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Morphology and Ultrastructure of the Antennal Chemoreceptors and Mechanoreceptors of Worker *Coptotermes formosanus* Shiraki *

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Summary. Three types of setae were found on the antenna of workers of *C. formosanus.* Sensilla basiconica function as chemoreceptors. They are non-socketed. with fixed plate base. thin walled, and perforated. Pore tubules are contained within the cuticular pores of s. basiconica. The pore tubules have direct contact with the dendritic branches within the sensilla. The other sensilla are tactile mechanoreceptors. The longest setae (sensilla trichodea) are thick walled, socketed. mononeuronic. and non-perforated. The shorter mechanoreceptors (sensilla chaetica) have the same characteristics as s. trichodea, exept that they are sometimes dineuronic. The numbers and distribution of the sensilla were established.
Key words: Chemoreceptors — Mechanoreceptors — Sensory receptors —Termites - infrastructure.

Introduction

The Formosan termite, *Coptotermes formosanus* Shiraki, is a serious pest of wood and cellulose products. It was recently discovered in the U.S.A. and is spreading (Anon., 1966). The ethology of this termite in respect to trail following pheromones has been studied to some degree (Merlins et al., 1971: Matsumura et al., 1972) but the sensory structures responsible for the reception of the stimuli have not been explored.

The present portion of our studies was conducted to determine the types, numbers, distribution, and ultrastructure of the antennal chemoreceptors and mechanoreceptors of workers of *C. formosanus* and to allow future investigative planning.

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Materials and Methods

Workers of *C. formosanus,* the largest of the worker-like individuals, were distinguished from other castes by their overall whitish color and the absence of wing stubs. The external structure of the antenna and the antennal sensilla was

examined with light and scanning electron microscopes (SEM). whereas the internal structure was studied with light and transmission electron microscopes (TEM). Termites were fixed in 5 %, formalin and immersed in 0.5 % crystal violet dye to locate the olfactory sensilla (Slifer. 1960). To obtain a gross picture of the antennal nervous systems *intra vitam* staining was used by injection of 0.5 % methylene blue in 0.75 % NaCl into the brain and subsequent fixation in 10 % aqueous solution of ammonium molybdate. For SEM observation, the termites were fixed in 5 % formalin, dehydrated in an acetone series (35. 50. 70. 90. and 100 %) and affixed to an aluminium stub with silver paint. Specimens were coated with gold palladium (60-40 %,) in a vacuum evaporator equipped with a tilting rotating stage. The specimens were subsequently examined in a JEOL-JSM U-3SEM, with accelerating voltages of 15, 30 or 25 kv. Setae were measured on the picture screen of the SEM. Specimens for the TEM were prepared from termite heads fixed in 2 % osmium tetroxide. After dehydration in an acetone series the specimens were embedded in Spurr low viscosity medium (Polyscience Inc.), at medium hardness. Sections were mounted on Effa Bar grids (E.F. Fullam) containing backing film. and stained in saturated uranyl acetate (during dehydration) and lead acetate. An AEI-EM-6B TEM was used for examination and photography.

Observation and Discussion

The antenna of *C. formosanus* is moniliform, flagellate, and 14-16 segmented. The scape is longer than the pedicel. The flagellar segments are of uniform size, except for the first (the meriston) which is shorter and sometimes undifferentiated from the next segment because of its regenerative character. Peg sensilla (basiconica sensilla, Richard, 1969) occur near the joints on the scape and pedicel. They probably function as proprioceptors because of their location.

