

Ultrastructure of the retina in the shrew (Insectivora: Soricidae)

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Abstract

Studied electron microscopically the retinæ of three central European members of the insectivore family Soricidae (*Sorex coronatus*, *Neomys fodiens*, *Crocidura russula*). All three species possess functioning retinæ with well developed photoreceptors as well as inner and outer synaptic layers. Rods and cones are present, but in *Crocidura* they are not easily distinguished. In this species and in *Neomys fodiens* a somewhat unusual organization of the receptors inner segment is encountered. In the inner plexiform layer, synapses of both, conventional and ribbon type, are observed in a ratio which is similar to that of other mammals. A slight degeneration seems to occur nonetheless, which affects the receptor cells, and which in *Crocidura* affects the inner plexiform layer as well.

Introduction

Behavioral studies have drawn attention to the orientation capacities of shrews and other insectivores. These studies and their interpretations (GOULD et al. 1964; GRÜNWALD 1969) have been accompanied by the assumption that shrews have reduced sight capacities. Authors experimenting with orientation in this group by means of whiskers or echolocation have been interested in maintaining that shrews are capable of light-dark-seeing only, but they have not given an anatomical or physiological basis for these proposals. Drawing chiefly on behavioral studies which suggest that shrews are able to discern light from darkness, it has been concluded that they cannot perform more complex functions. Furthermore, since their main sense of orientation appears to be based on senses other than vision, it has been concluded that their eyes do not function very well. In striking contrast to this, all investigations on soricid eyes which have been published thus far (VERRIER 1935; SCHWARZ 1935; KOLMER 1936; CEI 1946; SHARMA 1958; SOKOLOVA 1965; ROCHON-DUVIGNEAUD 1972; SATO 1977) state that they have a well developed retina. No case of degeneration has been encountered within the eight species that have been studied, and a reduction or a developmental arrest has been often explicitly denied. SHARMA (1958) after having described the *Suncus* retina, which does not appear to be degenerated, states that the sight in this shrew is very poor; however, he did not give any objective evidence to support this contention. Only ROCHON-DUVIGNEAUD (1972) indicated that the smallness of the eye gives rise to reduced acuity. This, however, does not necessarily follow (RODIECK 1973). There is disagreement among morphological investigators in relation to the types of photoreceptors that are present in shrew retinæ. Both rods and cones have been found in *Sorex araneus* (KOLMER 1936; ROCHON-DUVIGNEAUD 1972), *Crocidura leucodon* (SCHWARZ 1935) and *Neomys* (then *Crossopus*) *fodiens* (KOLMER 1936). According to the latter author and SCHWARZ (1935), *Crocidura russula* has rods and cones, while ROCHON-DUVIGNEAUD (1972) was unable to find these structures. No cones were found in *Suncus murinus* (SHARMA 1958). In *Crocidura suaveolens* (formerly *mimula*; VERRIER 1935) and the three species studied by CEI (1946) (*Blarina brevicauda*, *Chimarrogale himalayca*, *Anourosorex assamensis*) the photoreceptors have been reported

to represent an intermediate type showing characteristics of both rods and cones. However, it must be mentioned here that the description as well as the pictures of the retina of *C. suaveolens* contain typical rods, a fact which had been already noted by WALLS (1963). In *Sorex shinto*, SATO (1977) was not able to distinguish two kinds of receptor cells.

Since it appears that no electron microscopical investigation on the soricid retina has ever been published, the present study was undertaken in order to clarify some of these questions, and to provide an anatomical basis which might or might not correlate with the behavioral findings.

Materials and methods

Neomys fodiens, *Crocidura russula*, and *Sorex coronatus* have been investigated as representative of the three central european shrew genera. (The latter species had been separated from *S. araneus* as *S. gemellus* by OTT (1968). Recently, MEYLAN and HAUSSE (1978) presented compelling evidence that *S. gemellus* is identical to *S. coronatus* Millet, 1828. The objection that *gemellus* is a subspecies of *araneus* (CORBET 1978) does not fit to a biological concept of the species and will not be followed here).

Animals were trapped at different localities in Germany. After removal from the traps, eyes were dissected from the living animals and immersed immediately into cacodylate buffered glutaraldehyde. The retina was excised under the fixing solution, and after various fixation times, pieces of the retina fundus were rinsed in buffer, postfixed in osmic acid and prepared according to usual electron microscopical techniques. The ethanolic-phosphotungstic acid technique of BLOOM and AGHAJANIAN (1968) for the identification of synaptic junctions was used on a specimen of *Sorex araneus*.

