belong to the same evolutionary line. This phyletic relationship is probably an important fact in the interpretation of the harsh spiny fur of these taxa. However, if phylogeny may explain the distribution of a pattern, it does not give any clue for a functional explanation. This statement also derives from a study of hair morphology of the Heteromyidae by HOMAN & GENOWAYS (1978): several morphological structures are clearly related to certain

genera and therefore the expression of a shared apomorphy. But quite surprisingly, in certain species the structures deviate from the basic pattern and must be interpreted as special, but not yet explained functional adaptations.

The results on shrews show clearly the dualism between phylogenetic constraints and secondary adaptative modifications. Within the Soricinae, the deep ridged groove is a common conservative feature, shared between very different tribes. All these shrews are moreover characterized by an ecological preference for humid, temperate to cold habitats, which seems correlated with a very high basal metabolic rate (VOGEL 1980). Obviously, *Notiosorex* broke out from this evolutionary coadapted complex, invading a new adaptative zone, a very arid environment. This led on one hand to an unexpected lowered metabolic rate (LINDSTEDT 1980) and on the other hand to the loss of the typical soricine hair structure.

Within the Crocidurinae, the genus *Diplomesodon* presents a comparable situation. From biochemical genetics, this shrew should be placed in the genus *Crocidura* (MADDALENA 1990), but it deviates in many morphological features, justifying a separate genus. Here too, the invasion in a new adaptative zone led to new characters as responses to the new environment.

With the exception of the positive correlation of hair length and thermic insulation (SCHOLANDER 1955), up to now, functional interpretations of hair structures were guided by correlates with ecological factors, analogies and common sense, but rarely with experimental, e.g. physical tests. Real functional analyses are still lacking.

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