

## Sensory cells in the head skin of pond snails

### Fine structure of sensory endings

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**Summary.** Several types of receptor endings were identified with scanning electron microscopy and silver-impregnation techniques in the skin of the tentacles, lips, dorsal surface of the head and mouth region of the pond snails *Lymnaea stagnalis* and *Vivipara viviparus*. Sensory endings at the tips of dendrites of primary receptor neurones, scattered below the epithelium, differ in structure, i.e., the endings exposed to the surface of the skin possess different proportions of cilia and microvilli, which vary in number, length, and packing. Type-1 endings have microvilli and a few (1–5) cilia, 5–12  $\mu\text{m}$  in length. Type-2 endings have abundant (20–40), interwoven long (9–12  $\mu\text{m}$ ) cilia and random microvilli. Type-3 endings show typical packing of 10–25 cilia in the form of bundles or brushes. They may be composed either of long (9–18  $\mu\text{m}$ ) or short (2–7  $\mu\text{m}$ ) cilia, or of both long and short ones. Microvilli here are absent. Type-4 endings have only microvilli. Two other types of skin receptors do not extend their sensory endings to the surface and can be identified only in silver-stained preparations. Type-5 endings are branching dendrites of skin receptors cells that terminate among epithelial cells. In type-6, the sensory endings also terminate among epithelial cells but their cell bodies are located outside of the skin. In both species all skin regions examined possess the receptors of all six types differing only in their relative proportion. Possible functional roles of different receptors are discussed.

**Key words:** Skin receptors – Sensory endings – *Lymnaea stagnalis* – *Vivipara viviparus* – Head

The sensory systems of gastropods have been extensively examined physiologically (Jahan-Parvar 1972; Janse 1974; Salanki and Truong van Bay 1975; Lever 1977; Alkon et al. 1978; Grossman et al. 1979; Sokolov and Kovalev 1979). There is convincing physiological and behavioral evidence that not only specific sensory

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organs but the whole surface of the snail body is sensitive to various stimuli, especially to chemical and mechanical ones (Kiechebusch 1953; Wolter 1967; Janse 1974). Numerous scattered sensory cells have been revealed morphologically in the skin of gastropods. They form considerable clusters in the tentacles, lips, regions of the mouth, and pneumphostom, or the edge of the mantle (Hanström 1925; Schultz 1938; Rogers 1971; Zylstra 1972; Zaitseva 1980). At the same time attempts to relate morphological and functional properties of sensory cells have been restricted to sensory organs: statocysts, osphradium, tips of tentacles (Welsh and Storch 1969; Benjamin and Peat 1971; Rogers 1971; McKee and Wiederhold 1974; Zaitseva et al. 1978, 1980; Sokolov et al. 1980).

The elucidation of chemo- and mechanoreceptive systems requires information on the structure, variety, abundance, and distribution of receptors in the surface epithelium. However, the available data are not sufficient, since most of the studies consider the regions enriched with skin receptors, i.e., the tips of tentacles (Zylstra 1972; Wright 1974; Wondrack 1975), and rarely concern the scattered receptors (Crisp 1971; Hernadi and Benedeczki 1978; Zaitseva 1980).

Current classifications of skin receptors are highly arbitrary since they are based exclusively on the data of transmission electron microscopy and this technique provides only a tentative estimation of the number and distribution of cilia and microvilli and thus of the sensory endings. These classifications agree in one respect: there are sensory endings with cilia and microvilli, and others with microvilli (Crisp 1971; Zylstra 1972; Wright 1974; Wondrack 1975; Hernadi and Benedeczki 1978). Scanning electron microscopy (SEM) can directly reveal the structure of sensory endings and their distribution (Graziadei and Tucker 1970; Budelman et al. 1973; McKee and Weederhold 1974; Gwyneth and Salenddin 1978; Zaitseva et al. 1978, 1980). We used this technique for the study of the receptor endings in the head skin of the pond snails *Lymnaea stagnalis* (Pulmonata) and *Vivipara viviparus* (Prosobranchia).