Chemoreceptors

Sensilla basiconica (thin walled pegs, Prestage et al., 1963; sensilla basiconica. Abushama, 1965; peg organs. Richard, 1969) occur on mid and terminal flagellar segments and are the most numerous setae on the antennae of *C. formosanus.* They are particularly abundant on the distal portions of each segment from segments 6 and 7 to the end of the antenna. The number of s. basiconica on each segment increases distally, the terminal segment containing the most. A single antenna, for example, has 7 setae on segment 6, 22 on segment 7, 64 on segment 11 and 102 on the terminal segment, with a total count of 634 setae on all segments. The S. basiconica are thin walled with articulated bases. At the base, the setal wall is about 0.4 μ thick and near the tip about 0.2 μ. Sensilla are curved sharply toward the junction with the next segment. Their length varies from 9.0-33.3 μ. their base width from 1.38-2.33 μ and their plate base width from 2.38-5.67 μ.

The sensilla are innervated by multiple neurons., as many as 7 per sensillum. Each dendrite is enclosed in a thin cuticular sheath. The outer segment of the dendrite contains microtubules. Microvilli and the vacuole of the tormogen cell occur below the base of the hair. The dendrite assumes the structure of a cilium at the base of the outer segment and terminates at two basal bodies. The inner segment of the dendrite contains several rootlets arising proximally from the basal bodies. These findings agree with previous work on the ultrastructure of the olfactory dendrites in other

insects (Slifer. 1961, 1967: Ernst. 1969). There are 11 pairs of ciliary fibrils (Fig. 3) in the cilium. Distal to the cilium, the ciliary fibrils become microtubules. The microtubules occur in the dendritic branches which are in the setal lumen. The cuticular wall contains numerous flask-shaped cuticular pores (Fig. 1), most numerous in the mid region of the sensillum. Pore numbers decrease toward the distal region of the sensillum, as do the dendritic branches. The diameter of a flask-shaped pore is 900 Å, but ectally it narrows to 600 Å. The pore is about 0.15 µ long. The cuticular opening ranges from 100-140 Å in diam. (Fig. 2). Within each flask-shaped pore are 2 parallel pore tubules (Fig. 4) which extend from the dendritic branches to the cuticular pore. The diam. of the pore tubules ranges from 80-100 Å, and their length from 0.15-0.18 µ. They have distinct light centers and electron dense walls. The pore tubules contact the plasma membrane of the dendritic branch directly (Fig. 4). Although there is no evidence that the pore tubules are present in the continuous membrane lining the inner wall of the sensillum as proposed by Ernst (1969), his theory that they are extracellular structures constructed by trichogen cell is a possibility. Hawke and Parley (1971) agreed with Ernst (1969) that the "pore strands" in the cuticular pores of *Arenivaga* chemoreceptors were found in association with the cuticular structures rather than derived from the dendrites. Norris and Chu (1974) expressed the same opinion regarding the formations of the pore tubules in the chemoreceptors of *Periplaneta americana* L.

Mechanoreceptors

Two types of mechanoreceptors. sensilla trichodea and sensilla chaetica. were found. S. trichodea are straight and occur in a ring encircling each segment. They are the longest among the setae. Their length varies from 27.12 µ to 76.11 µ, the longest occurring on the distal flagellar segments. The average base width is 3.01 µ. The average number on each antenna is 145. They are socketed, thick walled, and mononeuronic (Fig. 5).

Sensilla chaetica are structurally similar to sensilla trichodea. but shorter and more abundant. They vary from 31.25-66.67 µ in length and 1.50-2.22 µ in base width. The estimated number per antenna is 361, and they practically cover the proximal portion of each segment, except for the basal segments. In addition to being thick walled they are movable because of their socket-like characteristics such as the presence of resilin-like material, sponge-like cavities, setal roots. vacuole and microvilli of the tormogen cell (Fig. 5). Sensilla chaetica are innervated by either 1 or 2 bipolar neurons (Fig. 7). This dineuronic characteristic of s. chaetica suggests that they may also serve as gustatory organs. The latter function, however, needs further study. Since both sensilla are trichoid or bristle-like, thick walled and set in membranous sockets, the primary purpose is considered to be that of tactile mechanoreceptors. The structure of the distal dendrite, however. differs from Thurm's (1964. 1965) descriptions of the hair-plate sensilla in the honeybee. C. *formosanus* tactile hairs contain dendrites or dendritic branches in their lumina (Figs. 6, 8), and there is no cuticular cap (scolopale) associated with the dendrite endings. A somewhat similar situation was reported by Zacharuch and Blue (1971) for the antennae of *Aedes aegypti* (L.) which have naked dendrites (without cuticular sheaths). They suggested that the sensilla also function as slow-acting chemoreceptors. In *C. formosanus.* however, the dendritic branches in the setal lumen are clearly enclosed in a cuticular sheath.

