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Fine structure of the galeal styloconic sensilla of larval *Lymantria dispar* (Lepidoptera: Lymantriidae)

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Abstract

Lepidopteran larvae possess two pairs of styloconic sensilla located on the maxillary galea. These sensilla, namely the lateral and medial styloconic sensilla, are each comprised of a smaller cone, which is inserted into a style. They are thought to play an important role in host-plant selection and are the main organs involved in feeding. Ultrastructural examination of these sensilla of fifth instar *Lymantria dispar* (L.) larvae reveal that they are each approximately 70 μ m in length and 30 μ m in width. Each sensillum consists of a single sensory peg inserted into the socket of a large style. Each peg bears a slightly subapical terminal pore averaging 317 nm in lateral and 179 nm in medial sensilla. Each sensillum houses five bipolar neurons. The proximal dendritic segment of each neuron gives rise to an unbranched distal dendritic segment. Four of these dendrites terminate near the tip of the sensillum below the pore and bear ultrastructural features consistent with contact chemosensilla. The fifth distal dendrite terminates near the base of the peg and bears ultrastructural features consistent with mechanosensilla. Thus, these sensilla each bear a bimodal chemo-mechanosensory function. The distal dendrites lie within the dendritic channel and are enclosed by a dendritic sheath. The intermediate and outer sheath cells enclose a large sensillar sinus, whereas the smaller ciliary sinus is enclosed by the inner cell. The neurons are ensheathed successively by the inner, intermediate, and outer sheath cells.

Keywords

sensillum; gustation; gypsy moth; ultrastructure; styloconic

Gypsy moth larvae, *Lymantria dispar* (L.) are major pest defoliators in most of the United States and destroy millions of acres of trees annually. This larva is highly polyphagous and displays a wide host plant preference, feeding on the foliage of hundreds of plants, but favoring leaves of deciduous hardwood trees, such as oak, maple, and sweet gum (Mosher 1915; Liebhold et al. 1995; Shields et al. 2003).

Lepidopteran larvae, such as gypsy moth larvae, possess gustatory and olfactory chemosensilla located on the antennae, maxillary palps, and epipharynx, as well as a pair of styloconic sensilla (lateral and medial) on each maxillary galea. Food plant recognition is predominantly governed by the activity of the styloconic sensilla (Schoonhoven 1972). In the literature, the lateral and medial styloconic sensilla have been referred to as “large cones” (Forbes 1910), “sensilla styloconica” and “Z2” and “Z1” (Schoonhoven and Dethier (1966), “sensilla styloconica” and Ss-I” and “Ss-II (Ishikawa 1967), “sensilla styloconica” and “SsII” and SsI (Ma, 1972); “uniporous pegs” and “LST” and “MST” (Albert 1980); “uniporous pegs” and “I” and

“m” (Devitt and Smith 1982), and “sensilla styloconica” and “LSS” and “MSS” (Grimes and Neunzig 1986).

The styloconic sensilla are considered to be bimodal contact chemo-mechanosensilla. Each sensillum bears four gustatory dendrites and a single mechanosensory dendrite. These eight pairs of gustatory cells are part of a total of approximately 59 paired chemoreceptor cells present in lepidopteran larvae (Schoonhoven and van Loon 2002). When the larvae are feeding, these sensilla are in continuous contact with the plant sap. Interestingly, Städler and Hanson (1975) reported in *Manduca sexta*, that while styloconic sensilla bear primarily a gustatory function, they also perform an olfactory role for short distances, such as in the detection of leaf odor.

