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Structural properties of bimodal chemo- and mechanosensitive setae on the pereiopod chelae of the crayfish, *Austropotamobius torrentium**

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Summary. The setae on the inner edges of the pereiopod chelae of *Austropotamobius torrentium* contain eight receptor-cell endings. Two units are mechanosensitive, four react only to amino acids, to amines, or to pyridines. The remaining two units are most probably also chemoreceptors.

All sensory cells possess long dendritic outer segments that extend to the tip of the seta, where a small pore is found. Structurally, two units differ from the other six by having (1) densely packed microtubules in their dendritic outer segments, (2) dense A-tubules with arms in their ciliary segments, (3) a well-developed ciliary rootlet in their dendritic inner segments, and (4) desmosomal junctions between the dendritic inner segment and the inner enveloping cell, which contains a scolopale. These features are probably general characteristics of crustacean mechanoreceptors.

The mechanoreceptors respond only to strong mechanical stimuli. This corresponds to the structural features of the setae, which lack specialized socket structures. Deflection of the setae may lead to longitudinal stress to the dendrites; the latter seem to be attached proximally to the inner enveloping cell and distally to the cuticle. Thus, the mechanoreceptor structure suggests a function analogous to scolopidial receptors.

The chemoreceptors are accessible to chemical stimuli via the subterminal pore. The walls of the setae, however, may be permeable as well.

It seems probable that action potentials were recorded also from the dendrites of the sensory cells.

Key words: Mechanoreception – Chemoreception – Sensory setae – Receptors, functional morphology – Crustacea

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The principles of how stimuli are transmitted to the sensory cell dendrites and which role modality-specific structures play in this process is a topic of current interest in arthropod sensory physiology. In insects, a great deal of insight in these mechanisms has been attained especially during the last two decades (cf. Thurm 1965, 1968; Hawke and Farley 1971; Moulins 1971; Steinbrecht and Müller 1971; Gaffal et al. 1975; Moran et al. 1976; Altner 1977; Altner et al. 1977, 1978, 1981; van der Wolk 1978; Gnatzy and Tautz 1980; French and Kuster 1981; French and Sanders 1981). In Crustacea, however, the body of information available on these questions is limited. This is mainly due to the fact that studies of structure and function have been seldom carried out in tandem. Only recently, Ache (1982) has stressed the point that the morphological and physiological data published to date do not provide a solid basis from which a substantial discussion of structure-function relationships could proceed.

Our investigation of bimodal sensory hairs on the pereiopod chelae of a decapod crustacean provides such combined morphological and physiological data on mechano- and chemoreceptors. Together with recent findings in other species (cf. Risler 1973; Mead et al. 1976; Wiese 1976; Ball and Cowan 1977; Chichibu et al. 1978; Crouau 1980, 1981; Tautz et al. 1981; Derby 1982) our results permit the definition of general morphological criteria by which mechanoreceptors in Crustacea are characterized. We show further that in Crustacea mechanosensitive hairs exist that react only to coarse stimuli and seem to function analogous to scolopidial organs.

Materials and methods

Animals and recordings. Experiments were performed on immature males and females of *Austropotamobius torrentium* with a body length of 40–60 mm. The animals were collected from local waters and obtained from commercial sources. They were kept in the laboratory for up to several weeks at 5–10° C.

For electrophysiological investigation, an isolated preparation of the propodite or dactylopodite of the second pereiopod was used. Out of the row of setae on the inner edge of the podites a group of these organs was cut off. Then a small window was cut into the cuticle. With a suction electrode of 5–10 µm tip diameter single afferent fibers were picked up. Extracellular recording (for details, see Hatt and Bauer 1980) and stimulation were carried out using a stimulation chamber, which delivered highly reproducible, steep changes in the concentrations of stimulants (Bauer et al. 1981).

Microscopic procedures. For scanning electron microscopy, chelae of second pereiopods were cut off, air dried and gold coated (Hummer II, Technics Inc., Alexandria, Virginia, U.S.A.). The material was examined with a Cambridge Stereoscan S4-10 scanning electron microscope. Dye-penetration experiments were carried out according to Slifer (1960). After immobilization by CO_2 whole animals were dipped into a solution of 0.5% crystal violet for 1–5 min and washed quickly in two changes of distilled water, then the chelae were cut off, dried under a heat lamp, cleared in xylene and mounted in resin for light-microscopical observation.

For transmission electron microscopy, OsO_4 fixation according to Zetterquist or to Dalton proved appropriate, especially when the tips of the chelae were previously cut off in order to faciliate diffusion of the fixative. Transverse serial sections of six podites from six individuals were used to reconstruct the dendrites.

These series had a length of up to 650 µm. Silver-grey sections were collected at intervals of 5, 10 or 15 µm. At points of special interest large numbers of ultrathin sections were collected. Such series comprised up to 20 µm. Another series of sections was cut through the distal portions of setae in order to collect data on the apical dendritic region and the terminal pore. One further specimen was serially sectioned longitudinally.

Results

A. Location, shape and cellular components of the sensilla

In *Austropotamobius torrentium* the first three pairs of pereiopods bear chalae. In animals with a body length of 40–60 mm, the length of the second pair of chelae is 6 mm in the propodite and 3 mm in the dactylopodite. The inner edge of the propodite as well as the dactylopodite bears a row of 41–55 stout, squat setae, which are about 170 µm long and 15 µm apart from each other (Fig. 1a, b). Our investigations did not reveal any difference between the sexes. The setae are not