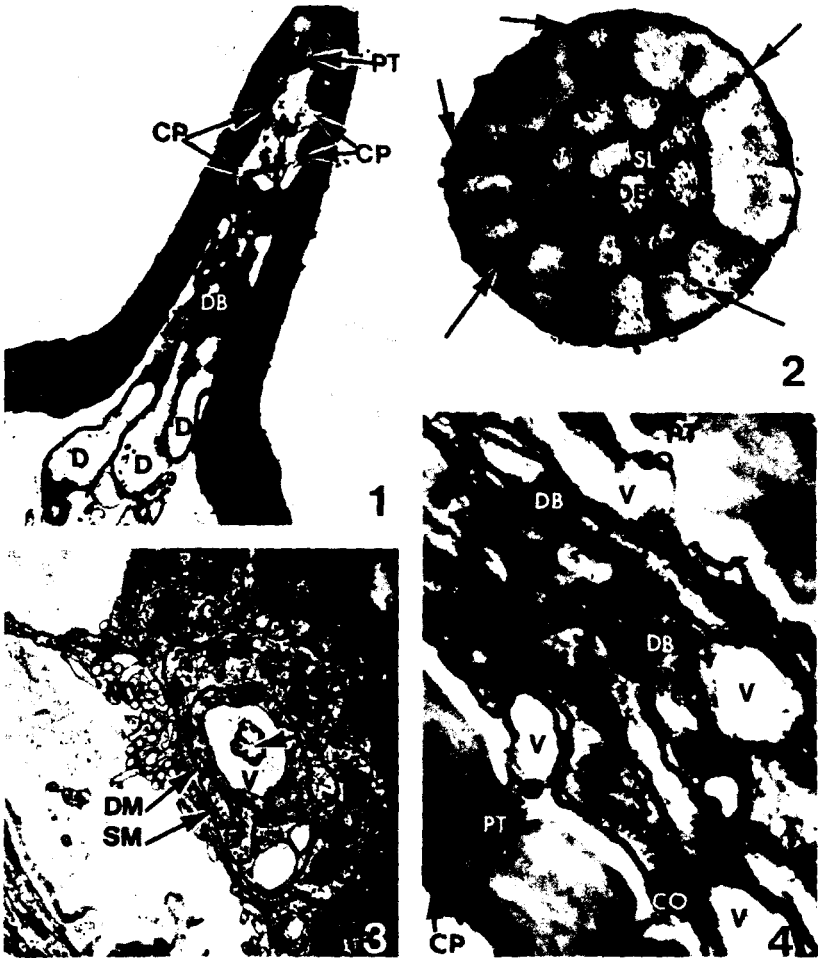

Fig. 1. Longitudinal section through sensillum basiconicum. Three dendrites (D) enter base of seta, each dividing into dendritic branches *(DB).* Cuticular pores *(CP)* appear at about l.3 length of seta proximally. Pore tubules *(PT)* within each cuticular pore. x 15,000

Fig. 2. Cross section through mid-region of sensillum basiconicum. containing 11 dendritic branches (DB) with narrow setal lumen *(SL}.* Note numerous cuticular pores (arrows) and microtubules in each dendritic branch, x 45,000

