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Centrin- and α-actinin-like immunoreactivity in the ciliary rootlets of insect sensilla

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Summary. Long ciliary rootlets are a characteristic feature of the dendritic inner segments of the sensory cells in insect sensilla. These rootlets are composed of highly ordered filaments and are regularly cross-striated. Collagenase digestion and immunohistochemistry reveal that the rootlets are probably not composed of collagen fibers. However, double-labeling experiments with phalloidin and anti-α-actinins show that antibodies to α-actinin react with the ciliary rootlets of the sensilla, but do not stain the scolopale, which is composed of actin filaments as visualized by phalloidin. Antibodies to centrin, a contractile protein isolated from flagellar rootlets of green algae, also stain the ciliary rootlets. Within the ciliary rootlets of insect sensilla, α-actinin may be associated with filaments other than actin filaments. The immunohistochemical localization of a centrin-like protein suggests that contractions probably occur within the rootlets. The centrin-like protein may play a role during the mechanical transduction or adaptation of the sensilla.

Key words: Ciliary rootlets – Sensilla – Mechanoreceptors – α-Actinin – Centrin – Cryofixation – Immunohistochemistry – *Periplaneta americana*, *Schedorhinotermes lamanianus* (Insecta)

Fibrous structures are commonly associated with the basal bodies of cilia in eukaryotic ciliated cells, including sensory processes of vertebrates and invertebrates (Pitelka 1974; Witman 1990). One of the most prominent of these structures is the long ciliary rootlet of arthropod sensilla. It is a characteristic structure of mechanosensitive Crustacean hair sensilla (e.g., Schmidt and Gnatzy 1984; Schmidt 1989, 1990) but is most prominent within the mechanosensitive arthropod scolopidia (e.g., Gray 1960; Howse 1968; Schmidt 1969, 1970, 1974; Michel 1974, 1975; Moran and Rawley 1975; Moran et al. 1975; Moulins 1976; Toh 1981; Bloom et al. 1981; McIver 1985; Wolfrum 1990). In comparison with other types of sensilla, e.g., olfactory pegs, the ciliary rootlets of the scolopidia are more prominent, being longer and thicker (Moulins 1976; McIver 1985). Therefore, this cytoskeletal element should play an important role in sensillum function in scolopidia (Wolfrum 1990). In comparison with rootlets of other ciliated cells and in the absence of evidence of any other function, it has been assumed that the ciliary rootlets in the sensory cells of the sensilla anchor the ciliary base (the basal bodies) at the tip of the dendritic inner segment (Moran and Rawley 1975). However, contractions mediated by a protein called centrin have been observed in the fibrous ciliary rootlets of some green algae (Salisbury and Floyd 1978; Salisbury et al. 1984).

An investigation of the composition of insect ciliary rootlets should provide more information concerning the properties and function both of these structures in sensilla and of other sensory structures. A prominent cytoskeletal element of the auxiliary cells of the scolopidia, the scolopale, has been characterized in previous studies (Wolfrum 1990, 1991 b). However, a detailed investigation on the ciliary rootlets of these sensilla is still lacking. In the present paper, the ultrastructure and composition of the ciliary rootlets in insect scolopidia are demonstrated by cytochemistry and immunohistochemistry.

In previous publications, some authors (Fawcett 1961; Füller and Ernst 1973; Michel 1974; Schmidt 1969, 1974) have speculated about the collagen nature of the rootlets. Therefore, the presence of collagen in the rootlets has been tested by both anti-collagen staining and collagen digestion. The presence of actinin and the localization of centrin have been ascertained by immunohistochemistry.

Materials and methods

Animals. Two insect species were used: *Periplaneta americana* (Blattodea) were taken immediately after molting from the colonies of the Institute, workers of *Schedorhinotermes lamanianus* (Isoptera) were kindly provided by Dr. M. Kaib, University of Bayreuth, FRG.

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Electron microscopy

Chemical fixation. Tannic acid fixation was used as described in Wolfrum (1990).

High-pressure freezing, freeze-substitution and embedding. Heads or antennae of the animals used were frozen in a Balzers high-pressure freezer HPM 010 (Balzers Union, Liechtenstein) (Müller and Moor 1984; Moor 1987) at about 2100 bar according to Studer et al. (1989) and Wolfrum (1990). The freeze-substitution procedure in dry acetone containing 2% OsO_4, and embedding in a mixture of Epon/Araldite were as described in Wolfrum (1990).

Collagenase digestion. Specimens were infiltrated with 0.1 M phosphate buffer, pH 7.1, for 10 min, and treated with buffered 0.5% Triton X-100 (Sigma, Deisenhofen, FRG) for 30 min at room temperature. After washing with buffer, the samples were incubated for 5 h at 37° C with collagenase from *Achromobacter iophagus* (EC 3.4.24.8) (15 U/ml, Boehringer, Mannheim, FRG); controls were incubated in phosphate buffer. The specimens were fixed for 30 min in buffered 2% glutaraldehyde, and for 45 min in buffered 2% glutaraldehyde plus 1% tannic acid at room temperature. After being washed with cold buffered 1% Na_2SO_4 to reduce precipitations of tannic acid and OsO_4, the specimens were post-fixed in buffered 1% OsO_4 for 45 min at 4° C. They were then stained en bloc with 1% uranyl acetate in 50% ethanol, followed by dehydration in graded ethanol and embedding in Durcupan ACM (Fluka).

