Fine Structure of the Terminal Organ of the House Fly Larva, Musca domestica L.*

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Summary. The terminal organs of the cephalic lobes of the house fly larva, Musca domestica L., were studied by scanning and transmission electron microscopy. Six different types of sensilla were found: (1) papilla sensillum, (2) pit sensillum, (3) spot sensillum, (4) modified papilla sensillum, (5) knob sensillum, and (6) scolopidium. The papilla, pit, spot, and modified papilla sensilla have the essential structure of contact chemoreceptors, *i.e.*, the unbranched dendritic tips are exposed externally through a single opening. However, a tubular body, which is a characteristic structure of tactile setae, is also present in some of the dendritic tips. We assume these sensilla serve a dual function—contact chemo- and mechanoreception. The role of the knob sensilla is obscure. The scolopidia present in the dorsal and the terminal organ are probably stress detectors. Two basal bodies occur in the dendritic ciliary region of all sensilla. Both of the basal bodies (except in the scolopidia) give rise to the distal ciliary microtubules as well as the proximal rootlets.

Key words: Sensilla — Insecta — Diptera — Musca domestica — Ultrastructure.

Introduction

The anterior tip of the house fly larva, *Musca domestica* L. (Diptera: Muscidae), has a pair of lobes each consisting of three different sensory organs which Bolwig (1946) called dorsal, terminal, and ventral. The fine structure of the dorsal organ has been described (Chu and Axtell, 1971; Richter, 1962). The terminal organ, called maxillary palp by Ludwig (1949), was studied by Bolwig (1946) by means of light microscopy and behavioral experiments. This report describes the fine structure of the terminal organ.

Materials and Methods

Cephalic lobes of house fly larvae (*Musca domestica* L., third-instar) were fixed in cold 5% glutaraldehyde with sodium-cacodylate buffer for 20 hours, and post-fixed in 1% OsO_4 with veronal-acetate buffer (Palade, 1952) for two hours. After dehydration in ethanol, the material was embedded in hard Epon 812 over propylene oxide. Sections were cut with a diamond knife on a Reichert Om U2 ultramicrotome and picked up with formvar-coated copper grids. Grids were stained with uranyl acetate (in 50% ethanol) and lead citrate (Venable and Coggeshall, 1965) for 20–30 min each and viewed with a Siemens Elmiskop 1 A.

For light microscopy, sections $(1-1.5 \mu$ thick) were double-stained with basic fuchsin and methylene blue-azure B (Ghidoni *et al.*, 1968).

For studying surface structure and distribution of sensory receptors, whole larvae, killed in hot water and coated with gold, were examined with a JEOL JSM-2 scanning electron microscope (SEM).

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Fig. 1. Digaram of a longitudinal section of the dorsal and terminal organ. A attachment cell; Ax axon; BM basement membrane; BN bipolar neuron; C cuticle; CR ciliary region; Ep epidermis; FS fluid-filled space; Gl glial cell; Hc haemocoel; IC inner cuticular ring; K knob sensillum; OC outer cuticular ring; PI papilla sensillum in the distal group; PII papilla sensillum in the dorso-lateral group; SI scolopidium in the ganglion of the terminal organ; SII scolopidium in the dorso-lateral group; T pit sensillum

Observations

The terminal organ is located at the tip of a cephalic lobe, ventral to the dorsal organ (Fig. 1). Large ganglia underlie both organs and connect to the central nervous system. The terminal organ (Fig. 2) is structurally more complex than the dorsal organ and contains at least six different types of sensory receptors arranged in two groups (distal and dorso-lateral).