Fig. 3. Cross section through ciliary region in outer segment of olfactory sensilla, just above basal bodies. Cilium (0 within vacuole (*V)* containing fine granular material and enclosed by sheath cell (Schwann cell). Note pairs of ciliary fibrils *(CF),* 9 peripherals and 2 in center ofdendrite; dendritic membrane *(DM},* sheath cell membrane *(SM*), mitochondria *(MC)* and microvilli (*MV*), x 17,600

Fig. 4. Longitudinal section through sensillum basiconicum, showing dendritic branches (DB), cuticular pores *(CP)* and pore tubules *(PT).* Note contact (CO) between pore tubule and dendritic branch, x 60,000

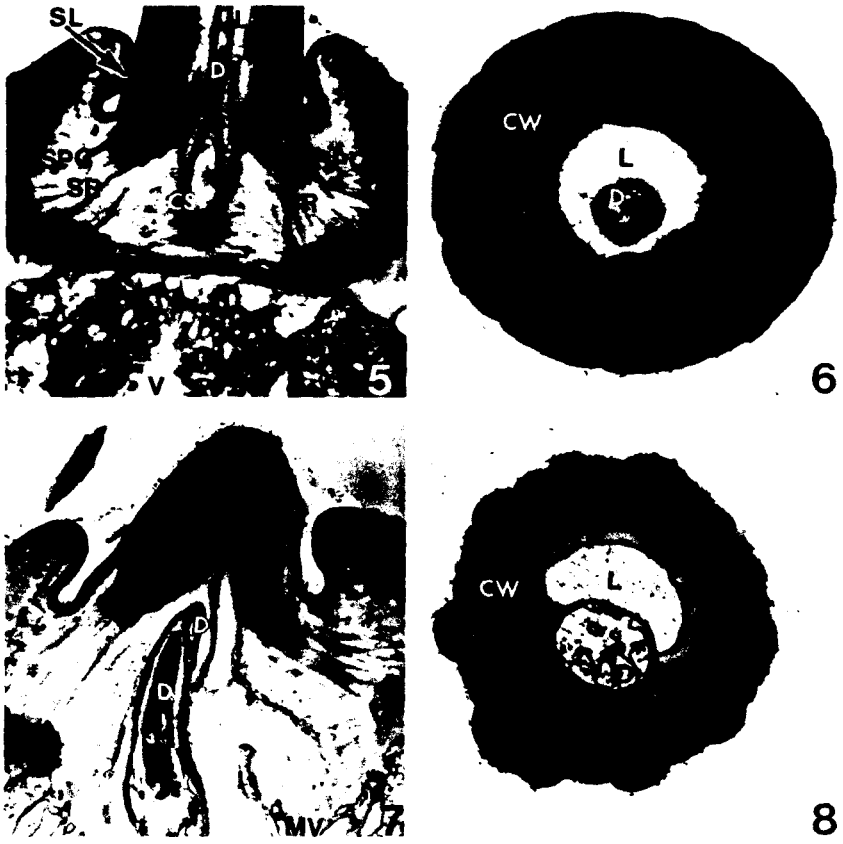

Fig. 5. Longitudinal section through sensillum trichodeum showing setal lumen *(L*). dendrite *(D)* enclosed in cuticular sheath *{CS).* socket lining *(SL),* spongelike cavity *(SPC*), setal roots (SR). microvilli *(MV)* of tormogen cell and vacuole *(V*). x 4,000

Fig. 6. Cross section through distal portion of sensillum trichodeum showing setal lumen *(L).* dendrile *(D).* cuticular wall *(CW);* single dendrite evidently divided into several branches, but still enclosed in common cuticular sheath, x 23,100

Fig. 7. Oblique section through socket area of sensillum chaeticum. showing two dendntes (*D*), x 24,400

Fig. 8. Cross section through mid-region of sensillum chaeticum. showing dendrite attached to one side of inner cuticular wall of hair lumen. Dendrite *(D)* divided into several branches within common cuticular sheath; large lumen (/.) and thick cuticular wall *(CW*), x 25.000.

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