Series of sections were cut using diamond knives on an Ultracut E ultramicrotome (Reichert-Jung, Nußloch, FRG). They were stained with uranyl acetate and lead citrate, and examined in a Zeiss EM 10/CR electron microscope (Zeiss, Oberkochen, FRG).

Fluorescence microscopy

Preparation. Unifixed specimens were placed in embedding media (Reichert-Jung, Nußloch, FRG) surrounded by boiled liver and cryofixed in melting iso-pentane. They were sectioned at a thickness of 10 µm in a cryostat (2800 Frigocut, Reichert-Jung) at about −20° C, and placed on coverslips precoated with 0.05% aqueous poly-L-lysine (Sigma) and encircled with a "Pap pen" (Science services, München, FRG).

Antibodies: Anti-α-actinin. α-Actinin from chicken gizzard was used to prepare two polyclonal anti-α-actinin sera from rabbit, purified by affinity chromatography. The first serum was kindly supplied by Dr. B. Jockusch, University of Bielefeld, FRG; the second anti-α-actinin serum was obtained from Sigma. *Anti-centrin.* A polyclonal rabbit antiserum to centrin, a 20 kDa polypeptide from the striated flagellar root of the green algae *Tetraselmis striata* (characterized by Salisbury et al. 1984), was a generous gift of Drs. M. Melkonian (University of Köln, FRG) and J.L. Salisbury (Majo Clinic, Rochester, Mich., USA). *Anti-collagen.* A polyclonal affinity-purified goat antibody against type-I collagen was obtained from South Biotechnology Associates (Birmingham, Ala., USA). *Secondary antibodies.* Fluorescein-isothiocynate (FITC)- or rhodamine-conjugated anti-rabbit-IgG antibodies against the whole molecule, both raised in goat (Sigma), and a FITC-coupled F(ab')2 fragment goat anti-rabbit-IgG (H + L) (Jackson Immuno Research, USA) were used. In all tests, the three anti-rabbit-IgGs reacted identically. FITC-conjugated anti-goat-IgG (H + L) was obtained from Dunn Labortechnik (Asbach, FRG).

Phalloidins. Rhodamine-coupled phalloidin (a generous gift from Dr. H. Faulstich, MPI for Medicine, Heidelberg, FRG) and FITC-coupled phalloidin (Sigma) were used as specific probes for filamentous actin (Wulf et al. 1979; Faulstich et al. 1988).

Double fluorescence staining. Cryosections were incubated first with 0.01% Tween20 in 0.15 M phosphate-buffered saline pH 7.2 (PBS) for 10 min and washed in PBS. After blocking with 0.5% fish gelatin (Sigma) plus 0.1% ovalbumin (Sigma) in PBS for 10 min, 10 µl of a dilution (1:100 anti-actinins; 1:50 anti-centrin; 1:10 or 1:20 anti-collagen in PBS) of one of the primary antibodies was placed on each section for 12 h at 4° C. Unbound antibodies were subsequently washed out three times with PBS. Subsequently, 10 µl of the specific secondary antibodies (1:40 anti-rabbit IgGs; 1:5 anti-goat IgG in PBS) were placed on the section for 1 h at room temperature. After being washed in PBS, the sections were incubated with 10 µl of one of the fluorescent phalloidins in PBS (rhodamine-coupled: 0.01 mg/ml, or FITC-coupled: 0.1 mg/ml) for 1 h at room temperature and washed three times in PBS. The sections were then mounted in Mowiol 4.88 (Farbwerke Hoechst, Frankfurt, FRG) containing 2% n-propyl-gallate.

Controls. Muscles of insects were used to demonstrate the specificity of the fluorescent phalloidins and the antibodies used. Both phalloidins reacted only in the light band of the muscles; both anti-α-actinins specifically stained the Z-line. The walls of blood vessels of the boiled liver, used for embedding where collagen is localized, the extracellular part of the basement membrane (basal lamina) of the insect compound eye, and the sarcolemma of insect muscle are known to contain collagen (Ashhurst 1968; Carlson and Chi 1979; Alberts et al. 1983), and acted as controls for anti-collagen immunostaining.