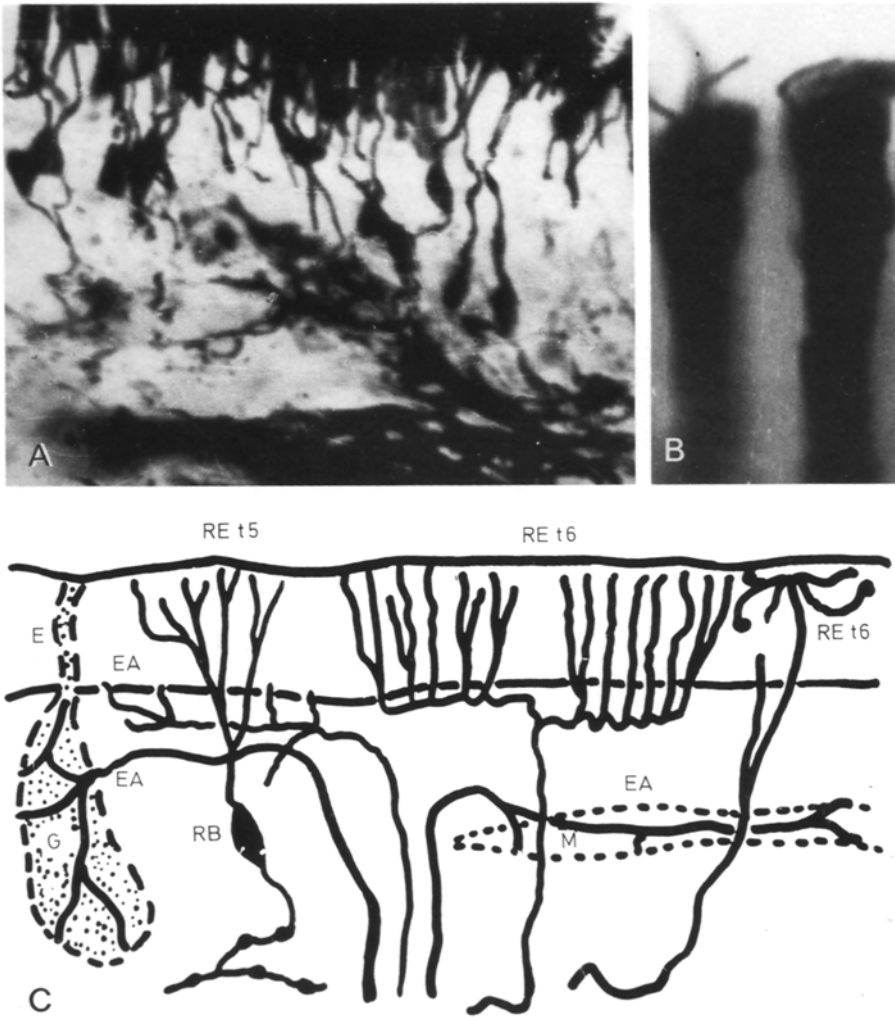
## Materials and methods

The tentacles, lips and pieces of skin from the dorsal surface and mouth region of the head of adults of *L. stagnalis* and *V. viviparus* were studied with light and scanning electron microscopy. For the examination of the general structure of the skin 1 µm araldite sections stained with toluidine blue-azure II-basic fuchsin were used. General topography and distribution of sensory cells were examined by means of the Golgi silver-impregnation technique.

SEM samples were fixed in 2% glutaraldehyde in physiological solution. For removal of the surface mucus pieces of tissue were incubated overnight in 16% glycerol and rinsed thoroughly in 20% ethanol. Following postfixation in 1% OsO<sub>4</sub> in physiological solution or phosphate buffer, pH 7.4, and partial dehydration in ethanols, the samples were quickly frozen in cooled propane at -180° and freeze-dried in vacuum (pressure 10<sup>-5</sup> torr) at -70°. The dried samples were mounted on stubs, coated in vacuum with carbon and silver, and examined with a JSM-U3 scanning electron microscope. Ciliary movements in living preparations were observed with phase contrast microscopy.

## Results

In silver-stained preparations primary bipolar sensory neurones are visible in the connective tissue beneath the layer of epithelial cells. Their dendrites pass to the surface between epithelial cells, where they form sensory endings. Axons of receptor neurones form nerve bundles going towards the CNS (Fig. 1A).