Electrophysiological studies on gypsy moth larvae (V.D.S., unpublished data), as well as other lepidopteran species, have revealed that gustation is mediated by four neurons within each styloconic sensillum (e.g., Ishikawa 1967; Schoonhoven and Dethier 1966; Dethier and Kuch 1971; Dethier 1973; Albert 1980; Shields and Mitchell 1995). Sensory input is encoded as patterns of nerve impulses and sent to higher processing centers in the brain of the insect. While many studies have focused on the electrophysiological responses of both lateral and medial stylconic sensilla of many lepidopteran species, detailed ultrastructural analyses of these taste sensilla are relatively sparse and have been carried out in only a few species (e.g., Ma 1972; Devitt and Smith 1982; Wieczorek 1976; Gaffal 1979; Shields 1994). This is surprising, considering the underlying physiological importance of these sensilla to the insect. In general, having a knowledge of the ultrastructure of these taste sensilla (e.g., number of neurons innervating each styloconic sensillum), prior to carrying out electrophysiological studies may contribute to advancing our understanding of taste recognition and coding. It may also allow us to unravel some of the principles that govern food selection behavior, providing us with a better understanding of the factors that make many lepidopteran larval species, e.g., *L. dispar*, such effective pests.

MATERIALS AND METHODS

Animals

L. dispar eggs (New Jersey strain) were obtained from USDA-APHIS, Otis Air National Guard Base (Falmouth, Massachusetts). The larvae were reared on a high wheat germ artificial diet (Bio-Serv, Frenchtown, NJ) and maintained at 24–26°C, ca. 60% humidity, and a 12 h light: 12 h dark photoperiod regimen (Shields et al. 2003). Fifth instar larvae, 12–18 h postmost, were used for all experiments.

Scanning Electron Microscopy

For scanning electron microscopy (SEM), heads were isolated, sonicated for 30 s in 1% Triton-X-100 detergent, rinsed several rinses of distilled water, and fixed for 24 h in chilled in 5% glutaraldehyde in Millonig's phosphate buffer (pH 6.9–7.1) containing 0.54% glucose. After fixation, the heads were rinsed in several changes of distilled water, followed by three rinses (15 min each) in phosphate buffer, postfixed in buffered 1% osmium tetroxide for 24 h, rinsed in several changes of distilled water, and sonicated for 20 s in phosphate buffer, serially dehydrated for 30 min, each, in an ascending ethanol starting at 70%, and critical point dried from CO₂ carbon dioxide (DCP-1, Denton Vacuum, Moorestown, NJ). The specimens were then mounted on aluminum stubs, evaporatively coated with gold-palladium (60:40) (DV-503 vacuum evaporator, Denton Vacuum, Moorestown, NJ) at 8.5 nm and viewed at 2.4 kV in a Hitachi S-4700 field emission scanning electron microscope.

Transmission Electron Microscopy

For transmission electron microscopy (TEM), heads were severed and the ventral mouthparts were dissected out in chilled 5% glutaraldehyde in Millonig's phosphate buffer containing 54% glucose. The specimens were then rinsed for 20 mins, each in two changes of phosphate buffer, postfixed for 2 h in buffered 2% OsO₄ in at room temperature, briefly rinsed in distilled water, block-stained in 1% uranyl acetate in 70% ethanol for 1 hour, and serially dehydrated for 10-min periods in ethanol, starting at 50%, and embedded in Spurr's resin (1 part ethanol: 1 part Spurr's for 2–4 h, followed by 1 part of the above mixture: 1 part ethanol for 4 h), and then put in a loosely capped container in a rotator, overnight. Following this, the specimens were then placed in fresh resin and left in a vacuum desiccator for 7 h. The samples were then placed in an oven at 70°C for 10 h. Ultrathin transverse and longitudinal sections were prepared from five specimens in cross section and two, in longitudinal section, on a Reichert-Jung Ultracut E microtome with a diamond knife (Diatome, Hatfield, PA). These sections were mounted on Pioloform-coated slotgrids and double stained with aqueous 2% uranyl acetate (30 min) and aqueous 0.2% lead citrate (5 min). The sections were viewed in a JEOL 100 S and a Zeiss EM 10 CA transmission electron microscope at 80 KV.

RESULTS

External ultrastructure of galeal sensilla

The labrum, mandibles, maxillae, labium, and hypopharynx comprise the ventral mouthparts and involved in feeding (Fig. 1, 2). The styloconic sensilla (lateral and medial) are found on the galea and comprise the maxilla, in addition to the maxillary palp (Figs. 3, 4). The galea bears five externally conspicuous sensilla: two uniporous, socketed styloconic sensilla (lateral and medial) and three aporous unsocketed basiconic sensilla, which occupy a ventro-anterior position (Fig. 4). These sensilla are all innervated by the lateral and medial branches of the galeal nerve, which eventually gives rise to the maxillary nerve and subesophageal ganglion. A campaniform sensillum, often distinct on the external midventral galeal wall of many lepidopteran larvae, was not identified in *L. dispar* larvae.

