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Sensory Organs in *Ips typographus (Insecta: Coleoptera)* – Fine Structure of Antennal Sensilla [1]

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Summary

The antennal sensilla in *I. typographus* are almost exclusively confined to the flattened terminal flagellar segment. The sensillar types have distinct distribution patterns in the three areas where they are found. Judging from the ultrastructural characteristics the following functions can be assigned to the sensillar types: chemoreception, single-walled and double-walled sensilla; chemoreception/mechanoreception, terminal-pore sensillum. Moreover there are two types of mechanoreceptors, one of which is connected to a bristle, whereas the other terminates within the cuticle of the flagellar segment.

Keywords: Bark beetle; Sensilla; Chemoreceptors; Mechanoreceptors; Electron microscopy.

1. Introduction

The spruce bark beetle, *Ips typographus*, is a serious forest pest, causing considerable damage to Norway spruce (*Picea abies*) in large areas of Europe. It has been shown that different substances emitted from the spruce and the aggregating beetles play an important role in the biology of this species (VITÉ and FRANCKE 1976). The interactions of different olfactory stimuli are only partly understood, but appear to result in an optimal density of bark beetles within the tree (VITÉ and FRANCKE 1976). Olfactory stimuli are not the only mode of communication in bark beetles: the presence of acoustical signals have long been known in other bark beetles, and have recently been described in *Ips typographus* (RUDINSKY 1979).

This study was undertaken to contribute to the knowledge of the antennal receptor system, *i.e.*, the sensillar sensory units in *Ips typographus*, and to provide a structural basis for physiological investigations.

2. Materials and Methods

The terminal flagellar segments of sexed, laboratory reared *Ips typographus* (L.) (SCHLYTER and CEDERHOLM 1981) were immersed in 3% glutaraldehyde in 0.2 M cacodylate buffer at 4 °C for 4 hours. To ensure penetration of the fixative the terminal segment was cut along its longitudinal axis. Postfixation was carried out in 1% OsO_4 for 2 hours. Dehydration in an alcohol series and blockstaining (1% phosphotungstic acid and 0.5% uranyl acetate) was followed by embedding in Vestopal W. Sections were made on an LKB ultramicrotome with glass knives and studied in a Zeiss EM 10. The sections were stained in lead citrate (0.5% in a 50 mM aqueous solution of NaOH).

For scanning electron microscopy (SEM) antennae were air-dried and coated with gold/palladium (40 : 60). The specimens were examined in a Cambridge Stereoscan Mark II:A.

3. Results

The antennae in *Ips typographus* are short, comprising two basal segments (scape and pedicel) and an antennal flagellum consisting of five segments. The terminal flagellar segment is flattened, having a length of 250 µm and a breadth of 200 µm. The antennal sensilla are almost completely confined to the ventral side of the terminal flagellar segment. The sensilla of the terminal segment are mainly found in three areas: an undulating band (area *A*) located at the middle part of the segment, distally another band (area *B*) and adjoining the latter

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an apical zone (area *C*) (Fig. 1). The types of sensilla and their distribution patterns are similar in areas *A* and *B*. The antennal sensilla have the same fine structural characteristics and moreover, the same distribution patterns in males and females.

3.1. Single-Walled Sensillum Type 1 (SW 1)

The SW sensillum is the most numerous type found on the antennae of *I. typographus*. They occur in areas *A*–*C*, but are especially dense in areas *A* and *B* (Fig. 2). The sensillar hair is 7–10 μm long with a basal diameter of about 1.5 μm. This sensillar type is usually innervated by two sensory cells, exceptionally by one or three: each giving rise to one sensory process which extends into the cuticular hair. In the basal part of the sensory processes the microtubules are arranged in a ciliar pattern, and this ciliar region is connected to the distal part of the dendrite by two axially arranged basal bodies and a rootlet system (Fig. 7). In the basal parts of the hair the sensory processes branch, and at higher levels the hair lumen is filled with a large number of branches (about 30, average diameter 0.1 μm), each containing 1–3 tubules (Fig. 5).

The walls of the cuticular hair are about 0.2 μm thick in the middle region, and are penetrated by a dense array of pores (about 40 pores/μm^2). At the surface of the cuticular hair the pores form longitudinal slit-like depressions, the pore funnels. The pore funnels are arranged in parallel rows along the longitudinal axis of the hair (Fig. 6). The pore channels, which measure 50–80 nm by 8 nm, lead from the pore funnels to the dilated pore kettles (diam. about 50 nm) (Figs. 5 and 6). The pore tubules originating from the pore kettles and which reach into the hair lumen have not been well preserved during the fixation processes. However, the pores of the SW sensilla in *I. typographus* have a structure similar to the SW sensilla of other species (STEINBRECHT & MÜLLER 1971).