**Fig. 1A–C.** Golgi preparations of skin in tentacles of *L. stagnalis*. **A** Arrangement of subepithelial sensory cells; grouping of dendrites and axons in bundles.  $\times 700$ . **B** Two sensory endings with different structure at surface of epithelium.  $\times 3,500$ . **C** Schematic drawing of variety of nerve fibers in skin of head. *E* epithelium, *M* muscle, *G* mucous gland, *EA* efferent axons, *RE t5*, *RE t6* receptor endings of types 5 or 6, respectively, *RB* cell body of receptor

Sensory cells are especially abundant at the tips and lateral and ventral surfaces of tentacles, and at the ventral surface and the front edge of the lips. In these regions, sensory neurones are often grouped in clusters of 10–30 cells. On the dorsal surface of the head only scattered receptors can be observed. Regions around the eyes at the tentacles of both species, as well as the central parts of the ventral surfaces of the lips, where the lip glands are located, are practically free of skin receptors (Fig. 2).

The main type of skin receptors is a neurone with one dendrite forming a single sensory ending on the surface (Fig. 1A). Although it is rather difficult to distinguish

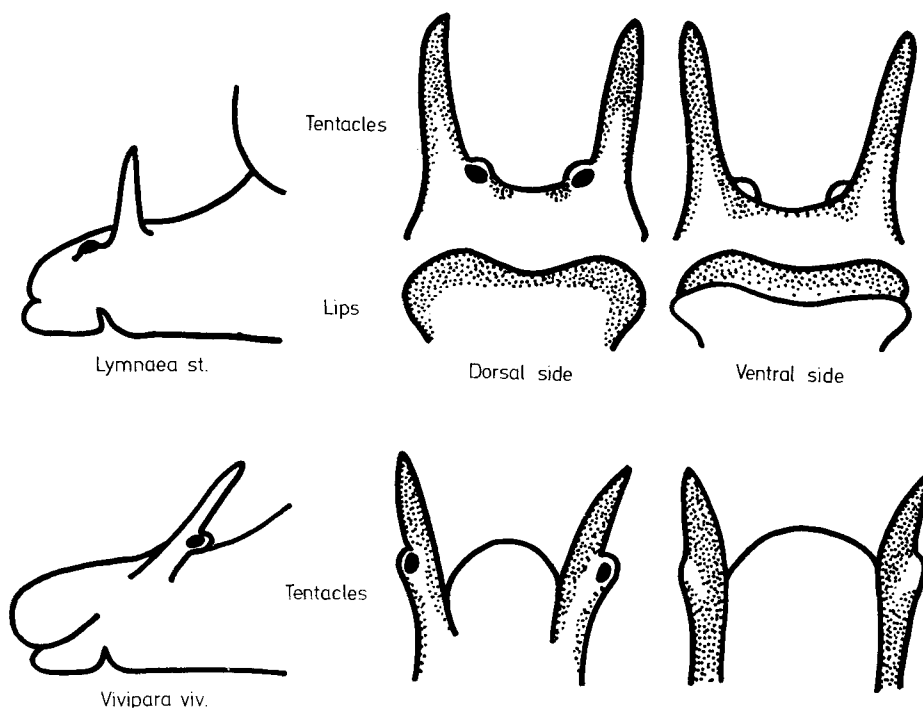


Fig. 2. Diagrams of distribution of rich sensory regions in head skin of *L. stagnalis* and *V. viviparus*

