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Ultrastructure of the Antennal Sensilla of the Oriental Fruit Fly *Bactrocera* (= *Dacus*) *dorsalis* (Hendel) (Diptera: Tephritidae)

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Wen-Yung Lee, Jui-Chun Chang, Tai-Lang Lin and Yu-Bing Hwang (1995) Ultrastructure of the antennal sensilla of the orienal fruit fly, *Bactrocera* (= *Dacus*) *dorsalis* (Hendel) (Diptera: Tephritidae). *Zoological Studies* **34**(1): 21-28. Ultrastructure of the antennal sensilla on the funiculus of *Bactrocera dorsalis* is distinguished into two groups: the single-walled sensilla and the double-walled sensilla. The single-walled sensilla are further divied into those with thick-walled-pore and those with thin-walled-pore. The former have thick cuticular sensillar wall about 0.18-0.38 μm in thickness. The pore openings are small and the density of pores is only 11 to 12 pores per square micron. One or two dendrites appear in each sensillar lumen and they connect with one or two sensory cells. The latter have a thin cuticular walls about 0.05-0.15 μm in thickness. The density of pores is about 25 pores per square micron. The pore openings are large with a circular pore below the cuticular wall. Twenty to sixty dendritic branches appear in the distal region of the sensillar lumen. In the clavate sensilla, besides the dendritic branches, there is a lamella or rolled dendritic structure on the midregion of the sensillar lumen, with one or two sensory cells at the base of the sensilla, below the cuticular part. The double walled sensilla contains an original cuticular sensilla wall and 10 to 12 ridges to make a double walled structure which appears as a stellate structure in cross section. These sensilla include two sensory neurons and two to four dendritic branches in the sensillar lumen.

Key words: Ultrastructure, Thick-walled-pore sensilla, Thin-walled-pore sensilla, Double-walled sensilla.

The antennae of insects are the major chemoreceptors for detecting and distinguishing airborne stimulants, as well as for evoking suitable behaviors, such as feeding, mating or oviposition. Seven types of sensilla on the funiculus (as referring to the third antennal segment) of *Bactrocera dorsalis* antennae have been morphologically described through use of the scanning electron microscopy by Lee et al. (1994). The seven morphological types are: the trichoid type I and type II, the basiconic type I and II, the clavate type I and II, and the styloconic (grooved) sensilla. The morphology and distribution, as well as the number, of each type of sensillum exhibits no sexual dimorphism in this fly. Although considerable information is available on the ultrastructure of antennal sensilla of Dipterans (Bay and Pitts 1976, Chu-Wang et al. 1975, Dickens et al. 1988, Hallberg et al. 1985, Lewis 1971, McIver 1960 1978, Slifer and Sekhan 1964, Sutcliffe et al. 1990, Venkatesh and Singh 1984), little is known about the detailed ultrastructure of the antennal sensilla of *B. dorsalis*. Accordingly, this investigation is along with our previous morphological studies on the antennal sensilla of *B. dorsalis*, extends our knowledge of the ultrastructure of the antennal sensilla in this insect.

MATERIALS AND METHODS

The *B. dorsalis* flies were obtained from the laboratory colony at the Institute of Zoology, Academia Sinica. The disected antennae of the flies were immersed in 2.5% glutaraldehyde in 0.1 M cacodylate buffer for 6 hrs at 6°C before

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shaking for two minutes to cleanse the surface of the antennae. A slight vacuum was applied to remove the air bubbles from inside and outside the tissue specimens. These antennae were post-fixed in 2% osmium tetraxide plus 0.1 M cacodylate buffer at 6°C for 2 hrs, then stained with 25% aqueous uranyl acetate after washing with distilled water. Dehydration was accomplished through a graded series of ethanol from fifty percent to absolute, then propylene oxide was used for infiltration. The specimens were embedded in Spurr's (1969) low viscosity medium. Thin sections (ca. 800 Å) were made with a diamond knife and were picked up on copper grids with 0.3% formvar supporting membrane, then stained with uranyl acetate in 50% alcohol and lead citrate. These preparations were viewed with Hitachi H-7000 transmission electron microscope at 75 kv or 100 kv a accelerating voltages.

