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Antennal chemosensilla and glands, and their possible meaning in the reproductive behaviour of *Trissolcus basalis* (Woll.) (Hym.: Scelionidae)***

ABSTRACT

The antennae of *Trissolcus basalis*, a solitary endoparasitoid of *Nezara viridula* (Heteroptera: Pentatomidae) eggs, have been investigated by SEM and TEM to map and describe the different types of chemosensilla and glands, some of which are reported for the first time in Parasitic Hymenoptera. A non chemoreceptor, sensillum campaniforme, has also been included since it is associated with glands. A functional interpretation has been attempted correlating the antennal structures with mating and host recognition behaviours previously reported.

Chemosensilla include one olfactory and four gustatory types, distributed thus:

i) one kind of olfactory sensilla («sickle-shaped sensilla»), present in both sexes, that are more extensive and more sensitive (as a whole) in the male (possible pheromone receptors?), while in the female they may be more versatile on account of a larger number of sensory cells per sensillum (could serve as receptors for synomones and kairomones);

ii) four kinds of gustatory sensilla, two of which («sensilla chaetica» possibly involved in reciprocal sex recognition, and «grooved peg sensilla» not clearly interpreted) are present in both sexes, while the third kind («papillary sensilla» possibly involved in host recognition-acceptance) is present only in the female, and the fourth one («sensilla conica» very difficult to interpret) exists only in the male.

Glands include three types distributed thus:

i) «dorsal glands» (both sexes), their secretion possibly involved in courtship;

ii) «ventral gland» (male only), probably secreting a recognition or aphrodisiac pheromone;

iii) «accessory glands» (female only), associated with papillary sensilla.

The importance of these antennal structures for *T. basalis* behaviour and Parasitic Hymenoptera biotaxonomy is briefly discussed.

Key words (in addition to those in the title): Anatomy, sensilla typology, morphology, ultra-

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structure, sensory neurons, sheath cells, secretory cells, olfaction, taste, pheromones, kairomones, mating behaviour, host-location-recognition, egg- parasitoid, *Nezara viridula*.

CONTENTS

1. INTRODUCTION

Trissolcus basalis (Woll.) is a solitary egg parasitoid of the crop pest *Nezara viridula* (L.) (Heteroptera: Pentatomidae) and is being used as an effective bio-control agent.

The female antennae have a five segmented «clava» defined (BIN, 1981) by the presence of nine ventral «plate sensilla» (sensu BIN, 1981; not SLIFER, 1969) presumed to be associated with host recognition (VINSON *et al.*, 1986). Two other types of sensilla, ventral «combed hairs» and latero-ventrally projecting «hair sensilla», have also been reported on the clava as well as on another antennomere (BIN, 1981).

The male antennae exhibit a peculiar 5th antennomere, the so called «sex-segment», in which an exocrine gland has been found (BIN & VINSON, 1986). Its secretion, released through a ventral peg-like process and presumably spread onto female receptors, has been proposed as being a mate recognition or aphrodisiac pheromone.

For both sexes, a preliminary map of the antennal structures was drawn up (BIN et al. 1986) in an attempt to associate these with behavioural mating steps. Some of the structures are common to both sexes, e.g. «sickle-shaped sensilla»

and «hair sensilla». Some others are only present in females, e.g. Bin's «plate sensilla» and «dorsal depressions», or only in males, e.g. «ventral peg» and «bulb sensilla». It has been suggested that mate recognition could be mediated by the female «placoid sensilla» and «dorsal depressions» and by the male «hair sensilla».

The above mentioned preliminary results indicated the need for investigations on topographical anatomy and fine structure of *T. basalis* antennae. The newly discribed and/or discovered sensilla and glands reported here for the female and male antennae are therefore a contribution to give a morpho-functional basis to defining behavioural processes such as mate recognition and host selection.

2. MATERIALS AND METHODS

2.1. Insects

Both *N. viridula* (Southern Green Stink Bug, SGSB) and *T. basalis* were held in a bioclimatic chamber at 22-23 °C, 60 % RH and under 16 h light, 8 h dark photoperiod. Adult SGSB's and nymphs were fed on young soybean plants (*Glycine max* (L.) Merril), raw peanut seeds (*Arachis hypogea* L.) and french beans (*Phaseolus* sp.). Food was changed daily and separate containers were used for nymphs and adults. Deposited eggs were collected daily to avoid adult cannibalism which sometimes occurs (JONES, 1985).