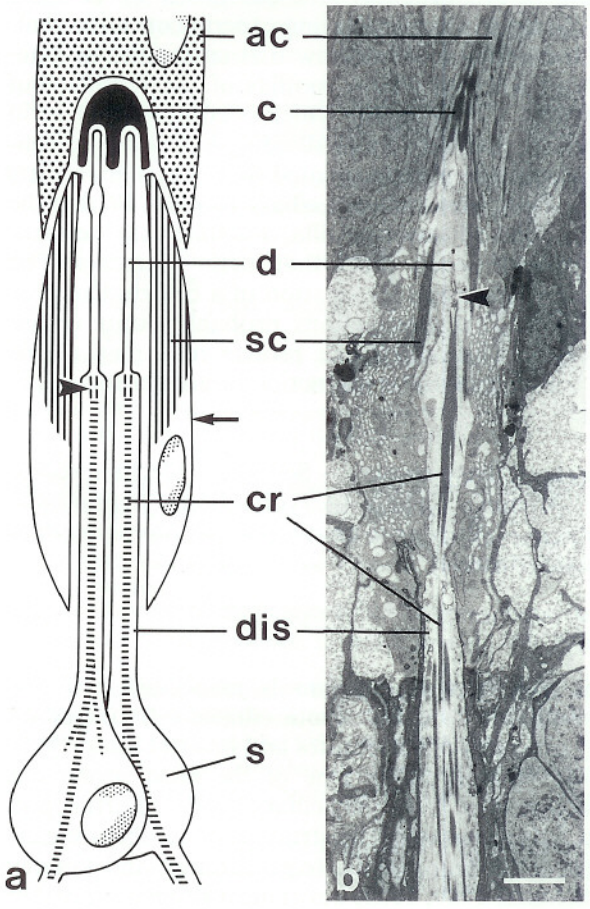


Fig. 1 a, b. Longitudinal sections through insect scolopidia. **a** Diagram and **b** lower-power electron micrograph of a scolopidium of *Periplaneta americana* (chemical fixation). The cap (*c*) lies between the attachment cell (*ac*) and the dendritic outer segment (*d*). The scolopale cell contains the prominent scolopale (*sc*). The ciliary rootlet (*cr*) projects from the basal bodies (*arrowheads*) at the tip of the dendritic inner segments (*dis*) down to the perikaryon of the sensory cell (*s*). Plane of transverse section in Fig. 2b is indicated by *arrow*. *Bar* in **b**: 3 µm; × 2500

The specificity of the phalloidins was additionally tested according to Wolfrum (1991a): after 30 min of preincubation with unlabeled phalloidin, the phalloidin fluorescence was notably reduced; after 2.5 h, no fluorescence could be observed in the usually stained scolopale of the scolopidia.

For additional controls of immunostaining, (1) the primary or secondary antibodies were omitted; (2) a secondary antibody against antibodies differing from the primary antibody was used; (3) non-immunoserum from rabbit was used instead of the primary antibodies. In no case was a reaction observed.

The mounted frozen sections were examined and photographed with a Zeiss Axiophot microscope or analyzed with the Zeiss LSM confocal laser scanning microscope. Fujichrome 100 color reversal films were used for photographic documentation.

Results

The ciliary rootlets in the mononematic and amphinematic scolopidia of the central chordotonal organ and the Johnston's organ of the antennal pedicel were investigated in the present study. There are no structural differences with respect to the ciliary rootlets of the species used, *Periplaneta americana* and *Schedorhinotermes lamanianus*. The ciliary rootlets originate at the basal bodies near the tip of the dendritic inner segment (Fig. 1). In both types of scolopidia, two sensory cells possess rootlets extending through the perikarya into the axons over a distance of up to 100 µm (Fig. 1). In the amphinematic scolopidia, there is additionally a third sensory cell whose dendritic outer segment terminates distally at the joint between the pedicel and the flagellum. In contrast to the other two sensory cells, the rootlet of this cell is shorter and ends within the dendritic inner segment.

The ciliary rootlets are not homogeneous massive strands. They are often hollow and branched (Fig. 1b) as, for example, in *Periplaneta americana* where up to 10–15 branches have been counted. The rootlets are composed of longitudinally oriented highly ordered filaments (about 4 nm in diameter) forming a characteristic regular cross-striation (Fig. 2). In cryofixed specimens, the period of the main bands (a-bands) is about 68 nm ($n=25$) (Fig. 2a). Two additional bands, the b- and the c-band are located between two main a-bands (Fig. 2a). Two sub-bands can be distinguished in the main a-bands, whereas three sub-bands are visible within the b-bands (Fig. 2a, c). The striation of ciliary rootlets of the sensilla is similar to that of D-periodic type-I collagen present within vertebrate tendons (Figs. 2a, 3a, c).

