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Antennal sensilla of *Anagrus atomus* (L.) (Hymenoptera: Mymaridae) female and their possible behavioural significance

ABSTRACT

The antennae of a hymenopteran Mymaridae female, *Anagrus atomus* (L.), have been investigated, through light microscopy as well as through scanning for the first time, and transmission electron microscopy, principally aiming at identification of sensory structures possibly involved in reproductive behaviour. Topographic distribution of the external components (cuticular appendages) of sensilla has been illustrated through "camera lucida" semischematic diagrams of the whole antenna, and especially the club, together with scanning electron micrographs. Topographic location of the same sensilla internal (cellular) components has been shown in the antennal club through transmission electron micrographs from serial cross sections. Seven categories of sensory structures have been identified (i.e., "apical sensilla", "grooved peg sensilla", "sensilla trichodea Type 1", "sensilla trichodea Type 2", "sensory ridges", "sunken peg sensilla", "tactile sensilla") and illustrated through semischematic diagrams and transmission electron micrographs from fine serial sections. On the basis of the nature of the sensilla and their location on the antennae, together with antennal use during the female reproductive behaviour, the behavioural meaning of the above mentioned sensilla has been hypothesised.

INDEX DESCRIPTORS (in addition to those in the title): contact chemoreceptor, olfactory sensilla, reproductive behaviour, sensory neurones, sheath cells, ultrastructure.

INTRODUCTION

Anagrus atomus (L.) is an egg parasitoid which develops on various leaf-hopper and plant-hopper species which insert their eggs in plant tissues.

The antennae of *A. atomus* females are obviously involved in reproductive behaviour, especially the antennal club, during the oviposition sequence, from searching for the host egg to checking and probing the latter before introducing the ovipositor into the same. Thus, various kinds of sensilla are expected to be present on the antennal flagellum, and involved in the oviposition behaviour.

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The female antenna displays a typically elongated scape, a pear-shaped pedicel, a flagellum made up of six funicular articles (F1-F6), and a 1-segmented club. Conspicuous "sensory ridges" (*Auctorum*) are present: one on flagellomeres F4 and F5, two on F6 and three on the club (CHIAPPINI, 1987).

Our aim was to study the antennal flagellum fine morphology of *A. atomus*, with special reference to the sensory structures possibly involved in the parasitoid host location-recognition-oviposition processes, as a first contribution to knowledge of the antennal ultrastructure of an adult Mymaridae, as well as to better understanding of its reproductive behaviour.

MATERIALS AND METHODS

BEHAVIOUR

The behavioural observations were done in the laboratory, under room conditions, utilising fresh material from the fields, i.e., host-plant leaves bearing leaf-hopper eggs parasitized by *Anagrus atomus* and already containing pupae of the latter, in order to obtain females of it; or fresh host-plant leaves bearing (or not) fresh leaf-hopper eggs to be presented to *A. atomus* females within Petri dishes as arenas for behavioural observations under a stereomicroscope.

MORPHOLOGY

Specimens of *Anagrus atomus* adult females, just emerged from the host eggs, prepared on whole mounts either in Faure's or Hoyer's embedding liquids, were directly observed under a light microscope; or dehydrated through graded ethanol series, CO_2 critical-point dried, gold coated, and studied under a Hitachi S 2300 scanning electron microscope, in order to locate and inventory all sensory structures detectable that way.

For transmission electron microscopy, entire specimens were soaked in KARNOWSKY'S (1965) fixative solution for three hours, next rinsed in cacodylate buffer several times and left in it over night at 4°C, then postfixed in 1% OsO_4 in cacodylate buffer for one hour and fifteen minutes, rinsed again in cacodylate buffer, dehydrated in a graded ethanol series until 90%, block stained with 1% uranylacetate in 95% alcohol for forty minutes, two more passages in absolute alcohol, and embedded through propylene oxide in Epon-Araldite. Sections, about 70 nm thick, sequentially stained with uranylacetate and lead citrate were examined through a Jeol JEM-1200EXII transmission electron microscope.

RESULTS AND DISCUSSION

The flagellum gross anatomy is quite simple, most of the antennal lumen being occupied by the cellular components (sensory neurones and relative sheath cells) of the antennal sensilla.

The haemocoel (H: Figs 4-10) is quite reduced, especially in the club, while a narrow blood vessel (BV: Figs 7-8) as well as two fine tracheae (TR: Figs 6-10) can be easily recognised both in the club and in the funicular articles.

It is noteworthy that in the club the epidermal cells persist relatively thick and frequently display irregular microvilli (MV: Figs 4-5) beneath a perforated cuticle (P: Fig. 5) resembling glandular cells of NOIROT and QUENNEDEY's (1974) Class 1.

Through light microscopy and S.E.M. examination, the following sensory structures can be detected (Figs 1-2) some of them already observed by LOU *et al.* (1996).

On the club there are:

-17-18 blunt tipped hairs (apparently chemoreceptors) belonging to three distinct categories of sensilla (especially considering the cellular components: see below), and irregularly distributed on the club, as follows:

-2 apical sensilla (Figs 1b, and 2: A), basiconica (*sensu* SNODGRASS, 1935), bearing a long hair, situated at the club tip;

-6 sensilla trichodea Type 1 (Figs 1b, and 2: T1), showing a hair somewhat shorter than the previous ones, and mostly distributed subapically;

-9-10 sensilla trichodea Type 2 (Figs 1b, and 2: T2), mostly situated ventrally, arranged in two rows on either side of the ventral edge of the club and having a hair very similar to Type 1;

-3 “sensory ridges” (*Auctorum*), i.e., 2 on the club lateral side and 1 on the club medial side (Figs 1b, 1c, and 2: SR);

-1 grooved peg sensillum, situated almost on the middle of the club ventral edge (Fig. 1c);

-1 sunken peg sensillum (*sensu* SNODGRASS, 1935) situated on the lateral side of the club distal third (Figs 1c, and 2: SP);

-numerous tactile sensilla, scattered all over the surface of club (Figs 1b, 1c, and 2: TS), and mixed with other hairs looking very similar to the former but not innervated.

On the funicular articles there are:

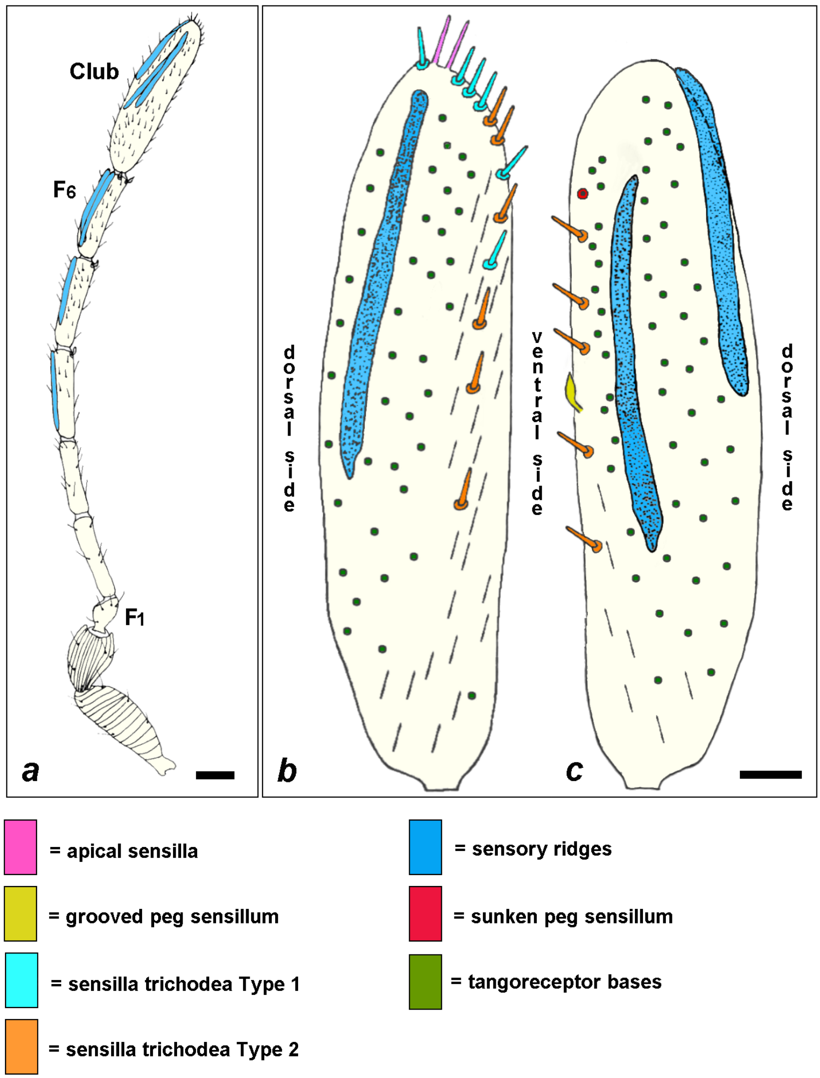

Fig. 1 - *Anagrus atomus* female. Diagram of the whole antenna (a), and the club medial (b) and lateral (c) view, displaying the sensillar distribution. Bars = 20 µm (a) and 10 µm (b) and (c). F1 and F6, funicular articles.

-"sensory ridges": 2 on article F6, and 1 on F5 and F4 (Fig. 1a);
-grooved peg sensilla: 2 or 3 on article F6, and usually 1 on F5 and F4 (Fig. 1a);
-sunken peg sensillum, only 1, on article F2.