Below the basal parts of the hair the sensory processes pass through a liquid-filled space (outer lymph cavity), which is surrounded by two enveloping cells: of these one surrounds the distal part of the outer lymph cavity, the other the proximal part. These two cells have a lamellar border towards the outer lymph cavity. The innermost enveloping cell (enveloping cell 1) forms a sheath around the dendrites of the sensory cells (Fig. 7). At the level of the ciliary region of the sensory processes, enveloping cell 1 gives rise to the cuticular sheath, which forms a thin, electron-dense envelop around the sensory processes. The cuticular sheath terminates at the level of the basal part of the hair. Inside the cuticular sheath the sensory processes are suspended in the inner lymph cavity (Fig. 7). Below the ciliar region the innermost enveloping cell forms thin lamellae (50 nm), which are arranged in whorl-like patterns (Fig. 7). The spaces between the lamellae are continuous with the inner lymph cavity. Proximally the lamellar pattern disappears and the dendrites are located within the innermost enveloping cell.

The general arrangement of sensory and enveloping cells described above is also found in the other sensillar types on the antennae of *Ips typographus*. However, the arrangement of enveloping cells has not been studied in the MBS and MCS sensilla (see below).

3.2. Single-Walled Sensillum Type 2 (SW 2)

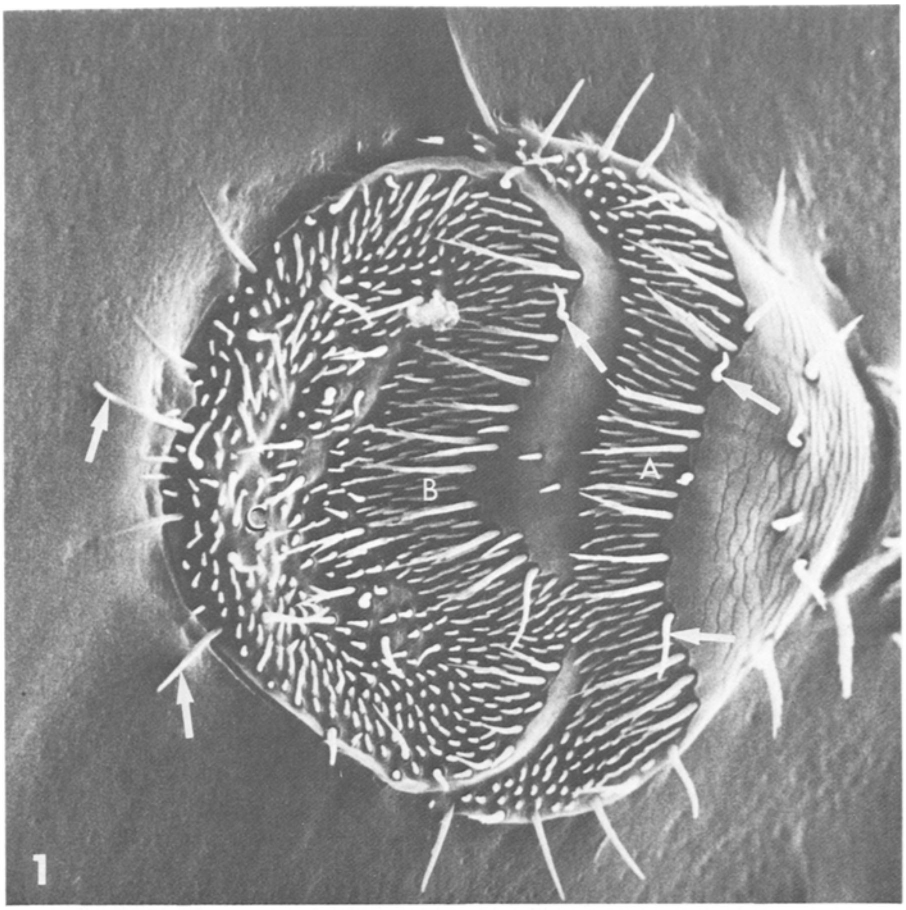
This sensillar type is predominantly found in area *C*. The sensillar hair is about 20 μm long, and its external shape is more slender than that of the SW 1 sensilla (Fig. 3). The basal diameter of the hair is about 2 μm. This sensillar type is innervated by one or two sensory cells which give rise to branched sensory processes within the cuticular hair. Compared to the SW 1 sensilla the branching is not as extensive (Fig. 8), also the branching takes place at more distal levels of the cuticular hair in SW 2 sensilla. The density of pores is lower in the SW 2 sensilla. In contrast to SW 1 sensilla, the pore kettles of SW 2 sensilla smaller and the pores are connected with the hair lumen through liquid channels (Fig. 8).