Cyto- and immunohistochemistry

Collagenase digestion. Treatment with collagenase had no effect on the ciliary rootlets of the scolopidia. The ciliary rootlets and their typical cross-striation were preserved after treatment in all samples studied ($n=10$)

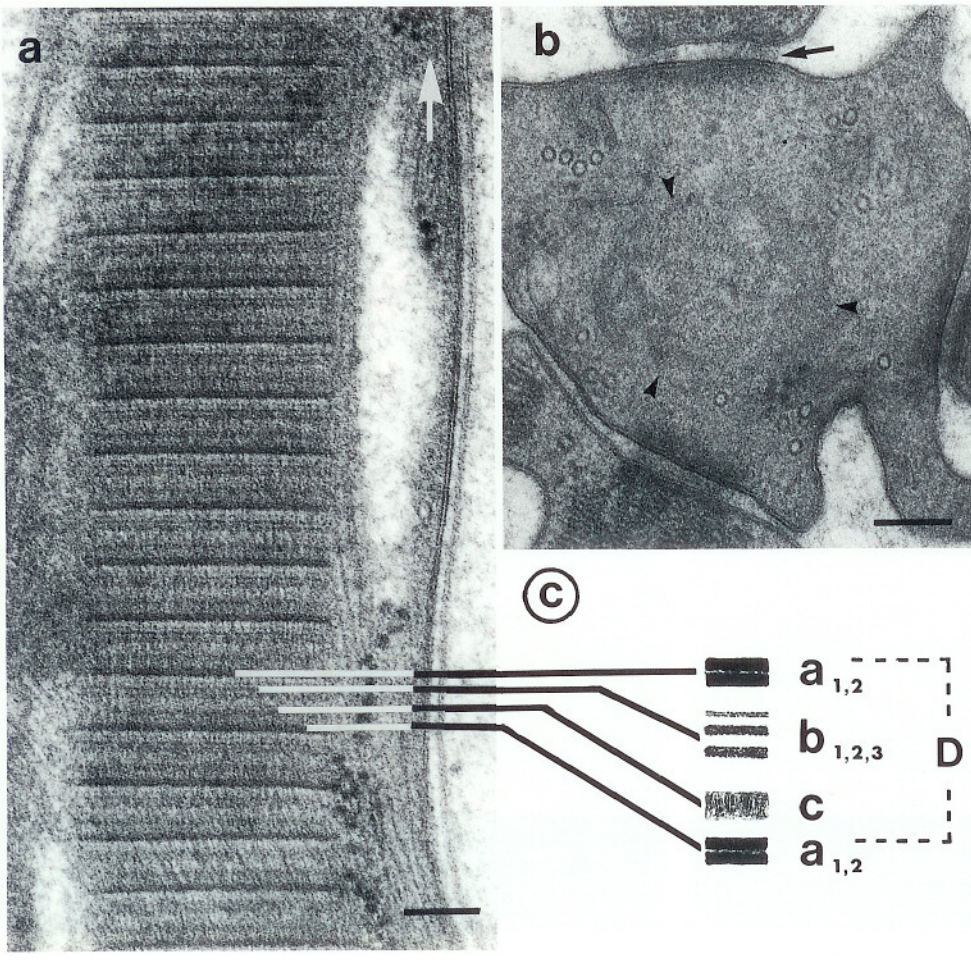


Fig. 2a–c. Ultrastructure of ciliary rootlet in scolopidia of *Schedorhinotermes lamanianus* (high-pressure freezing preparation). **a** Longitudinal section; the ciliary rootlet within the dendritic inner segment is regularly cross-striated. *Arrow* points distally to the basal bodies.
b Transverse section; the ciliary rootlet is indicated by *arrowheads* within the dendritic inner segments. Desmosomes (*arrow*) link the dendritic inner segment with the scolopale cell containing the actin filaments of the scolopale. Plane of section is indicated in Fig. 1b. **c** Scheme of cross-striation pattern: three bands *a*, *b* and *c* are visible; two sub-bands can be seen within the a-band and three sub-bands within the b-band. The periodicity *D* (distance between the main a-bands) is about 68 nm. *Bars* in **a** and **b**: 0.1 µm; ×99000