Fig. 2. Frontal view of the tip of the left cephalic lobe showing two groups of the terminal organ. Distal group: $K_{1.2}$ knob sensilla; $P_{1.3}$ papilla sensilla; $T_{1.5}$ pit sensilla; single arrow, spot sensillum. Dorso-lateral group: M modified papilla sensillum; P papilla sensillum; double arrows, spot sensillum. SEM. $\times 9000$

Distal Group

The distal group, at the extreme tip of the cephalic lobe, is composed of a cylindrical portion with a cluster of sensilla (Figs. 2, 3). The cylindrical portion is elliptical in cross-section $(19 \times 25 \,\mu)$ and $18 \,\mu$ long. It is coated by two concentric



Fig. 3. Transverse section through the middle part of the cylindrical portion showing the dendrites innervating the sensilla in the distal group (compare with Fig. 2). The dendrites innervating each sensillum are encircled by one inner and one outer enveloping cell. In this section, papilla and spot sensilla are only surrounded by an inner enveloping cell, but in the proximal sections they are encircled by two enveloping cells. FS fluid-filled space; IC inner cuticular ring; K_{1-2} dendrites of knob sensilla; OC outer cuticular envelope; P_{1-3} dendrites of papilla sensilla; S dendrite of spot sensillum; T_{1-5} dendrites of pit sensilla; *, a tubular body present in the dendritic tip. $\times 9030$



Fig. 4. Diagram of a papilla sensillum showing 3 dendrites (D), one of the dendritic tips possessing a tubular body (TB). C cuticle; CT cuticular tube. Insert: Typical arrangement of microtubules (MT) around each microfilament (F) in the tubular body

cuticular envelopes in the same manner as the cylindrical portion of the dorsal organ, *i.e.*, the outer envelope is composed of epicuticle, exocuticle and endocuticle and is separated from an inner cuticular ring by a narrow, fluid-filled space. Four different types of sensilla (named from their gross appearance) are found in the distal group: (1) three "papilla" sensilla, (2) five "pit" sensilla, (3) two "knob" sensilla, and (4) a "spot" sensillum. A scolopidium lies internally beneath these senilla.

Papilla Sensilla. The three papilla sensilla (P_1, P_2, P_3) occupy about half of the surface of the distal portion (Fig. 2). They appear identical when examined with the SEM, but they are innervated by different numbers of bipolar neurons. P_1 and P_3 are each innervated by three bipolar neurons and P_2 by five bipolar neurons (Fig. 3). There is a single pore, 0.3μ in diameter, at the center of each papilla (Figs. 4, 5). The characteristic feature of this sensillum is that one of the dendritic tips has a "tubular body" (Thurm, 1964) and ends about 1 μ proximal



Fig. 5a—c. Papilla sensillum. a Longitudinal section through the pore (arrow) showing 2 dendrites exposed to the outside. C cuticle; CT cuticular tube; TB tubular body. ×27000.
b Cross section at level 2 (Fig. a). DS dendritic sheath. ×34000. Insert: Cross section at level 1. ×24000. c Cross section of the same dendrites further proximally of level 2. Note doublet neurotubules appear at the periphery of the dendrites. ×19000

to the pore. The outer dendritic tips do not have tubular bodies and extend further distally. The dendrite is enlarged in the region of the tubular body (Fig. 4). The tubular body is composed of parallel microtubules in groups of four to six connected by an electron-dense substance enclosing a space containing a central microfilament (Fig. 4 insert). This pattern is also observed in all the tubular bodies in other sensilla of the terminal organ. The dendrite containing a tubular body was on the side towards the center of the terminal organ (Fig. 3) in all specimens examined. Proximally, the dendrites of each sensillum are bathed in a highly electron-dense fluid and encircled by a dendritic sheath (cuticular sheath; scolopale) which is contiguous with a thick, cuticular tube (Fig. 5).

About 16μ below the base of the cylindrical portion, a constricted ciliary region divides each dendrite into an inner (proximal) and an outer (distal) segment (Figs. 6, 7). Two basal bodies lie, in tandem, proximal to the constricted region.