APICAL SENSILLA

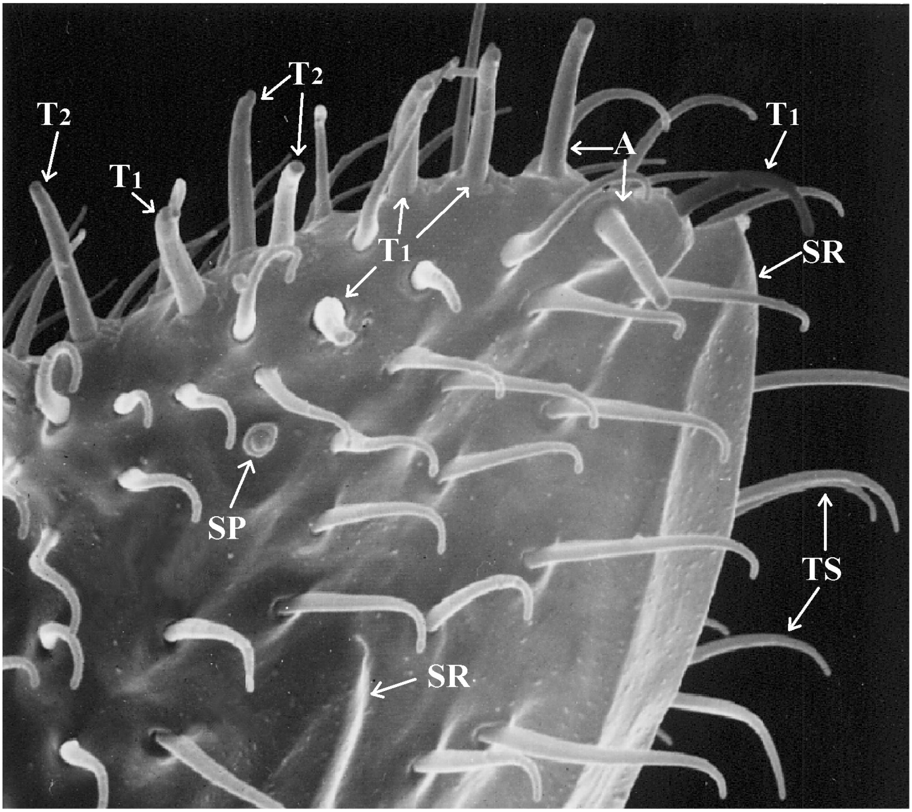

Fig. 2 - Scanning electron micrograph of the club distal portion. A, apical sensilla; SP, sunken peg sensillum; SR, sensory ridges; T1, sensilla trichodea Type 1; T2, sensilla trichodea Type 2; TS, tactile sensilla.

The cuticular components of the apical sensilla (Figs 1b, and 2: A) consist of a hair-shaft set without any socket on the club wall (i.e., basiconicum), being proximally smooth and fluted on the rest, having an unpartitioned lumen and terminating with an irregular apical pore system (Fig. 11a).

The cellular components are represented by three sensory neurones (A: Figs 3-6) and only one big sheath cell (Fig. 11a, c, and d, and A: Figs 3-7).

All the sensory neurones send their outer dendritic segments into the hair-shaft lumen, reaching almost to the tip (D: Fig. 11a, and b).

The sheath cell lines with dense microvilli a single narrow sinus (obviously including both ciliary and sensillar sinus) which extends inwards into a very deep labyrinth (LA: Fig. 11c, and d). The sheath cell partially encloses the sensory neurone inner dendritic segments to which it attaches with extended

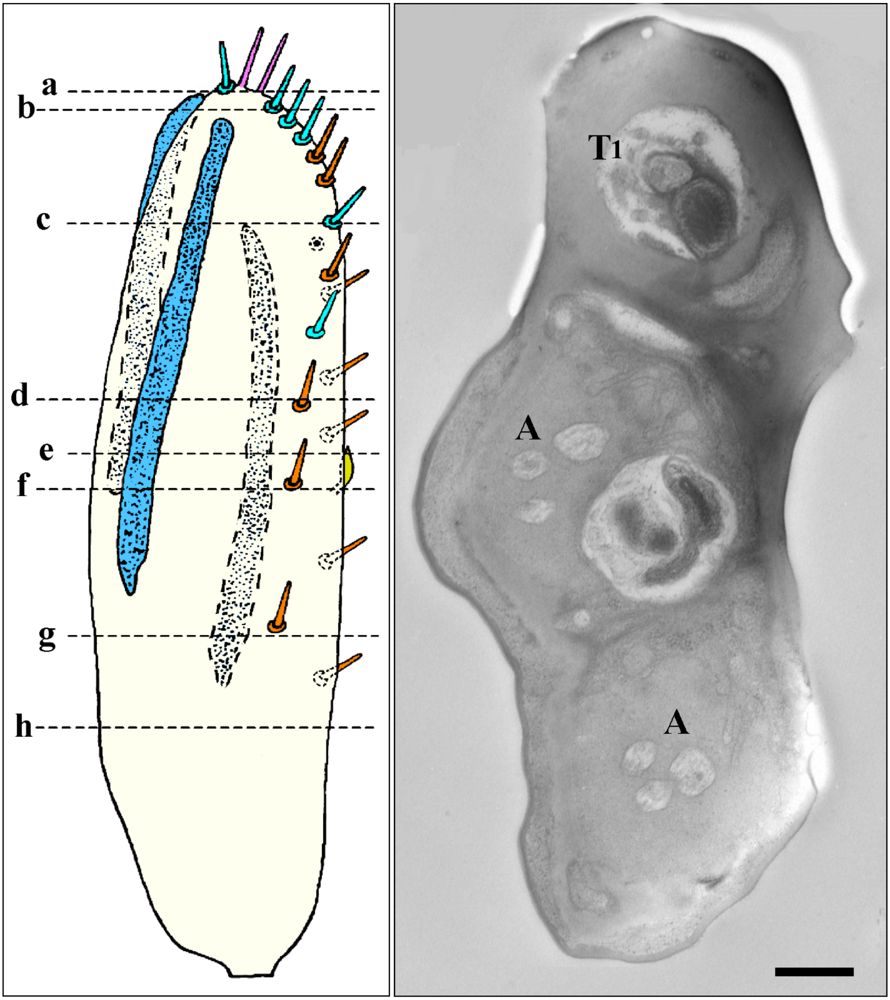

Fig. 3 - Schematic diagram of the antennal club (medial view, dorsal side on the left) indicating levels (a), (b), (c), (d), (e), (f), (g), (h), through which fine cross sections have been cut; and transmission electron micrograph of section through (a) level (club dorsal side on the top). Bar = 0.5 µm. Symbols as in Figs 1 and 2.

septate junctions (ID: Fig. 11a, and c).

It is remarkable that the sheath cell does not produce any dendritic sheath.

These sensilla might be gustatory, although the hair-shaft lumen lacks a distinct dendritic channel, the outer dendritic segments are naked all their length, and there is no mechanosensitive element. They are most probably involved in the recognition of the microhabitat, i.e., the host-plant tissue

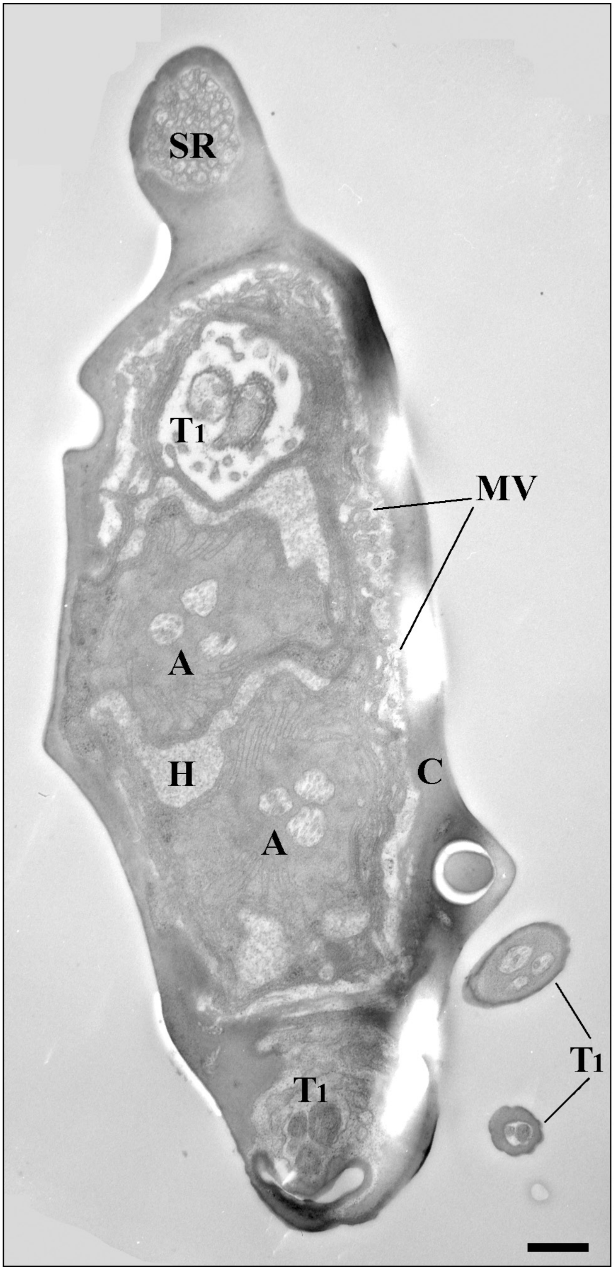

Fig. 4 - Transmission electron micrograph of club cross section through (b) level (see diagram on Fig. 3). Bar = 0.5 µm. Symbols as in Fig. 2, and: C, cuticle; H, haemocoel; MV, microvilli.