Observations

Photoreceptor cells: All three species appear to possess both rods and cones (fig. 1a–c; outer segments of the retina were often separated from the rest of the cell in the course of the fixation process; fig. 5). However, the proportions of the two receptor cell types differ between the species, and in different regions of the retina. The highest relative number of cones is found in *Sorex coronatus*, attaining in certain regions a ratio of 2 rods: 1 cone, while in *Neomys* the ratios are between 3:1 and 13:1. The difficulty of identifying, and therefore counting, cones in *Crocidura russula* will be discussed in further sections of this publication.

Rods: Rod outer segments (fig. 2a) do not differ from those found in other vertebrates. There is always a ciliary stalk connecting it to the inner segment with a centrosome at its base.

The inner segments, which are always composed of an ellipsoid and a myoid, display species differences. In *Sorex coronatus* the ellipsoid is enlarged in its scleral part and densely filled with mitochondria (fig. 2b). In the fusiform inner segments of *Neomys* and *Crocidura* (fig. 2c, d; 1c) there is a mitochondria-free central region which is surrounded by a peripheral mantle of mitochondria. The central region contains numerous ribosomes and microtubules. The mitochondrial cristae often are arranged in a very orderly manner, similar to outer segment membrane stacks, particularly in *Crocidura*. The myoid contains ribosomes, endoplasmic reticulum (ER), some Golgi bodies, and numerous microtubules, which are arrayed parallel to the long axis of the cell. When it is stretched out, the inner segment becomes pear-shaped, a fact which has been already noted by SCHWARZ (1935). The inner segments normally are connected to neighbouring cells by desmosome-like junctions.

Rod nuclei are smaller than cone nuclei; they are generally spherical and dark. They are arranged in 4 (*S.c.*, *C.r.*) to 8 (*N.f.*) rows. The nuclear zone is connected to the receptor terminal by a narrow region containing bundles of microtubules. In the receptor terminals (fig. 3a–d) numerous electron dense or lucent synaptic vesicles are encountered with a diameter of about 40 nm.

Synaptic lamellae (ribbons) often are very short. The percentage distribution of synaptic ribbons in *Crocidura* (table 1) indicates that most ribbons in this species are smaller than 250 nm, while in *Sorex* most of the synaptic lamellae are between 50 and 350 nm. In either case,