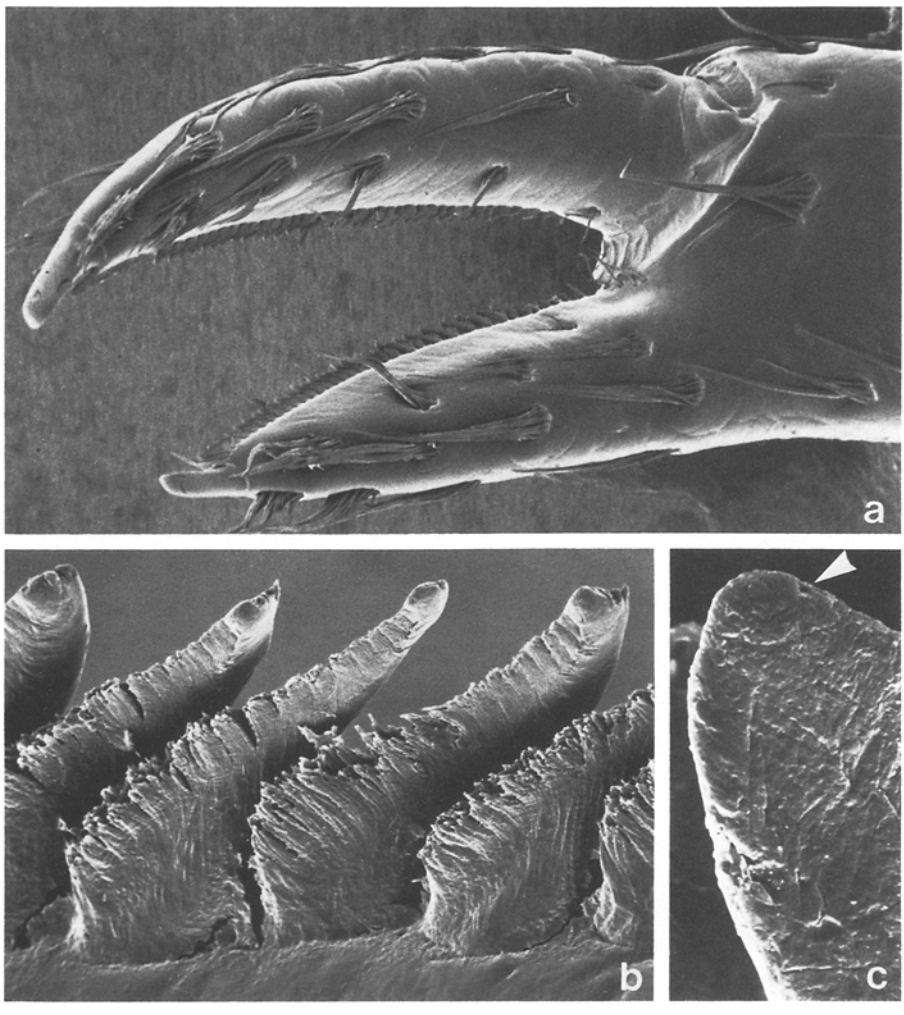


Fig. 1a–c. Location and shape of the fringed setae on the pereiopod chelae of *Austropotamobius torrentium*. **a** Chela of second pereiopod. A row of stout setae lines the inner edge of the propodite and the dactylopodite. **b** The flattened setae are fringed at their rear edge. **c** Subterminally, a pore (*arrowhead*) is visible. (a) ×40; (b) ×600; (c) ×1400

erect but instead are inclined at an angle of about 50 degrees to the tip of the podite. Their lateral aspect is triangular, resembling a sail with its tip pointing distally toward the tip of the chelae. Its rear edge, which faces the joint of the chelae, is fringed roughly (Fig. 1b). Only near the tip do the setae have an unbroken outline. Subterminally, a small apical pore is visible, displaced to the fringed side (Fig. 1c). The bases of the setae are somewhat constricted, measuring about 35 μm in diameter. The setae are not solid cuticular structures; a dendritic channel runs longitudinally through them at their non-fringed side (Fig. 2a).

The setae are innervated by eight bipolar sensory cells (Fig. 2c, d). Exceptions have been observed with six or more than eight units. All eight dendritic outer segments are unbranched and extend to the tip of the hair, where an amorphous, osmiophilic material clogs the pore. Within the dendritic channel, processes of enveloping cells are also found. They occupy only a small part of the hair channel, which widens from 0.5 μm at the tip, to about 4 μm basally. The dendrites measure only 0.05–0.3 μm in diameter. Thus, within the setae, there is an ample receptor lymph cavity. At the base of the setae, the dendritic channel is bent about 10° proximally to the edge of the chela. It penetrates the cuticle, which is about 70–80 μm thick in this region. A cuticular sheath and multiple wrappings of enveloping cell processes are now visible around the eight dendritic outer segments (Fig. 3a).

After having crossed the cuticle (Fig. 3b) of the podite, the numerous profiles of the enveloping cells form a bulge beneath the bundle of dendrites. Only thin leaflets of these cells, together with very thin processes of epidermal cells, separate the dendrites from the inner surface of the cuticle. Thus, the bundle of dendritic outer segments, which measures about 1.3 μm in diameter, may run only 1–3 μm beneath the cuticle. About 150 μm proximally, at a level where the enveloping cell perikarya are located, the distance to the cuticle increases slightly. Finally, about 470 μm distant from the bases of the hairs, immediately before the sensory cell perikarya, this distance varies between 3 and 60 μm. Running proximally, the dendrites turn to the medial side of the chelae.

About 140 μm proximal to the bases of the setae, the ciliary region of the dendrites occurs (Fig. 4). The total length of the dendritic outer segments is therefore about 330 μm. The inner segments are of the same length. The perikarya of the sensory cells measure about 10 μm. The ciliary region is surrounded by an inner lymph cavity, which measures about 3 μm in diameter.

B. Physiological properties of the setae in pereiopod chelae of Austropotamobius torrentium

From our electrophysiological recordings, four chemosensitive types of units can be distinguished. They react only to amino acids, or to amines or to pyridines. These responses are highly specific. The units are characterized by broad reaction spectra, which are clearly reproducible, and by their response characteristics and the form of their action potentials (for details see Bauer and Hatt 1980). Figure 5a shows typical reponses of the chemosensitive cells and the time course of an average action potential for each type.

In addition to these units there are also mechanosensitive receptor cells within the setae of the pereiopod chelae of *A. torrentium*. Rapidly adapting bursts of action