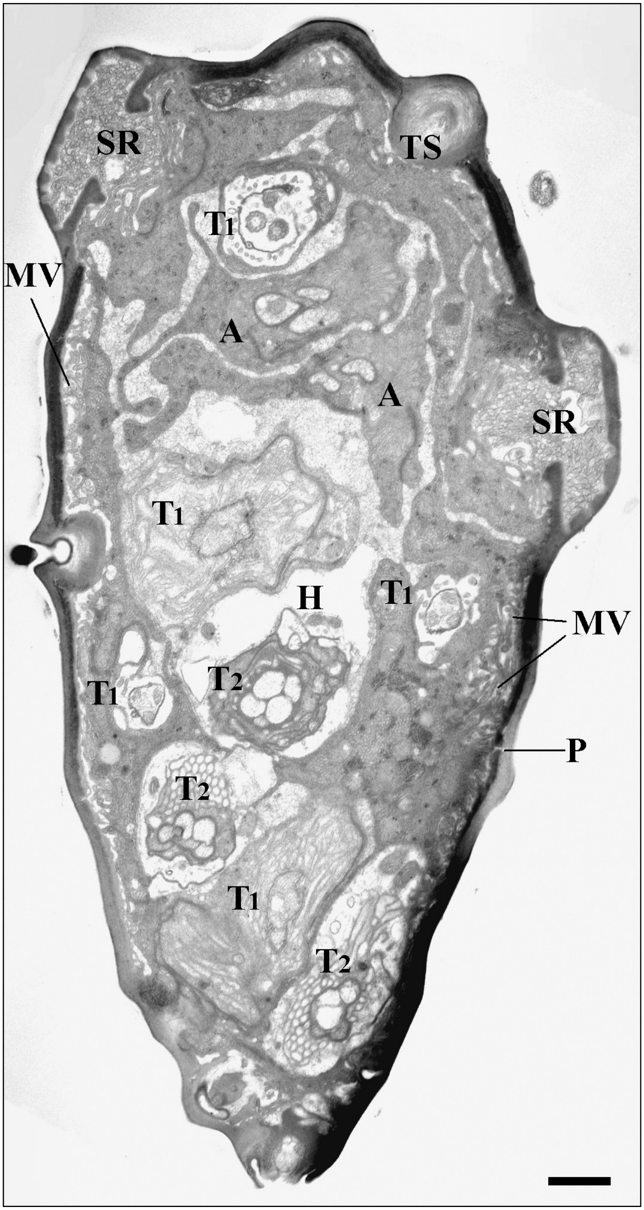

Fig. 5 - Transmission electron micrograph of club cross section through (c) level (see diagram on Fig. 3). Bar = 1 µm. Symbols as in Fig. 4, and: P, club wall pore; T2, sensilla trichodea Type 2; TS, tactile sensilla.

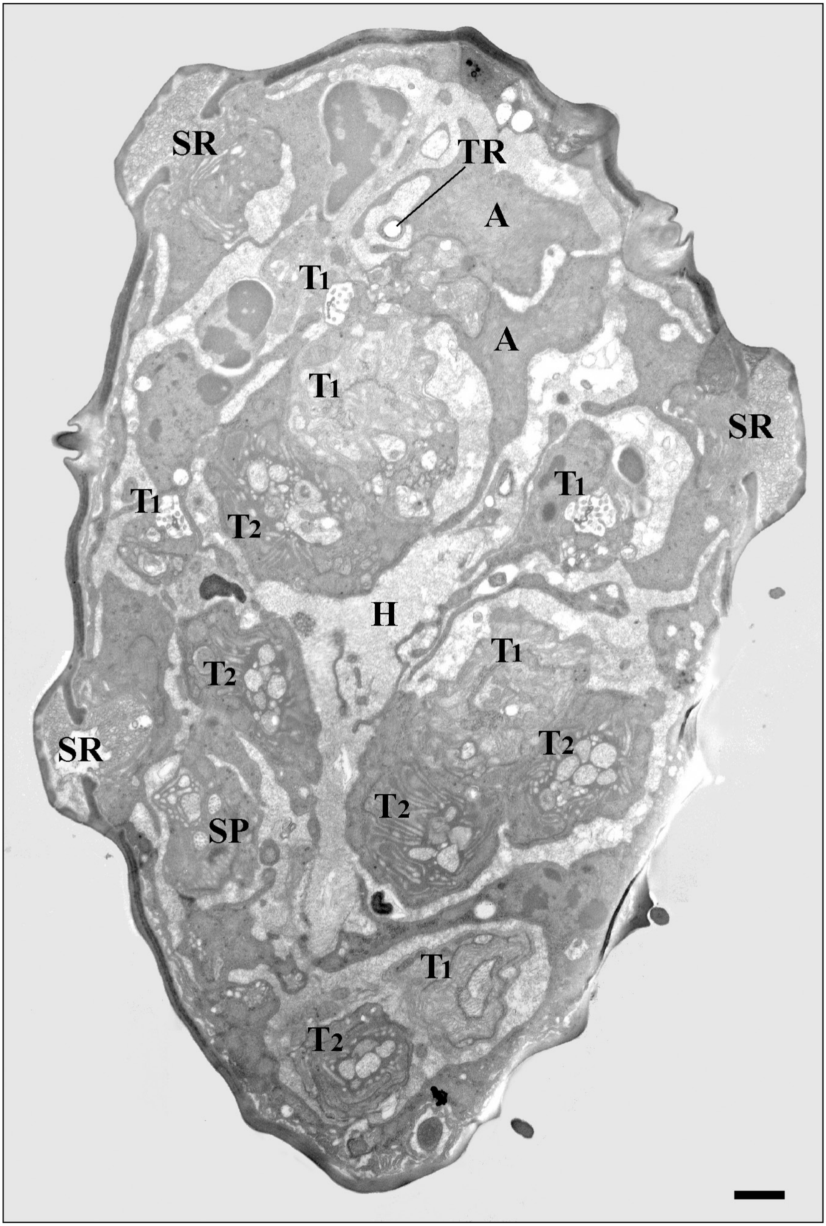

Fig. 6 - Transmission electron micrograph of club cross section through (d) level (see diagram on Fig. 3). Bar = 1 μm. Symbols as in Fig. 5, and: SP, sunken peg sensillum; TR, trachea.

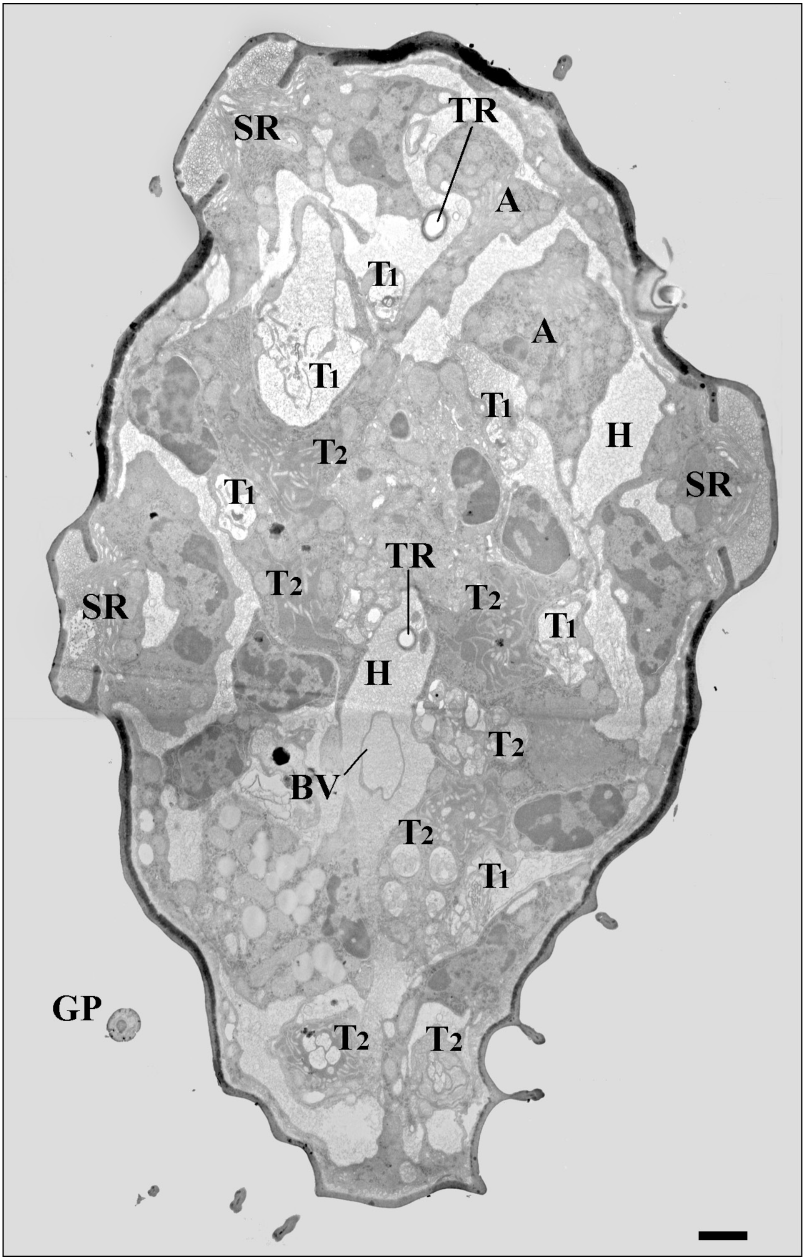

Fig. 7 - Transmission electron micrograph of club cross section through (e) level (see diagram on Fig. 3). Bar = 1 µm. Symbols as in Fig. 6, and: BV, blood vessel; GP, grooved peg sensillum.