Fig. 6. Diagram of the dendritic ciliary region in a papilla sensillum

The distal basal body is wider than the proximal one, ciliary tubules extend from both of the basal bodies. Nine double-tubules extending from the distal basal body are located at the periphery of the constricted region, whereas either singleor double-tubules (the number varies from 3 to 12) extending from the proximal basal body pass through the center of the constricted region. In between these two groups of ciliary tubules in the constricted region lies a so-called "fibrillar body" (Smith, 1969; Chu and Axtell, 1971). Striated rootlets with a periodicity of 740 Å arise from both of the basal bodies and unite into a big root proximally. The inner dendritic segment possesses numerous organelles (mitochondria, vesicles, endoplasmic reticulum, ribosomes, rosette-like particles of glycogen and few neurotubules) whereas the outer segment contains only neurotubules and a few small vesicles. The dendritic sheath gradually disappears near the constricted ciliary region while the highly electron-dense fluid fades in the extracellular space between the dendrites and the inner enveloping (trichogen) cell.



Fig. 7a—e. Dendritic ciliary region in a papilla sensillum. a Longitudinal section of a dendrite. B_1 distal basal body; B_2 proximal basal body; FB fibrillar body; R rootlets. $\times 38000$. b and c Cross section at the constricted ciliary region showing 9 double-ciliary tubules at the periphery of the dendrite and 4 or 11 ciliary tubules in the center. Fibrillar body is located in between these 2 groups of ciliary tubules. $\times 50000$, $\times 37000$. d Cross section through the distal basal body. Ciliary tubules in the center arise from the proximal basal body. $\times 40000$. e Cross section through the proximal basal body. Arrow indicates the rootlets extending from the distal basal body. $\times 43000$

Pit Sensilla. Five pit sensilla occur at the periphery of the distal group; three of them are located laterad and the other two mesad (Fig. 2). They are innervated by different numbers of bipolar neurons; T_1 is innervated by 4 neurons, T_2 by 5, T_3 by 2, T_4 by 2, and T_5 by 3 neurons (Fig. 3). All the unbranched distal ends of the dendrites from T_2 , T_3 and T_4 are exposed to the outside through a pore (0.5 μ in diameter) in the center of each "pit" (Fig. 8) and have no tubular bodies. In T_1 and T_5 , one dendritic tip possesses a tubular body and terminates about 3 μ below the opening while the other dendritic tips extend distally to the pore (Figs. 9, 10). The location of the dendrite with a tubular body was consistent in all the materials studied (Fig. 3).



Fig. 8. Longitudinal section through the opening (arrow) of a pit sensillum showing 3 dendritic tips (D) communicating to the outside. C cuticle; CT cuticular tube. $\times 20000$

Fig. 9. Cross section of 3 dendrites at level 2 (Fig. 10). DS dendritic sheath; TB tubular body. $\times 27600$. Insert: Cross section at level 1. $\times 19000$

The dendrites of the pit sensilla have the same ultrastructure in the ciliary region as those of the papilla sensilla. Distal to the ciliary region, the group of dendrites innervating each sensillum is loosely surrounded by an electron-dense dendritic sheath (Fig. 9) which has some inward branches. The dendrites are bathed in an electron-transparent fluid (sensillum liquor) which appears distinctly lighter than the fluid of the papilla sensilla (Fig. 3).

Knob Sensilla. The two knob sensilla differ in size $(K_1 = 1.6 \mu \text{ diam}; K_2 = 2.2 \mu \text{ diam})$. Each knob sensillum is innervated by one bipolar neuron (Fig. 3) but they differ in their fine structure. In the smaller (K_1) , the dendrite contains granular material and a few neurotubules in the part distal to the junction of the "knob" and the cuticular tube (Fig. 11). In contrast, the larger (K_2) is filled with dendritic lamellae (Fig. 12). The lamellae begin in the cuticular tube and become more numerous distally. Each lamella contains only a few neurotubules. Distal to the ciliary region of both sensilla the dendrite is bounded by an electron-dense dendritic sheath which terminates at the stalk of the "knob".