RESULTS

The antennae of *B. dorsalis* consist of three segments; the scape, the pedicel and the funiculus. The chaetica and the microtrichoids occur on the scape and the pedicel. Many sensilla are distributed on the funiculus among the microtrichoids. A sensory pit is located on the external surface, about one-fifth of distance from the proximal region of the funiculus.

The ultrastructure of the cuticular wall of these sensilla on the funiculus of *B. dorsalis* can be distinguished into two groups: Single-walled sensilla and double-walled sensilla. Single-walled sensilla are further divided into those with thick-walled-pore and those with thin-walled-pore.

Thick-walled-pore sensilla

Thick-walled-pore sensilla characterize the trichoid type I sensilla (Fig. 1), with a thick cuticular wall. The thickness of the cuticular wall is about 0.25-0.38 μm at the base and about 0.18-0.2 μm at the distal region. The thickness appears to decrease from the base to the tip of the sensilla. The external openings of the pores are very small, ranging from 100 to 200 Å. The distance between any two openings is about 0.35-0.5 μm; thus, the density of the openings on the sensilla is only about 11-12 pores per square micron. Internally, each pore connects to the sensillar lumen through a funnel-like structure. The lumen is filled with an electron dense material. One or two dendrites appear in each sensillum. Individual dendrites contain different numbers of microtubules.

The structures at the base of the sensillum are composed of one or two sensory cells connected with the outer dendritic segment. A receptor lymph cavity surrounds the outer dendritic segment. Epidermal cells appear at the sides of the sensory cells (Fig. 1a).

Thin-walled-pore sensilla

Thin-walled-pore sensilla occur in several morphological types on the funiculus of the *dorsalis* fly antennae: trichoid type II sensilla, clavate sensilla and basiconic sensilla. Their ultrastructures (Figs. 2, 3) are similar and they have thin cuticular walls, ranging from about 0.05 to 0.15 μm. The external opening of each pore is about 300-800 Å. The distance between any two openings is about 0.1-0.2 μm or even less. Therefore, the density of the pores on these sensilla is about 25 pores per square micron. These sensilla are also called multiple-pore sensilla. Below the cuticular wall, each pore widens to form a cuticular chamber (Figs. 2b, 3b) referred to as the "pore kettle" by Ernst (1969) with diameters two or more times those of the pore openings. Several tubules radiate to the sensillar lumen from the pore kettle. The outer dendritic system (Figs. 2a, 3a) appears as one dendrite at the basal part of the sensillum which ramifies toward the distal region into about twenty to sixty dendritic branches scattered in the sensillar lumen (Figs. 2b, c). The dendritic branches contain a different numbers of microtubules.

In the clavate sensilla (Fig. 3), in addition to the ultrastructure described above, the outer dendritic segment has lamellar membranes (Fig. 3b), or circular membranes (Fig. 3c) in a regular arrangement up to the midregion of the sensillar lumen, with several microtubules located between the membranes.

The sensory cell of the thin-walled-pore sensilla is commonly associated with the outer dendritic system. The enveloping epidermal cells are at the sides of the sensory cell (Fig. 3a).

Double-walled sensilla

Double-walled sensilla occur in the styloconic sensilla (the grooved sensilla). Dethier et al. (1963) referred to these sensilla as the stellate, or coronal pegs from their appearance in cross section. With the stellate grooved structure of the outer wall and the original cuticular wall as the inner wall, these sensilla form a double-walled structure (Fig. 4c). In cross section, these sensilla show ten to twelve stellates for the most part (Figs. 4c, d) with numbers gradually decreasing toward the tip of the sensillum (Fig. 4b).

The thickness of the double walls is about 0.21-0.25 μm; the outer stellate cuticule is about 0.15-0.20 μm thick; the inner cuticular wall (the original wall) is about 0.05-0.08 μm thick. In cross section (Figs. 4b, c, d), the grooves appear as clefts between two stellates. A radial spoke channel leads from each groove to the sensillar lumen. The extrasensillar lumens within the double wall and the sensillar lumen are filled with an electron-dense material (referred to as the receptorlymph).