3.3. Double-Walled (DW) Sensillum

This sensillar type is found in area *A*. The cuticular hair projects about 7 μm above the antennal surface (Fig. 4). The apical part of the hair has longitudinal slit-like pores forming radial channels connecting the surface and hair lumen (Fig. 9). The DW sensilla are innervated by 2–6 sensory cells which give rise to unbranched sensory processes terminating in the apical part of the hair. The sensory processes in DW sensilla are tightly enveloped in a prominent cuticular sheath which terminates below the pores such that the hair lumen is virtually lacking. Below the hair one of the sensory processes exhibits a lamellar pattern, the lamellae partially being joined by septate junctions (Fig. 10). Above the ciliar region the sensory processes attain a rounded outline in cross section and become separated before joining the dendrites.

3.4. Terminal Pore (TP) Sensillum

The TP sensilla are found along the margins of the antennal club as well as along the proximal limits of



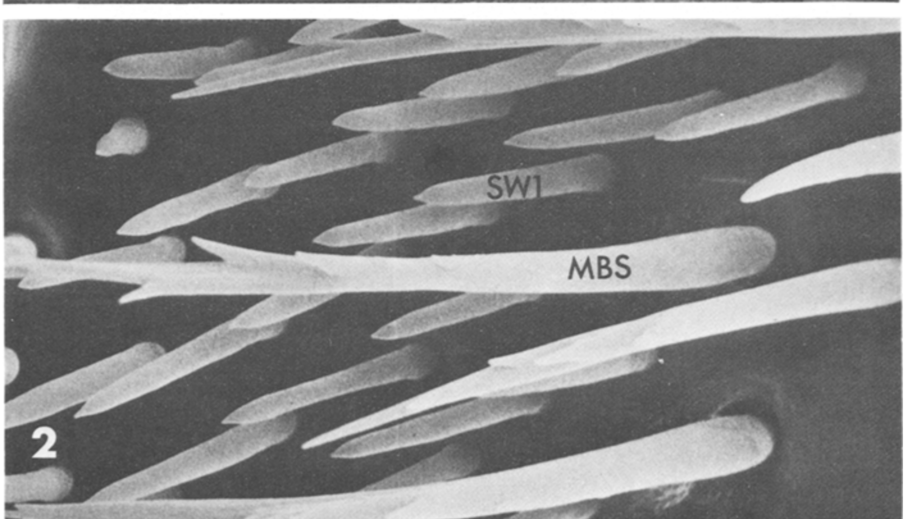
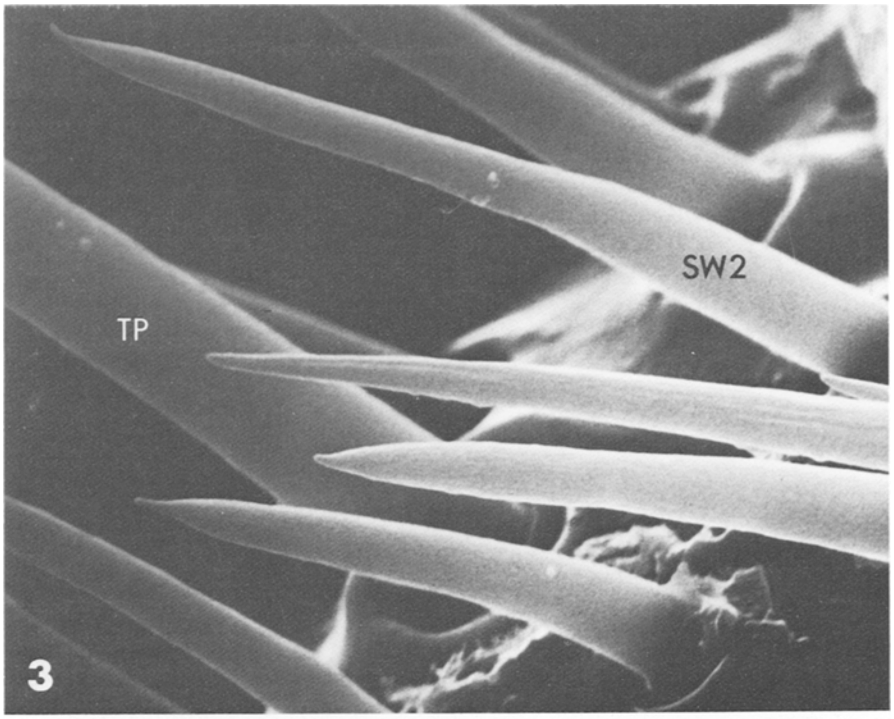