Each uniporous styloconic sensillum comprises a small socketed peg or cone that inserts into the fibrous cuticular sockets of a taller style (Figs. 3, 4). The styles of each sensillum stand erect on the superior galeal surface (Figs. 3, 4). The lateral styloconic sensillum is positioned in closest proximity to the maxillary palp (Fig. 3). Both styloconic sensilla are similar in height; however lateral sensilla appear slightly taller (70.5 µm) than medial sensilla (67.9 µm). A more detailed account of external ultrastructural features, including measurements of the styloconic sensilla, as well as the other galeal sensilla of *L. dispar*, has already been described in Shields (1996). The peg of the medial styloconic sensillum is deflected laterally (toward the maxillary palp) (Figs. 3, 4) and a slightly subapical pore is positioned ventrally, measuring 179 nm ± 15 (S.E.) (Fig. 4a). The medial style is also rotated laterally (Figs. 3, 4). The peg of the lateral styloconic sensillum is deflected ventrally and a slightly subapical pore is positioned laterally, measuring 317 nm ± 15 (S.E.) (Fig. 4b).

Fine structure of the styloconic sensilla

A schematic representation of a uniporous styloconic sensilla is shown in Fig. 18. The lateral and medial styloconic sensilla are each innervated by five bipolar neurons. Their staggered cell bodies lie within the galea at various depths. From each cell body, a dendrite extends distally and an axon, proximally (Fig. 18). Each dendrite is divided into a distal (outer) thin segment and a proximal (inner) thicker segment (Fig. 18). Approximately midway along its length, an abrupt constriction occurs and demarcates the ciliary region (Fig. 18). The distal dendritic segment contains only microtubules, whereas the proximal dendritic segment and cell bodies

contain organelles, such as mitochondria, vesicles, Golgi bodies, free ribosomes, and rough and smooth endoplasmic reticula.

Conspicuous fenestrated fibrils are located directly beneath the slightly subapical terminal pore of each styloconic sensillum (Fig. 5a). In addition, an electron-dense, possibly viscous exudate originating from the underlying dendritic channel, was visible in the pores of some specimens (Figs. 5a, 6a). Four, unbranched distal dendrites are enclosed by the dendritic sheath and extend within the dendritic channel into the peg of each sensillum (Figs. 5–7, 18), terminating at varying distances beneath the pore (Fig. 18). No gap junctions were observed between the distal dendrites. The distal dendrites lie in close proximity with one another within the dendritic channel (Figs. 5–14, 18) and are bathed in fluid, continuous with that found in the ciliary sinus, proximally (Figs. 15, 18). The dendritic sheath completely separates the dendrites within the dendritic channel from the sensillar sinus (Fig. 18). Near the pore, the dendritic sheath is fused with the cuticular wall of the peg (Fig. 18).

Near the base of the peg, the remaining fifth unbranched distal dendrite terminates in a tubular body in both lateral and medial styloconic sensilla (Figs. 8–10, 18). The tubular body is comprised of an accumulation of longitudinally oriented microtubules in an electron-dense matrix. This dendrite is closely apposed to one side of the dendritic sheath and peg cuticle (Figs. 8–10, 18). At the level of the tubular body and just proximal to its termination (Fig. 11), the distal dendrite containing the tubular body appears to be held in place by at least one longitudinal inward fold of the dendritic sheath (Figs. 8, 9). The dendritic channel is apposed to one side of the peg and continues proximally in close association with the wall of the style (Figs. 8, 9).