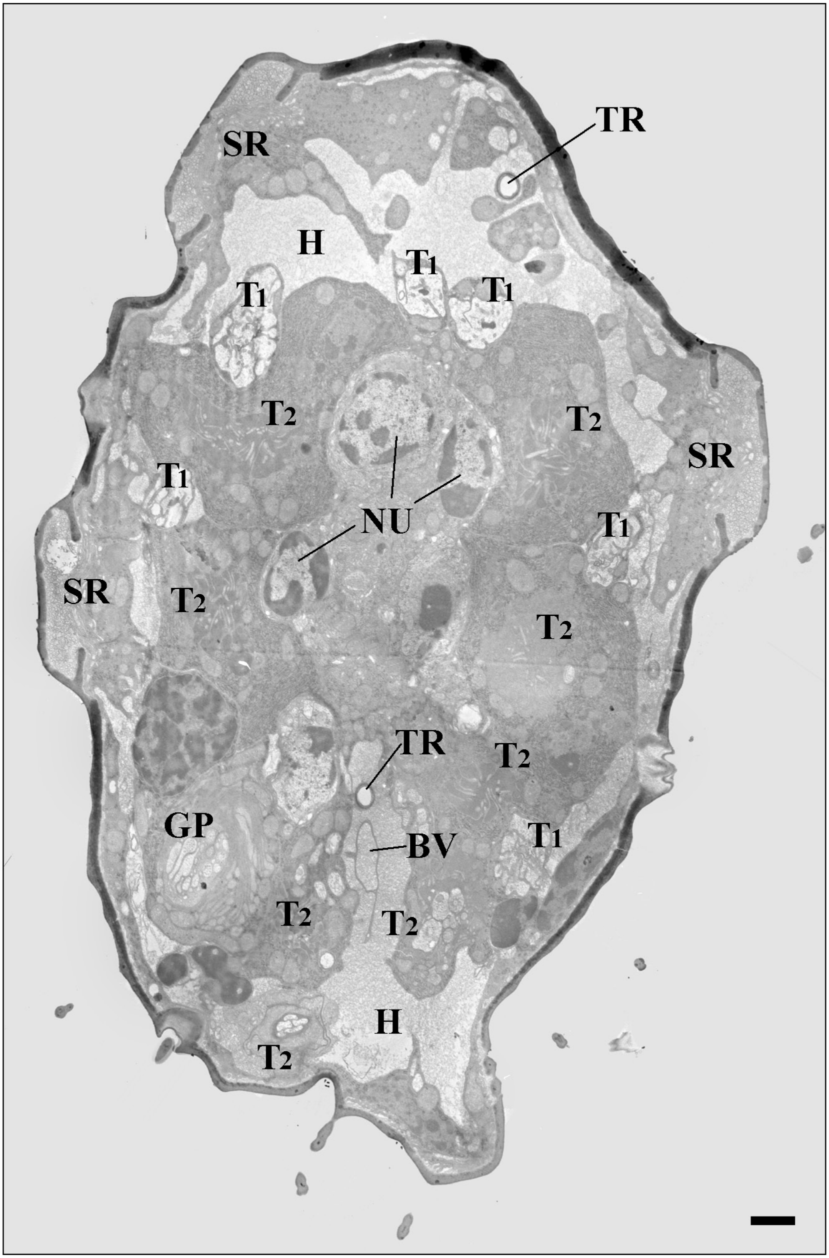

Fig. 8 - Transmission electron micrograph of club cross section through (f) level (see diagram on Fig. 3). Bar = 1 µm. Symbols as in Fig. 7, and: NU, sensory neurone nucleus.

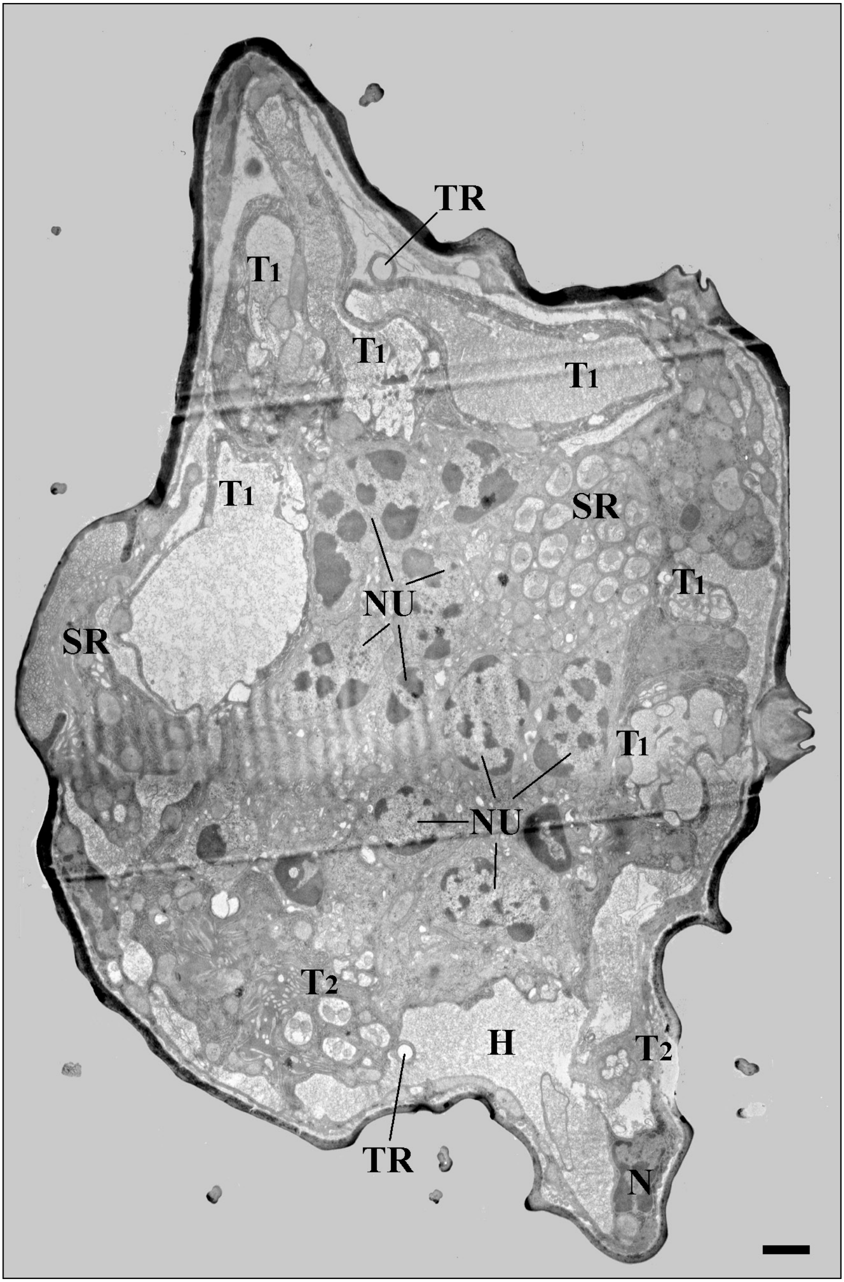

Fig. 9 - Transmission electron micrograph of club cross section through (g) level (see diagram on Fig. 3). Bar = 1 µm. Symbols as in Fig. 8, and: N, sheath cell nucleus.

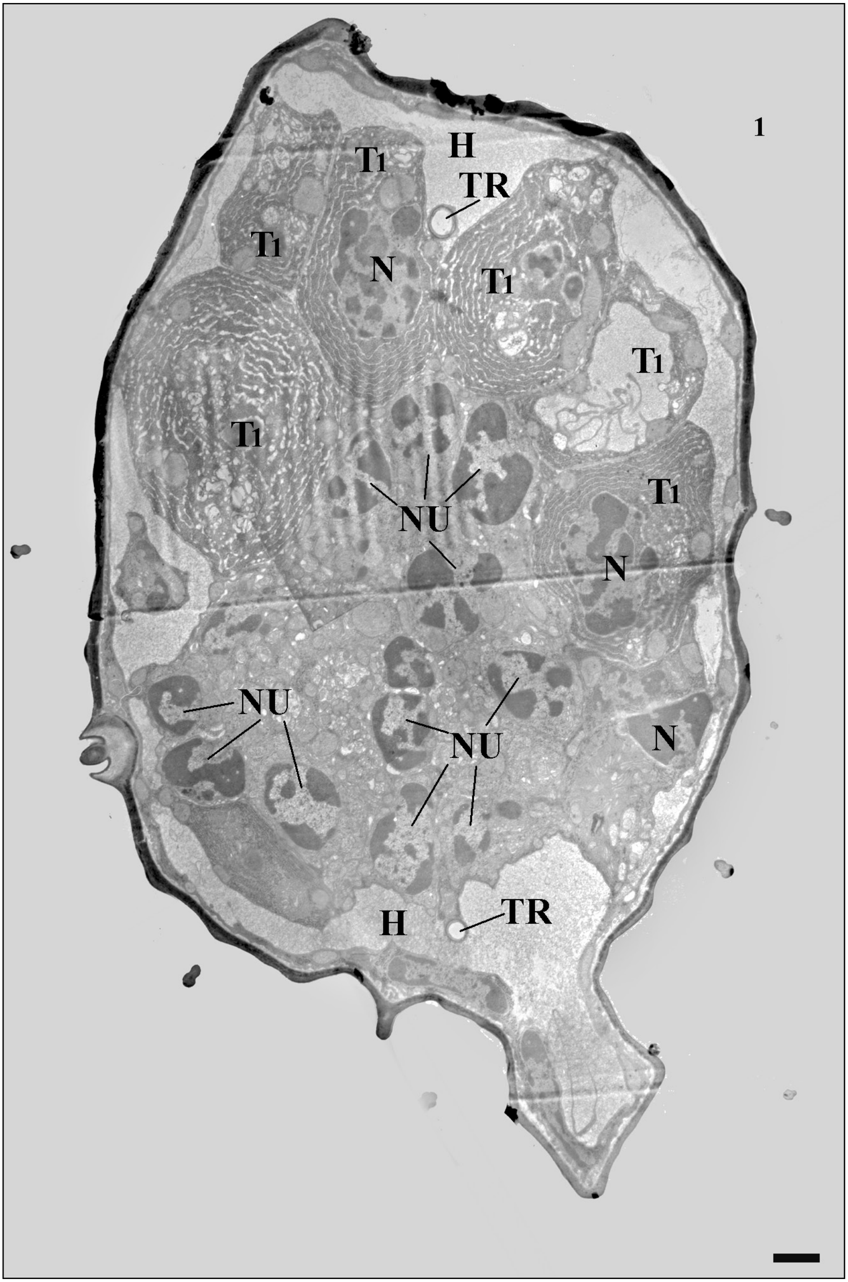

Fig. 10 - Transmission electron micrograph of club cross section through (h) level (see diagram on Fig. 3). Bar = 1 µm. Symbols as in Fig. 9.