Fig. 1. The terminal flagellar segment. The sensilla are present in three areas (*A*. *B* and *C*), which have characteristic distribution patterns of the sensillar types. *Arrows*, terminal pore sensilla. SEM, ×410

Fig. 2. Mechanosensory bristles (*MBS*) are found along the proximal margin of areas *A* and *B*. *SW 1*, single-walled sensillum type 1. SEM, ×2,750



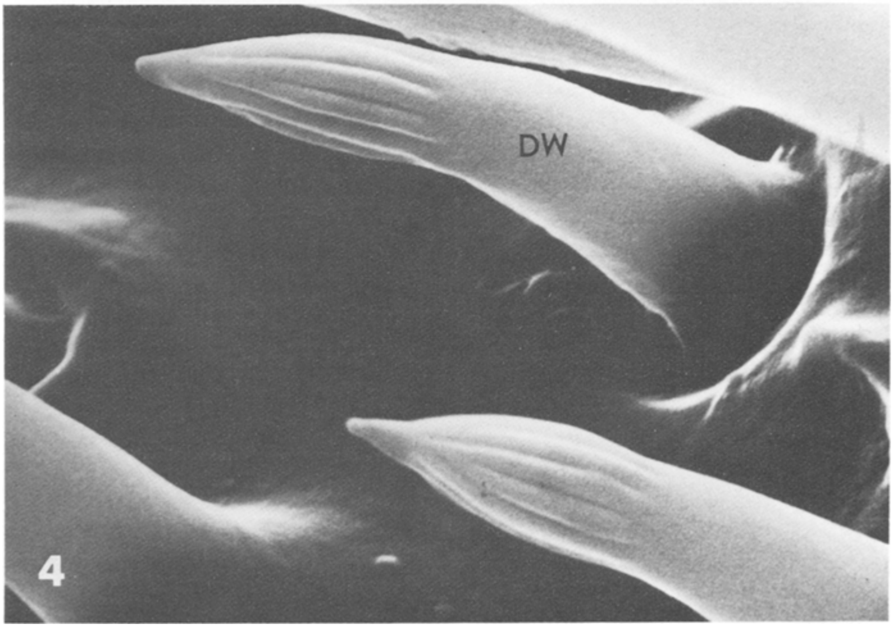
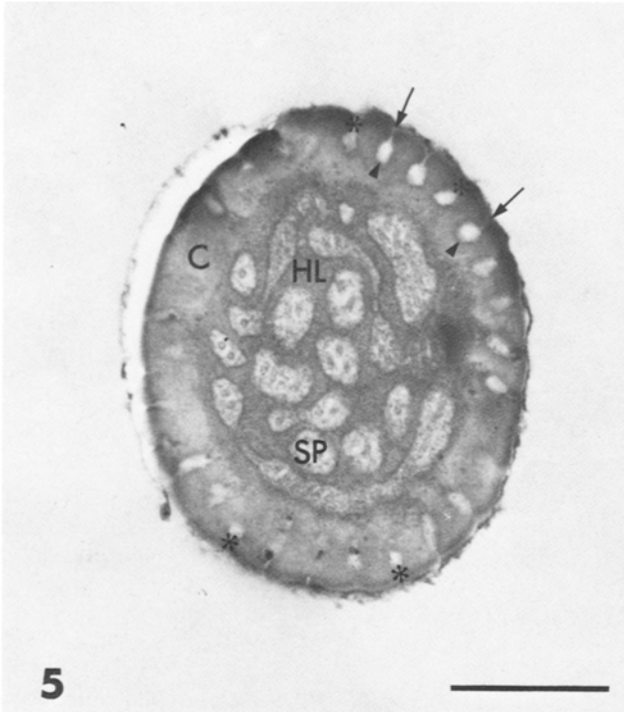
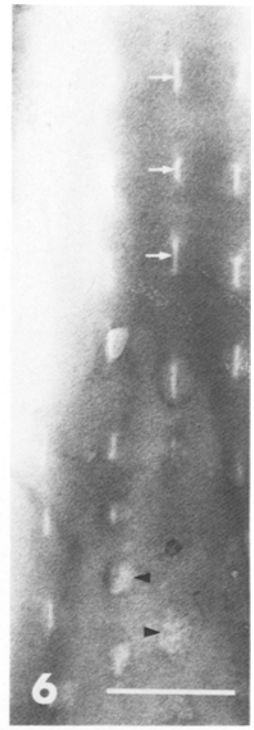


Fig. 3. Single-walled sensilla type 2 (*SW2*) are found in area *C*. *TP*, terminal pore sensilla found along the margin of the terminal flagellar segment. SEM, ×6,700