Adults of *T. basalis* were maintained in glass tubes supplied daily with a mixture of honey (10%), vanilla flavored powdered sugar (10%), yeast (10%) and benzoic acid (1%) (SAFAVI, 1968). Host eggs were exposed to parasitoids for 24 h, removed and placed in another tube for incubation. Males and females, which emerge in 11-13 days, were kept in the same tube to allow mating.

2.2. Morphological studies

For T.E.M. observations, *Trissolcus basalis* females and males, newly emerged in the laboratory from eggs of *Nezara viridula* were immediately immersed in Karnowsky's fixative (1965) with 2% Acrolein. Then antennae were detached, cut into pieces (to make the fixative penetrate better) and left for 4 hours at 4°C, next washed overnight in cacodylate buffer, postfixed in 1% Osmium tetroxide for 1h 30' (females) or 2h (males), rinsed in the same buffer, dehydrated in graded ethanol series, block stained with 1% Uranyl acetate in 95% ethanol solution for 1h (during dehydration process), embedded through propylene oxide in Epon-Araldite. Thin sections obtained by a L.K.B. «Nova»

ultramicrotome, sequentially stained with Uranyl acetate and Lead citrate, were examined through a Philips EM 400T. For S.E.M. observations, newly emerged females and males, anesthetized in CO_2 , were beheaded, and the heads immediately, or previously treated with Neutrase (BIN and VINSON, 1986) to clean the papillary sensillum apertures (Fig. 7b), or with KOH (BIN e VINSON l.c.) (Fig. 9),were gold coated in a Balzers Union SCD O4O sputter unit, and viewed through a Philips 501 B or a Jeol JSM-35 (Figs 7b;9).

2.3. Behavioural studies

A brief description of the methods used in published (BIN & VINSON, 1986; BIN *et al.*, 1986) and unpublished studies (BIN *et al.*, submitted) follows.

The behaviour of the newly emerged male was observed under a stereo microscope, kept in a glass tube. For mating behaviour observations, individual males and newly emerged virgin females (at most 24 h old) from artificially isolated, parasitized eggs were paired in an arena (0.4 cm high and 1 cm in diameter). Their behaviour was observed directly or videorecorded under a stereo microscope and various steps were timed using a stop watch.

Ablation of antennomeres and other operations were conducted on adults initially anesthetized with CO_2 and then held dorsally on a piece of double stick tape glued to a piece of filter paper placed on a cool plate (-1, $-3°C$) so that the specimen was immobilized. Specific antennomeres were removed with a scalpel.

Host location was examined by bioassay using groups of 5-10 inexperienced, 2-3 days old females. Females were placed in a two-choice (Y) olfactometer with a 20 ml/min air flow, 24-27°C internal temperature, illuminated by a 60 W incandescent lamp at 20 cm distance. Each trial lasted 10 min at which time the number in each arm and those not responding were recorded. To avoid any position influence, the olfactometer was rotated 180° after each bioassay. After five replicates the olfactometer was washed in series of solvents with an increasing polarity (n-Hexane; Acetone; distilled water), and finally oven-dried at 60°C.

For host acceptance, bioassays were carried out using females at most 24 h old as above, released individually on host egg- masses in 3 cm diameter Petri dishes and directly observed and/or videorecorded under a stereo microscope.

2.4. Explanation of symbols used in the Figs:

AG,	accessory gland(s)	pBB	proximal basal-body
dBB	distal basal-body	BM	basement membrane

BV	blood vessel	MC	microvillar cavity
CA	sensillum campaniforme	ML	microlamellae
CB	cell boundaries	MT	microtubules
CH	sensillum chaeticum	MV	microvilli
CMA	crypto-multiporous area	NU	nucleus
CR	ciliary rootlets	P	pore(s)
CS	ciliary sinus	PA	papilla
CU	cuticle	PG	glandular peg
iCU	inner cuticular layer	PS	papillary sensillum
oCU	outer cuticular layer	PT	papillary sensillum pit
D	outer dendritic segment(s)	R	ribosomes
cD	ciliary constriction(s)	RE	rough endoplasmic reticulum
iD	inner dendritic segment(s)	RF	reinforcement
DB	dendritic branches	S	secretion
DC	ductule cell	SC	sheath cell(s)
DG	dorsal gland	iSC	inner sheath cell
DS	dendritic sheath	oSC	outer sheath cell
DU	ductule	SCO	sensillum conicum
EA	end apparatus	SEC	secretory cell
G	Golgi apparatus	SH	shaft
GC	glial cell	SJ	septate junctions
GD	glandular depression	SK	sickle-shaped sensillum
GO	glandular outlet(s)	SN	sensory neuron cell bodies
GP	grooved peg sensillum	SO	socket
GR	groove(s)	SS	sensillar sinus
H	haemocoele	TB	tubular body
HL	hinged lid(s)	TR	tracheole(s) or tracheal branches
LY	lysosome(s)	V	secretion vesicle(s)
M	mitochondrion(s)	VG	ventral gland

3. RESULTS AND DISCUSSION

3.1. Antennal topographical anatomy concerning chemosensilla and glands

Trissolcus basalis antennae are geniculate, markedly different in size and shape according to the sex, but both sexes have almost the same types of sensilla and glands (Table 1).