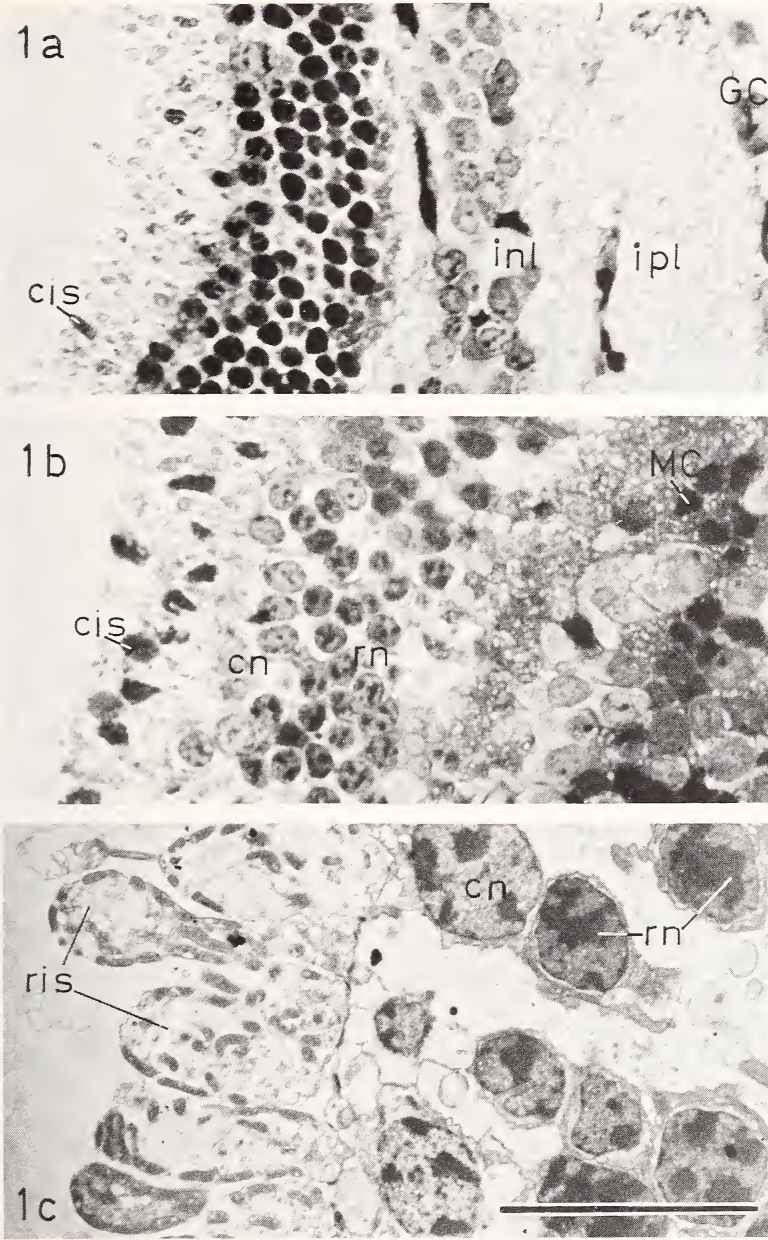


Fig. 1. a: *Sorex coronatus* semithin section of the whole retina. All nuclear and synaptic layers appear well developed; the retina is vascularized. Outer segments often are torn off or are not stained. A few cone inner segments (cis) can be discerned. The layer of the large ganglion cells is only one row thick. inl = inner nuclear layer; ipl = inner plexiform layer; GC = ganglion cell ($\times 1000$). – b: *Neomys fodiens* semithin section. Scleral half of the retina is shown. More cone inner segments are found than in the previous figure. Note the large number of Müller cells (MC). cn = cone nucleus; rn = rod nucleus. ($\times 1000$). – c: *Crocidura russula*, ultrathin section through receptor cell layer. An outer segment with ciliary stalk has been preserved in the upper left corner. Note unusual mitochondria arrangement in the ovoid or pear-shaped inner segments (ris). Cone (cn) and rod nuclei (rn) are shown. (Bar $10 \mu\text{m}$)