Fig. 4. Double-walled sensilla (*DW*) present in area *C*. SEM, ×13,000

areas *A* and *B* (Figs. 1 and 3). The TP sensilla are 40–50 μm long, and have a basal diameter of about 3 μm. The cuticle of the slender, slightly curved hair is smooth, lacking pores in the cuticular walls. This sensillar type is innervated by 5–6 neurones. The unbranched sensory processes are of two types (Fig. 12): one terminates with a basal body at the base of the hair indicating a mechanosensory function, whereas the others proceed into the cuticular hair (Fig. 11) terminating below a small pore. The pore has a diameter of about 0.1 μm and is filled with electron dense material. The sensory processes are enveloped in a cuticular sheath which terminates in the extreme distal part of the hair. At the level of the tubular body





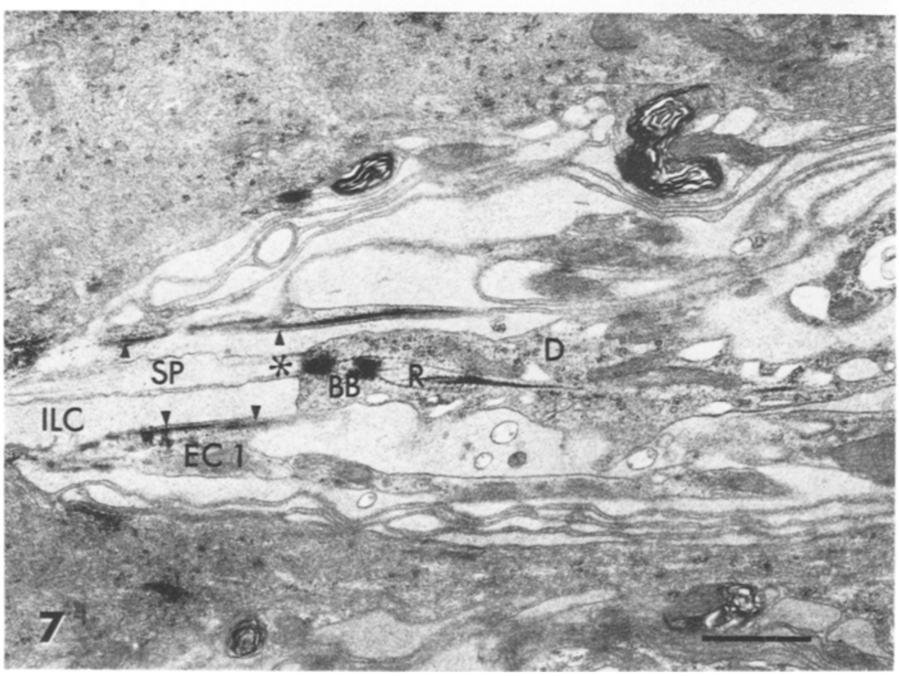
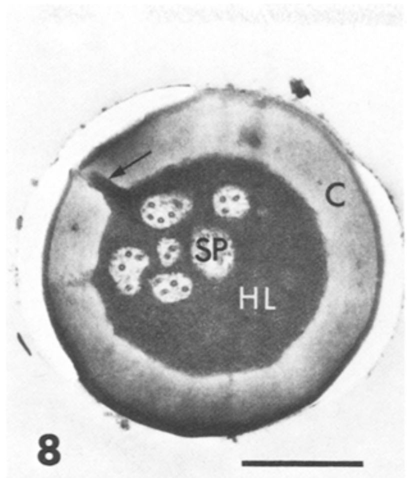
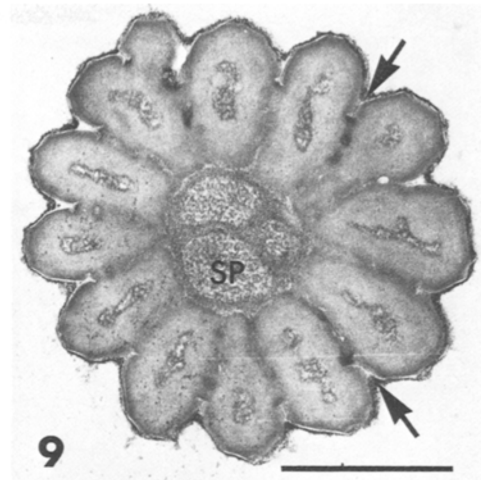