Female antennae (Fig. 1) are formed by 11 antennomeres: scape (1st), pedicel (2nd), and flagellum (3rd to 11th) consisting of a short funicle (3rd to 6th) and a relatively big «clava» (sensu Bin, 1981) (7th to 11th). There are four kinds of chemosensilla and two kinds of glands all situated on the flagellum, in number and distributed as follows: (i) «sickle-shaped sensilla» (SK, Figs 1a, 3b, 8) about 36 altogether on the dorsal side of the flagellomeres, about 4 sensilla per subsegment: irregularly located and frequently reduced to 3 on antennomeres 3rd-4th and 11th, 3 on 5th, and 4 (exceptionally 5) regularly distributed (one

pair on either side of the dorsal gland depression, DG) near the distal margin of the other flagellomeres; (ii) «papillary sensilla» (PS, Figs 1b, 3a, 8) 9 on the ventral side of clavomeres, and distributed according to Bin's formula 2-2-2-2-1; (iii) «sensilla chaetica» (CH, Figs 1c, 3a, 8), about 27 present altogether, on the ventral side of antennomeres 6th to 10th, in number of 4 and regularly located on each antennomere 7th to 10th, only 3 on antennomere 6th, and about 8 irregularly distributed on the last antennomere; (iv) «grooved peg sensilla» (GP, Figs 1d, 21: a, b), about 6 altogether, 1 near the lateral (outer) distal margin of each antennomere 4th to 6th (exceptionally, 7th as well), and 3 (rarely 2) before the apex of antennomere 11th; (v) «dorsal glands», whose nume-
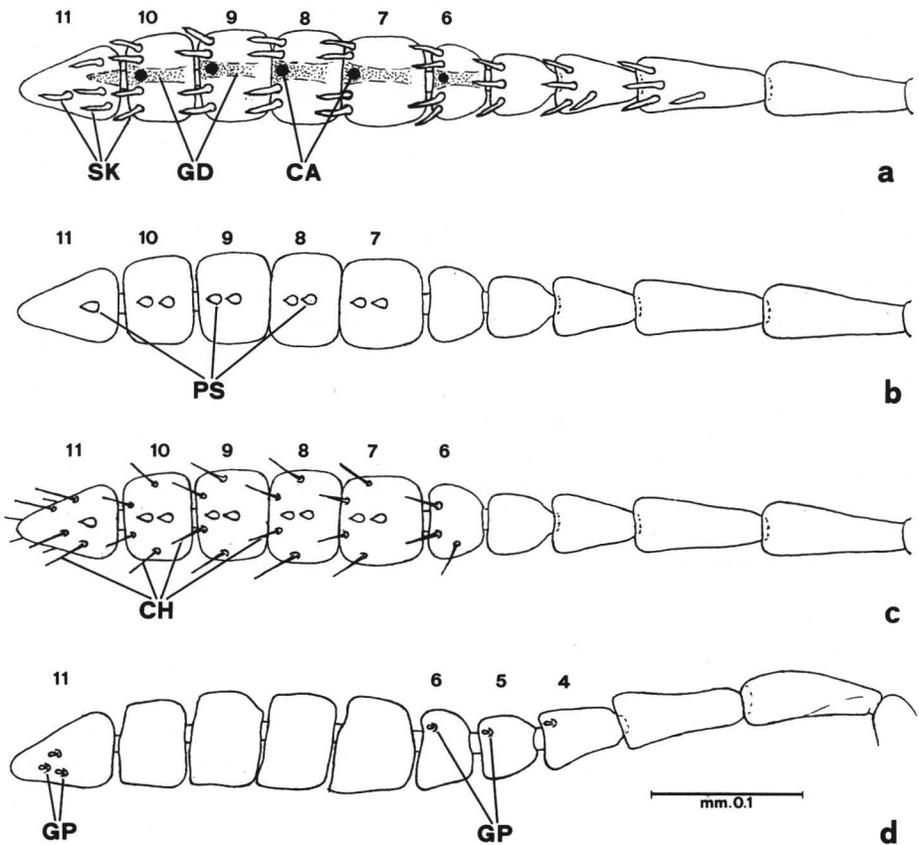
Fig. 1 - Outline of female antennae: a) dorsal view showing only «sickle-shaped sensilla» (SK), «glandular depressions» (GD), and relative «sensilla campaniformia» (CA); b) ventral view with only «papillary sensilla» (PS); c) the same with «sensilla chetica» (CH) added; d) lateral view showing «grooved peg sensilla» (GP, not to scale) only.