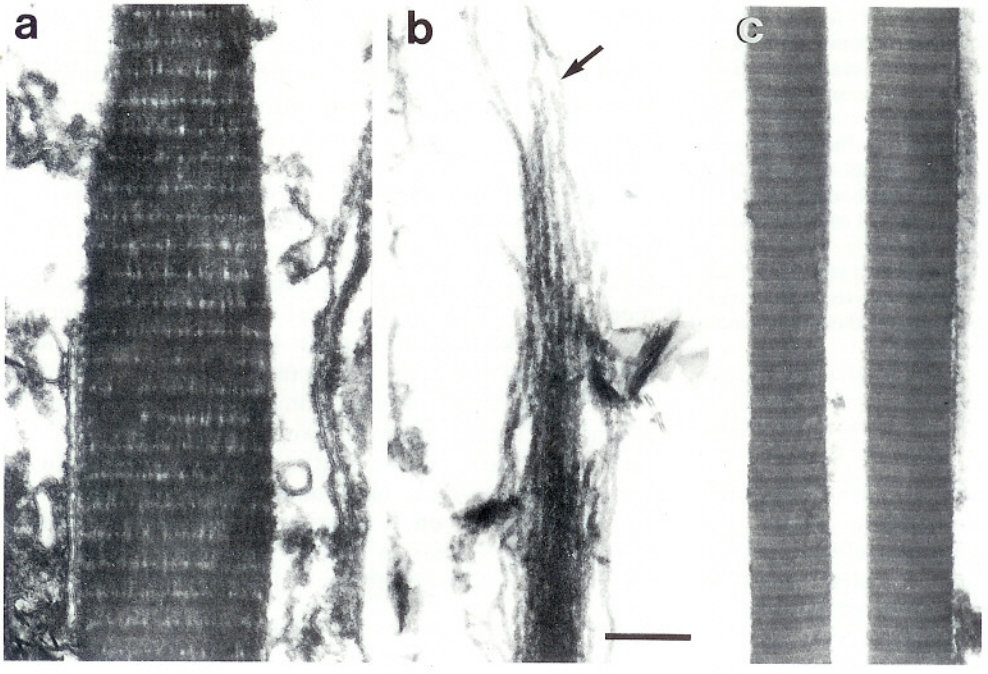


Fig. 3a–c. Collagenase digestion. Longitudinal sections through: **a** the ciliary rootlet of a scolopidium of *Periplaneta americana* treated with collagenase; **b** a collagen fibril of mouse tendon that has been digested into collagen microfibrils (*arrow*) by collagenase treatment; **c** control collagen fibrils of mouse tendon following the same treatment as in **a** and **b**, but without collagenase. *Bar*: 0.2 μm; ×58500

(Fig. 3a). In contrast, collagen fibrils of tendons of white mice, used as control tissues, were digested by the collagenase, producing microfibrils (Fig. 3b) or were even completely destroyed.

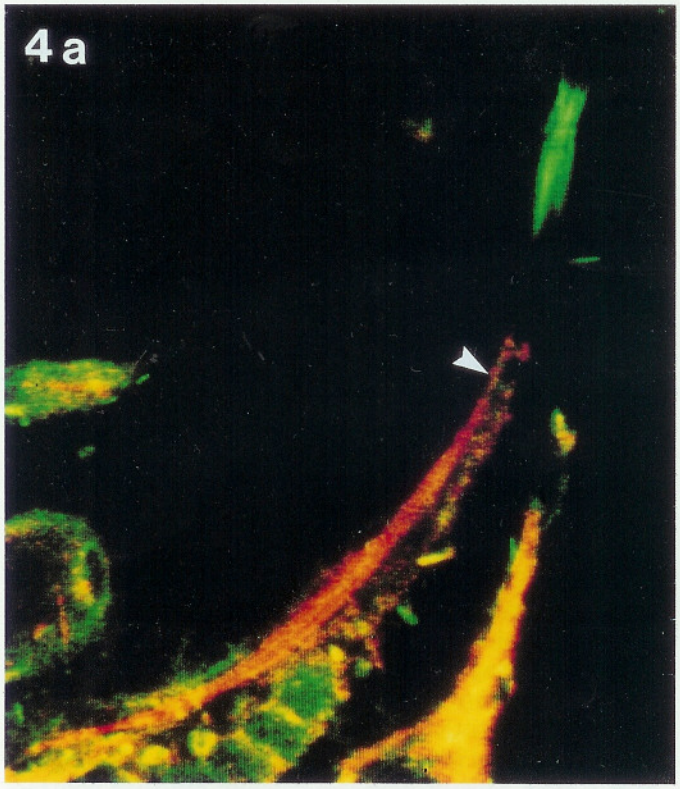
Anti-collagen. The polyclonal antibody to type-I collagen did not react with the ciliary rootlet of the scolopidia. Instead, it labeled all tissues used for controls, where collagen fibrils are known to be present: the walls of blood vessels within the cooked liver used for embedding, the extracellular part of the basement membrane of the compound eye of insects, and the sarcolemma of insect muscles (Ashhurst 1968; Carlson and Chi 1979; Alberts et al. 1983).

Anti-α-actinin. An α-actinin-like immunoreactivity demonstrated by both antibodies is present in both types of scolopidia. The rhodamine-immunofluorescence is visible in two stripes that project from the region of the scolopale-tube (detected by the phalloidin staining of their actin filament bundles (see also: Wolfrum 1990, 1991b)) down to the somata of the scolopidia (Fig. 4a). The cap, the scolopale, and the ciliary rootlets are visible with the scolopidia under Nomarski optics (Fig. 4b). The staining pattern of the double-exposure reconstruction (Fig. 4a) and superposition on the Nomarski picture (Fig. 4b) reveal that the antibodies to α-actinin react with the striated ciliary rootlets of the sensory cells of the scolopidia. In addition, the double-label experiments reveal that neither antibody to α-actinin reacts within the scolopale of the scolopidia (Fig. 4; Wolfrum 1991b).