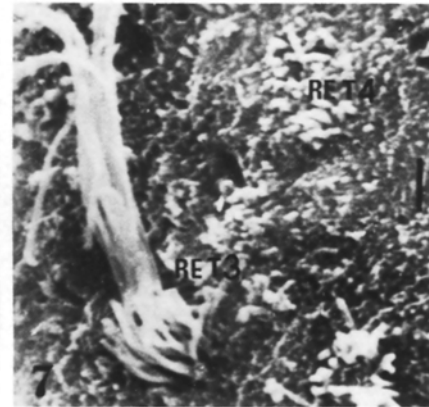
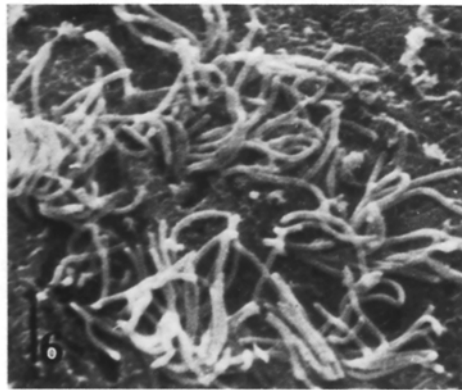
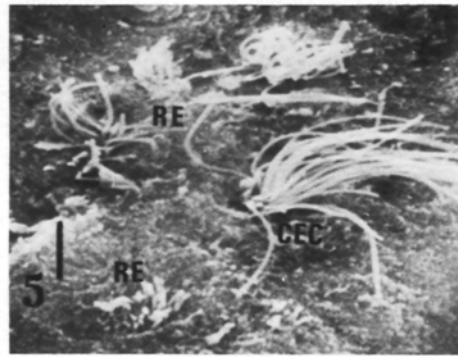
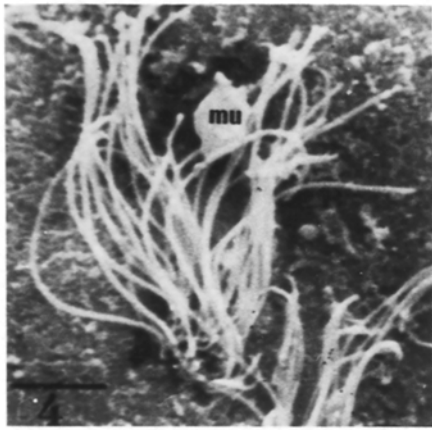
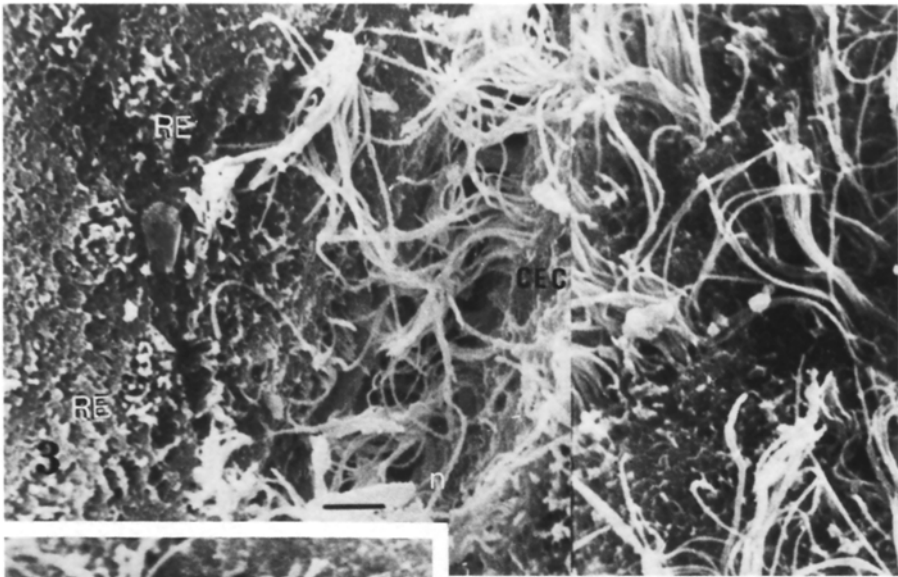
fine details in the structure of sensory endings with silver-staining, it is evident that they are not uniform (Fig. 1 B). Tentatively they may be divided into endings without, with a few, or with numerous cilia.

Sensory neurones with branching dendrites are rare in the skin. The characteristic feature of these receptors is that the branches of their dendrites reach to but do not extend beyond the epithelial surface (Fig. 1 C).

Golgi-stained preparations reveal also the fine branches of nerve fibers that seem to have no connections with cell bodies of receptor neurones in the skin. Those terminating on mucus glands or the base of epithelial cells apparently belong to motor neurones located in the CNS (Fig. 1 C). Processes ramifying near the surface, without recognizable cell bodies (Fig. 1 C), seem to represent free nerve endings of central sensory neurones.

SEM reveals the distribution of sensory endings among epithelial cell. Sensory endings are usually surrounded by epithelial cells with a microvillar surface, that prevail in the skin of these molluscs. Ciliated epithelial cells, scattered between microvillar ones, are most numerous in areas of concentration of skin receptors (Fig. 2), where they form ridges (Fig. 3). Numerous (40–60) long (up to 20  $\mu\text{m}$ ) cilia of these cells (Fig. 4) are mobile, and their beating favours the exchange of liquid and mucus at the skin surface and accordingly the perception of chemical stimuli.