The double-wall sensillum usually includes two sensory neurons which connect to the outer dendritic system at the basal region. The dendrite

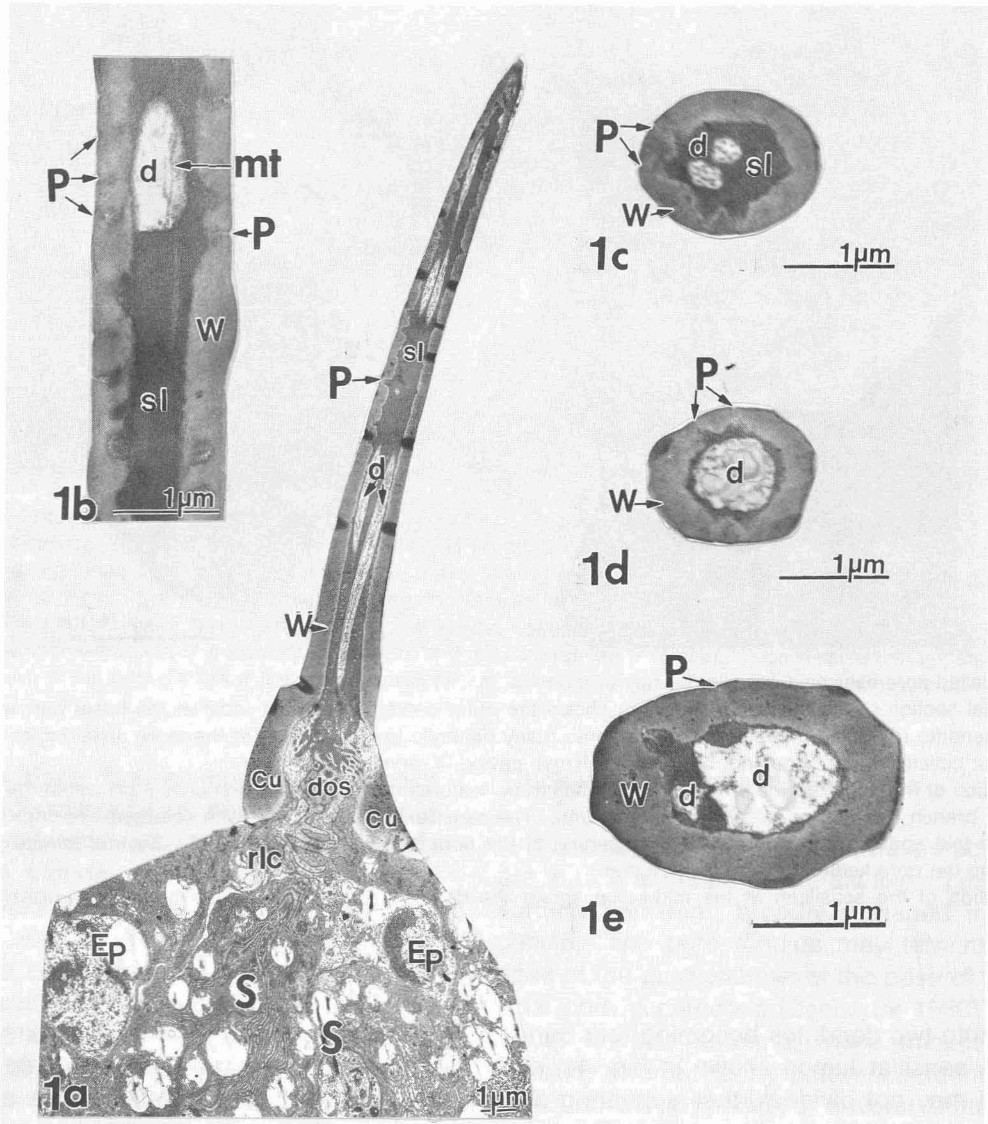

Fig. 1. Thick-walled-pore sensilla.

1a. The longitudinal section shows two dendrites (d) within the sensillar lumen (sl). Two sensory cells (S) appear between the epidermal cells (Ep) at the base of the sensillum. Cu: cuticle, dos: outer dendritic segment, P: pore opening, rlc: receptor lymph cavity, W: sensillar wall.

1b. A sensillum at the base has one dendrite (d) within the sensillar lumen (sl). The small openings of pores (P) are located in the thick cuticular wall (W). mt: microtubule.

1c-1d. Cross sections of the sensilla at the midregion; that in Fig. 1c has two dendrites (d) within the sensillar lumen (sl) and that of Fig. 1d has one. A few pores (P) can be seen in the cuticular wall (W).