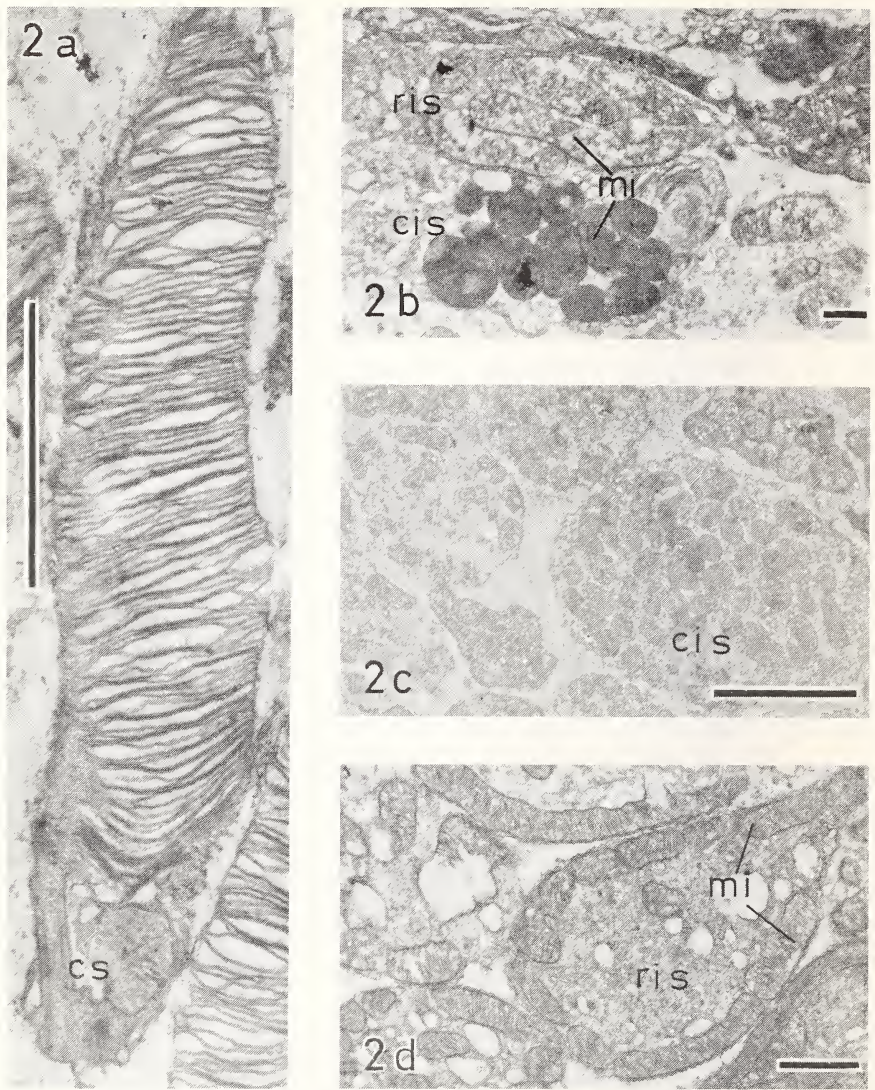


Fig. 2. Receptor inner and outer segments (bars $1\mu\text{m}$). a: *S.c.*, rod outer segment showing normally developed membrane stacks, connected to the inner segment by a ciliary stalk (cs). – b: *S.c.*, rod (ris) and cone (cis) inner segments showing light and dark mitochondria (mi) respectively. – c: *N.f.*, cross section through rod and cone inner segments. The cone inner segment (cis) is filled with mitochondria, though not densely, while in the rod inner segments the mitochondria form a mantle layer around a central core. – d: *C.r.*, oblique sections through rod inner segments (ris), showing the peripheral position of the mitochondria (mi)

the long ribbons (up to 1500 nm or more) which are regularly found in other species (GRÜN 1980) are entirely lacking in the shrew retinae.

Horizontal and bipolar cell dendritic invaginations which may be identified by their triad arrangement sometimes appear filled with electron dense material (fig. 3a). *Neomys* and particularly *Crociodura* seem to possess a reduced number of small, simple invaginations which frequently contain unusual amounts of vesicles or vacuoles.

Table 1

Size distribution of receptor terminal synaptic ribbons in *Crocidura* and *Sorex*

size classes (nm)	percentage of synaptic ribbons <i>Crocidura</i>	<i>Sorex</i>
50–150	28.6	16.6
150–250	37.2	33.2
250–350	11.5	33.2
350–450	14.3	8.3
450–550	2.8	—
550–650	4.3	—
650–750	—	8.3
750–850	1.4	—