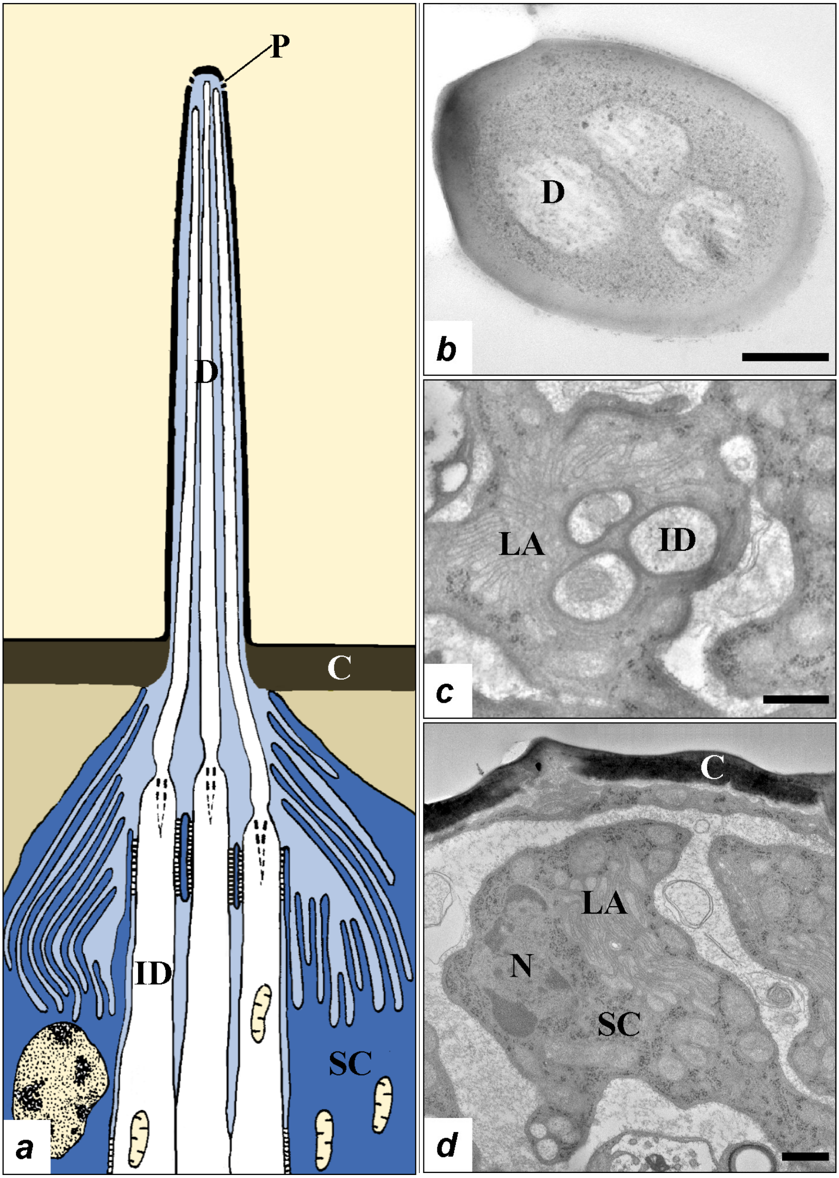

Fig. 11 - Apical sensillum. Schematic diagram (a), and transmission electron micrographs of cross sections through: the distal end of the hair-shaft (b), the inner dendritic segments (c), and the innermost portion of the sheath cell (d). Bars = 0.2 µm (b), 0.5 µm (c) and (d). C, cuticle; D, outer dendritic segment; ID, inner dendritic segment; LA, sheath cell labyrinth; N, sheath cell nucleus; P, pore system; SC, sheath cell.

wounded by the leaf-hopper ovipositor. In fact, the *Anagrus* female walks quickly up and down on the wounded leaf, in search of the host eggs, bearing the antennae slightly diverging, directed towards the leaf surface so as to form a 50° angle with the latter, and constantly tapping the substratum with her antennal club tips; furthermore the tapping frequency increases while the female slows her walking on finding a leaf-hopper egg.

Sensilla trichodea Type 1

The cuticular apparatus of sensilla trichodea Type 1 (Figs 1b, and 2: T1) consists of a fluted hair-shaft, set in a flexible socket, gradually tapering to the tip, having an unpartitioned lumen, and terminating with a single apical pore (P: Fig. 12a, and b).

The cellular components consist of four sensory neurones (Fig. 12a, and d; T1: Figs 4-7) and only one sheath cell (Fig. 12a, and d; T1: Figs 4-10).

Of the four sensory neurones, three send the outer dendritic segments into the hair-shaft lumen while the fourth one terminates with a tubular body at the hair-shaft base, thus representing a mechanosensitive element. The three dendrites which enter the hair-shaft lumen terminate at different levels close to the hair tip (Fig. 12a, and c).

The sheath cell is remarkably large, and displays a big nucleus lying at its base and a perinuclear cytoplasm very rich in rough endoplasmatic reticulum (Fig. 10: T1). This cell lines a wide sinus (including both ciliary and sensillar sinus); within that, there is a sort of dendritic sheath, quite strong and irregularly shaped, exceptionally extended downwards, and frequently interrupted (perforated) (DS: Fig. 12a, and d).

These sensilla, morphologically speaking, must be considered gustative although the hair-shaft lumen lacks a distinct dendritic channel, and the dendritic sheath is quite unusual. They are most probably involved in examination/selection of the host eggs. In fact, after the piece of behaviour reported above, the *Anagrus* female, bearing its antennae almost parallel to each other, sometimes brushes the scar above the host egg with the antennal club ventral side.

Sensilla trichodea Type 2

The cuticular components of sensilla trichodea Type 2 (Fig. 1b, and c; Fig. 2: T2) consist of a fluted hair-shaft arising from a flexible socket and tapering to the tip. The hair-shaft lumen is unpartitioned and terminates with an apical pore system (Fig. 13a, and b).

The cellular components consist of five sensory neurones and two sheath cells (Fig. 13a, and f; T2: Figs 5-9).

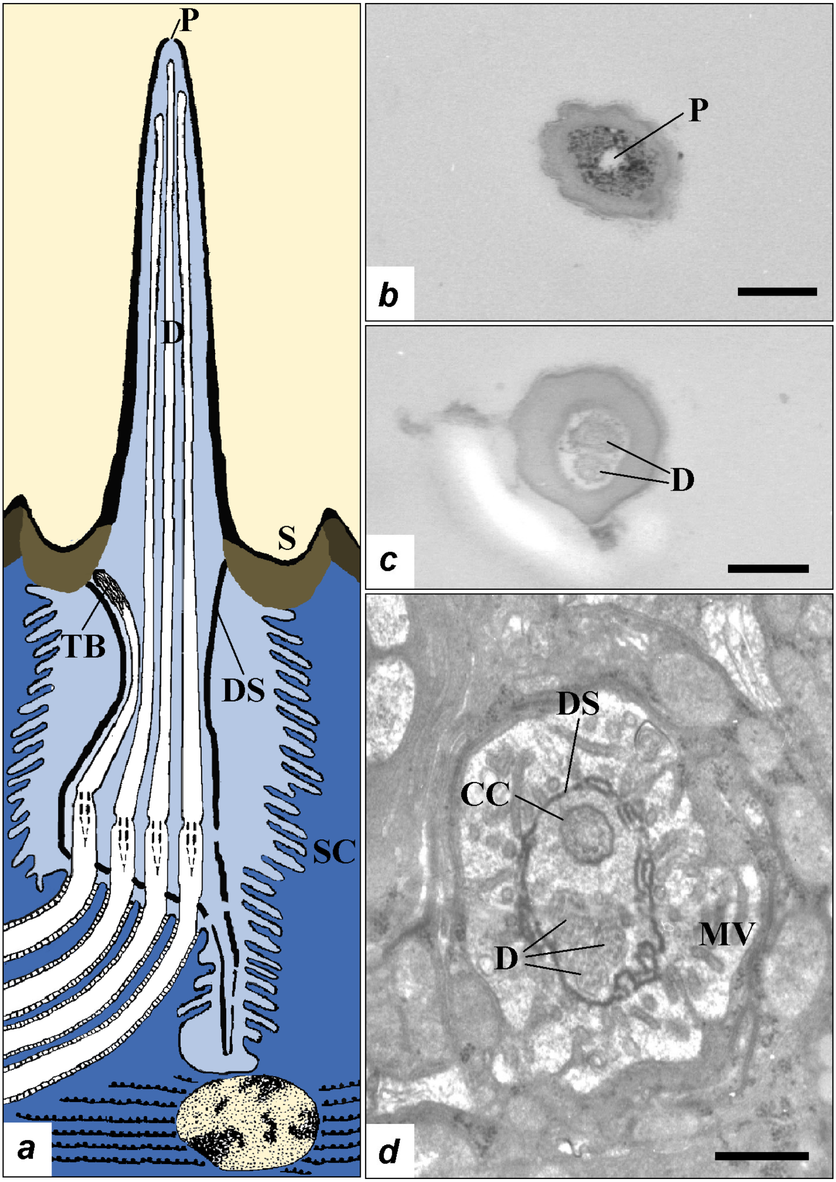

Fig. 12 - Sensilla trichodea Type 1. Schematic diagram (a), and transmission electron micrographs of cross sections through: b, the very distal end of the hair-shaft; c, just below the latter, showing two of the three outer dendritic segments; d, the ciliary region. Bar = 0.25 μm (b) and (c), and 0.5 μm (d). Symbols as in Fig. 11, and: CC, ciliary constriction; DS, dendritic sheath; MV, microvilli; S, socket; TB, tubular body.