The surface of both "knobs" appears rough. The knob wall is similar to the body cuticle, *i.e.*, composed of epicuticle, exocuticle and endocuticle, and some pore canals are present (Figs. 11 b, 12 b). Surprisingly, no pore openings were found in the "knob" part. However, an opening $(0.3 \ \mu \ \text{diameter})$ was found at the junction between the cuticular tube and the knob part of each sensillum (Figs. 11 c,



Fig. 10. Diagram of a pit sensillum showing 3 dendrites (D). One of the dendritic tips possesses a tubular body (TB) and the other two are exposed to the outside through an opening. Ccuticle; CT cuticular tube

12 c). The dendritic sheath is interrupted only on the side towards the pore and further distally, the sheath disappears.

The fine structure of the constricted ciliary region of the dendrites resembles that of the papilla sensillum.

Spot Sensillum. A spot sensillum, located at the lateral side of the distal group, is innervated by one bipolar neuron (Fig. 2, single arrow). The dendritic tip has a tubular body and communicates to the outside through a fine pore $(0.14 \,\mu$ diameter).

Scolopidium. The scolopidium sensillum (SI), with its distal end attached to the ventral side of the epidermis of the cephalic lobe, lies in the center of the ganglion at right angle to the dendrites of the other sensilla (Fig. 1). Two bipolar neurons innervate this scolopidium with their cell bodies lying inside the neuron mass of the ganglion. The dendrites pass through a wide extracellular space surrounded by the scolopale cell and terminate separately in the cap (Figs. 13, 14 a).



Fig. 11 a—d. Small knob sensillum (K_1). a Longitudinal section showing the dendrites containing granular substance and a few neurotubules (arrow) in the "knob" portion. *C* cuticle; *CT* cuticular tube. ×24000. b Cross section of the "knob". *PC* pore canal. ×26000. c Longitudinal section through the opening (arrow). ×14000. d Cross section through the opening. Arrow indicates the dendrite freely exposed to the outside without covering by the dendritic sheath (*DS*). ×29000

Each dendrite has a cup-shaped dilatation before entering the scolopale rods (Fig. 13), similar to the scolopidium of the locust tympanal organ (Gray, 1960). Two basal bodies lie in tandem at the proximal end of the transition zone. Distal to the transition zone, the dendrites remain the same diameter until the ciliary dilatation; they taper within the cap. Nine double-tubules arising from the distal basal body ascend the entire length of the dendrite and may finally fuse into a ring in the distal end (Fig. 14 b). A prominent geometric cross pattern inclusion lies in the ciliary dilatation proximal to the cap. Based on several longitudinal and cross sections, the inclusion body is made of several layers of five to six parallel bars each which are stacked together at a 60° orientation with each other. From some electron micrographs it appears that each bar is composed of two parallel microtubules. Rootlets arise from the distal basal body and extend proximally to form a big solid root with a macro-periodicity of about 720 Å. Numerous microtubules are around the cylindrical root and run parallel with its longitudinal axis (Fig. 14f).



Fig. 12a and b. Large knob sensillum (K_2) . a Longitudinal section showing the lamellated dendrite (D). Arrow indicates the dendritic sheath (DS) termination. C cuticle; CT cuticular tube. $\times 15000$. b Cross section of the "knob" at level 1 (Fig. 12a). Note the neurotubules are arranged in a single row in each dendritic lamella. PC pore canal. $\times 19000$. Insert: Cross section of the same sensillum at level 2 showing the reduced number of dendritic lamellae. $\times 10500$. c Longitudinal section through the pore (arrow). $\times 16000$. Insert: Cross section through the pore showing the absence of the dendritic sheath in the area adjacent to the pore. $\times 18000$

The scolopale cell contains 10 scolopale rods which concentrically surround the extracellular space with the distal dendrites inside. The scolopale rods are composed of packed microtubules embedded in an electron-dense amorphous material. Distally, the rods fuse together into a scolopale ring. The cytoplasm of the scolopale cell contains numerous irregularly shaped vacuoles. The long and pointed cap located at the distal end of the scolopale ring is an amorphous extracellular structure (Figs. 14a, b). Dendritic tips penetrate almost the entire length of the cap and are closely associated with the cap material.