Near the apical termination of the intermediate sheath cell, the dendritic sheath develops longitudinal infoldings, which partly or wholly compartmentalizes some of the distal dendrites (Figs. 12–14), not including the mechanosensory one. The dendritic sheath wraps all five neurons and terminates just distal to the ciliary sinus (Figs. 15, 18). Just prior to the ciliary region, the microtubules within the distal dendritic segments become peripherally distributed. As the narrow distal dendritic segment inserts into the broader proximal one, the microtubules are arranged along the periphery of the dendrite in a typical $9 \times 2 + 0$ pattern. At the distal end of the proximal dendritic segment, two longitudinally oriented, centriole-like basal bodies are arranged in tandem (Fig. 15, 18). They each bear a $9 \times 3 + 0$ microtubular arrangement. Striated rootlets extend proximally from each distal basal body towards the cell body of each neuron (Figs. 15, 18).

The lateral and medial styloconic sensilla are each associated with three sheath cells: inner, intermediate, and outer (Fig. 18). The outer sheath cell encloses the large sensillar sinus and bears a microvillate outer surface (Fig. 18). The intermediate sheath cell envelopes the inner sheath cell for most of its length and lines part of the sensillar sinus (Fig. 18). The inner sheath cell wraps the neuronal cell bodies, the proximal dendritic segment and the basal part of the distal dendritic segments, near where the dendritic sheath terminates (Figs. 15–18). This sheath cell also encloses the ciliary sinus (Figs. 15, 18). Near the proximal end of the dendritic sheath, the inner sheath cell also becomes thinner and more highly infolded into the ciliary sinus and forms elongate, longitudinal, desmosomal junctions of the zonula adhaerens type with the dendrites (Figs. 15, 18). Along the inner border of the inner sheath cell, clusters of longitudinally oriented 6 nm diameter actin-like fibrils and 23 diameter microtubules become embedded in a dense, amorphous matrix and form a close association with the proximal dendrites through these junctions (Fig. 15). All three sheath cells contain mitochondria, vesicles, microtubules, free ribosomes, Golgi bodies, and rough endoplasmic reticula. More proximally, the three sheath cells eventually successively draw to one side, each ending in an

expansion containing the nucleus. Micrographs showing structures proximal to those in Figs. 16 and 17 are not included in this paper, but are similar to those reported in Shields, 1994.

DISCUSSION

The present ultrastructural study examines the fine structure of the galeal lateral and medial uniporous styloconic sensilla of *L. dispar* larvae. These sensilla play an important role during feeding and have been tested electrophysiologically in *L. dispar* and confirmed to be gustatory in function (Dethier and Kuch 1971; Schoonhoven 1972; Shields 2006). The lateral and medial styloconic sensilla stand erect on the galeal surface and are positioned in close proximity to one another; the lateral sensillum is closest to the maxillary palp. At the tip of the peg of each sensillum a terminal pore is found, which is positioned slightly subapically. Stimulating chemicals enter through the terminal pore and diffuse towards the four underlying gustatory neurons. In *L. dispar*, the distal dendrites of these neurons extend into the lumen of the peg and terminate at various levels below the pore. A similar arrangement of neurons has been reported in the uniporous sensilla of other lepidopteran species (e.g., Ma 1972; Shields 1994, Asaoka 2003). In only 1% of the specimens of *L. dispar*, terminal branching of one or two of the distal dendrites was observed, a feature also described in some other lepidopteran species (e.g., Schoonhoven and Dethier 1966; Shields 1994). While distal dendritic branching is a feature commonly observed in olfactory (multiporous) sensilla, it is rarely observed in gustatory (uniporous) sensilla (Zacharuk 1980; Zacharuk and Shields 1991). Potentially, the presence of gap junctions may play a role in mediating interactions between the taste cells within a sensillum, however no gap junctions were observed to occur between the distal dendrites.

A fifth dendrite terminates in a tubular body near the base of the peg and is presumed to be mechanosensitive, based on its ultrastructure. The tubular body of the mechanosensory neuron of *L. dispar* is composed of longitudinally-oriented microtubules embedded in an electron-dense matrix and is similar to those described in the styloconic sensilla of other lepidopteran species (e.g., Schoonhoven and Dethier 1966; Ma, 1972; Wieczorek 1976; Gaffal (1979); Albert (1980); Devitt and Smith 1982; Shields 1994; Asaoka 2003). It is tightly apposed to one side of the dendritic sheath and peg cuticle and often appears to be held in place by at least one longitudinal fold of the dendritic sheath. This neuron is thought to monitor contact of the sensillum with the substrate during feeding (Ma 1972).