1e. The cross section of a sensillum at the base which shows one big and one small dendrite (d) in the sensillar lumen. P: pore opening, W: sensillar wall.

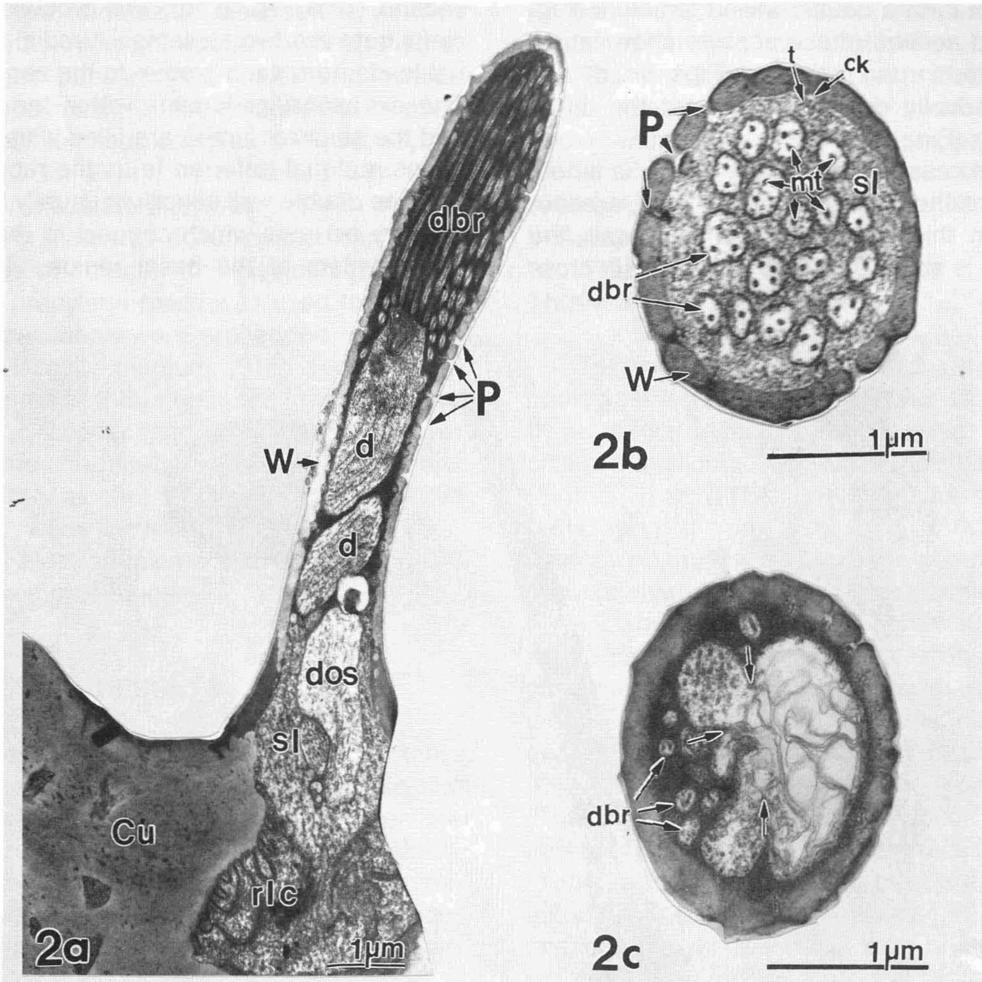

Fig. 2. Thin-walled-pore basiconic sensillum.

2a. Longitudinal section of the basiconic sensillum shows the outer dendritic segment (dos) at the basal part of the sensillum. A single dendrite (d) at the midregion is divided into many dendritic branches (dbr) in the more distal region of the sensillar lumen. Cu: cuticle, P: pore opening, rlc: receptor lymph cavity, W: sensillar wall.

2b. Cross section of the upper region of the basiconic sensillum features many dendritic branches (dbr) within the sensillar lumen (sl). Each branch has one or more microtubules (mt). The sensillar wall (W) is thin with enlarged openings of pores (P). A pore kettle (ck) appears continuous with the opening of the pore below the cuticular wall. Several minute pore tubules (t) extend from the pore kettle to the sensillar lumen.