Fig. 13. Diagram of the scolopidium in the ganglion of the terminal organ

The scolopale cell is connected to an epidermal cell by an elongated attachment cell whose nucleus lies near the attached area (Fig. 1). At the junction near the cap and the scolopale ring, the attachment cell possesses numerous microtubules arranged longitudinally (Figs. 13, 14a). A basement membrane and an extensive extracellular space in between separate the scolopidium from the other cells in the ganglion.



Fig. 14a—f. Scolopidium sensillum. a Oblique section through the distal part of a scolopidium showing 2 dendritic tips projecting into the cap C). AC attachment cell; CD ciliary dilatation; E extracellular space; MT microtubules; SC scolopale cell. ×19000. b Cross section through the cap at level 1 (Fig. 14a). The left dendrite (D) has "9+0" arrangement while the right one has a ring structure. ×43000. c Cross section of a ciliary dilatation at level 2. Arrow indicates one of the nine double-tubules at the periphery. ×55000. d Cross section at level 3 showing arms in the double-tubules. ×83000. e Cross section of distal basal body. ×72000. f Slightly oblique section through the inner dendritic segment showing numerous microtubules (MT) running parallelly with the long axis of the root (R). ×24400

Ganglion

The ganglion of the terminal organ is located beneath the epidermis in the interior of the cephalic lobe adjacent to the ganglion of the dorsal organ (Fig. 1). It is composed of bipolar neurons, glial cells, enveloping cells (trichogen and tormogen cells), epidermal cells and some other cells of uncertain origin. The terminal organ does not have a large central fluid-filled vacuole like that of the dorsal organ (Chu and Axtell, 1971).

All the cell bodies of the 35 bipolar neurons, which innervate the distal group and a spot sensillum in the dorso-lateral group, are located in the proximal part of the ganglion. The axons of the neurons leave the ganglion proximally and converge to form a compact nerve which joins the central nervous system. Again, the neuron cell bodies and axons are wrapped by the cell processes of the "tunicated type" of glial cells (Smith, 1968).

Dorso-Lateral Group

The dorso-lateral group consists of 4 different types of sensilla (Figs. 1, 2): (1) a "papilla" sensillum, (2) a modified "papilla" sensillum, (3) a "spot" sensillum, and (4) a scolopidium sensillum.

Papilla Sensillum. Structurally, this sensillum (PII) is the same as the papilla sensillum in the distal group (Figs. 1, 2). It is innervated by 3 bipolar neurons. Remarkably, the neuron cell bodies are located in the ganglion of the dorsal organ instead of the terminal organ.

Modified Papilla Sensillum. The modified papilla sensillum (Fig. 2) looks like the papilla sensillum but is innervated by only one dendrite, surrounded by an electron-opaque fluid. The dendritic tip with a tubular body is exposed to the outside through a pore (0.13 μ in diameter) at the junction between two knobbles (Fig. 15).

The prominent feature of this sensillum is that the neuron is independently situated in the haemocoel, not in the ganglion of either the dorsal or the terminal organ.

Spot Sensillum. A spot sensillum, innervated by one bipolar neuron, is located next to the modified papilla sensillum (Fig. 2, double arrows) and appears as a tiny pit (0.2 μ in diameter) in the SEM. The dendritic tip with a tubular body is exposed to the outside through that pit (Fig. 16). The neuron cell body is located in the ganglion of the terminal organ.

Scolopidium. A scolopidium sensillum $(S\Pi)$ occurs near the papilla sensillum of the dorso-lateral group (Fig. 1). The fine structure of this scolopidium is similar to that of the one in the distal group except it is innervated by only one bipolar neuron. The neuron cell body is located in the ganglion of the dorsal organ near that of the papilla sensillum. The dendrite, surrounded by a scolopale cell and its attachment cell, is suspended in the haemocoel.