In *L. dispar*, the dendritic sheath encloses the dendritic channel until the level of the distal termination of the intermediate sheath cell. At this level, the dendritic sheath develops inward folds and completely compartmentalizes some of the distal dendrites. In *L. dispar*, complete compartmentalization of the mechanosensory distal dendrite did not occur. In contrast, Ma (1972) and Asaoka (2003) described the complete compartmentalization of this distal dendrite in the styloconic sensilla of two lepidopteran species. Interestingly, Shields (1994) reported the complete compartmentalization of all five distal dendrites in only 1% of the specimens of *Mamestra configurata*. The compartmentalization of dendrites may provide stability to them in this region.

Cytoskeletal elements in the inner sheath cell, consisting of actin-like microfilaments and microtubules were observed in *L. dispar*, similar to those observed in other lepidopteran larvae (e.g. Shields 1994; Asaoka 2003). These structures are associated with desmosomal junctions of the zonula adhaerens type (Zacharuk 1980) between the distal region of the proximal dendritic segments and the inner sheath cell. It is likely that these junctions provide stability and protection to the proximal dendritic segments (Zacharuk 1985), they can also be sites of secretion, providing nutrients to the dendrites (Scott and Zacharuk 1971).

The lateral and medial styloconic sensilla are each associated with three sheath cells: inner, intermediate, and outer, as described in the sensilla of other lepidopteran larvae (e.g., Shields 1994). While the role of the inner sheath cell most probably is to secrete nutrients into the ciliary sinus (Philips and Vande Berg 1976; Zacharuk 1980; 1985), the intermediate and outer sheath cells presumably sequester nutrients for cellular maintenance and sinus liquor production (Philips and Vande Berg 1976; Zacharuk 1980; 1985).

The present study complements an earlier paper by Shields (1996), which examined the permeability and diffusion pathways of both styloconic sensilla of *L. dispar*, as well as five other lepidopteran species, to aqueous chloride solutions of the heavy metal ions, cobalt, mercury, and lead. Based on the detailed knowledge of the fine structure of the lateral and medial styloconic sensilla of *L. dispar* presented here, it is now possible to better understand the results of the diffusion pathway study. Only the results from the cobalt and mercury permeability experiments are discussed here. The diffusion pathways (i.e., how cobalt and mercury ions entered and diffused within the lateral and medial styloconic sensilla) were easily visualized following sulfiding of the preparation which resulted in a black precipitate. Such diffusion pathways are, in fact, meant to simulate the fate of taste chemicals entering into the sensilla and interacting with the underlying distal dendrites when the insect is feeding. Similar studies have also been carried on different insect species using the same or other dyes (e.g., Slifer 1954; Schafer and Sanchez 1976; Baker 1987; Albert et al. 1993).

In *L. dispar*, as well as in the other lepidopteran species investigated, cobalt ions permeated through the terminal pore and into the dendritic channel housing the distal dendrites of both lateral and medial styloconic sensilla (Shields 1996). In contrast, mercury ions became trapped within the terminal pore and did not diffuse beyond this point. It is clear from the fine structure of the apparent plug of fenestrated fibrils, found directly beneath the pore in *L. dispar* in this study, that it may act to confer selectivity by allowing the diffusion of certain chemicals, but not others (Zacharuk 1980; 1985; Zacharuk and Shields 1991). The underlying mechanism for diffusion could be as follows (Shields 1996): if the fibrillar pore matrix is presumably comprised of sulfhydryl proteinaceous components, it would likely bind mercury ions irreversibly and create a plug, preventing diffusion. Such a result would not occur with the use of cobalt ions. A similar fibrillar pore matrix has been described in other lepidopteran larva (e.g., Ma 1972; Gaffal 1979; Shields 1994).