Anti-centrin. Indirect immunofluorescence reveals that antibodies to centrin react with insect scolopidia. The localization of the reaction is ascertained by both double-labeling using anti-centrin followed by phalloidin staining, and by superposition of the resulting double-exposure double-fluorescence micrograph (Fig. 5a) on the Nomarski picture (Fig. 5b): rhodamine-phalloidin stains the actin filament bundles of the scolopale (Fig. 5a; see also Fig. 4 and Wolfrum 1990, 1991b), whereas the anti-centrin FITC-immunofluorescence occurs within the scolopidia mainly in two strands (and also in fibrillar bundles) that project proximally (Fig. 5). The respective localization of both the phalloidin-reaction and anti-centrin-reaction, and an additional superposition of the immunofluorescence and the Nomarski picture show that the anti-centrin-like immunoreactivity is located in the ciliary rootlets of the scolopidia. The stained fibrillar bundles in Fig. 5a correspond to the branched part of the ciliary rootlets (Fig. 1b).

Fig. 4a, b. Anti-α-actinin/phalloidin double-labeling in longitudinal section through a scolopidium of *Periplaneta americana*. Confocal laser scanning reconstructions: **a** indirect immunofluorescence of anti-α-actinin (rhodamine; *red*) and phalloidin-FITC fluorescence (*green*); **b** Nomarski optics. FITC-phalloidin reacts specifically with the actin filament bundles of the scolopale proximal to the cap, indicated by an *arrow*. Anti-α-actinin does not co-localize with phalloidin fluorescence; the rhodamine-immunofluorescence corresponds to the location of the ciliary rootlets (*arrowheads*) of the scolopidium. *Bar*: 10 μm; ×1000

Fig. 5a, b. Anti-centrin/phalloidin double-staining in longitudinal sections through scolopidia of *Periplaneta americana*. **a** Indirect immunofluorescence of anti-centrin (FITC; *green*) and phalloidin-rhodamine fluorescence (*red*); **b** Nomarski optics. Rhodamine-phalloidin reacts specifically with the actin filament bundles of the scolopale proximal to the cap, indicated by an *arrow*. Anti-centrin FITC-immunofluorescence corresponds to the location of the ciliary rootlets (*arrowheads*) of the scolopidia. In **a** branched rootlets are indicated by an *asterisk*; compare with Fig. 1b. *Bar*: 10 μm; ×1100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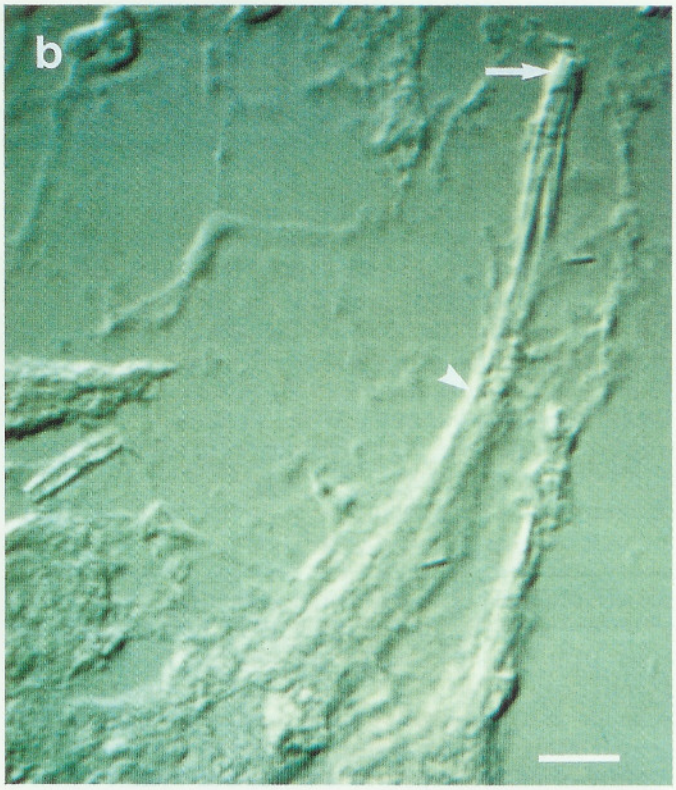
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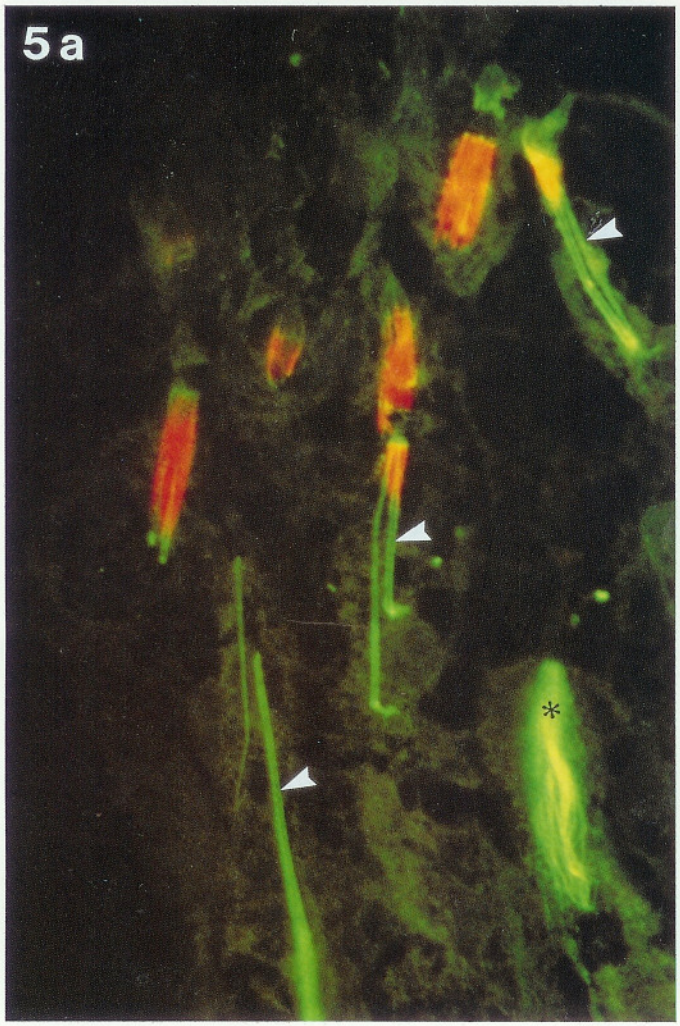
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Discussion