Other Sensilla

Two spot sensilla, identical in their fine structure, are separately located laterally and medially on the cephalic lobe. Each is innervated by one bipolar neuron. The dendritic tip with a tubular body is exposed to the outside through a



Fig. 15. Oblique section through the pore (arrow) of a modified papilla sensillum showing the dendritic tip with a tubular body (TB) exposed to the outside. C cuticle. $\times 11700$

Fig. 16. Longitudinal section through the pore (arrow) of the spot sensillum of the dorsolateral group showing the dendritic tip with a tubular body (TB) exposed to the outside. C cuticle. $\times 18000$



Fig. 17. Longitudinal section through the pore of a spot sensillum located medially on the cephalic lobe showing the dendritic tip with a tubular body (TB) exposed to the outside. The big arrow indicates the direction of the dendrite embedded in the cuticle. $\times 16000$

pore $(0.4 \,\mu$ in diameter) (Fig. 17). The striking feature of this sensillum is that most of the dendrite is embedded in the cuticle. The location of the neuron cell bodies was not determined.

Discussion

At least 6 different types of sensilla are found in the terminal organ. Our results clarify and alter several of the previous findings by light microscopy (Bolwig, 1946): (1) The papilla sensillum in the dorso-lateral group of the terminal organ is not a scolopidium. (2) The scolopidium located vertically in the center of the ganglion does not simply penetrate through the ganglion, but rather has the neuron cell bodies located within the ganglion. (3) In the dorso-lateral group the spot sensillum is innervated by the neuron in the ganglion of the terminal organ whereas the papilla sensillum and the scolopidium have their neurons in the ganglion of the dorsal organ. This explains the connection between the dorsal and terminal organ which was observed by Keilin (1927) and Hertweck (1931). (4) A minute structure (designated "X" by Bolwig) located medially on the cephalic lobe is the spot sensillum.

Bolwig (1946) stated: "The whole structure of the terminal and ventral organs of the cephalic lobes as well as the fact that their nerves extend to the central nervous system below the oesophagus gives good reason to believe that the organs have a gustatory function.". He made several behavioral experiments, but was unable to prove the hypothesis. In the present study, we found that all sensilla, except the knob sensilla and the scolopidia, have an opening through which the naked dendritic tips are externally exposed. They are similar to those of known contact chemoreceptors in insects (Dethier, 1955; Schoonhoven and Dethier, 1966; Larsen, 1962; Adams et al., 1965; Wensler and Filshie, 1969; Hansen and Heumann, 1971). We assume that these sensilla play a role in contact chemoreception. Thurm (1964, 1965) showed that the tubular body in the distal end of the dendrite in certain mechanoreceptors is the point of transduction of mechanical stimuli. Some dendritic tips (in the papilla, pit, modified papilla, and spot sensilla) possess a tubular body and may also communicate to the outside through the opening. Therefore, on the basis of the ultrastructural evidence in our study, these sensilla probably serve a dual function—contact chemo- and mechanoreception. Their actual function still demands electrophysiological investigation. The tubular body is composed of microtubules and microfilaments which are arranged in a regular pattern. Re-examination of the dorsal organ reveals the same fine structural arrangement in the tubular bodies. A similar pattern is also observed in the tubular bodies of haltere sensilla (Smith, 1969) and tarsal taste hairs (Hansen and Heumann, 1971) of calliphorid flies.

The role of the knob sensilla is unknown. The different dendritic endings (granular vs lamellated) suggest different functions in the two types. No pores were found in the "knob". The only opening in each sensillum is situated at the junction between the "knob" and the cuticular tube. The opening is considered to be a "basal pore" (Chu and Axtell, 1971) through which the dendritic sheath is pulled out during the molting process rather than a means of communication to the exterior. This interpretation is based on the following observations: (1) The opening lies at the base of the sensillum. (2) The dendritic sheath is interrupted only on the side towards the opening. (3) The dendritic sheath continues further distally before disappearing.