2c. Cross section of the sensillum at the midregion shows the dendrite dividing into many branches (arrows). dbr: dendritic branches.

may divide into two dendrites becoming four dendrites in the sensillar lumen shown in Fig. 4c, or the dendrite may not divide further appearing as two dendrites in the sensillar lumen as in Fig. 4d. At the terminal region, the sensillar lumen is filled with the electron-dense material and no dendritic endings can be observed (Fig. 4b).

The sensory pit

The sensory pit contains the thin-walled basiconic sensilla, the grooved double-walled sensilla and several small microtrichial hairs. The ultrastructure of the thin-walled basiconic sensilla and the grooved double-walled sensilla are the same as thin-walled-pore sensilla and double-walled sensilla on the funicular surface. It is not necessary to described them here.

DISCUSSION

The typical insect sensillum is a hairlike structure with the upper cuticular part protruding from

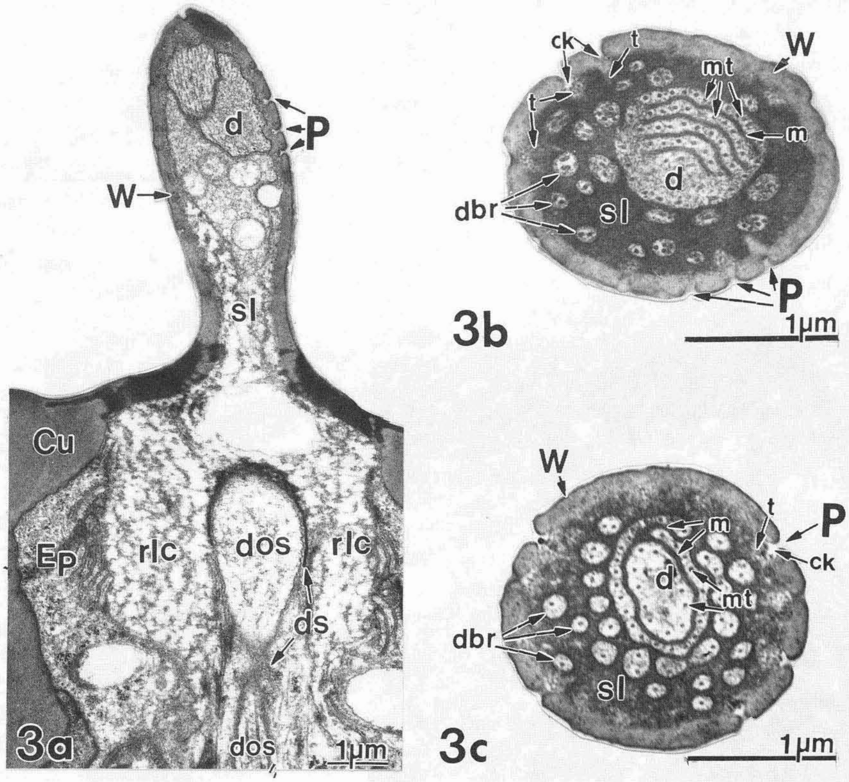

Fig. 3. Thin-walled-pore clavate sensillum.
3a. Longitudinal section of the clavate sensillium, two dendrites (d) appear within the sensillar lumen (sl). An outer dendritic segment (dos) is surrounded by the dendritic sheath (ds) within the receptor lymph cavity (rlc). Epidermal cells (Ep) are at the sides of the sensory cell. Cu: cuticle, P: pore opening, W: sensillar wall.
3b-3c. Cross sections of a clavate sensillum at the midregion, the dendrite (d) has a lamellar (Fig. 3b) and a circular (Fig. 3c) structure. The microtubules (mt) are arranged between two membranes (m) of lamella. A pore kettle (ck) appears continuous with the opening of the pore (P) below the cuticular wall (W). sl: sensillar lumen. dbr: dendritic branches, t: pore tubules.

the antennal surface; one or more sensory cells and related epidermal cells are below the antennal surface. The epidermal cells usually involve sheath producing cells, tricogen cells and tormogen cells. The bipolar sensory neuron projects an outer dendritic segment toward the hairlike structure and an axon to the central nervous system. A large subcuticular cavity, the receptor space, joins the hair lumen and surrounds the dendrite (Keil and Steinbrecht 1982, Zacharuk 1980).