Striated ciliary rootlets are associated with the base of motile and non-motile cilia (Pitelka 1974). The appearance of these fibrous rootlets is, however, very variable (Sandoz et al. 1988; Harrison 1989). Whereas they are always composed of longitudinally oriented filaments (4–5 nm in diameter) showing a regular cross-striation, the periodicity of this complex striation varies between 21 nm and 900 nm (Larson and Dingle 1981; Pitelka 1974). The periodicity measured in the present study (68 nm) lies within the range of the periodicity of ciliary rootlets as found in arthropod sensilla, viz., between 55–75 nm (Gaffal and Bassemir 1974; Schmidt and Gnatzy 1984). The large variation in the periodicity in ciliary rootlets may be reflected by differences in their composition (Sandoz et al. 1988), but may also be caused by different preparation methods, including physiologically induced changes in rootlet length (e.g., contractions: Salisbury and Floyd 1978). The complex sub-striation, shown in detail for the antennal scolopidia of the lacewing *Chrysopa* (Schmidt 1969, Fig. 7), documented for other arthropods by several authors (e.g., Michel 1975; Moran and Rawley 1975; Toh and Yokohari 1985; Schmidt and Gnatzy 1984), and corroborated in the present study in cryofixed specimens, is similar in ciliary rootlets of all arthropod sensilla studied so far. Therefore, the rootlets are probably composed of the same principal components.

Components of the ciliary rootlets

The periodicity of the ciliary rootlets in the sensilla is similar to that of D-periodic collagens that show a periodicity of about 67 nm in longitudinal ultrathin sections (Ashhurst and Bailey 1980; Chapman et al. 1990). For this reason Schmidt (1969, 1974) and others, e.g., Füller and Ernst 1973; Michel 1974) have assumed a collagen-like nature of the ciliary rootlets in insect sensilla. However, the following evidence indicates that the rootlets are most probably not composed of collagen: (1) Ciliary rootlets are intracellular structures; in contrast, D-periodic collagen fibers are restricted to the extracellular space. All events involved in the formation of collagen fibrils (the cleavage of the extension peptides of the procollagen, the assembly into collagen microfibrils and mature collagen fibrils) take place within the extracellular milieu after secretion of the procollagen into the extracellular space (Prockop et al. 1979a, b; Trelstad 1982). Collagen fibrils within cells are restricted to lysosomes during collagen disassembly (Yajima 1986). (2) The ciliary rootlets withstand collagenase treatment, whereas the collagen fibrils present in control preparations of vertebrate tendons are digested. (3) Antibodies to type-I collagen, the major type of collagen present in animals, do not react with the ciliary rootlets of the insect sensilla. (4) Moreover, in another ciliated system, viz., the molluscan ciliated gill epithelium, the cilliary rootlets are also not composed of collagen fibrils (Stephens 1975). After extraction of the isolated basal apparatus of the gill, the soluble proteins were separated by SDS-gel electrophoresis. Proteins with the molecular weight of collagen or procollagen were not present in the SDS-gels.

The present immunohistochemical localization of an α-actinin-like protein in the ciliary rootlets of the scolopidia is the first localization of α-actinin or any related protein in ciliary rootlets. Moreover, the double-staining tests reveal that in the rootlets, this α-actinin-like protein is not associated with actin filaments, as found in skeletal muscle (Pollard and Cooper 1986) or desmosomal plaques (Geiger et al. 1981; Drenckhahn and Franz 1986). However, in the Z-line of skeletal muscle, α-actinin is an anchoring protein not only for actin filaments, but also for other filamentous proteins, such as titin (or connectin) and nebulin, which probably influence muscle elasticity (Maruyama 1986; Wang and Wright 1988; Nave and Weber 1990; Nave et al. 1990). Therefore, one might speculate that, in the ciliary rootlets, an α-actinin-like protein is associated with such elastic filamentous proteins.