It is rather difficult to distinguish the sensory endings with cilia from the adjacent epithelial ciliated cells in the regions of their high density (Fig. 3).



**Fig. 3.** Example of distribution of ciliated epithelial cells and receptor endings; ridge of epithelial ciliated cells, at left uniform endings of type 4 receptors. Scale: 4  $\mu$ m

**Fig. 4.** Ciliated epithelial cell. Scale: 4  $\mu$ m

**Fig. 5.** Ganglion-like grouping of different receptors surrounded by "free" space, note one ciliated epithelial cell in this group. Scale: 4  $\mu$ m

**Fig. 6.** Close grouping of similar endings of type 3 receptors at edge of lip. Scale: 2  $\mu$ m

**Fig. 7.** Group of heterogeneous endings at surface of tentacle. Scale 2  $\mu$ m zu Figs. 3–7: RE receptor ending, CEC ciliated epithelial cell, mu droplet of mucus

Therefore, we concentrated on separate sensory endings while analyzing their variety. The main types of sensory endings extending to the surface of the skin are common to both species.

Type I receptors possess a few (1–5) wriggling cilia that extend from the central part of the dendrite tip (Fig. 8A). The remaining area of the ending (1.5–3.5  $\mu\text{m}$  in diameter) is occupied by rather long microvilli. The length of the cilia varies from 5 to 12  $\mu\text{m}$ .

A typical feature of type 2 endings is the presence of numerous (20–40) long (9–12  $\mu\text{m}$ ) interwoven cilia spreading along the surface (Fig. 8B). The diameter of these endings is 2.5–3.5  $\mu\text{m}$  but the bases of cilia are concentrated in the small central pit. Microvilli show a random distribution.

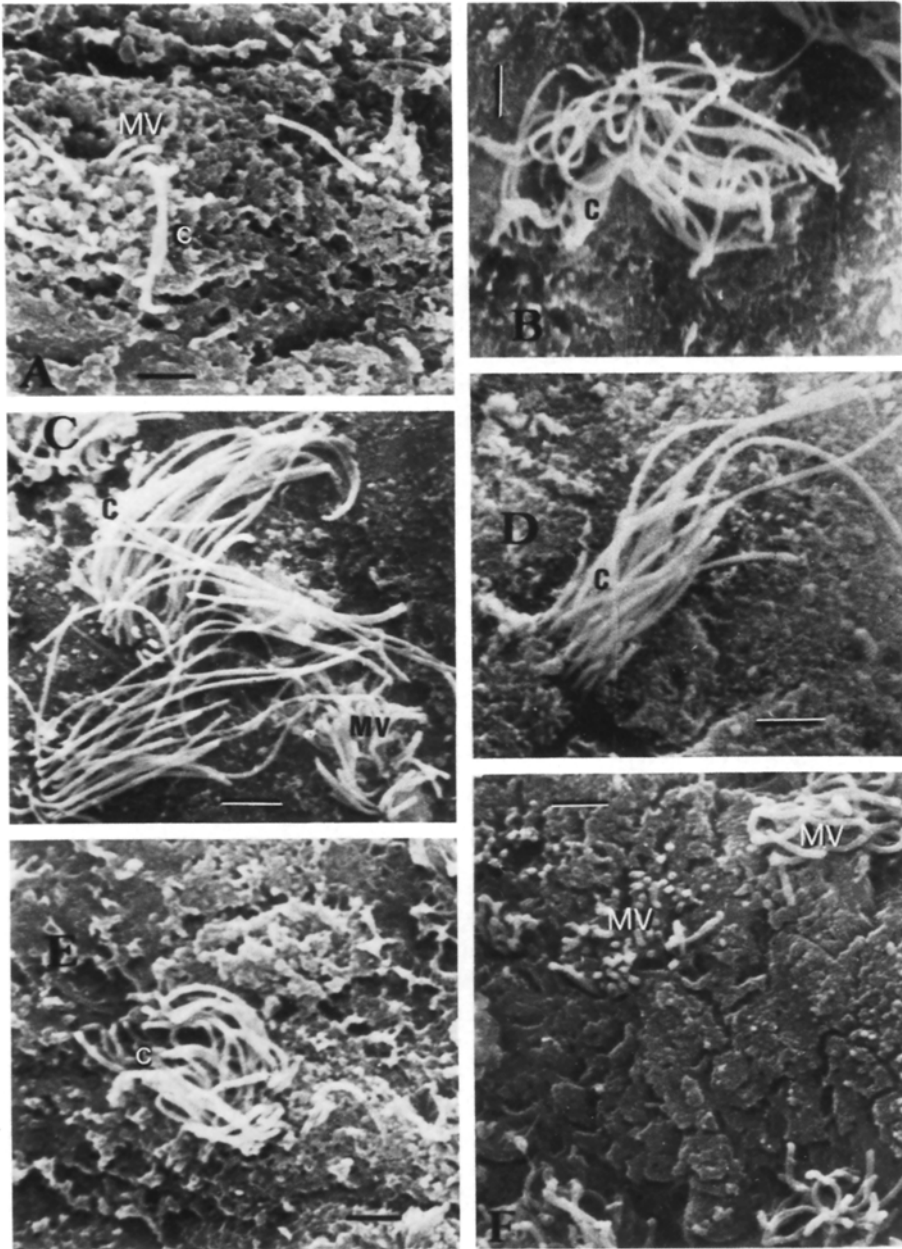
Type 3 receptors can be recognized according to a typical pattern of ciliary packing. Cilia arise from the whole surface of the ending and are directed upward. The endings of this group may have cilia of different length: long (9–12  $\mu\text{m}$ ), short (2–6  $\mu\text{m}$ ) or both kinds together. Accordingly, the shape of the endings resembles the bundle with the base of 1.5–2.5  $\mu\text{m}$ , when they are formed by 8–20 long or mixed cilia (Fig. 8C), or the brush 1–2.5  $\mu\text{m}$  in diameter composed of 6–12 short ones (Fig. 8E). Perhaps the sensory endings described as variants of the third type (Fig. 8) are in fact different kinds of receptors.