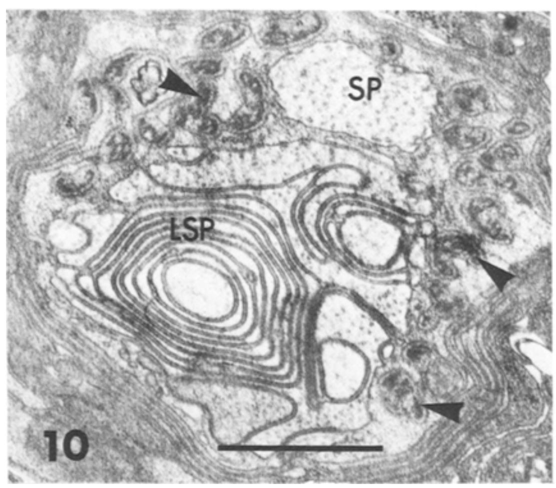
Fig. 5. Transverse section through the basal part of the hair of a single-walled sensillum type 1 (SW 1). At this level the branching of the sensory processes is not completed. Branches of the sensory processes (*SP*) are suspended in the hair lumen (*HL*). The cuticle (*C*) is penetrated by a large number of pores. Each pore starts as a small depression, pore funnels (*arrows*). The slit-like pore channels (*asterisk*) connect the pore funnels and the pore kettles (*arrowheads*). Scale: 0.5 μm

Fig. 6. Tangential section through the cuticular walls of a single-walled sensillum type 1 (SW 1) showing the longitudinal pore channels (*arrows*) and pore kettles (*arrowheads*). Scale: 0.25 μm

Fig. 7. Longitudinal section through a single-walled sensillum type 1 (SW 1). Enveloping cell 1 (*EC 1*) forms an array of thin lamellae around the dendrites (*D*), and gives rise to the cuticular sheath (*arrowheads*). The sensory processes (*SP*) are connected with the dendrites by a ciliar region (*asterisk*) and a system of basal bodies (*BB*) and rootlets (*R*). *ILC*, inner lymph cavity. Scale: 1 μm







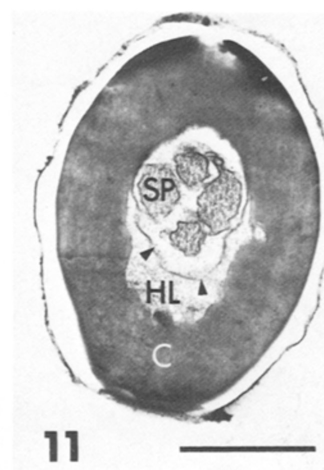


Fig. 8. Transverse section through the cuticular hair of a single-walled sensillum type 2 (SW 2). The liquid channels (*arrow*) are well developed in this sensillar type. *C*, cuticle; *HL*, hair lumen; *SP*, sensory process. Scale: 0.5 μm

Fig. 9. Transverse section through a double-walled (DW) sensillum. Radial pores (*arrows*) connect the sensory processes (*SP*) with the outside of the hair. Scale 0.5 μm

Fig. 10. Transverse section through a double-walled sensillum(DW) immediately above the ciliar region of the sensory processes (*SP*). One of the sensory processes exhibits a lamellar pattern (*LSP*). The proximal continuation of the cuticular sheath is present in enveloping cell 1 as shown by the dense depositions (*arrowheads*). Scale 1 μm

Fig. 11. Transverse section through the basal part of the hair of a terminal pore sensillum (TP). Four sensory processes (*SP*) are present within a cuticular sheath (*arrowheads*). *C*, cuticle; *HL*, hair lumen. Scale 1 μm

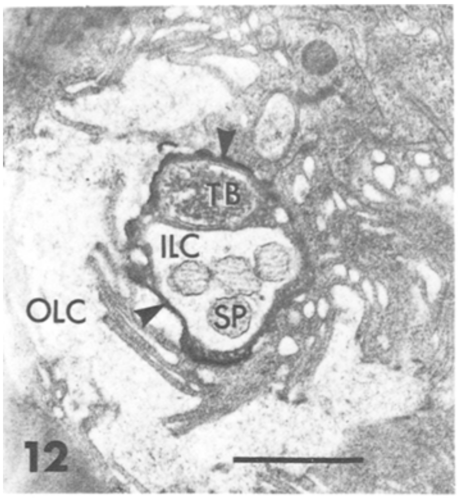
the aberrant sensory process is enveloped in a separate pocket of the cuticular sheath (Fig. 12).