Interestingly, the large variation in terminal pore diameter between lateral and medial styloconic sensilla of *L. dispar* ($317 \text{ nm} \pm 15 \text{ (S.E.) nm}$ versus $179 \text{ nm} \pm 15 \text{ (S.E.)}$, respectively) described in the present study, appeared to correlate well with differences observed in the diffusion of cobalt ions (Shields 1996). Lateral sensilla were found to be more permeable than medial sensilla in *L. dispar*. However, this correlation did not hold up for all lepidopteran larvae tested in that study.

In addition to cobalt ions permeating through the terminal pore and into the dendritic channel of *L. dispar*, Shields (1996) also found that cobalt ions diffused into the sensillar sinus in three locations: i) near the tip of the sensillum; ii) in the region of the insertion of the peg into the style, and iii) at the apex of the style and termination of the intermediate sheath cell, where the distal dendrites became temporarily partly or completely compartmentalized by the dendritic sheath. These pathways could be explained by hypothesizing that the dendritic sheath is permeable in some regions. The results of the present ultrastructural study in *L. dispar* do, in fact, support this hypothesis. The appearance of the dendritic sheath in the region of the terminal pore was thinner, as well as porous. In the region of the insertion of the peg into the style and at the apex of the style, the dendritic sheath appeared to be porous. These apparent small pores within the dendritic sheath could have allowed the diffusion of cobalt ions from the dendritic channel surrounding the dendrites to the surrounding sensillar sinus. Dendritic sheath porosity

in the region where the distal dendrites became temporarily partly or completely compartmentalized was also observed ultrastructurally by French and Sanders (1979).

The smaller pores (i.e., sidewall pores), identified ultrastructurally by TEM and SEM surrounding the terminal pore, could not be ruled out in having contributed to the diffusion of cobalt ions into the sensillar sinus near the tip of peg (Shields 1996). Results of the diffusion study indicated that cobalt, but not mercury ions, were permeable through these pores (Shields 1996). Zacharuk (1980; 1985) also postulated that materials could be sequestered and transported from the sensillar sinus to the cuticular surface of the peg.

In some specimens of *L. dispar*, an electron exudate was observed ultrastructurally just below the terminal pore in both lateral and medial styloconic sensilla. This exudate was also noted on the cuticular surface surrounding the terminal, slightly subapical, pore in some specimens of *L. dispar*, as viewed by SEM (not shown since the successful visualization of pores by SEM often requires special cleaning procedures to minimize or remove such deposits). Blaney and Chapman (1969), Pietra and Angioy (1982), and other authors, noted the importance of pore extrusion from the dendritic channel and proposed that it continually fills the pore, possibly to act as a conduction medium. Chapman and Bernays (1989) suggested that as the insect first encounters a leaf surface, initial stimulation of its contact chemoreceptors would likely involve compounds derived from dry surfaces, rather than those released in plant sap. These stimulating compounds would then combine and dissolve in the conduction medium prior to binding to receptor sites on the distal dendritic terminals, resulting in the generation of nerve impulses (Zacharuk 1980; 1985; Zacharuk and Shields 1991). In blowflies, Pietra et al. (1980) suggested that this substance contained acid mucopolysaccharides and could act as a selective filter for stimulating compounds. Alternatively, such pore extrusions may temporarily block materials from entering into the terminal pore, as is commonly observed when viewing this region with the aid of scanning electron microscope. This temporary blockage may explain why some styloconic sensilla are not responsive to stimuli when performing electrophysiological experiments.

While this ultrastructural study has provided detailed information regarding the morphology of both the lateral and medial styloconic sensilla, electrophysiological studies are underway to determine the molecular receptive range and sensitivity capabilities of these sensilla to various stimulants and deterrent compounds.

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Figs. 1–4.