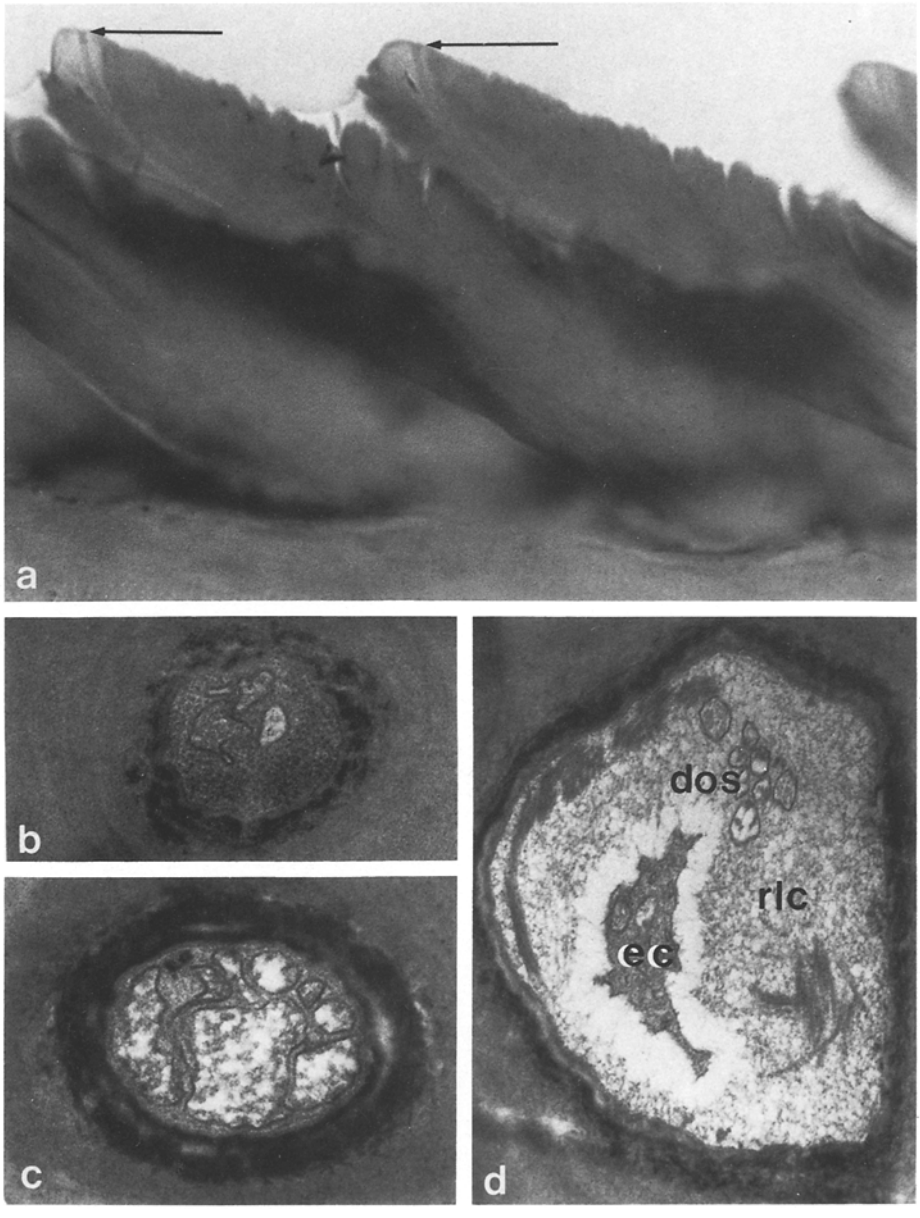


Fig. 2a–d. Dendritic channel and dendritic outer segments in the fringed setae on the pereiopod chelae of *Austropotamobius torrentium*. **a** Whole mount of a chela showing two setae; crystal-violet preparation. The dendritic channel is clearly visible; pores are indicated by *arrows*. Around the pore, a conical region of the cuticle is free of dye. **b, c** Transverse sections through setae near the tip showing four (**b**) and eight (**c**) dendritic outer segments embedded in an electron-dense substance. **d** Transverse section through basal region of a seta. Eight dendritic outer segments (*dos*) and a process of an enveloping cell (*ec*) are visible within the outer receptor lymph cavity (*rlc*). Within the receptor lymph, flocculent and fibrous material is found. (a) ×1000; (b) ×48 000; (c) ×40 000; (d) ×25 000

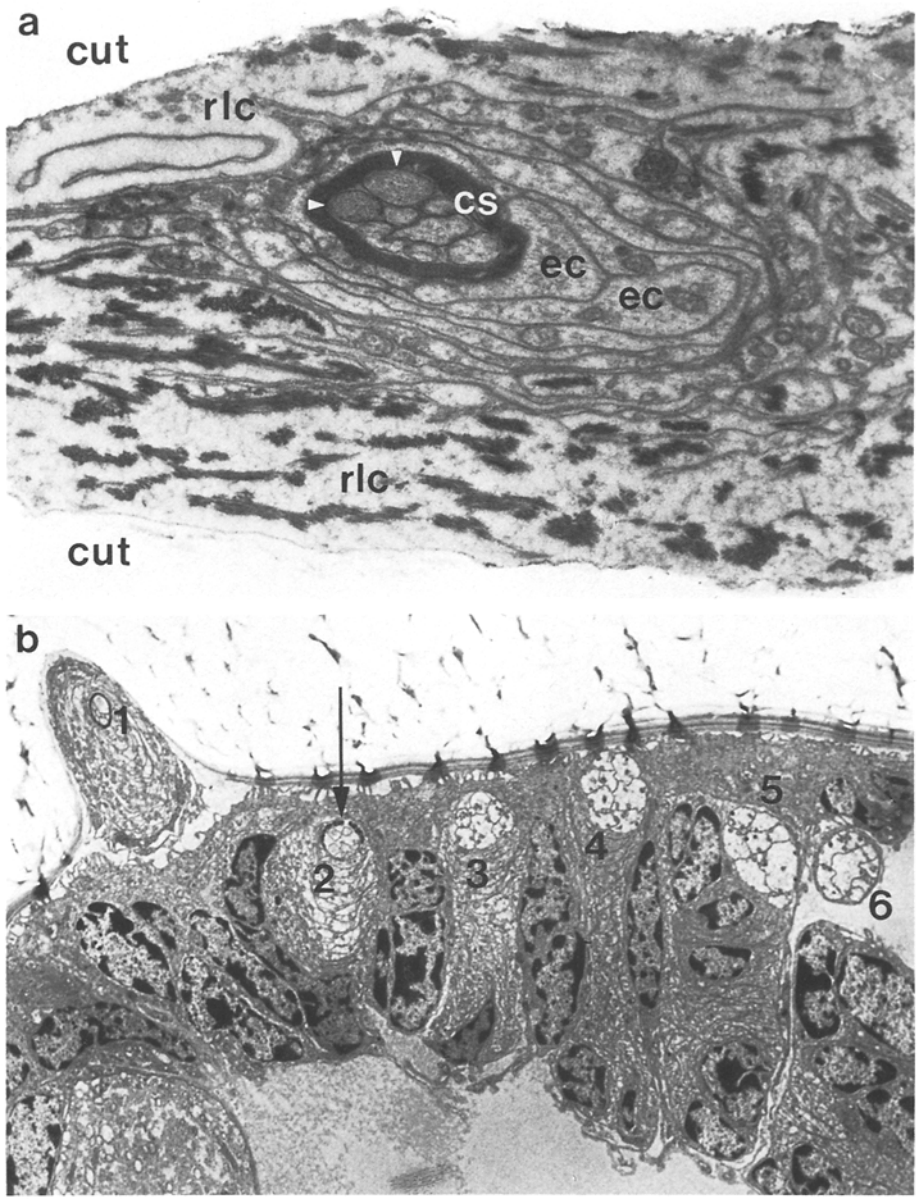


Fig. 3a, b. Dendrites of the receptors of the fringed setae on their course through the cuticle of a chela of *Austropotamobius torrentium*. **a** Transverse section through dendritic channel within the cuticle (*cut*). Eight dendritic outer segments within an electron-dense cuticular sheath (*cs*) are enwrapped by enveloping cell processes (*ec*). Around them an extension of the outer receptor lymph cavity (*rlc*) containing fibrous material is visible. Two dendritic outer segments show a denser packing of microtubules (*arrowheads*) than the other six. **b** Bundles of dendrites from six setae (*1–6*) beneath the cuticle at different distances from the seta. Bundle *2* is cut near the ciliary region of the dendrites. The scolopale (*arrow*) around this bundle is clearly visible. Bundles *3–6* contain dendritic inner segments. (a) ×15000; (b) ×2100