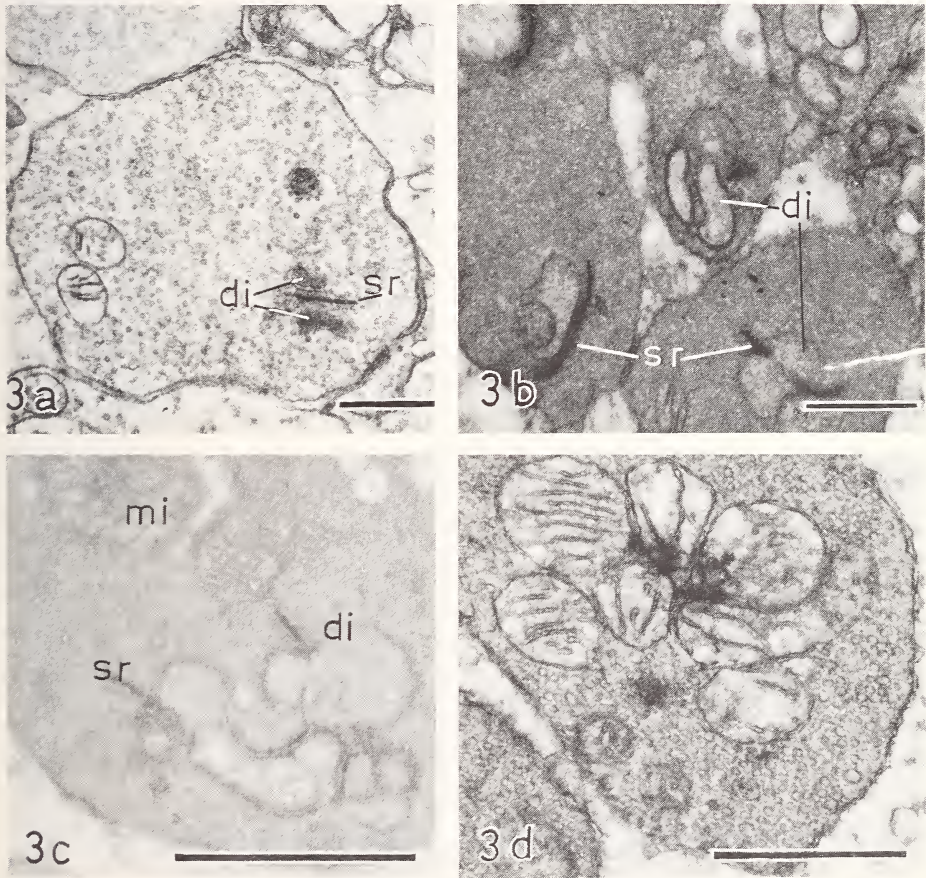


Fig. 3. Receptor cell terminals (bars 1 μ m). a: *S. c.*, cone (?) terminal, showing numerous synaptic vesicles, a synaptic ribbon (sr) and dendritic invaginations (di), filled with electron dense material. – b: *N. f.*, cone (?) terminal. Note the vesicular material in the dendritic invaginations. – c: *C. r.*, rod (?) terminal. Note the vesicles in the dendritic invaginations, the short ribbon, and the numerous mitochondria close to the synaptic site. – d: *N. f.*, rod (?) terminal, showing numerous mitochondria (mi)

It is a general feature of mammalian photoreceptor terminals to contain mitochondria; however, the soricids have a striking number of them, displaying up to 60% of the terminal area covered by these organelles which often are located very near to the synaptic sites.

The rod terminal of *Sorex* is rather small, irregularly shaped and dark. In *Neomys* and *Crociodura*, it is light and more spherically shaped.

Cones: The structure of cone outer segments does not differ from other vertebrate cones, with exception of the typical cone shape, which was hardly to be found. Most cone outer segments are similar in appearance to short rods.

The inner segment of *Sorex* cones is fusiform, and both the cytoplasm and mitochondria appear dark (fig. 2b), rendering a dark and conspicuous aspect to the inner segment as a whole (fig. 1a, b). In *Neomys* (fig. 2c) the dark mitochondria are dispersed loosely throughout the whole inner segment; these mitochondria are neither densely packed, nor do they form a mantle. The inner segment is cone shaped and more voluminous than in the rods. No myoid region had been encountered. In *Crociodura*, it is very difficult to distinguish two kinds of photoreceptors. While the presence of rods is not subject to any doubt, the existence of cones can only be inferred from the presence of two types of receptor cell nuclei (though the difference is not very conspicuous, in contrast to what is found in *Sorex* and *Neomys*), from the existence of short outer segments, and from some single receptors which display dark staining of cytoplasm and mitochondria and lack a myoid. The combination of these evidences speaks in favour of the presence of cones (see fig. 5). The terminals of these cones are wholly like that of rods.

Synaptic vesicle numbers or diameters do not reveal any differences between receptor types or species.

Outer plexiform layer: In *Sorex* and *Neomys*, this relatively thick layer is formed by well-developed neuronal processes containing neurotubules and neurofilaments. The outer plexiform layer of *Crociodura* is somewhat reduced in thickness and neuronal processes are not clearly identified as being axons or dendrites.

Horizontal cells: In all three species, these cells and their nuclei are dark and irregularly shaped.

Intermediate neurons: This layer, comprising the perikarya of the bipolar cells, amacrine cells, and the non-neural Müller cells, is composed of only a few cell rows. It is always thinner than the layer of receptor cells. The large spherical nuclei of the bipolar cells are surrounded by a rather broad cytoplasmic rim containing many free ribosomes, a small amount of ER, and large mitochondria. The amacrine cells are similar to them, but they appear somewhat darker and their cytoplasmic rim is even more expanded, containing ER and Golgi bodies. The chromatin is more dispersed than in bipolar cell nuclei. The highest proportion of amacrine cells is found in *Neomys*; in *Crociodura* it is low.

The nuclei of the glial Müller cells (fig. 1b) are found in the intermediate neuron layer; their processes protrude sclerad as well as into the inner plexiform layer. These processes and the perinuclear cytoplasm are very dark, which is at least partly due to the presence of glycogen granules. The darkly stained and irregularly shaped Müller cells are very conspicuous, and often are found to form regional clusters.