All fine structural studies of insect scolopidia show a ciliary dilatation in the outer dendritic segment. However, the inclusion inside the dilatation differs in different organs: fibrous structures in the locust tympanal organ (Gray, 1960), an electron-dense "sieve-like" structure in the antennal scolopidia of a fruit fly (Uga and Kuwabara, 1965), several axial structures in the termite antennal connective organ (Howse, 1968), a dense granular material in a cockroach subgenual organ (Howse, 1968) and in the noctuid moth ear (Ghiradella, 1971), some electron-dense substance in Johnston's organ of a lacewing and a mosquito (Schmidt, 1970), a single rod in Johnston's organ of a termite (Howse, 1968), and a central core of fibrous material in the cockroach leg (Young, 1970). Our results show a geometric cross pattern in the terminal organ of the house fly larva. The significance of the ciliary dilatation and its inclusion body is unknown. From physiological experiments, it is known that scolopidia function as mechanoreceptors (Howse, 1968; Young, 1970) but which fine structural component of a scolopidium responds to the mechanical stress is obscure. Young (1970) stated that an increase in the longitudinal tension stimulates the scolopidia. If so, the scolopidium situated across the ganglion of the terminal organ may detect a vertical stress and the one in the dorso-lateral group may detect a horizontal stress.

In each dendrite, two basal bodies lie in tandem at the proximal end of the ciliary region. The unique feature in this region is that the ciliary microtubules, except those of scolopidia, arise from the distal basal body as well as from the proximal basal body. Ciliary microtubules have been shown to arise only from the distal basal body in insect sensilla (Steinbrecht, 1969; Slifer, 1970). Rootlets arise also from both basal bodies instead of only from the distal basal body as is commonly found in insects. The other cases of rootlets extending from both basal bodies are the chordotonal organ of the lacewing (Schmidt, 1969) and the tarsal taste hairs of the blowfly (Hansen and Heumann, 1971). Re-examination of the dome of the dorsal organ of the fly larva reveals that the ciliary microtubules and rootlets also arise from both basal bodies.

References

- Adams, J. R., Holbert, P. E., Forgash, A. J.: Electron microscopy of the contact chemoreceptors of the stable fly, *Stomoxys calcitrans* (Diptera: Muscidae). Ann. Ent. Soc. Amer. 58, 909-917 (1965).
- Bolwig, N.: Senses and sense organs of the anterior end of the house fly larvae. Vid. Medd. dansk nat.-hist. Foren 109, 81–217 (1946).
- Chu, I.-W., Axtell, R. C.: Fine structure of the dorsal organ of the house fly larva, Musca domestica L. Z. Zellforsch. 117, 17–34 (1971).
- Dethier, V. G.: The physiology and histology of the contact chemoreceptors of the blowfly. Quart. Rev. Biol. 30, 348-371 (1955).
- Ghidoni, J. J., Campbell, M. M., Adams, J. G., Thomas, H., Ramos, E. E.: A new multicolored staining procedure for one micron section of epoxy embedments. Proc. Electr. Micr. Soc. 26th Meeting, New Orleans, 240–241 (1968).
- Ghiradella, H.: Fine structure of the noctuid moth ear. 1. The transducer area and connections to the tympanic membrane in *Feltia subgothica* Haworth. J. Morph. 134, 21-46 (1971).
- Gray, E. G.: The fine structure of the insect ear. Phil. Trans. Roy. Soc. (B) 243, 75-94 (1960).
- Hansen, K., Heumann, H.-G.: Die Feinstruktur der tarsalen Schmeckhaare der Fliege Phormia terraenovae Rob.-Desv. Z. Zellforsch. 117, 419–442 (1971).
- Hertweck, H.: Anatomie und Variabilität des Nervensystems und der Sinnesorgane von Drosophila melanogaster (Meigen). Z. wiss. Zool. 139, 559-663 (1931).
- Howse, P. E.: The fine structure and functional organization of chordotonal organs. Symp. Zool. Soc. Lond. 23, 167–198 (1968).