The outer dendrite system usually ramifies into two branches or remains single in the sensillar lumen of thick-walled-pores sensilla. It may subdivide into more than ten branches in thin-walled-pore sensilla. All these outer dendritic segments are within the receptorlymph of the sensillar lumen. Air or odor molecules are presumed to enter or diffuse to the lumen along the pores of the cuticular hair wall and reach the dendrites either via direct contacts or via the receptorlymph (Keil and Steinbrecht 1982).

Thick-walled-pore sensilla

The cuticular wall of thick-walled-pore sensilla are thick and the pores are slit-like on the sensillar surface becoming broadly v-shaped in the wall cuticle. The pore tubules may terminate at the apex of the pore channel at the base of the superficial pore constriction (Zacharuk 1980). Besides on *B. dorsalis* antenna, these thick-walled-pore sensilla, referred to by different terminology, are found on the antennae of several Dipterans: the long single walled sensilla of *B. oleae* (Hallberg et al. 1980), the thick-walled multiporous pitted sensilla of *Anastrapha ludens* (Dickens et al. 1988), the thick-walled sensilla tricholea of *Musca autumnalis* (Bay and Pitt 1976), the thick-walled multiporous sensilla of the syrphid flies (Hood Henderson and Wellington 1982), the sharp-tipped trichodea of *Culicoides furens* (Chu-Wang et al. 1985), the short, pointed tipped sensillum tricho-