rous outlets terminate on a longitudinal dorsal depression, here called «glandular depression» (GD, Figs 1a, 3b, 24), in number of 6 altogether, one per antennomere 6th to 11th, and having each gland (except on 11th antennomere whose gland is distally shortened) near the distal end a single «sensillum campaniforme» (CA, Figs 1a, 24) associated with it; (vi) «accessory glands» (AG, Fig. 8), so called here as they are closely connected with «papillary sensilla», opening into the pit of these just above and below the papilla base (Figs 7b: PT; 8: AG; 9: GO).

Male antennae (Fig. 2) consist of 12 antennomeres: a long scape (as in the female), a shorter (much shorter than in female) pedicel and a moniliform flagellum composed of 10 subsegments or flagellomeres (antennomeres 3rd to
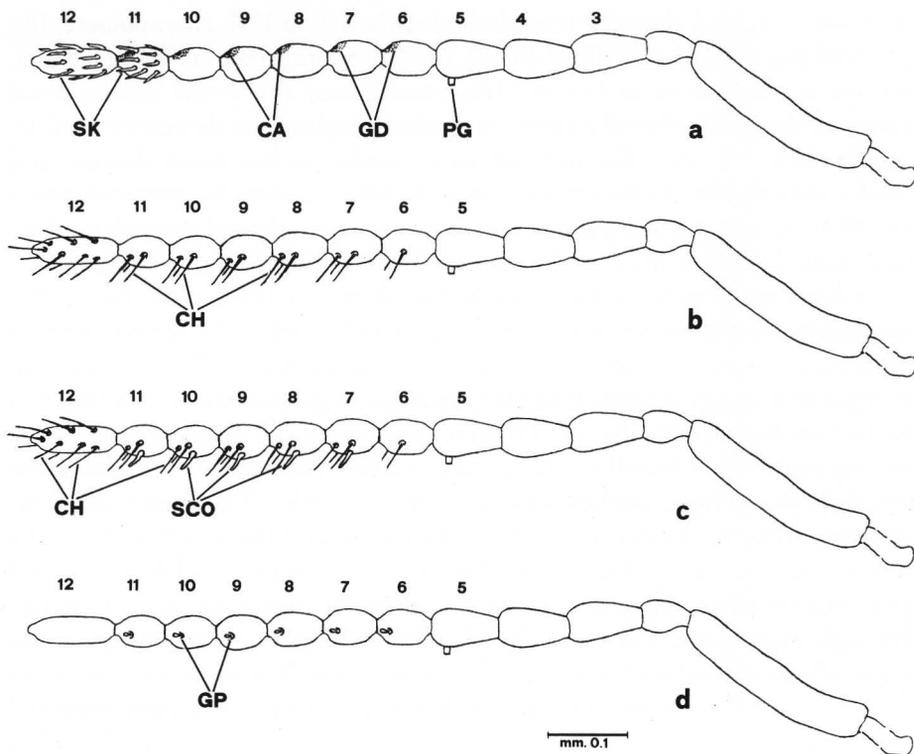
Fig. 2 - Outline of male antennae: a) lateral aspect displaying «sickle-shaped sensilla» (SK, not to scale, omitted on antennomeres 3rd to 10th), «glandular depressions» (GD) with relative «sensilla campaniformia» (CA), and «glandular peg» (PG); b) side aspect with only «sensilla chaetica» (CH); c) the same with «sensilla conica» (SCO) added; d) lateral view showing «grooved peg sensilla» (GP, not to scale) only.