- Keilin, D.: The chordotonal organs of the antenno-maxillary complex in the larva of cyclorrhaphous Diptera. Ann. Mag. nat.-hist. 20, 334–336 (1927).
- Larsen, J. R.: The fine structure of the labellar chemosensory hairs of the blowfly, *Phormia regina* Meig. J. Insect Physiol. 8, 683–691 (1962).
- Ludwig, C. E.: Embryology and morphology of the larval head of *Calliphora erythrocephala* (Meigen). Microentomol. 14, 75-111 (1949).
- Palade, G. E.: A study of fixation for electron microscopy. J. exp. Med. 95, 285–297 (1952).
- Richter, S.: Unmittelbarer Kontakt der Sinneszellen cuticularer Sinnesorgane mit der Außenwelt. Eine licht- und elektronenmikroskopische Untersuchung der chemorezeptorischen Antennensinnesorgane der *Calliphora*-Larven. Z. Morph. Ökol. Tiere 52, 171–196 (1962).
- Schmidt, K.: Der Feinbau der stiftführenden Sinnesorgane im Pedicellus der Florfliege Chrysopa Leach (Chrysopidae, Planipennia). Z. Zellforsch. 99, 357-388 (1969).
- Schmidt, K.: Vergleichend morphologische Untersuchungen über den Feinbau der Ciliarstrukturen in den Scolopidien des Johnstonschen Organs holometaboler Insekten. Verh. Dtsch. Zool. Ges., 64. Tagg, 88–92 (1970).
- Schoonhoven, L. M., Dethier, V. G.: Sensory aspects of host-plant discrimination by lepidopterous larvae. Arch. néerl. Zool. 16, 497–530 (1966).
- Slifer, E. H.: The structure of arthropod chemoreceptors. Annu. Rev. Ent. 15, 121-142 (1970).
- Smith, D. S.: Insect cells. Edinburgh: Oliver & Boyd 1968.
- Smith, D. S.: The fine structure of haltere sensilla in the blowfly, *Calliphora erythrocephala* (Meig.), with scanning electron microscopic observations on the haltere surface. Tissue & Cell 1, 443–484 (1969).
- Steinbrecht, R. A.: Comparative morphology of olfactory receptors. In: Olfaction and Taste, ed. by C. Pfaffmann. New York: Rockefeller Univ. Press 1969.
- Thurm, U.: Mechanoreceptors in the cuticle of the honey bee: Fine structure and stimulus mechanism. Science 145, 1063–1065 (1964).
- Thurm, U.: An insect mechanoreceptor. Part 1: Fine structure and adequate stimulus. Cold Spr. Harb. Symp. quant. Biol. 30, 75–82 (1965).
- Uga, S., Kuwabara, M.: On the fine structure of the chordotonal sensilium in antenna of Drosophila melanogaster. Jap. J. Electr. Micr. 14, 173-181 (1965).
- Venable, J. H., Coggeshall, R. E.: A simplified lead citrate stain for electron microscopy. J. Cell Biol. 25, 407-408 (1965).
- Wensler, R. J., Filshie, B. K.: Gustatory sense organs in the food canal of aphids. J. Morph. 129, 473–492 (1969).
- Young, D.: The structure and function of a connective chordotonal organ in the cockroach leg. Phil. Trans. Roy. Soc. (B) 256, 401–428 (1970).

Note Added to Proof: After the present article was in press, two papers by Gnatzy and Schmidt [Z. Zellforsch. 122, 190–209 (1971)] and Schmidt and Gnatzy [Z. Zellforsch. 122, 210–226 (1971)] appeared. They demonstrated that the opening canal in the mechanoreceptors is an "ecdysial canal" which is formed by deposition of the cuticle around the dendritic sheath during moulting. Therefore, the pore is not involved in sensory reception and in the present article those dendritic tips with a tubular body (in the papilla, pit, modified papilla, and spot sensilla) may only play a role in mechanoreception. A similar interpretation of the scolopidium-like sensillum in the dorsal organ of the house fly larvae is possibly correct rather than the previous assumption of a dual function—mechano- and chemoreception.

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