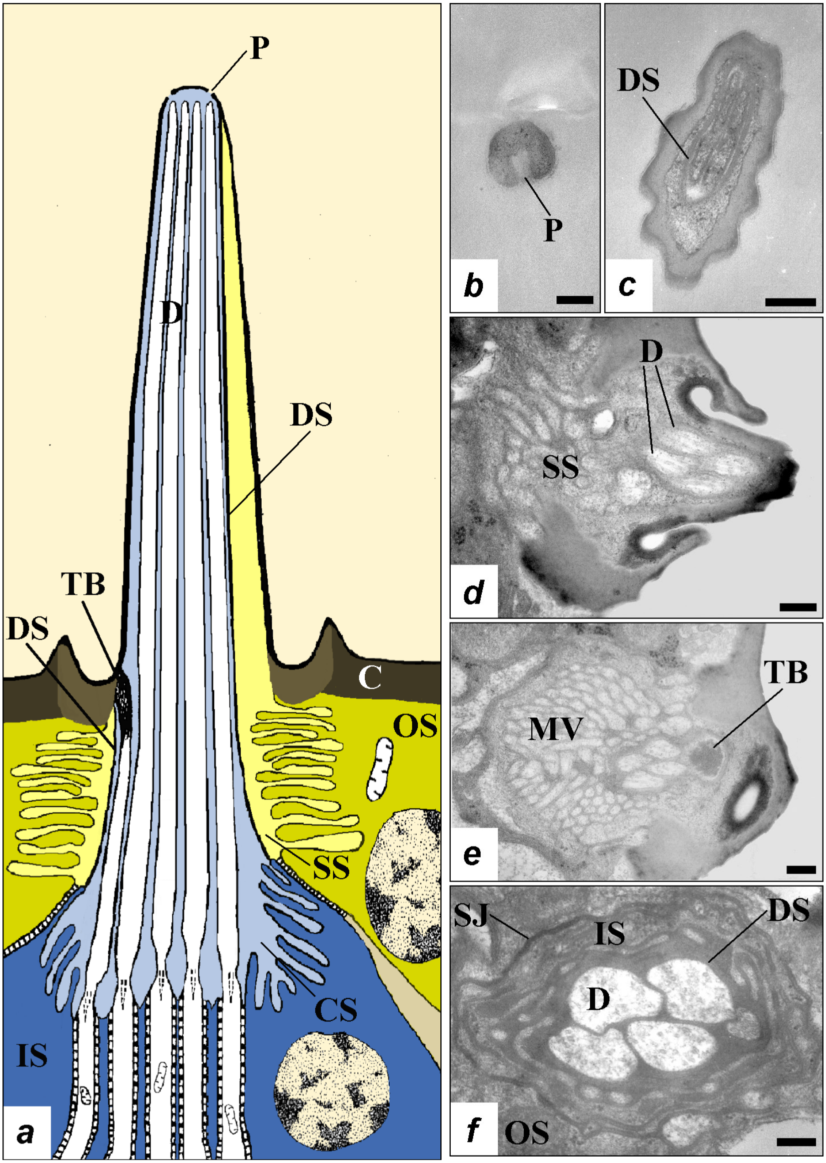

Fig. 13 - Sensilla trichodea Type 2. Schematic diagram (a), and transmission electron micrographs of cross sections through: b, the distal end of hair-shaft; c, the middle of hair-shaft; d, the socket region; e, just beneath the latter; and f, just above the ciliary constrictions. Bars = 1 µm (a), 0.1 µm (b), and 0.2 µm (c), (d), (e), (f). Symbols as in Fig. 12, and: CS, ciliary sinus; IS, inner sheath cell; OS, outer sheath cell; SJ, septate junctions; SS, sensillar sinus.

Of the five neurones, four have outer dendritic segments which enter the hair-shaft lumen (Fig. 13c, and d), unbranched and still encased in the dendritic sheath (Fig. 13a, and c). The fifth neurone ends with a tubular body at the hair-shaft base (TB: Fig. 13a, and e), thus representing a mechanosensitive element.

The inner sheath cell (thecogen) produces a very thick dendritic sheath (Fig. 13f) extended within the hair-shaft lumen almost to the tip of that, and lines a ciliary sinus extended inwards into a deep labyrinth.

The outer sheath cell surrounds the inner one and lines, with packed microvilli, a wide sensillar sinus which is divided from the ciliary sinus by the above mentioned dendritic sheath (Fig. 13a).

These sensilla, morphologically speaking, must be contact-chemoreceptors, just like sensilla trichodea Type 1. Their behavioural significance must be similar to that of the latter, but probably tuned to different substances, e.g., the host plant sinomone/s and the host egg kairomone/s, alternatively. The problem might be resolved through electrophysiological bioassays.

SENSORY RIDGES

The cuticular components of the sensory ridges (Figs 1, and 2: SR) correspond to the remains of modified olfactory multiporous hairs, lying on the antennal wall and longitudinally merging with it so that their lumen is continuous with the club lumen (Fig. 14a).

They are thick-walled sensilla with bell-shaped pores (Fig. 15a).

The cellular components consist of some twenty sensory neurones (Figs 9: SR, and 15b) and two clearly distinct (inner and outer) sheath cells (Fig. 15a).

The sensory neurone perycarions lye near the club base (Fig. 10) while the dendrites run upwards and branch before entering the outer process (the ridge) lumen, which they fill.

It is noteworthy that the wall pores are internally connected to the dendritic branches through electrondense material (Fig. 15a).

The inner sheath cell lines a ciliary sinus and, together with the outer sheath cell, a comparatively narrow sensillar sinus, with loose microvilli which can invade even the ridge lumen (Fig. 15a).

These sensilla, morphologically speaking, must be olfactory, and they are apparently involved in the microhabitat (i.e., a leaf of the leaf-hopper host-plant potentially bearing eggs) recognition. In fact, an *Anagrus* female introduced into a Petri dish and presented with a host-plant leaf bearing leaf-hopper eggs, just before leaping onto the leaf, stops walking and keeps the antennae in an upright position, slightly rotating them, so as to capture airborne odour molecules and to establish their provenience.

GROOVED PEG SENSILLUM

The cuticular components of the grooved peg sensillum (Figs 1c, and 16b) consist of a peg-like structure displaying a fir-like and grooved body on a smooth stalk set on the club wall without any flexible socket. There are four or five longitudinal, slit-like wall grooves, each one about 20-30 nm wide and 130-170 nm deep, having irregular pores at their bottom (Fig. 17a, b, and c). The peg lumen is divided into two concentric compartments (the inner one being the dendritic channel) by a quite thick cuticular wall. The latter is connected to the outer peg wall by a sort of cuticular bridges (Figs 16a, and 17c).

The cellular components consist of three sensory neurones (Figs 8: GP, and 17e, and f) and two sheath cells.

All of the sensory neurones enter the dendritic channel in the peg lumen (Figs 16a, and 17c).

The inner sheath cell (thecogen) is quite large and has a big nucleus at its basal part where it encases the three sensory neurones' inner dendritic segments. Furthermore, it lines a ciliary sinus, inwardly extended in a very deep labyrinth with packed microlamellae (Fig. 17f), and outwardly widened and lined by microvilli, closely packed and quite short and wide (Fig. 17e), which abut on the dendritic sheath. The latter encases the outer dendritic segments all along their length, to the dendritic channel of the peg (Fig. 16a).

The outer sheath cell envelopes the previous one and lines, with loose and irregular microvilli, a wide sensillar sinus continuous with the sensillar channel in the peg lumen (SS: Figs 16a, and 17d).

The function of these sensilla is not easily conceivable. They look like the "grooved basiconica" described by MESSADEQ *et al.* (1995) and CRIBB (1997), and interpreted as possible hygroreceptors.

SUNKEN PEG SENSILLUM

The sunken peg sensillum cuticular components (Figs 1c, and 2: SP) consist of a deep, curved pit, occupied all along its length by a sort of peg set on the pit bottom without any joint membrane and terminating with a solid portion almost on line with the pit entrance which is somewhat projecting from the club wall (Fig. 18a, and b).

The cellular components consist of three sensory neurones (Figs 6: SP, 18a, and 19b) and two sheath cells.

Two of the sensory neurones send their outer dendritic segment into the peg lumen, ending at different levels towards the peg tip; while the third neurone terminates beneath the pit base with a dendrite tapering but not forming any tubular body (Figs 18a, and 19b).

The inner sheath cell (thecogen) lines a narrow ciliary sinus and produces a thick dendritic sheath (DS: Fig. 19a, and b).