As type 4 we classify the receptors whose sensory endings have at the surface only microvilli (Fig. 8F). The length of microvilli varies, sometimes even in the same ending, from very short (0.5  $\mu\text{m}$ ) to rather long (up to 3.5  $\mu\text{m}$ ). The regular arrangement of microvilli in the form of a central rosette or as a peripheral border was more often observed in the case of *V. viviparus*. These endings may be small (1  $\mu\text{m}$ ) or large (up to 2.5  $\mu\text{m}$ ) in diameter.

Phase contrast examination of living skin preparations reveals, besides the regular beat of the ciliated epithelial cells, movements of individual cilia and of groups of cilia spreading along the surface. Thus, it seems likely that cilia at the surface of some sensory endings, namely of types 1 and 2, are mobile. It is difficult to draw definite conclusions about the mobility of cilia in endings of the third type as they are too similar to the epithelial ciliated cells.

Sensory endings of all types were observed in both species in all regions of the head. Therefore, it is possible to report only on the preferential localization of definite types. At the front edge of the lips in both molluscs, type 3 receptors with short cilia are pre dominant and closely grouped (Fig. 6). Type 3 receptors with long cilia are typical of the dorsal surface of the head where sensory endings are sparsely scattered. Endings of types 1 and 4 are abundant in the tentacles, the lips and the mouth region while type 2 endings frequent in tentacles of *L. stagnalis* are random in *V. viviparus*. We rarely observed in *V. viviparus* endings of the third type with mixed cilia (Fig. 8D) of the kind that were found in the lips and mouth region of *L. stagnalis*.

The number and density of sensory endings vary greatly in different regions. In rich sensory regions of the head, i.e., at the tip of tentacles or at the edges of lips the density of skin receptors may be up to  $5 \times 10^5$  per  $1 \text{ mm}^2$ . Sensory endings are usually separated from each other by microvillar epithelial cells (Figs. 5, 8), and only in the regions of their highest concentration do these endings lie side by side (Fig. 6).



**Fig. 8A-F.** Types of sensory endings of skin receptors in head. **A** Two endings of type I. **B** Type 2 ending. **C** Two endings of type 3 with long cilia, and type 4 endings with long microvilli. **D** Type 3 ending with mixed cilia. Note microvillous surface of epithelial cells that in other micrographs is masked by residual surface mucus. **E** Type 3 ending with short cilia. **F** Type 4 endings with long microvilli, top and bottom, and short microvilli, middle. Scale in all cases 2  $\mu\text{m}$ . *C* cilia, *MV* microvilli

Sometimes sizable areas are occupied by receptors of the same (usually third or fourth) type (Figs. 3, 6) but more frequently adjacent sensory endings are of different types (Figs. 5, 7, 8C).