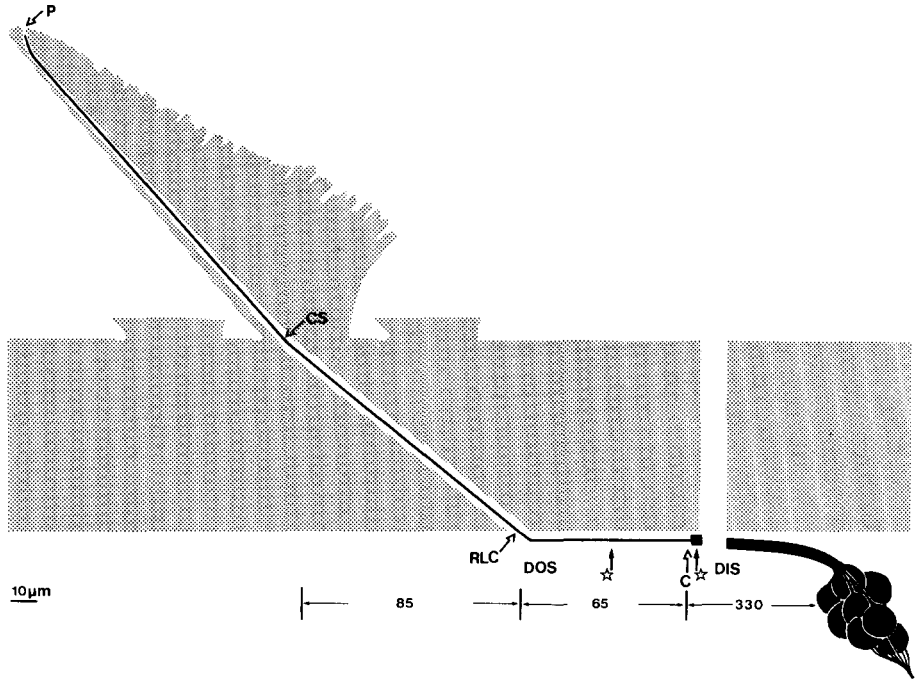


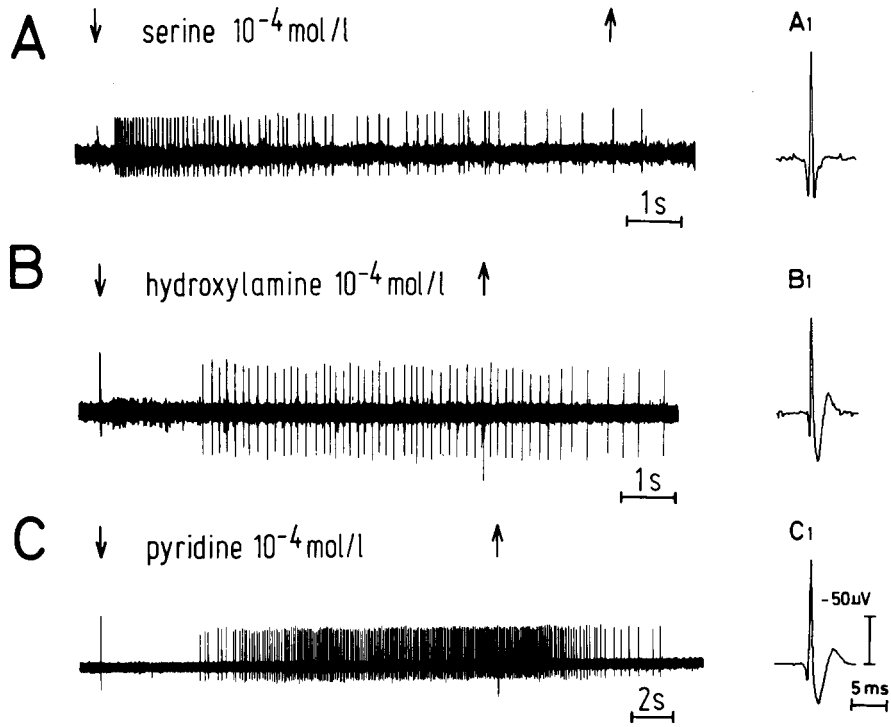
Fig. 4. Schematic representation of a fringed seta on the pereiopod chelae of *Austropotamobius torrentium*. Sensory cell perikarya and bundle of dendrites are black. Distances between characteristic levels indicated in µm. *CS* distal end of cuticular sheath; *DIS* dendritic inner segments; *DOS* dendritic outer segments; *P* subterminal pore; *RLC* proximal limitation of outer receptor lymph cavity. The *arrows* marked with *stars* indicate the extension of the scolopale within the inner enveloping cell

potentials could be elicited in afferent neurons by pressing down the setae (Fig. 5b, A) or by direct lateral displacements. The impulse frequency depended on the direction, amount and velocity of the displacement. Maximal frequencies were obtained when the tip of the seta was pushed down with high velocity. The shortest interspike intervals in response to very strong mechanical stimulation were between 9 and 10 ms. Occasionally, we obtained simultaneous responses from two different mechanosensitive units, which could easily be distinguished by different spike amplitudes (Fig. 5b, B). No differences were observed in the maximal response with regard to the direction of deflection.

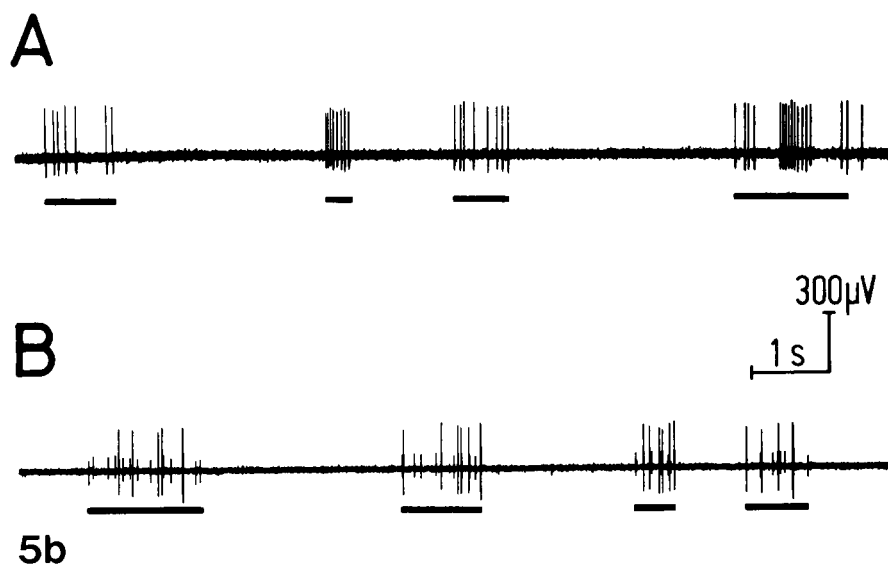
The mechanosensitive units showed no or a very low spontaneous activity ($0.1\,s^{-1}$ at 13° C). Only direct displacements by a capillary led to responses. Rapid changes of the flow rate within the stimulation chamber and strong vibrations proved ineffective. The mechanoreceptors have not yet been studied quantitatively.