The outer sheath cell lines a wide sensillar sinus (SS: Fig. 19a), with loose

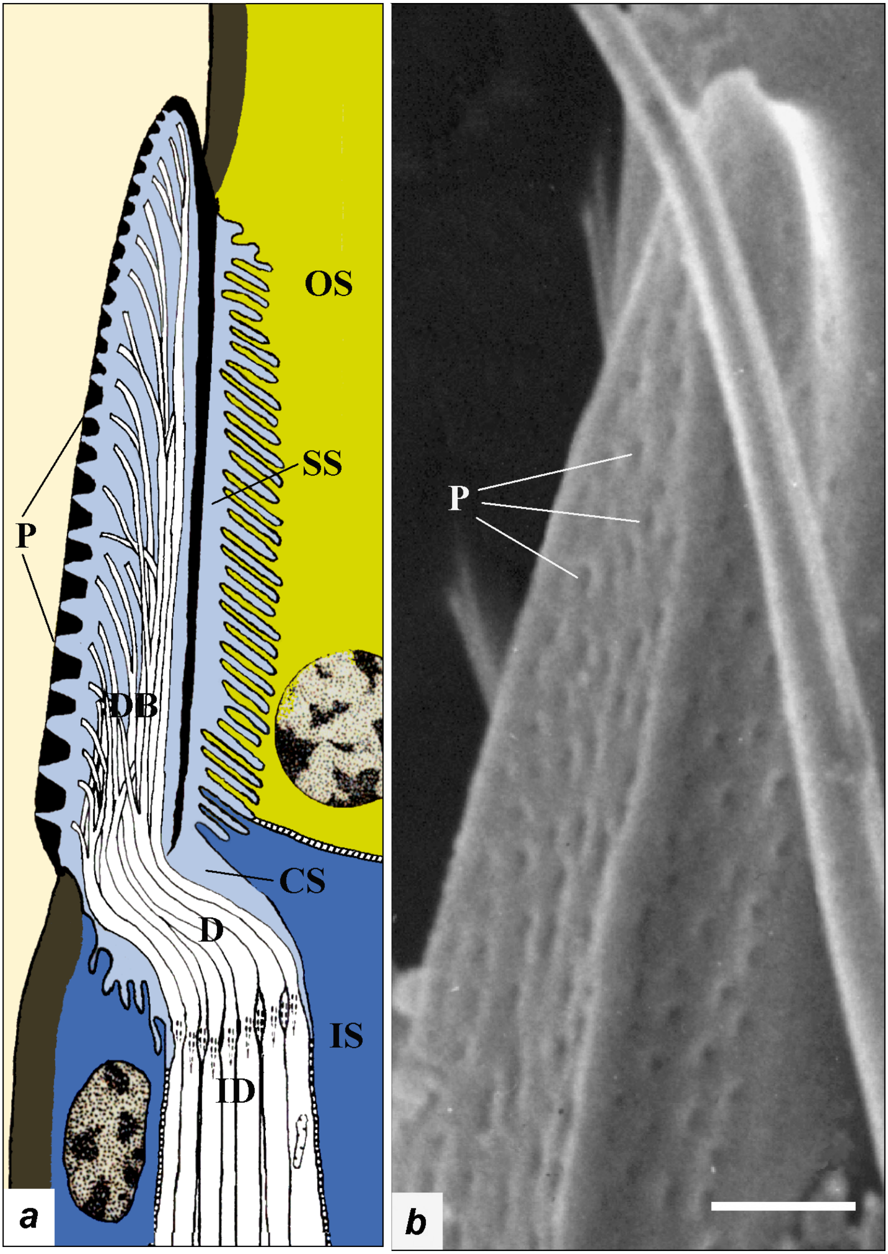

Fig. 14 - Sensory ridge. Schematic diagram (a), and scanning electron micrograph (b) displaying its multiporous wall. Bar = 1 µm (b). Symbols as in Fig. 13, and: DB, dendritic branches.

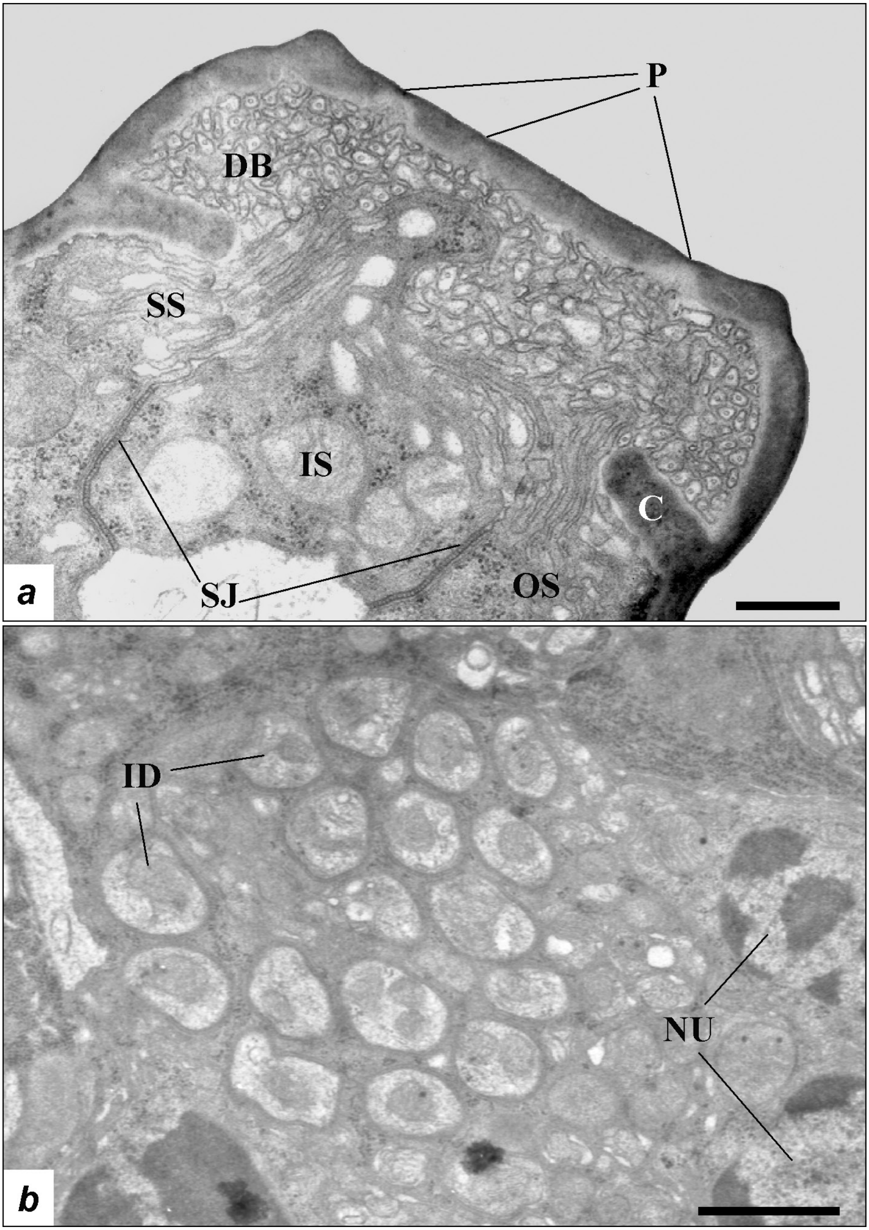

Fig. 15 - Sensory ridge. Transmission electron micrographs of cross section details through the ridge (a), showing dendritic branches within it, and the sinus; and (b), through the inner dendritic segments' level. Bars = 0.5 µm (a) and 1 µm (b). Symbols as in Figs 13 and 14, and: NU, sensory neurone nucleus.

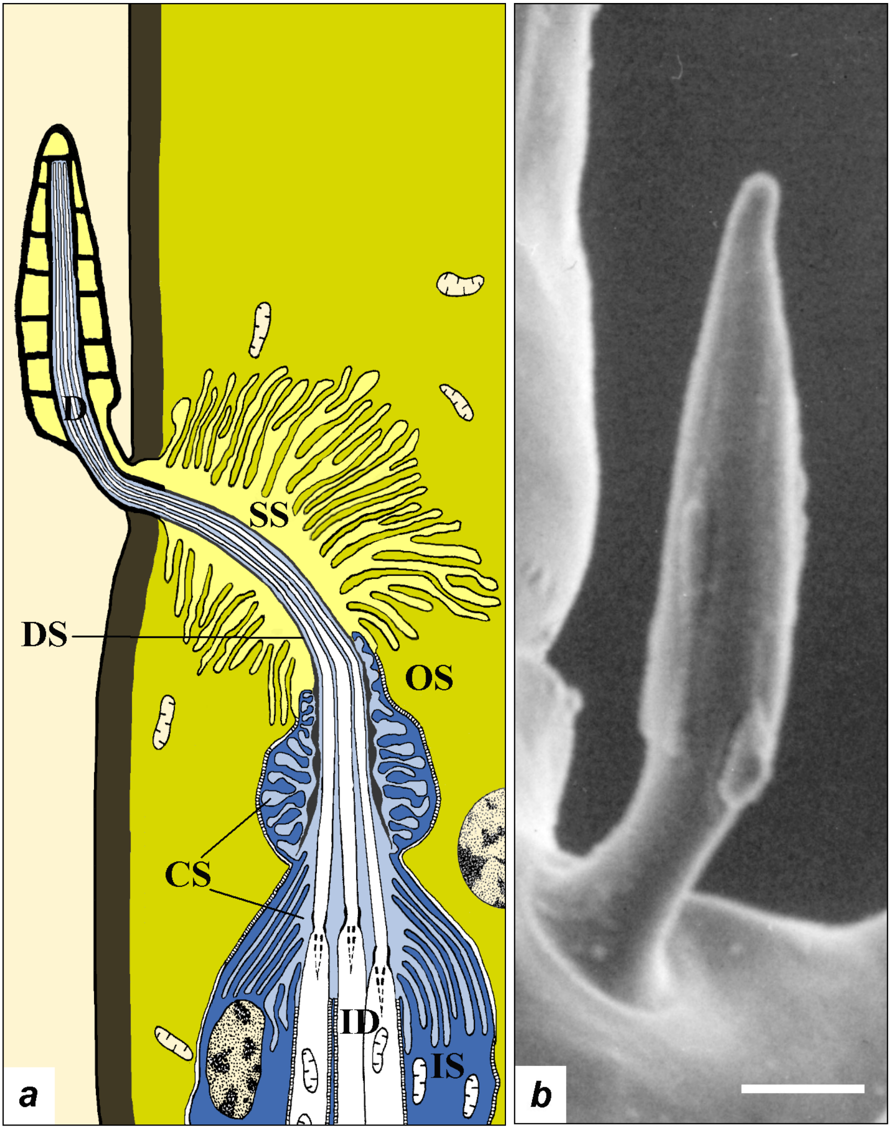

Fig. 16 - Grooved peg sensillum. Schematic diagram (a), and scanning electron micrograph (b) showing external aspect. Bar = 1 µm (b). Symbols as in Fig. 14.