Inner plexiform layer: This layer is well developed in *Sorex* and *Neomys*, with numerous axons, axon terminals, and dendrites. Within the terminals, synaptic vesicles occur dispersed or clustered near to a synaptic junction (fig. 4a, b, c, e). Dense core vesicles are found regularly, though not in large numbers (fig. 4b, e). The specific structure of synaptic junctions as revealed by the E-PTA technique has been studied in *Sorex araneus*, a species closely related to *S. coronatus* (fig. 4f), and in *Crociodura*. In either species, a typical conventional synapse is found, which is composed of a presynaptic density, cleft densities and postsynaptic dense

projections. Bipolar cell terminals are identifiable by a typical synaptic ribbon (fig. 4b, c), normally connected to a synaptic dyad composed of an amacrine cell and a ganglion cell dendrite (DOWLING and BOYCOTT 1967). Figure 4d shows two ribbon junctions onto a common postsynaptic amacrine cell. Reciprocal synapses have been found (fig. 4c), but no serial synapses. Multivesicular bodies are very conspicuous enclosing 3 to 5 vesicles. Axons contain neurotubules, neurofilaments and axonal synapses. Dendrites are generally very large.

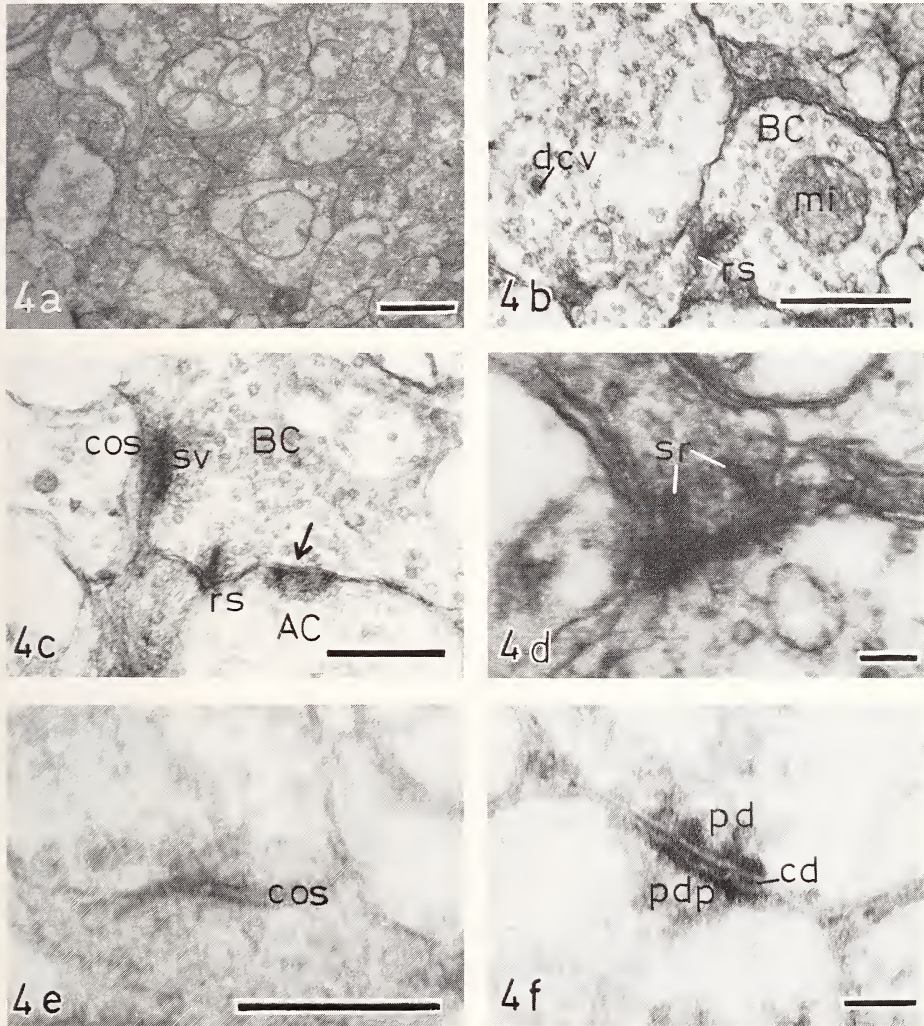


Fig. 4. Innerplexiform layer. a: C. r., Though the synapse layer appears by no means degenerated, there are relatively few synaptic junctions. Note the large mitochondria. (Bar $1\ \mu\text{m}$). – b: N. f., bipolar cell terminals (BC), showing dense core vesicles (dcv) and a ribbon synapse (rs). (Bar $0.5\ \mu\text{m}$). – c: S. c., bipolar cell terminal, making a conventional synapse (cos) and a ribbon synapse onto a ganglion cell dendrite as well as an amacrine cell (AC), from which it receives a reciprocal synapse (arrow). sv = synaptic vesicles (Bar $0.5\ \mu\text{m}$). – d: S. c., bipolar cell making two ribbon synapses onto a common postsynaptic cell. (Bar $0.1\ \mu\text{m}$). – e: C. r., conventional synapse (cos) with synaptic vesicle cluster in contact to the junction, and a dense core vesicle. (Bar $0.5\ \mu\text{m}$). – f: *Sorex araneus*, conventional synapse, showing pre-synaptic densities (pd), cleft densities (cd) and postsynaptic dense projections (pdp). (E-PTA technique; bar $0.1\ \mu\text{m}$)