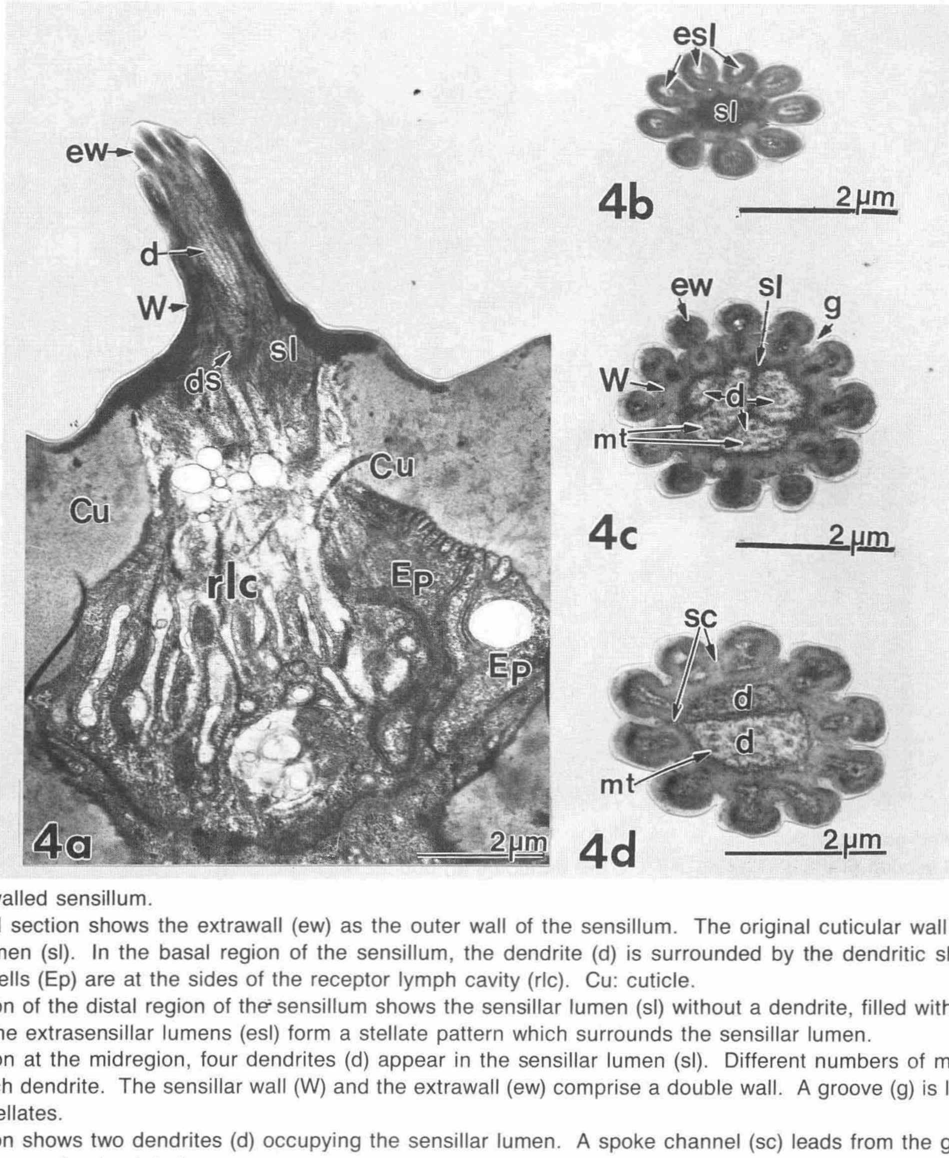

Fig. 4. Double-walled sensillum.

4a. Longitudinal section shows the extrawall (ew) as the outer wall of the sensillum. The original cuticular wall (W) is near the sensillar lumen (sl). In the basal region of the sensillum, the dendrite (d) is surrounded by the dendritic sheath (ds). The epidermal cells (Ep) are at the sides of the receptor lymph cavity (rlc). Cu: cuticle.

4b. Cross section of the distal region of the sensillum shows the sensillar lumen (sl) without a dendrite, filled with electron-dense material. The extrasensillar lumens (esl) form a stellate pattern which surrounds the sensillar lumen.

4c. Cross section at the midregion, four dendrites (d) appear in the sensillar lumen (sl). Different numbers of microtubules (mt) occur in each dendrite. The sensillar wall (W) and the extrawall (ew) comprise a double wall. A groove (g) is located between each two stellates.

4d. Cross section shows two dendrites (d) occupying the sensillar lumen. A spoke channel (sc) leads from the groove (g) to the sensillar lumen. mt: microtubules.

deum of *Aedes aegypti* (McIver 1978) and the sensillum trichodeum of *Simulium arctieum* (Sutcliffe et al. 1990).

Thin-walled-pore sensilla

Thin-walled-pore sensilla on the funiculus of *B. dorsalis* have larger pores with greater density than in thick-walled-pore sensilla. Meanwhile, these sensilla show evidence of pore kettles and pore tubules associated with the dendrites in the sensillar lumen, which thick-walled-pore sensilla do not show. Zacharuk (1980) mentioned that in thin-walled-pore sensilla, the pores open into an enlarged circular pore kettle, the pore tubules extend from the inner wall and scatter into the underlying dendritic chamber. He also stated in 1985 that the thin-walled multiple pores sensilla (MPPS) have a wider odor response spectrum than the thick-walled MPPS because of their enlarged pore openings. As to the postantennal organ of Collembola, their pore kettles have external openings and provide channels from the kettles to underlying sensillar chambers. A dense secretion often underlines the sensory cuticle and fills the pore kettle. This apparently serves as an outward secreting and inward stimulus-conducting mechanism (Altner and Thies 1976).

Thin-walled-pore sensilla are common on dipteran antennae, such as the short single-walled sensilla of *B. oleae* (Hallberg et al. 1984), the thin-walled multiporus pitted sensilla of *A. ludens* (Dickens et al. 1988), the sensilla basiconica of *Drosophila melanogaster* (Venkatesh and singh 1984), the thin walled peg of *Sarcophaga argyrostoma* (Slifer and Sekhon 1964) the basiconic sensilla of *Stomoxys calcitrans* (Lewis 1971), the thin-walled sensillum basiconcium of *M. autumnalis* (Bay and Pitt 1976), the blunt tipped sensilla trichodea of *Ae. aegypti* (Mclver 1978), the multiporous thin sensilla of some Syrphidae (Hood Henderson and Wellington 1982) and the sensilla basiconic of *S. arcticum* (Sutcliffe et al. 1990). An atypical thin-walled-pore sensillum with unbranched dendrites appears in some sensilla basiconic of *S. arcticum* (Sutcliffe et al. 1990). These sensilla are not found in *B. dorsalis* antenna, nor are there any records from other Dipterans.