Cell bodies of skin receptors are often grouped in clusters and their dendrites extend to the surface as a common bundle (Fig. 1A). At the skin surface the clusters of receptors are expressed as rather compact groups of sensory endings surrounded by "free space", the areas of microvillar epithelial cells (Fig. 5).

## Discussion

In its main features the organization of the sensory system in the head skin of *L. stagnalis* and *V. viviparus* is the same, and common for gastropods. Receptors are scattered over the whole surface of the head. Similar receptors were found in the skin at the front edge of the foot of *L. stagnalis* (Zaitseva 1980). The tips of tentacles or the edges of lips, the regions specialized for the perception of sensory signals, differ from the rest of the skin only by the concentration of receptors. In these areas of the head the skin receptors are closely grouped while as a rule they lie individually or as small clusters.

The clusters of skin receptors are apparently a kind of subepithelial ganglion repeatedly described for gastropods (Zylstra 1972; Zaitseva 1980). Such grouping of receptors facilitates the integration of sensory information. It is interesting that receptors of different types may be joined in one cluster (Fig. 5).

The essential feature in the organization of this varied sensory system is the presence of receptors in all its regions. SEM data help to account for the results of behavioral and physiological studies that demonstrate the polymodal sensitivity of the whole head of gastropods (Kiechebusch 1958; Wolter 1967; Salanki and Truong van Bay 1977).

The total number of different skin receptors identified, is at least six. If we take into account that receptors of the third type have pronounced variations, i.e., possess long, short, and mixed cilia (Fig. 8C, D, E), and the fourth type combines the receptors with long and short microvilli and their different arrangement (Fig. 8F), the number of types of receptors in the skin of the head should rise to nine. It is clear that the abundance of different receptors can provide perception and discrimination of various sensory stimuli by the surface of the head.

Receptors of the skin were previously studied with SEM in a single case, in the mantle of *Helisoma duryi* (Gwyneth and Saleuddin 1978), where principally the same types of sensory endings were observed. It is rather difficult to compare directly our classification of the skin receptors and those based on the data of transmission electron microscopy since different criteria were used. Ultrastructural descriptions, as a rule, state only the presence of sensory endings with cilia and microvilli and with microvilli only (Crisp 1971; Navoni 1973; Hernadi and Benedeczki 1978). More detailed studies on the tentacles or ommatophore revealed 4–6 types of sensory endings (Zylstra 1972; Wright 1974; Wondrack 1975) which in their main features are similar to those described here.

It should be noted that great similarity in the structure of the skin receptors and their arrangement is apparently peculiar for gastropods. Practically identical types of skin receptors were identified in the head of the pond snails *L. stagnalis* and *V.*