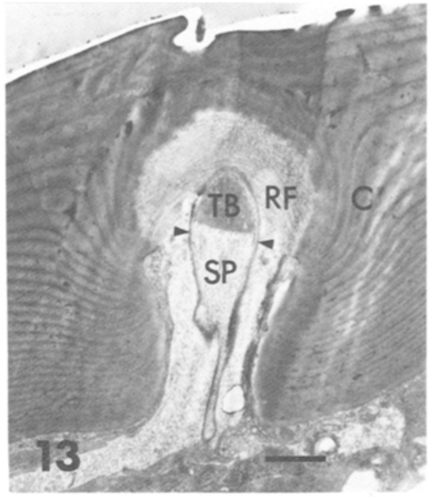
3.5. Mechanosensory Cuticle Sensillum (MCS)

The MCS sensilla are present in low numbers on the terminal flagellar segment. This sensillar type terminates within a cavity of the cuticle. The distal part of the sensory process forms a well developed tubular body which has a length of 1.5 μm and a maximal diameter of 1.0 μm. The sensory process is entirely enveloped in a cuticular sheath, which in its distal part is anchored to the cuticular walls of the cavity by a system of radial fibres (Fig. 13). The arrangement of the enveloping cells of MCS sensilla has not been studied.

3.6. Mechanosensory Bristle Sensillum (MBS)

The mechanosensory bristles are present at the proximal margins of areas *A* and *B* (Fig. 2). The bristles have two rows of teeth along their sides and are about 40 μm long. The bristles are directed towards the tip of the club, roughly parallel to the antennal surface. In cross section the bristle is homogeneous except for a narrow lumen containing an electron dense material, which usually becomes cracked during the sectioning.





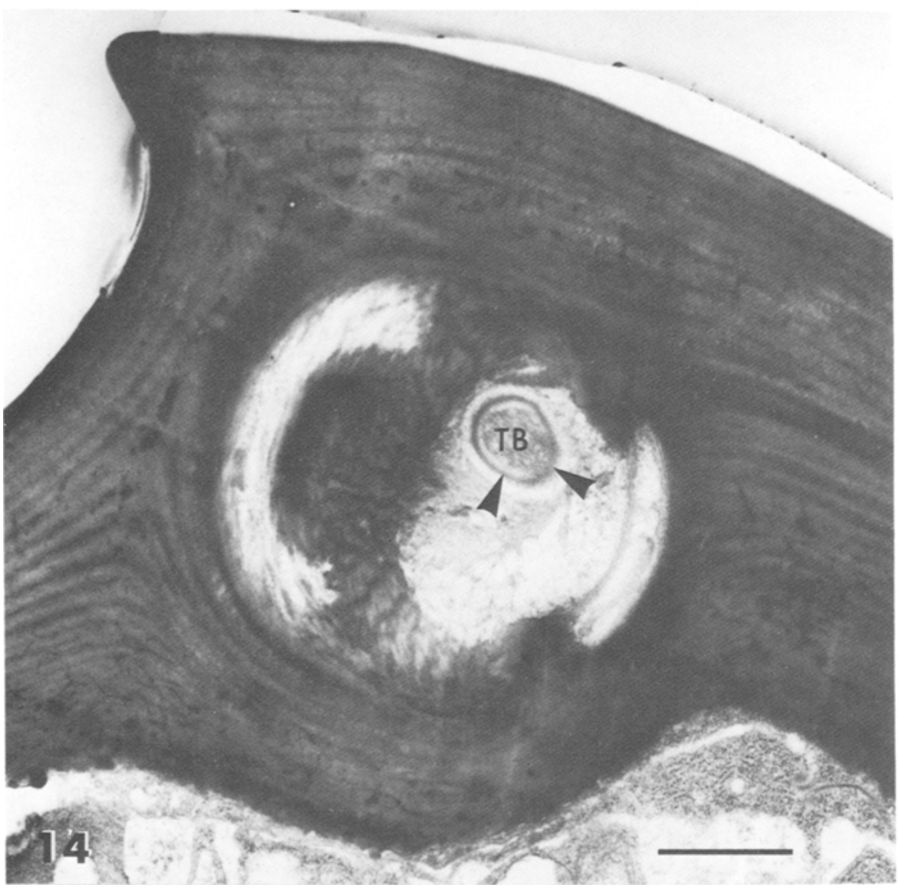


Fig. 12. Transverse section through a terminal pore sensillum (TP) below the hair. One mechanosensory unit (*TB*) and four chemoreceptive sensory processes (*SP*) are located within the cuticular sheath (*arrowheads*). *ILC*, inner lymph cavity; *OLC*, outer lymph cavity. Scale 1 μm

Fig. 13. Longitudinal section through a mechanosensory cuticular sensillum (MCS). The distal part of the sensory process (*SP*) is developed as a tubular body (*TB*). The cuticular sheath (*arrowheads*) which envelops the sensory process is connected with the cuticle (*C*) by a system of radial fibres (*RF*). Scale: 1 μm

Fig. 14. Transverse section through the basal part of a mechanosensory bristle sensillum (MBS). The sensory process terminates as a tubular body (*TB*) beneath the bristle. The tubular body is enclosed within a well developed cuticular sheath (*arrowheads*). Scale: 1 μm