C. Modality-specific structures and stimulus transmitting systems

Since mechano- and chemosensitive units have been observed in the setae on the pereiopod chelae of *A. torrentium*, two questions arise: (1) Do the sensory cells



5a



5b

Fig. 5a, b. Impulse activity of chemo- and mechanosensitive units in fringed setae on the chelae of *Austropotamobius torrentium*. **a** Recordings from three different chemosensitive units with the corresponding average action potentials. A shows the response of an amino acid-sensitive unit after application of serine, B that of an amine-sensitive unit to hydoxylamine, C that of a pyridine-sensitive unit to pyridine. The action potential amplitude in A was 120 µV, in B 220 µV and in C 200 µV. The drugs were applied in concentrations of 10^{-4} mol/l. Onset and end of stimulation are indicated by *arrows*. A_1, B_1, and C_1 show the respective averaged action potentials. **b** Recordings from a single afferent fiber of a mechanosensitive unit showing responses to seta deflection at varying velocities. Stimulation is indicated by the heavy lines below (A). Simultaneous recordings from both mechanosensitive units of a seta to mechanical displacements of the seta (B)

demonstrate stimulus-specific structures, and (2) how are the stimuli transmitted to the dendritic outer segments?

1. Differences in the structure of sensory cells. We found conspicuous differences in the fine structure of the dendritic processes, according to which two types of units can be distinguished. In two dendritic outer segments the density of microtubules is considerably higher than in the other six (Fig. 6a). When one compares outer segments of approximately the same diameter, the number of microtubules in these segments ranges from at least 1.5 times to 3.7 times the number in the other. Near the ciliary junction this difference becomes less obvious, but from serial sections it can be seen that the dendrites with the more densely packed microtubules run at the outer surface of the bundle of dendrites, i.e., at the face directed toward the cuticle (cf. Fig. 3a). These dendritic outer segments are further characterized by four other features: (1) Their ciliary junctions appear about 5 μm distal to those of the other six units (Fig. 6b). (2) Although all ciliary segments are of the $9 \times 2 + 0$ type, in the two segments in question the A tubules of the doublets bear two arms and are more electron dense than the B tubules (Fig. 6c). (3) In all inner dendritic segments a ciliary rootlet is developed. Only in the two outermost dendrites it is well developed and reaches about 60 μm in length, whereas in the other six it is less well developed and maximally 10 μm in length (Fig. 7). (4) Only the two outermost dendritic inner segments are bound specifically to the inner enveloping cell.

This enveloping cell shows a semicircular array of longitudinally oriented microtubules embedded in an electron-dense matrix (scolopale). In this region the two dendritic inner segments are bound to the membrane of the enveloping cell by numerous desmosomes (Figs. 6b, 7a). Within the desmosomes, bridges of the electron-dense matrix reach the membrane. The supporting structures in the enveloping cell terminate proximally at about the level of the ciliary junctions of the other six dendrites. Further proximally, beyond the termination of the ciliary rootlets, no differences between the eight units were observed; they form a uniform bundle. The perikarya are also identical. The perikarya from several setae form clusters that are suspended within the hemolymph space (Fig. 8). Neurilemma cells form thin but incomplete wrappings around them. The axons have a diameter of 0.4–1 μm and appear uniform. They run medially and centrally.

2. Stimulus-transmitting structures. Chemical stimuli should reach the dendritic outer segments via a terminal pore and/or via channels for diffusion in the wall of the setae. The walls of the setae do not show the helicoidal structure of the exocuticle (cf. Neville 1975) of the chelae. It can be considered as a continuation of the epicuticle. Its thin surface layer, however, which is only about 70 nm thick, was found only in the basal portions of the setae. It cannot be excluded that it is artificially disrupted and lose in apical regions.

About 40 μm above the basal constriction, the diameter of the setae is greatest. The outline of the setae is wedge-shaped in cross sections. At the broad edge near the dendritic channel, the cuticular wall measures about 6 μm. Laterally, it is about 10 μm thick and in the proximal fringed rim it measures up to 50 μm.