SEM micrographs. The specimens in Figs. 1–4 were critical point dried. Fig. 1. Frontal view of whole head showing an abundance of trichoid hairs covering the entire head surface. Bar = 1 mm. Fig. 2. Ventro-anterior view of the ventral mouthparts. la, labium; ma, maxilla. Bar = 500 μ m. Fig. 3. Superior-ventral view of the left maxilla (ma) showing the galea (g), maxillary palp (p), lateral (l with arrow) and medial (m with arrow) styloconic sensilla and dorsal guard hairs (h). Bar = 100 μ m. Fig. 4. Superior-ventral view of the tip of a left galea (g) and lateral (l) and medial (m) styloconic sensilla. Each styloconic sensillum consists of a small terminal conical peg (c with arrow) inserted into a socket on a large style (s with arrow). The style of the medial styloconic sensillum is laterally rotated (toward the lateral styloconic sensillum), and curved. The peg of the medial sensillum is laterally deflected, whereas the peg of the lateral sensillum is ventrally deflected. In addition, three aporous basiconic sensilla are also visible: a spire-shaped sensillum (sp with arrow) positioned near the medial styloconic sensillum, in addition to basiconic lateral (lb with arrow) and medial (mb with arrow) sensilla. Bar = 50 μ m. The insets show a higher magnification view of the slightly subapical position of the terminal pore of a medial (a) and lateral (b) styloconic sensillum, in addition to the sidewall pores (white arrows) surrounding the terminal pore. Inset bars in A and B = 1 μ m.

Figs. 5–10.

TEM micrographs. Fig. 5. Cross section of a lateral styloconic sensillum taken near the tip of the peg showing four distal dendrites enclosed by the dendritic channel and dendritic sheath (arrow) and surrounded by the sensillar sinus (ss) and peg cuticle (pcu). Bar = 1 μ m. The inset shows a longitudinal section through the tip of the subapical pore (white arrow) of a lateral styloconic sensillum taken from another specimen. The pore contains an electron-dense, possibly viscous exudate from the dendritic channel, as well as an apparent plug of fenestrated fibrils (asterisk) located directly beneath the pore. The dendritic sheath is fused with the cuticular wall of the peg and is thinner and possibly porous in this region. The black arrow indicates a pore canal from one of the sidewall pores containing pore tubules. Bar = 0.2 μ m. Fig. 6. Higher magnification of Fig. 5 showing the four distal dendrites (asterisks). At this level, the distal dendrites contain only microtubules and are tightly apposed to one another and obliterate the view of the dendritic channel. ss, sensillar sinus. Bar = 0.5 μ m. The inset shows a longitudinal section from another lateral styloconic sensillum showing four distal dendrites (asterisks) lying in the dendritic channel and tightly apposed to one another. Just below the pore, there appears to be electron-dense material, possibly a viscous exudate (arrow) originating from the dendritic channel. ss, sensillar sinus. Bar = 0.4 μ m. Fig. 7. Cross section of a medial styloconic sensillum, similar to Fig. 6, showing four distal dendrites (asterisks) lying within the dendritic channel (dc), enclosed by the dendritic sheath (arrow), and surrounded by the sensillar sinus (ss). Note the longitudinally-oriented microtubules in the distal dendrites. Bar = 0.2 μ m. Fig. 8. Cross section, proximal to Fig. 6, of a lateral styloconic sensillum at the level of where the peg inserts into the style. Five distal dendrites are visible, four gustatory (black asterisks) and one mechanosensory (white asterisk) lying within the dendritic channel (dc). The mechanosensory distal dendrite contains a tubular body at this level, composed of longitudinally-oriented microtubules and embedded in an electron-dense matrix, which is unevenly distributed in some areas. The tubular body is tightly apposed to one side of the dendritic sheath (arrow) and peg cuticle (pcu) and appears to be held in place by at least one longitudinal fold (f with arrow) of the dendritic sheath. The dendritic sheath appears to be perforated by a pore (black arrow). Bar = 0.5 μ m. Fig. 9. Cross section of a medial styloconic sensillum, similar to Fig. 8. Note the four gustatory dendrites and the single mechanosensory dendrite (asterisk) containing a tubular body lying within the dendritic channel (dc). Note the longitudinal fold (f with arrow) of the dendritic sheath that may also bear a pore; pcu, peg cuticle. Bar = 0.3 μ m. Fig. 10. Lower magnification of Fig. 9 nearing the termination of where the peg cuticle (pcu) inserts into the style cuticle (scu). The dendritic channel contains five distal dendrites and is enclosed by the dendritic sheath and surrounding sensillar sinus (ss). At this level, the dendritic channel is apposed to one side of the peg cuticle. Bar = 3 μ m.