The ultrastructures of lamellar and circular menbranes at the midregion of the outer dendritic segment appear in the clavate sensilla of *B. dorsalis* antenna. These sensilla belong to the thin-walled-pore snesilla based on the presence of a thin cuticular sensillar wall and the multiple pores. These lamellated structures are also reported in the clavate sensilla of *S. calcitrans* antennae by Lewis (1971), in the sensilla coeloconic and internal sensilla of the antennal tip of the mosquito *Deinocerites cancer* by Mclver and Siemicki (1976), and in the thin-walled sensilla (mpp) of several *Syrphus* with a large rolled dendrite rolled by Hood Henderson and Wellington (1982). The lamellation can be the result of different processes in which the outer dendritic segment is branched, one of them is flattened and interdigitated or rolled (Altner and Prillinger 1980). Mclver and Siemicki (1976) discribed ussed the function of the lamelled dendrite as possibily sensitive to infrared radiation or mechanical stimuli.

Double-walled sensilla

Double-walled sensilla are not numerous in most insects and are located primarily on the antennae (Zacharuk 1985). However, these sensilla are found in large numbers on *B. dorsalis* and *B. tryoni* (Giannakakis and Fletcher 1985) and also known from the antennae of *B. oleae* (Hallberg et al. 1984), *Sarco. argyrostoma* (Slifer and Sekhon 1964), *S. calcitrans* (Lewis 1971), *M. autumnalis* (Bay and Pitts 1976, *Syrphus* (Hood Henderson and Wellington 1982), and *S. arcticum* (Sutcliffe et al. 1990). The main characteristic of these sensilla is a stellate, grooved appearence in cross section. These sensilla do not have pore tubules. Zacharuk (1985) reported that a dense substance from the dendritic chamber (sensillar lumen) fills the spoke canals and apparently flows out over the groove surface. This was presumed to be the trapping and conduction mechanism for the chemical stimulant.

Thick-walled-pore sensilla have a thick cuticular wall and small pore openings while thin-walled-pore sensilla have a thin cuticular wall and enlarged pore openings. Both types of sensilla have pore tubules and have been shown to be chemosensory, and primarily olfactory. Thick-walled-pore sensilla seem to be more selective, some may be stimulated by pheromones, and thus are referred to as "specialist" sensilla on this basis. Thin-walled-pore sensilla generally have a wider range of chemosensitivity and are referred to as "generalist." Some of thin-walled-pore sensilla with lamelled dendrites were shown in some biting flies to respond to carbon dioxide (Zacharuk 1985). Double-walled sensilla consist of the original cuticular wall plus a ridged structure. These sensilla do not have pore tubules but have spoke canals, some of which are thermo- and hygrosensory, and some are thermo- and chemosensory (Altner and Prillinger 1980).

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東方果實蠅*Bactrocera* (=*Dacus*) *dorsalis*觸角感覺毛之微細結構

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利用穿透性電子顯微鏡研究東方果實蠅觸角感覺毛之微細結構，可分為兩類，單層感覺毛(single-walled sensilla)和雙層感覺毛(double-walled sensilla)。單層感覺毛又分有厚壁有孔感覺毛(thick-walled-pore sensilla)和薄壁有孔感覺毛(thin-walled-pore sensilla)。形態學上之毛狀第一型感覺毛(trichoid type I sensilla)屬於厚壁感覺毛，毛壁厚，厚度約0.18-0.38μm，壁孔小而疏。毛腔內具神經細胞(sensory cell)一或兩個。在形態上之毛狀第二感覺毛(trichoid type II sensilla)，突出感覺毛(basiconic sensilla)和棒狀感覺毛(clavate sensilla)屬薄壁有孔感覺毛，其毛壁薄，厚度約0.05-0.15μm，壁孔大而密，感覺毛上部之毛腔具有許多經樹突分支(dendritic branches)，基部在體壁內具一或兩個神經細胞。棒狀感毛之微細構造，毛腔內除樹突分支外，還有呈層狀或環狀之樹突。雙層感覺毛為形態學上之時針感覺毛(styloconic sensilla)或稱為溝感覺毛(grooved sensilla)。由於原來體壁外著腔內具 2 或 4 條樹突，係由兩個基部之神經細胞發出之神經樹突，不分支或分支而呈 2 或 4 條樹突。

關鍵詞：微細構造, 厚壁有孔感覺毛, 薄壁有孔感覺毛, 雙層感覺毛。

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