With the methods used, four thin concentric layers of different appearance can

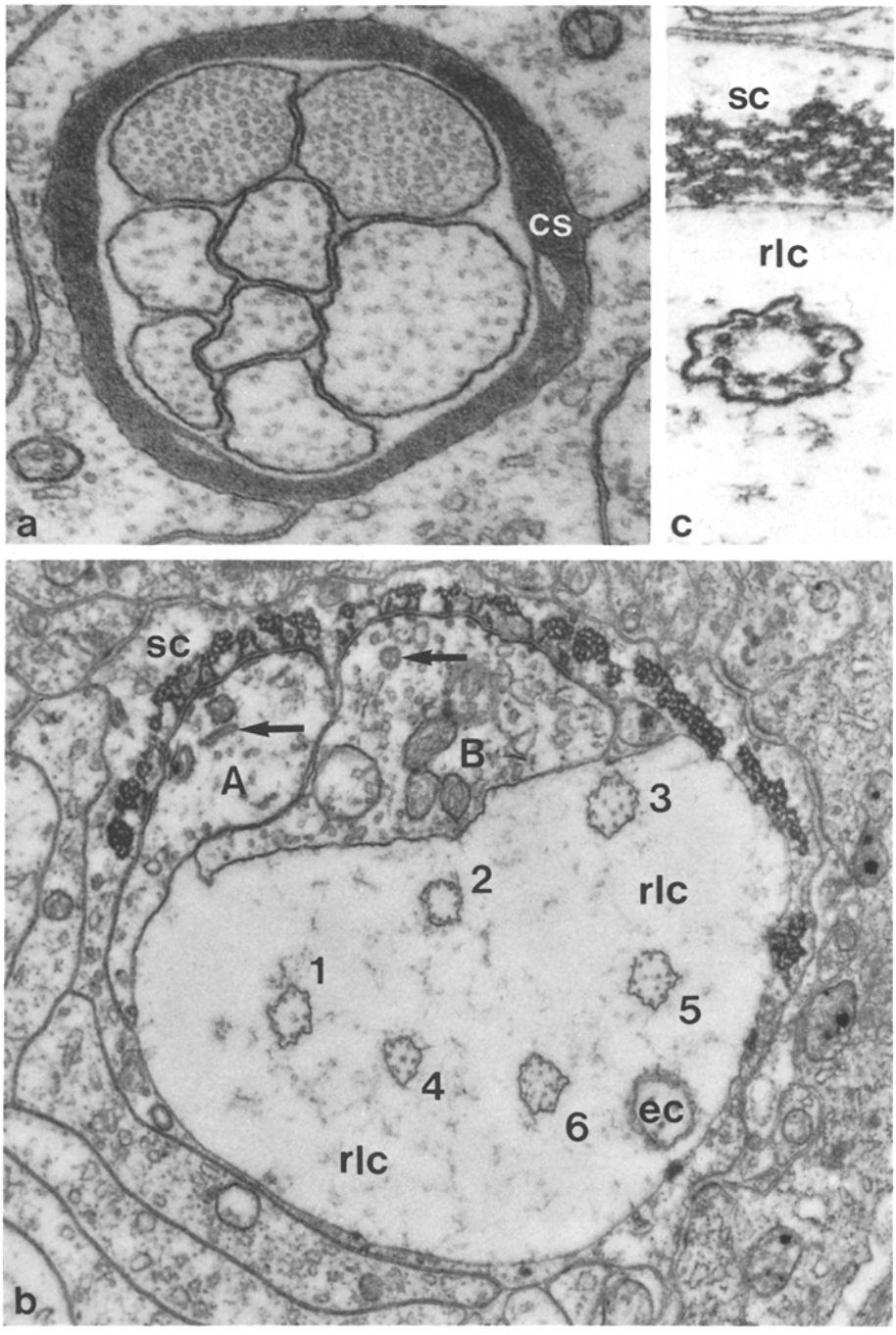


Fig. 6a–c. Structure of the dendrites of the sensory cells in the fringed setae. **a** Eight dendritic outer segments within the cuticular sheath (*cs*); two segments show a conspicuously dense packing of microtubules. **b** Ciliary region. The two dendrites (*A, B*), with the dense tubular packing in the outer segments shown in (**a**), have already reached their inner segment region. They are each characterized by a ciliary rootlet (*arrows*) and by desmosomal junctions with the inner enveloping cell, which contains a scolopale (*sc*). The other dendrites (*1–6*) are shown at their ciliary segment. They are surrounded by the inner receptor lymph cavity (*rlc*); *ec* process of the inner enveloping cell. **c** Transverse section through ciliary segment of a dendrite with a dense array of microtubules in the outer segment. For further explanation, see text. *rlc* Inner receptor lymph cavity; *sc* scolopale. (a) ×60 000; (b) ×24 000; (c) ×90 000

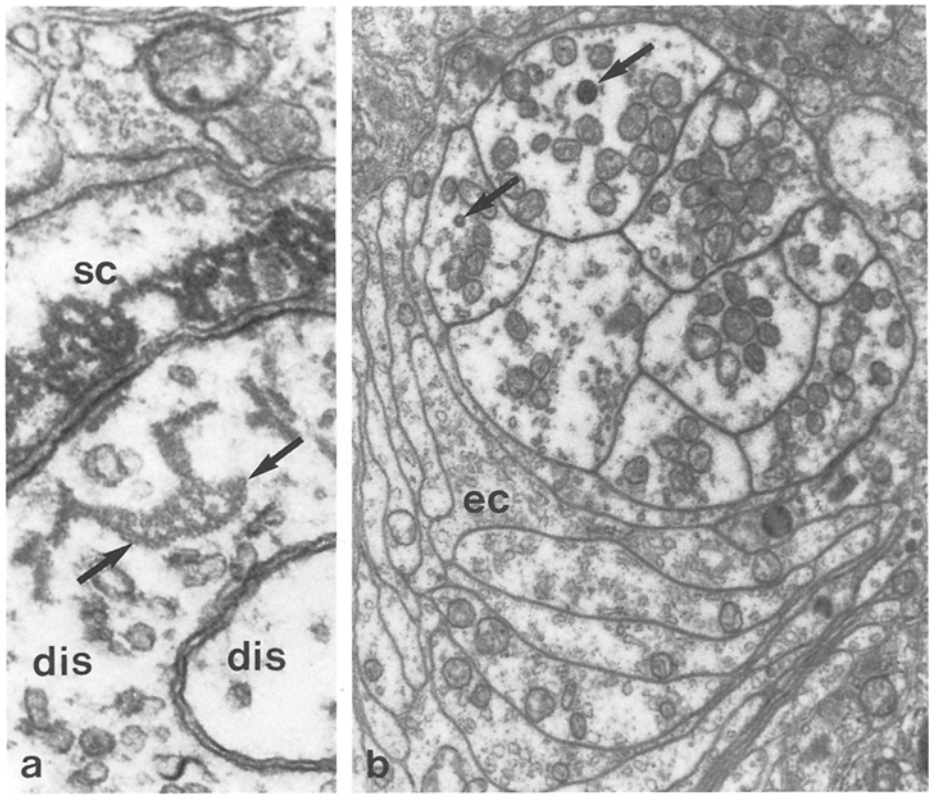


Fig. 7a, b. Dendritic inner segments. **a** One of the two dendritic inner segments (*dis*) is characterized by the presence of a strong ciliary rootlet (*arrows*). It is connected with the inner enveloping cell by desmosomes, which are continuous with the scolopale (*sc*). **b** Bundle of eight dendritic inner segments enwrapped by enveloping cell processes (*ec*). In two dendrites a ciliary rootlet is visible (*arrows*). (a) ×70000; (b) ×18000

be distinguished around the dendritic channel (Fig. 9). The innermost layer, which is not clearly discernible in all sections, is of medium electron density. It is only about 30 nm thick. It is surrounded by a dense layer (about 20 nm), a lighter layer (30–50 nm), followed by a flocculent, electron-dense layer (about 100 nm). Apically, the two dense layers appear to fuse and to be continuous with the substance that clogs the pore.

These four inner layers are surrounded by the main portion of the cuticular wall, which, in our sections, appears nearly homogeneous. Only near the central core of the four thin layers is a faint concentric filamentous pattern visible (Fig. 9). Several widely spaced, light channels (Fig. 9), most of them about 20 nm in diameter, run longitudinally within the cuticular wall. Due to their small diameter they could not be traced over longer distances. They do not produce a "spongy" texture of the cuticle as in typical aesthetascs (Ache 1982), nor do they show special structural differentiations as do pore systems in insect sensilla (Altner and Prillinger 1980).