Table 1. *Comparison of sensillar types found on the antennal club of Ips typographus and four other species of bark beetles: Scolytus multistriatus* (BORG and NORRIS 1971), *Dendroctonus ponderosae* (WITHEHEAD 1981), *D. frontalis* (DICKENS and PAYNE 1978) and *Trypodendron lineatum* (MOECK 1968)

Ips typographus	*Scolytus multistriatus*	*Dendroctonus ponderosae*	*D. frontalis*	*Trypodendron lineatum*
SW 1	Basiconica A	Multiporous peg	Basiconica	Basiconica
SW 2	Trichodea	Multiporous peg	Trichodea II	Trichodea II
DW	–	Fluted cone	Fluted sensillum	–
TP	–	Long uniporous peg	–	Trichodea III
MBS	Chaetica	–	–	Chaetica
MCS	–	–	–	Campaniforma
Other types	Basiconica B	Short uniporous peg	Trichodea III	–

The basal parts of the bristles are connected to the surrounding cuticle by an articulating membrane and radially arranged fibres. In the most basal part of the hair there is a sensory process which terminates as a tubular body (Fig. 14). The tubular body is eccentrically inserted into the bristle base, usually being displaced towards the side facing outward. The tubular body is about 1 μm long and has a maximal diameter of about 0.7 μm. The sensory process, including the tubular body, is enveloped in a cuticular sheath. Below the tubular body the sensory process has an irregular outline in cross section. The arrangement of enveloping cells has not been studied in the mechanosensory bristles.

4. Discussion

The fine structure of the antennal sensilla has previously been described in four species belonging to *Scolytidae* (Table 1). In Table 1 the presence of corresponding sensillar types in five bark beetle species, including *Ips typographus* are compared to show that the variation in the fine structure of any sensillar type appears limited this taxon. The variation of the antennal sensory system among bark beetles is restricted to the presence of sensillar types in a given species. In addition the arrangement of the sensillar fields is variable (PAYNE *et al.* 1973).

The table also illustrates the difficulties of the nomenclature of insect sensilla. In the present study the classification follows that of ALTNER (1977), in which the sensilla are placed in four categories: single-walled, double-walled, terminal pore and poreless. It has been shown that these four categories of sensilla are sensitive to specific modalities of stimuli (ALTNER 1977). The poreless sensilla as defined by ALTNER are lacking on the antennae of *Ips typographus*, however, in other insects this sensillar type has been shown to function in thermo/hygroreception. The MCS and MBS sensilla which have one single sensory process terminating as a tubular body also lack pores but these types of sensilla are not included in the poreless category by ALTNER. The presence of tubular bodies indicates that these sensilla are mechanoreceptors (McIVER 1975).

The single-walled sensilla of insects are chemoreceptors (ALTNER 1977) and the specific functions of single-walled sensilla of bark beetles have been described in *Ips confusus* and *Dendroctonus frontalis*. In *I. confusus* a sensitivity of the SW 2 sensilla to pheromones was supposed (BORDEN and WOOD 1966), whereas both the SW 1 and SW 2 sensilla of *D. frontalis* exhibited sensitivity to pheromones and host terpenes (DICKENS and PAYNE 1978).

Of the other sensillar types present on the antennae of *I. typographus*, the TP sensilla have the structural characteristics of bimodal chemo-/mechanoreceptors (ALTNER 1977, GAFFAL 1979). The DW sensilla of *I. typographus* have the same structure as chemoreceptive DW sensilla (ALTNER 1977). However, since the DW sensilla in some other species have been shown to contain thermoreceptors (ALTNER *et al.* 1977), this role can not be excluded in *I. typographus*. Moreover, the lamellated sensory process of the DW sensilla in *I. typographus* is similar to that of poreless sensilla in which thermoreception has been demonstrated (ALTNER 1977). Lamellated sensory processes have not been described so far in sensilla with pores (ALTNER and PRILLINGER 1980).

The antennal sensilla of *I. typographus* belong to the following functional classes: three are chemoreceptors, one is a combined chemo-/mechanoreceptor and two are mechanoreceptors. Compared with other insects, *e.g.*, lepidopterans (STEINBRECHT 1973, HALLBERG 1981) the number of chemoreceptive sensillar types is low. This low number of chemoreceptive sensillar types of this species may reflect the mode of living of these beetles, which spend a large part of their lives in the excavated tunnel system under the bark. Moreover, acustic signals are used in its communication (RUDINSKY 1979), and it has been proposed that the MBS sensilla may function in sound perception in the absence of tympanic organs (BORDEN and WOOD 1966).

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