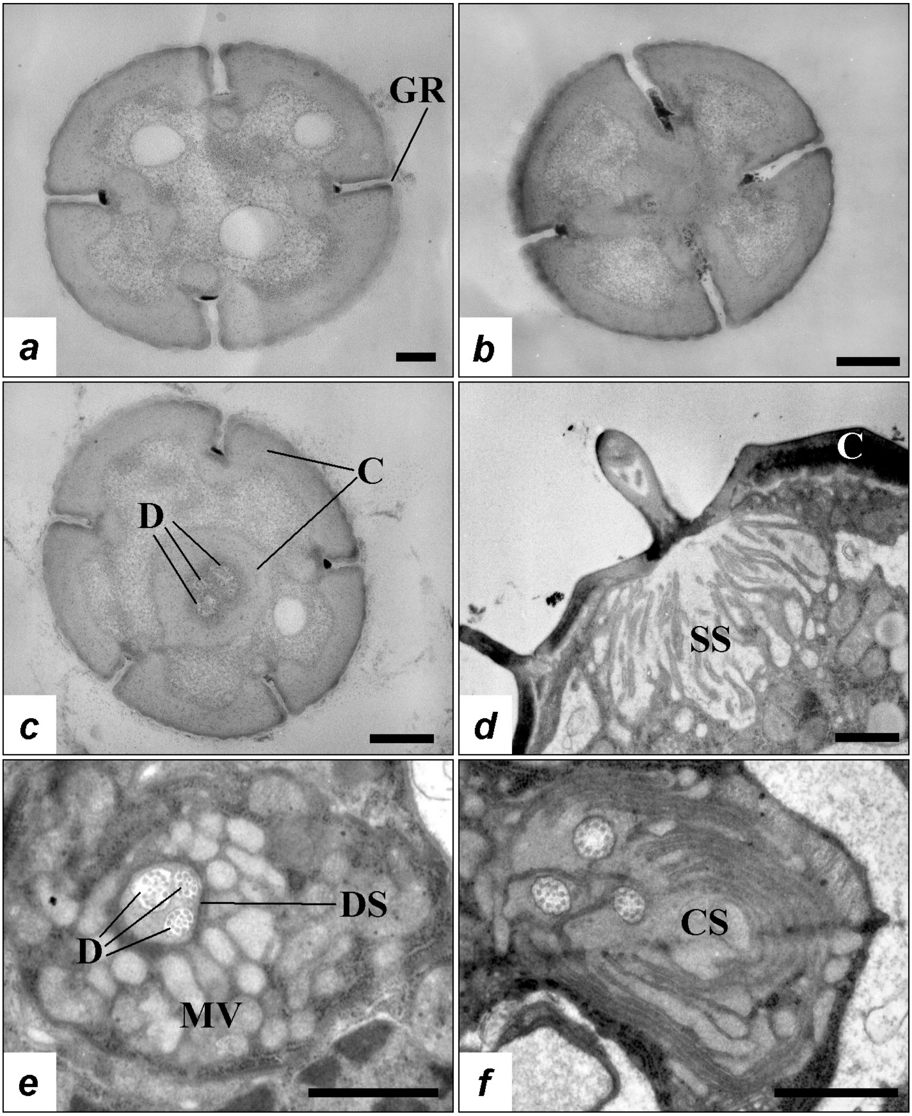

Fig. 17 - Grooved peg sensillum. Transmission electron micrographs of cross sections through: above the distal end of the dendritic channel (a), the top of dendritic channel (b), the middle of the peg body (c), the peg base (d), just beneath the latter (e), the ciliary constrictions (f). Bars = 0.1 µm (a), 0.2 µm (b) and (c), and 1 µm (d), (e) and (f). Symbols as in Fig. 16, and: GR, groove.

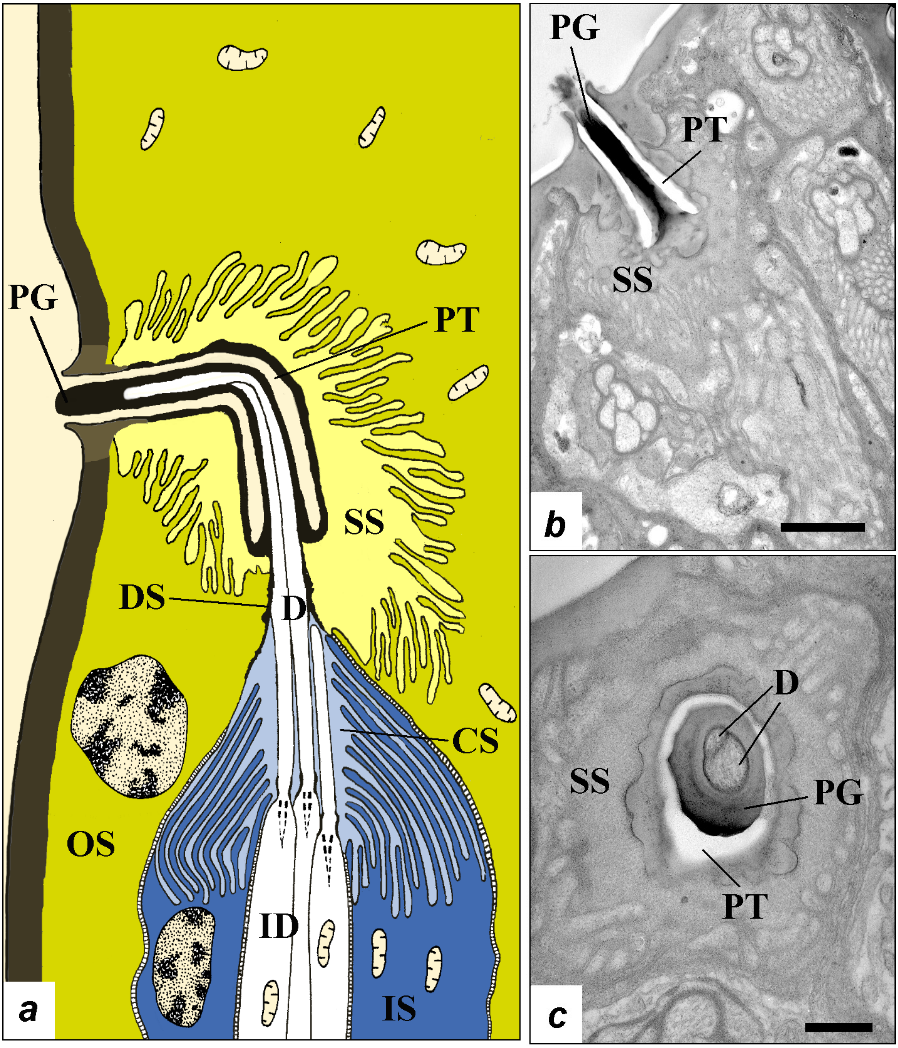

Fig. 18 - Sunken peg sensillum. Schematic diagram (a), and transmission electron micrographs of cross sections through: the outer portion of the peg, above its bend (b), and the inner portion of the peg, below its bend (c). Bars = 1 µm (b), 0.4 µm (c). Symbols as in Fig. 16, and: PG, peg; PT, pit.

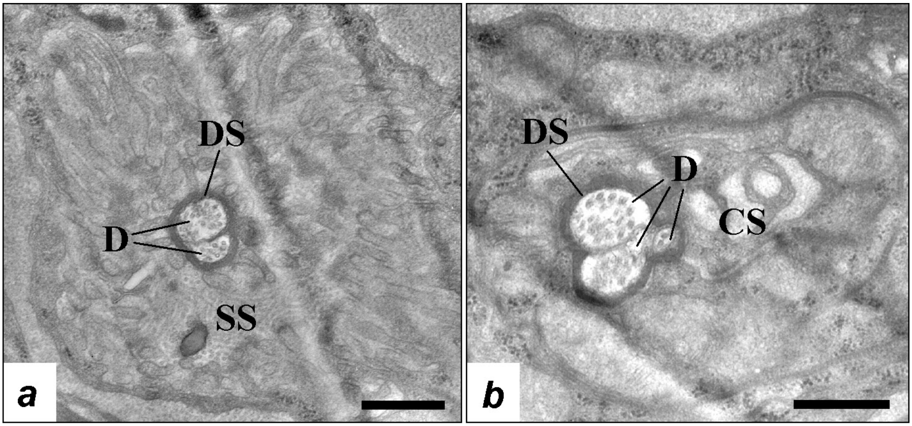

Fig. 19 - Sunken peg sensillum. Transmission electron micrographs of cross section details through the two dendrites entering the peg (a), and the termination of the outer dendritic segment of the third sensory neurone (b). Bars = 0.5 µm (a) and (b). Symbols as in Fig. 18.

microvilli abutting on the dendritic sheath. The sensillar sinus is apparently filled with granular electrondense material (Fig. 19a).

The function of these sensilla is not easily conceivable. They look like the "basal sensillum" described by SOLINAS *et al.* (1987) and interpreted as possible hygro/thermo receptor.

TACTILE SENSILLA

The tactile sensilla display a cuticular apparatus consisting of a long, thin hair-shaft, tapering from the base to a sharp pointed tip (Figs 1b and c, and 2: TS), and set in a flexible socket (TS: Fig. 5). The hair-shaft is finely fluted and shows an empty lumen.

They are innervated with a single sensory neurone whose dendrite terminates with a tubular body at the hair-shaft base.

These sensilla must be involved in the examination/recognition of the physical features of the leaf-hopper oviposition site on the host-plant leaf.

ACKNOWLEDGEMENTS

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RIASSUNTO

SENSILLI ANTENNALI DELLA FEMMINA DI *ANAGRUS ATOMUS* (L.) (HYMENOPTERA: MYMARIDAE) E RELATIVO PROBABILE SIGNIFICATO COMPORTAMENTALE

Le antenne della femmina di un imenottero Mymaridae, *Anagrus atomus*, vengono studiate in microscopia ottica ed elettronica a scansione e, per la prima volta, a trasmissione, principalmente al fine di identificarne le strutture sensoriali presumibilmente impegnate nel comportamento riproduttivo della specie. La distribuzione topografica degli elementi esterni (appendici cuticolari) dei sensilli viene illustrata con disegni semischematici dell'antenna intera e della clava in particolare, effettuati al microscopio ottico con camera lucida, unitamente a micrografie elettroniche a scansione. La localizzazione topografica delle parti interne (componenti cellulari) degli stessi sensilli viene evidenziata nella clava mediante micrografie elettroniche a trasmissione di sezioni fini trasversali seriate. Sette categorie di sensilli vengono così identificate ("apical sensilla", "grooved peg sensilla", "sensilla trichodea Type 1", "sensilla trichodea Type 2", "sensory ridges", "sunken peg sensilla", "tactile sensilla") ed illustrate con disegni semischematici riassuntivi e con micrografie elettroniche a trasmissione di sezioni fini seriate. Sulla base della natura dei sensilli e della loro posizione sull'antenna, unitamente al portamento delle antenne medesime durante il comportamento riproduttivo della femmina, viene ipotizzato il significato comportamentale dei sensilli in questione.

Parole chiave: cellule avvolgenti, comportamento riproduttivo, neuroni sensoriali, sensilli gustativi, sensilli olfattivi, ultrastruttura.

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