The subterminal pore of the setae measures 0.5 µm in diameter. It is located

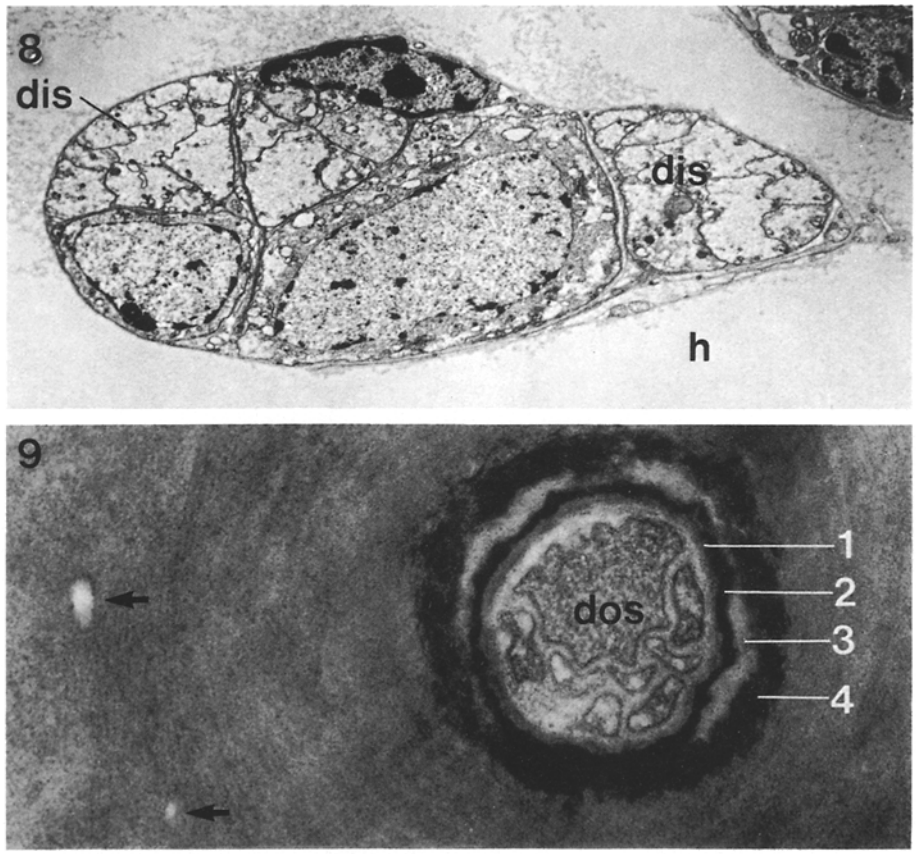


Fig. 8. Three bundles of dendritic inner segments (*dis*) at their origin from the sensory cell perikarya. These form a cluster within the hemolymph space (*h*) within the chela. × 3400

Fig. 9. Structure of the wall of a seta on the pereiopod chelae of *Austropotamobius torrentium*. Four layers (*1–4*) are distinguished immediately around the dendritic channel. Two fine, electron-lucent channels (*arrows*) are visible within the cuticle, which shows a concentric filamentous pattern around the central dendritic channel; *dos* dendritic outer segments. × 60 000

about 5 μm below the tip, and leads into the dendritic channel, which, near the tip, curves to reach its longitudinal position within the seta (Fig. 2a).

About 1 μm beneath the pore at least one dendrite is visible (Fig. 2b). All eight dendrites are present within an area not exceeding the next 12 μm proximally. In the experiments using crystal violet (Fig. 2a) the dye was seen within the cuticular wall after an incubation time of more than 1 min. Only a conical region at the tip of the setae and the bases of the setae remained free of dye. It remains unclear whether the dye also proceeds into the dendritic channel.

In the region of the insertion of the setae into the surrounding cuticle of the chelae no special cuticular differentiations were found.

Discussion

A. Function and structure of the sensory cells in the fringed setae on the pereiopod chelae of Austropotamobius torrentium

Electrophysiological investigations have enabled us to ascribe a function to six of the eight units that occur in the setae. There are two mechanoreceptive and four chemoreceptive sensory cells. The latter react to amino acids, to amines or to pyridines. Recent results show that there are two types of pyridine receptors (Hatt and Bauer 1982).

The function of two other units remains unclear. In several experiments, units were observed that displayed spontaneous activity but did not respond to the substances mentioned above. In four cases, however, a stimulation with plant extracts caused an increase of impulse frequency. Although not yet investigated systematically, it seems probable that these units are also chemoreceptive. This assumption is consistent with the fact that *Austropotamobius torrentium* is also herbivorous. No sensory cell was sensitive to both chemical and mechanical stimuli.

Our structural findings agree with these physiological results. Two sensory cells are not only different from the other six but also show cytological properties that make them candidates for being mechanoreceptors. These features are (1) a comparatively dense assemblage of the microtubules within the dendritic outer segment, (2) the occurrence of dense A-tubules with arms in the ciliary segment, (3) the presence of a distinct ciliary rootlet within the dendritic inner segment, and (4) a specialized connection of the dendritic inner segment to the inner enveloping cell.

B. Structure and function in the mechanoreceptors

The present study is one of the rare investigations on crustacean mechanoreceptors, in which both electrophysiology and transmission electron microscopy have been applied jointly in order to collect reliable information on receptor specialization and on the process of stimulus transmission. Gaffal et al. (1975) and Seelinger (1977) investigated sensory hairs in the apical sensory cone on the antenna of an isopod (*Hemilepistus reaumuri*); Wiese (1976) studied mechanoreceptors for near-field water displacements on the surface of the telson in *Procambarus clarkii*. Other investigators have studied solely the fine structure but give a functional interpretation of their findings partially based on behavioral observations (Schöne and Steinbrecht 1968; Risler 1973, 1977; Strickler and Bal 1973; Mead et al. 1976; Ball and Cowan 1977; Crouau 1978, 1979, 1980, 1981; Guse 1978, 1980; Keyser 1981; Kouyama et al. 1981). Comparing the data from these studies it is apparent that no simple uniform scheme can be drawn for the structure of crustacean mechanoreceptive hairs as is possible for those of insects (Thurm 1968; Gaffal et al. 1975; McIver 1975; Altner and Prillinger 1980).

The main differences are the following: (1) In Crustacea the number of mechanoreceptive units is observed to vary between a single one (Gaffal et al. 1975; Mead et al. 1976; Crouau 1980, 1981) and three (Schöne and Steinbrecht 1968; Risler 1973; Ball and Cowan 1977; Crouau 1978, 1979; Guse 1978: Kouyama et al. 1981). In many cases two mechanoreceptors are present (Wiese 1976; Guse 1978;

Crouau 1980, 1981; Keyser 1981, our observations). (2) A highly specialized socket region is developed in some cases (Gaffal et al. 1975; Mead et al. 1976; Wiese 1976; Ball and Cowan 1977; Keyser 1981). Such socket structures have also been observed in light- or scanning electron-microscopical preparations complementary to electrophysiological investigations (Chichibu et al. 1978; Riemay 1980; Derby 1982). They may also be present in the setae studied by Tautz et al. (1981). Other setae, similar to those studied by us, lack any differentiation of the socket. (3) The dendritic outer segments may extend to the tip of the hairs or setae (Mead et al. 1976, our observations), however, have also been observed to end at the socket region (Gaffal et al. 1975; Mead et al. 1976; Ball and Cowan 1977; Chichibu et al. 1978; Crouau 1978, 1979) or within the hairs at some distance from the tip (Crouau 1980, 1981, cf. also Chichibu et al. 1978). In this case the structure of the hair wall changes at this level. Schöne and Steinbrecht (1968) and Kouyama et al. (1981) reported that the mechanoreceptive dendrites near the hair base are connected to an extracellular chorda, which enters the hair. (4) A tubular body has been observed only in some cases; it seems to be present only in those dendritic outer segments that are bound to a specialized socket.