Figs. 11–17.

TEM micrographs. Fig. 11. Cross section, proximal to Fig. 8, of a lateral styloconic sensillum showing a higher magnification of the five distal dendrites within the dendritic channel (black arrow). At this level, the dendrites occupy much of the space within the channel. The tubular body of the mechanosensory dendrite is no longer visible; however the dendrite (asterisk) is still tightly apposed to one side of the dendritic sheath (white arrow). Note the longitudinally-oriented microtubules within the distal dendrites. Bar = 0.2 μ m. Fig. 12. Cross section, proximal to Fig. 11, of a lateral styloconic sensillum showing five distal dendrites within the dendritic channel (white asterisk). The dendritic sheath extends longitudinal folds (white arrow) into the dendritic channel, sometimes resulting in the partial or complete compartmentalization of some

of the five distal dendrites. One of the folds (white arrow) has pushed into one of the dendrites, giving the appearance that a sixth distal dendrite is present (black asterisk). This is, rather, a dendritic branch. At this level, apical, finger-like projections of the intermediate sheath cell (n) surround the dendritic sheath. Bar = 0.5 μ m. Fig. 13. Higher magnification of Fig. 12. The arrows indicate possible pores perforating the dendritic sheath. Note the longitudinally oriented microtubules within the distal dendrites and longitudinal folds of the dendritic sheath. asterisk, dendritic channel; n, intermediate sheath cell. Bar = 0.5 μ m. Fig. 14. Cross section, similar to Figs. 12 and 13 and proximal to Fig. 11, of a medial styloconic sensillum showing five distal dendrites within the dendritic channel (asterisk). Apical, finger-like projections of the intermediate sheath cell (n) are also apparent. ss, sensillar sinus. Bar = 0.5 μ m. Fig. 15. Cross section, proximal to Fig. 13, of a lateral styloconic sensillum showing five proximal dendrites (single and double asterisks) through the ciliary sinus (cs). The dendrites are now wrapped by the inner sheath cell (i), since the dendritic sheath has already terminated. Along the inner border of the highly infolded inner sheath cell, are discrete complexes of actin-like microfilaments together with microtubules (arrows). These complexes are embedded in a dense amorphous matrix and project into the ciliary sinus. The inner sheath cell also forms desmosomal junctions of the zonula adhaerens type with the proximal dendrites. Three of the proximal dendrites (single asterisks) are cut at a level through the proximal basal body, while the remaining two proximal dendrites (double asterisks) are cut at a level just proximal to the proximal basal body. Bar = 0.5 μ m. Fig. 16. Cross section, proximal to Fig. 15, of a lateral styloconic sensillum, proximal to the termination of the ciliary sinus. All five proximal dendrites (asterisks) are individually wrapped by the inner sheath cell (i), which has become thinner and microvillated. The proximal dendrites and inner sheath cell contain numerous mitochondria (arrows). n, intermediate sheath cell; o, outer sheath cell; scu, style cuticle. Bar = 1 μ m. Fig. 17. Cross section, similar to Fig. 16 and proximal to Fig. 14, of a medial styloconic sensillum. asterisks, proximal dendrites; i, inner sheath cell; m, intermediate sheath cell; o, outer sheath cell; ss, sensillar sinus; scu, style cuticle. Bar = 2 μ m.

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Fig. 18.

Diagrammatic reconstruction of a uniporous styloconic sensillum of *Lymantria dispar* in longitudinal section. All five of the sensory cells are shown. ax, axon; cb, cell body; cs, ciliary sinus; dbb, distal basal body of proximal dendritic segment; dc, dendritic channel; dd, distal dendritic segment; ds, dendritic sheath; i, inner sheath cell; n, intermediate sheath cell; o, outer sheath cell; pcu, peg cuticle; pd, proximal dendritic segment; po, terminal pore; pbb, proximal basal body of proximal dendritic segment; r, rootlets; scu, style cuticle; ss, sensillar sinus; tb, tubular body.