Table 2

Number of synaptic junctions and ratio of conventional to ribbon junction in the inner plexiform layer of the species studied

	total	conventional	ribbon	conventional ribbon
<i>Sorex coronatus</i>	1.75	1.30	0.45	2.9
<i>Neomys fodiens</i>	2.18	1.80	0.40	4.4
<i>Crocidura russula</i>	2.15	1.50	0.70	2.3

Junctions have been counted in the electron microscope over defined areas and computed to $100\mu\text{m}^2$

In *Crocidura*, the ratio of terminals to dendrites is low; more terminals with few or no synaptic vesicles are found in this species than in the other two species. The number of mitochondria in axon terminals is rather high, similar to values that have been found in receptor terminals.

Table 2 indicates the number of synaptic junctions as computed for an area of $100\mu\text{m}^2$. All species, particularly *Sorex coronatus*, are characterized by a low total number of synapses as compared to other vertebrates. *Crocidura russula* displays a high ratio of ribbon (= bipolar cell) synapses while *Neomys*, on the other hand, has the highest ratio of conventional (= amacrine cell) to ribbon synapses.

Ganglion cells: These cells possess the largest perikarya with many ribosomes, abundant ER, mitochondria, and Golgi bodies. In all three species, the ganglion cells appear to be highly metabolically active. The size of their perikarya together with the fact that they form only one row (fig. 1a) results in a very high ratio of receptor cells to ganglion cells (10 or 12 : 1 in *Sorex* and *Crocidura*, and up to 13 : 1 in *Neomys*).

Discussion

The eyes of the three species of central European shrews studied here have well-developed, functioning retinæ. Inner as well as outer photoreceptor segments do not show any reductions, as they have been demonstrated, for instance, in cave dwelling animals (BESHARSE and BRANDON 1974). All the structures known to be involved in light reception and impulse transmission have been found. Rods are capable of active stretching movement. The synaptic layers show all features of an active neural tissue. While the number of synaptic junctions in the soricid inner plexiform layer is low in comparison with other vertebrates, the ratio of conventional to ribbon synapses fits well into other mammalian data (DOWLING 1968; DUBIN 1970; DUBIN and TURNER 1977), suggesting a normal anatomical organization of the inner plexiform layer. These results confirm the conclusions of SATO (1977), who indicated that the visual system of the soricids is well developed in comparison to that of the fossorial moles.

However, there are signs of slight degenerations, and the degrees of these degenerative changes characterize the three shrew species covered in this survey. In *Sorex*, the principal deviations from the organization of the normal vertebrate retina mainly concern the dendritic invaginations; in *Neomys*, they revolve around the number of inner segment mitochondria, the formation of dendritic invaginations and the number of cones in relation to rods (if one regards the duplex retina as being the original soricid type). *Crocidura* displays additional reductions in the number of intermediate neurons (apparently reducing the number of Müller cells) and in the differentiation of the synaptic layers.

The high proportion of ribbon synapses in *Crocidura russula* corresponds to the reduced