Applied immunohistochemistry reveals that antibodies to centrin cross-react with the ciliary rootlets in insect scolopidia. Centrin is the major component of the striated flagellar or ciliary rootlets of the flagellate green algae, *Tetraselmis striata* (Salisbury et al. 1984), and occurs in other algae (e.g., Salisburg et al. 1987; Höhfeld et al. 1988; Koutoulis et al. 1988; Melkonian et al. 1988). This protein is a calcium-sensitive contractile phospho-protein of molecular weight 20 kDa (Salisbury et al. 1984; Martindale and Salisburgy 1990). The rootlets of these algae contract in response to elevated calcium concentrations (Salisbury and Floyd 1978; Salisbury 1983), centrin being largely responsible for this contraction (Salisbury et al. 1984). Since a centrin-like protein is localized in the ciliary rootlets of the scolopidia, contractions modulated by calcium may also occur in these rootlets. Here, a centrin-like protein could be associated with the α-actinin-like protein.

Functional significance of the ciliary rootlets

Ciliary rootlets in insect sensilla may, as in other ciliated cells, anchor the proximal basal body within the cytoplasm of the inner dendritic segments (Moran and Rawley 1975). The present observations indicate that the ciliary rootlets of scolopidia may additionally be involved in sensory transduction or adaptation: mechanosensitive insect sensilla generally show a wide range of adaptation behavior, from slow adaptation to very rapid adaptation, unless the stimulus is strongly oscillatory (McIver 1985; French 1988). A slow sensory adaptation has been noticed in scolopidia by Moran et al. (1977). Two hypotheses have been discussed regarding the way in which arthropod scolopidia receive stimuli. (1) Young (1970) claims that an increase in longitudinal tension on the sensory dendrites provides the necessary adequate stimulus. (2) Moran et al. (1977) assume that a lateral displacement of the extracellular cap and the dendritic tips induces an active sliding of the dendritic microtubuli doublets; this, in turn, causes a bending of the base of the dendritic outer segments and a displacement of the distal basal body in the dendritic inner segment. These

events should result in changes of the membrane permeability and a generator current.

Both hypotheses allow for a contraction or a relaxation of the ciliary rootlets being produced. This would serve in sensory transduction or adaptation of the scolopidia.

(1) If the mechanical force of a contraction of the ciliary rootlets is transmitted via the basal bodies within the dendritic inner segments to the sensory outer segments, the latter would longitudinally be placed under tension. This would reinforce the longitudinal tension of the dendrites proposed for the adequate stimulus by Young (1970). In contrast, relaxation of the ciliary rootlets would increase the force that would be necessary to place the dendrites under tension. This would represent a mechanism for sensory adaptation.

(2) Previous investigations on the scolopale, the second prominent cytoskeletal component of the scolopidia, support the hypothesis of Moran et al. (1977) (Wolfrum 1990, 1991 b). The actin filament bundles composing this structure may bend during stimulation of the scolopidia, and probably produce the necessary force to restore the cap and the dendritic tip after stimulation. Additionally, during stimulation of the scolopidia, the distal basal body and the attached ciliary base are probably tilted, and the dendritic outer segment is bent at their ciliary necklace. This has been noticed not only by Moran et al. (1977), but also by other authors (e.g., Toh and Yokohari 1985; own observations). Contraction of the ciliary rootlets could be involved in the hypothesis of Moran et al. (1977) as follows: (1) a contraction may reinforce the shift of the distal basal body and therefore the bending of the ciliary necklace during stimulation; or (2) after this shift, a contraction may build up the force required to restore the distal basal body and the ciliary necklace to their starting position; (3) an involvement in sensory adaptation of the scolopidia may also be possible, since a contraction of the rootlet may effect the degree of displacement of the distal basal body, and therefore the range of bending of the ciliary necklace.

If any of these processes occur in the sensory cells, they might be triggered by an increase in the intracellular calcium concentration (Salisbury and Floyd 1978; Sleigh 1979). Since the elasticity of the scolopale, which may also be functionally important, may additionally be influenced by changes in calcium concentration (Wolfrum 1991 b), both the range of elasticity of the scolopale and the range of contraction of the ciliary rootlets could be coupled in the scolopidia.

The present findings in the ciliary rootlets of insect sensilla may change our understanding of ciliary rootlets in arthropod sensilla. Further studies should elucidate whether these findings can be extended to other ciliary rootlets of sensory cells (e.g., the rod cells of the vertebrate eye; Spira and Milman 1979), which could have wide implications for sensory physiology.

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