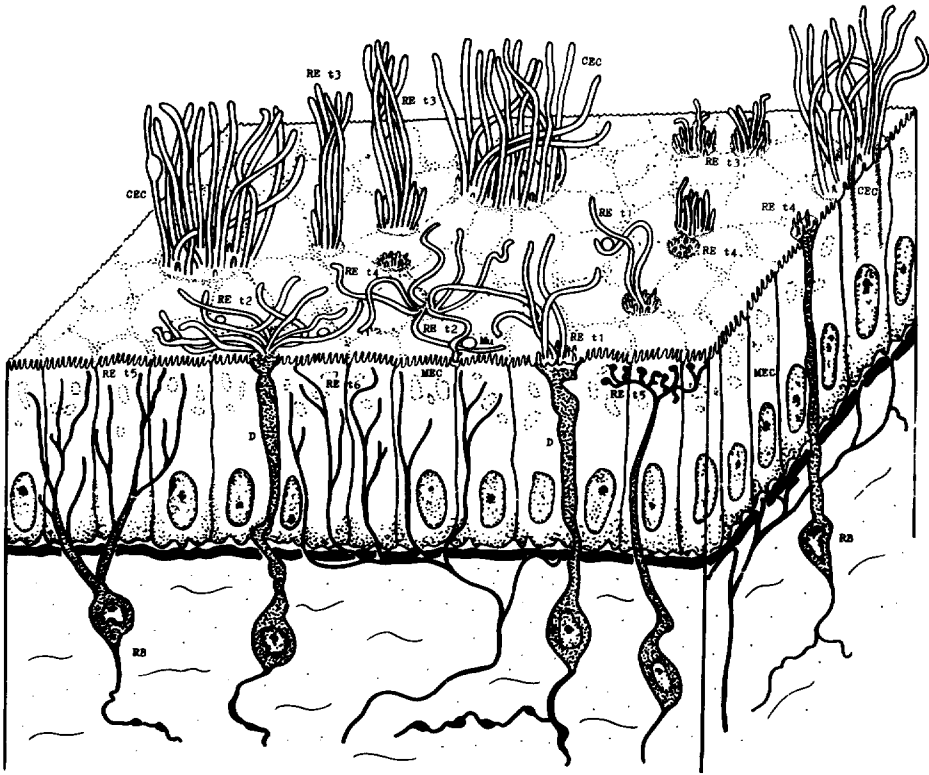


Fig. 9. Diagram of epithelium rich in sensory region on tentacles of *L. stagnalis* showing different types of receptors. *RE t1*, *RE t2*, *RE t3*, *RE t4*, *RE t5*, *RE t6*, corresponding types of sensory endings; *RB* cell body of receptor, *D* dendrite of receptor, *MEC* microvillous epithelial cell, *CEC* ciliated epithelial cell, *Mu* droplet of mucus

*viviparus*, and of the terrestrial snail *Helix vulgaris* (Zaitseva 1980) with silver impregnation.

It is difficult to offer a definitive conclusion on the functional specialization of different skin receptors when data are available only on their morphological features. Some authors consider the ciliated sensory endings as chemoreceptive and those with microvillar surface as mechanoreceptive (Navoni 1973) while others suppose that both chemo- and mechanoreceptors may have cilia (Crisp 1971). Most authors agree that sensory endings with microvilli and a few cilia, similar to our types 1 and 4, belong to the chemoreceptors (Zylstra 1972; Wright 1974; Wondrack 1975) since receptors of similar structure were found in the specialized chemosensitive organs of molluscs (Kohn 1961; Welsh and Storch 1969). This approach, based on the comparison of the structure of sensory endings from skin and from specialized organs, seems to be valid.

We are prone to think that perception of various chemical signals, i.e., distant or olfactory, versus contact or gustatory, by the skin of gastropods is realized by microvillar receptors of the fourth type and by receptors with mobile cilia of the first and second types. Receptors of type 2 are abundant in the skin of the tentacles and

the lips and are similar in structure to the chemoreceptors of the osphradium (Sokolov et al. 1980).

Receptors of the third type with standing bundles of cilia are apparently mechanosensitive. They prevail at the edges of lips and at the dorsal surface of the head as well as in the skin of the foot (Zaitseva 1980). Long roots of cilia, typical of tactile receptors, were found in similar sensory endings in the tips of tentacles (Zylstra 1972; Wondrack 1975).

Sensory endings terminating inside the epithelium may also perform a tactile function. Skin receptors with branching dendrites, similar to those described as type 5, were repeatedly found in the tentacles of snails (Hanström 1925; Schulz 1938; Rogers 1971); they are common in invertebrates. It was established electrophysiologically that the main part of the primary mechanoreceptive neurones with vast receptive fields in the skin of *L. stagnalis* are located in the CNS (Janse 1974). It seems reasonable to assume that free sensory endings of the central sensory neurones, i.e., receptors of the sixth type, are just this type of tactile receptors in the skin. Similar tactile receptor neurones located in the central ganglia were also described in *Aplysia* (Bailey et al. 1979; Rosen et al. 1980) and in a leech (Nicholson and Baylor 1968).

Besides the tactile, the olfactory, and the gustatory sensitivities, the skin of the head of gastropods is photosensitive (Stoll and Bijnsma 1973). Zylstra (1972), proceeding from the comparison with the optic receptors of molluscs, came to the conclusion that light "off" receptors of skin may have sensory endings with microvilli or a few cilia. Some variants of receptors of the first or the fourth types may be associated with this kind of skin sensitivity.

If there exist non-specialised receptors for pain and temperature they may represent some variants of type 6, similarly to receptors of this modality in higher animals.

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