Correlated with this structural variability, significant differences in functional properties are to be expected. For the receptors in the present material, it is evident that only strong mechanical stimuli lead to an excitation. Displacements of the setae from the resting position lead to phasic bursts that show rapid adaptation after maximal deflection. From the physiological observations it seems doubtful as to whether the mechanoreceptors could provide more than only very rough information on the presence of food materials or on substrate particles that are touched during locomotion. The same considerations have recently been published for the "hedgehog hairs" in *Homarus americanus* (Derby 1982), which are homologous to those we investigated.

The hypothesis is further supported by the lack of structural differentiations of the setae which could serve a finely graded stimulus transmission. The setae do not possess elaborate joint structures at their insertion into the surrounding cuticle. On the contrary, it is by no means obvious how the stimulus is actually transmitted to the dendrites of the sensory cells.

A lateral indentation of the dendrites at a distinct point is hardly conceivable. It is more likely, however, that longitudinal stress is exerted on the dendritic outer segments, when a seta is reflected. The dendritic outer segments lie within a receptor lymph cavity that extends from the ciliary section (C in Fig. 4) to the terminal pore. Particularly those two units, the dendritic outer segments of which show a conspicuously dense packing of microtubules, are tightly connected to the innermost enveloping cell by desmosomes. A scolopale is present, which can be thought to enhance the rigidity of this cell in the region of contact. Longitudinal stress could occur with seta deflection if the distal ends of the dendritic outer segments were firmly connected to the cuticle of the hair. There is no unequivocal evidence for such an attachment; however, from the micrographs of the tip region it is seen that the dendrites are embedded in an electron-dense matrix, which could well provide such a fastening.

Thus, the mechanoreceptors could be stimulated analogously to those in scolopidial organs. This type of stimulation has been suggested also for the sensory

hairs in the statocyst of *Astacus fluviatilis* (Schöne and Steinbrecht 1968) and antennal hairs in *Procambarus clarkii* (Kouyama et al. 1981). In these cases, however, an extracellular strand (chorda) is developed to which the dendritic tips are bound and which is continuous with the cuticle of the sensory hair. The dendritic outer segments thus are expanded between the region of the desmosomal contacts near the ciliary segment and this point of attachment to the chorda, which, in the cases mentioned, lies near the hair base. Although corresponding in the basic properties, the system in the fringed setae of *Austropotamobius torrentium* studied by us seems less differentiated.

In summary, our observations support the view that, in Crustacea, mechanosensitive hairs show structural features reflecting differences in the mechanism of adequate stimulation. Regardless of these differences, structural features can be defined that seem to characterize all types of crustacean mechanoreceptors. These characteristics are (1) a comparatively dense packing of microtubules in the dendritic outer segment, (2) the presence of dense A-tubules with, most probably, dynein arms in the ciliary segment, (3) the presence of a distinct ciliary rootlet within the dendritic inner segment, and (4) the connection of the dendritic inner segment to the innermost enveloping cell by desmosomes and the presence of a specialized cytoskeleton (scolopale) within this cell.

This combination of features has been observed in several mechanosensitive sensory hairs (or is visible in published micrographs of these hairs; cf. Risler 1973; Mead et al. 1976; Ball and Cowan 1977; Guse 1978; Crouau 1980, 1981).

Apparently this combination is also present in mechanosensitive proprioceptors, although most authors do not present data on the dendritic ciliary segment. Mill and Lowe (1971) have stressed the point that a scolopale, desmosomes and ciliary rootlets are characteristic of the limb proprioceptor in *Cancer pagurus*. Also the observations of Moulins and Clarac (1972) in a chordotonal organ in *Astacus leptodactylus* fit well into this structural scheme. Moulins (1976), in a review of the ultrastructure of arthropod chordotonal organs in general, mentioned the characteristics listed above, which, as it seems now, are not only found in these proprioceptors but can be regarded as a common structural denominator for mechanoreceptors in Crustacea in general.

C. Transmission of chemical stimuli to the receptors in the fringed setae of Austropotamobius torrentium, accessibility and function of the receptor lymph cavity

From our physiological recordings it is highly probable that six units within the fringed setae on the pereiopod chelae of *Austropotamobius torrentium* are chemoreceptors. As in insect chemoreceptors, the sensory cells show no modality-specific structures (Altner 1977; Hansen 1978; Altner and Prillinger 1980). However, pores within the cuticular wall of a sensillum indicate that the outer receptor lymph cavity is accessible to stimuli present in the surrounding medium. In the setae examined here, the stimuli should reach the dendrites via the terminal pore (Fig. 1c, 2a). From our experiments with crystal violet, however, it cannot be excluded that the lateral walls are permeable as well. So far we are not able to interpret the observation that crystal violet does not fill an apical conical portion of the hairs (Fig. 2a). Local accumulation of crystal violet due to differences in

cuticular fine structure have been reported to occur in "aesthetasc" hairs (Ghiradella et al. 1968; Snow 1973; Andersson 1975).

From our observations no argument can be derived as to whether the ionic composition of the outer receptor lymph could be under control of the enveloping cells. An electrogenic ion transport, which contributes to the sensory function of a sensillum, has been observed to be performed by enveloping cells in insects (for a review, see Thurm and Küppers 1980).

Thurm and Wessel (1979) have demonstrated the presence of an epidermal voltage source in terrestrial Crustacea (*Armadillidium*), which, however, is of another nature than that found in insects.

D. Dendritic action potentials

The dendrites of the receptor cells in the setae are about 700 µm long, with the inner and outer segments having approximately the same length (cf. Fig. 4). The distance between the base of the setae and the perikarya of the sensory cells is about 470 µm. In several electrophysiological recordings, the electrode was located within this range. The distance can be measured exactly in mechanoreceptors by stimulating individual setae distal to the position of the electrode. In these cases it seems probable that the electrical activity was recorded from dendrites rather than from perikarya or axons. On the other hand, these action potentials do not differ in their time course or amplitude from those registered at distances of more than 1 mm from a seta, which are certainly axonic responses.

An origin of spikes at a dendrite has been reported by Mellon and Kennedy (1964) for bipolar receptors in tactile hairs of *Procambarus clarkii* and by Pabst and Kennedy (1967) for cutaneous mechanoreceptors in the same species.

Further experiments are in progress on impulse generation and propagation in the receptors described in this paper.

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