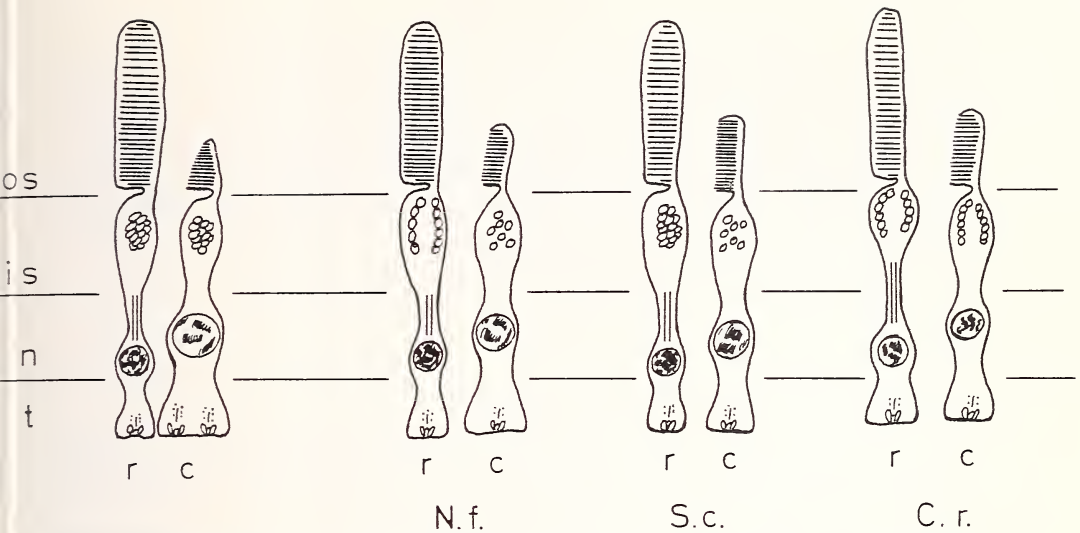


Fig. 5. Diagrammatic presentation of rods (r) and cones (c) of *Neomys fodiens* (N.f.), *Sorex coronatus* (S.c.), and *Crocidura russula* (C.r.), in comparison to typical vertebrate visual cells (left pair). The "cone" of C.r. is a hypothetical compilation of several aspects found among the visual cells of this species. Essential differences are found in the structure of the inner segments (is), mainly in the arrangement of the mitochondria, and in the outer segments (os) of the cones. n = nuclear region, including myoids, t = terminal region

number of amacrine cells in this species. Since these cells are mainly involved in lateral connections, the *Crocidura* retina seems to be characterized by a more direct transmission from bipolar to ganglion cells, while *Sorex* – and particularly *Neomys* – might be assumed to contain a higher degree of information processing within the retina. This would certainly result in different visual properties of the retinæ (RODIECK 1973).

The soricid retina is a duplex retina which, however, contains a low portion of cones and a reduced number of interneurons and ganglion cells. It has been suggested that these features are characteristic of animals with nocturnal or dawn activity (WALLS 1963). The eyes of these animals are characterized by the ability of rods to migrate, a spherical lens, and a tubular eye shape. These characteristics fit to all three shrews species examined in this survey.

The nature of the photoreceptors in this group has been a matter of some controversy. As has been stated in the introductory section, ROCHON-DUVIGNEAUD (1972) only found rods, SCHWARZ (1935) and KOLMER (1936) reported rods and cones, while VERRIER (1935) only observed cones which seemed to look like rods, which caused her to assume the existence of a single intermediate type of photoreceptor cell. This study presents sufficient, though not compelling, evidence for the existence of two types of receptors, one of which is a rod, while the other one is not easily identified and might reasonably be called a rod-like cone (fig. 5).

This designation would justify the published positions of the authors cited above.

As far as can be judged from an investigation limited to morphological considerations, *Crocidura* seems to have the least developed retina. *Neomys* should be regarded as having characteristics which lie intermediate between the two other species; its high number of large amacrine cells may be an adaptation to aquatic life.

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Zusammenfassung

Ultrastruktur der Retina von Spitzmäusen (Insectivora, Soricidae)

Verhalten und Ökologie legten den Schluß auf eine reduzierte Sehfähigkeit oder mangelnden Gebrauch der Augen nahe. Da bisherige lichtmikroskopische Untersuchungen keine Hinweise darauf erbrachten, wurde an je einem Vertreter der drei einheimischen Gattungen die Ultrastruktur der Retina untersucht. *Sorex coronatus*, *Crocidura russula* und *Neomys fodiens* besitzen vollständig entwickelte Retinae. Die Rezeptorzellen sind in Zapfen und Stäbchen differenziert, obwohl bei *Crocidura* diese Unterscheidung nicht sehr deutlich ist. Die innere plexiforme Schicht zeigt einen typischen Aufbau und enthält konventionelle und „ribbon“-Synapsen. Das Verhältnis dieser Synapsentypen entspricht dem von anderen Säugern bekannten. Leichte Degenerationserscheinungen finden sich in den Rezeptorzellen aller drei Arten, bei *Crocidura* auch in der inneren Synapsenschicht.

Es wird angenommen, daß alle drei Arten voll funktionsfähige Augen haben.

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