12th) the apical of which is notably longer than the preceding one. These antennae bear almost the same kinds of chemosensilla and glands as in the female except for the lack of «papillary sensilla» (and relative «accessory glands»), replaced by «sensilla conica», and the addition of a «ventral gland», i.e. BIN — VINSON's (1985) «sex gland». The numbers and distribution of the said structures are as follows: (i) «sickle-shaped sensilla» (SK, Figs 2a, 30, 31, 41a, 44a), in number of about 170 altogether, 26-27 on each antennomere 3rd and 4th, about 20 on 5th, 13-14 on 6th to 11th, and about 17 on 12th; on 3rd-5th and 12th they are irregularly distributed whereas on the other subsegments they are roughly arranged in two whorls (a subproximal and a subdistal); (ii) «sensilla conica» (SCO, Figs 2c, 30, 31, 36a, 41a), in total 5, one per antennomere 7th to 11th, rather central on the subsegment ventral side; (iii) «sensilla chaetica» (CH, Figs 2b, 30, 31, 36), about 27 altogether (as in the female), located on the ventral-subventral side distal half of antennomeres 6th to 11th, 2 on 6th and 3 on 7th to 11th, and about 10 irregularly distributed on 12th antennomere; (iv) «grooved peg sensilla» (GP, Figs 2d, 30, 31, 41), 6 altogether (as in the female), but one per antennomere 6th to 11th, located near the lateral (outer) distal margin of these; (v) «dorsal glands», and relative «glandular depressions» (GD, Figs 2a, 30b, 31), very like and the same number as but much shorter (and distally shifted) than in the female, while the relative «sensilla campaniformia» are identical; (vi) «ventral gland», whose secretion is released through a «glandular peg» (PG, Figs 2a, 44a), located on the 5th antennomere ventral side.

In both sexes most of each flagellomere lumen is filled with the cellular components of the above mentioned sensilla and glands. The sensory neuron cell bodies (as observed in *Nasonia vitripennis* by SLIFER, 1969) are almost all arranged in a rather central, irregular, «massive ring» (the masses are larger in the female, Figs 10, 25, 26, 32, 33) which surrounds and partially embeds the two antennal nerve branches and a quite narrow haemocoele containing the antennal blood vessel, tracheal branches and tracheoles. The sheath cells that are responsible for the secretion of the cuticular parts of the sensilla encircle the dendrites of these and fill the region below the same sensilla, while the normal epidermal cells lying elsewhere below the antennal cuticle are much flattened although their nuclei can be easily identified. Also the secretory structures (especially female «dorsal glands» and male «ventral gland») occupy a considerable portion of the lumen of the flagellomeres involved. The intersegmental passages are very narrow and contain only the blood vessel, tracheal branches and the two antennal nerve branches, that flow together within the scape to form, as known, the antennal trunk nerve.

It is noteworthy that this, at least in the female, shows as many axons as the antennal sensory neurons altogether, thus excluding any periferal fusion of sensory axons, according to ZACHARUK (1985).

Tab. 1 - Numbers and distribution of chemosensilla and glands (not including the «accessory glands») on the male and female antennae. Ten samples at least cheked with SEM; numbers in blackets observed occasionally.

Chemosensilla		Antennomeres involved										Total per antenna
		12th	11th	10th	9th	8th	7th	6th	5th	4th	3rd	
SK	male	ca. 17	13-14	13-14	13-14	13-14	13-14	13-14	20	26-27	26-27	ca. 170
	female		3-4	4	4	4	4	4	3	3-4	3-4	ca. 36
SCO	male		1	1	1	1	1					5
PS	female		1	2	2	2	2					9
CH	male	ca. 10	3	3	3	3	3	2				ca. 27
	female		ca. 8	4	4	4	4	3				ca. 27
GP	male		1	1	1	1	1	1				6
	female		3(2)				(1)	1	1	1		ca. 6
Glands												
DG	male		1	1	1	1	1	1				6
	female		1	1	1	1	1	1				6
VG	male (only)								1			1

3.2. Fine morphology
3.2.1 Female chemosensilla and glands

Sickle-shaped sensilla (SK). The cuticular components consist of an outstanding, rather rigid hair-shaft (Figs 3b, 21, 24) ranging in length 15-17 μm, notably expanded at the base to closely fit the round and rigid socket (3-3.2 μm in diameter), sharply bent anteriorly just above the base (2.1-2.4 μm in diameter) and then running, slightly diverging from antennal surface, to an acutely pointed tip; the shaft wall facing the antenna is non-porous all the length but the tip (Fig. 4: a, c, d) and bears two longitudinal internal reinforcements (RF, Fig. 4: a, c) that partially divide the shaft lumen into two compartments, while elsewhere the shaft is typically thin-walled and multiporous, with simple, bell-shaped pores whose outlets are very fine (Fig. 4).

There are not pore tubules, but some electrondense material (a chemical mediator between stimulating molecules and dendritic sites of stimulation ?) very frequently connects the pore outlets to the dendritic branches (Fig. 4b).

The cellular parts per sensillum consist of: a) medially 28 sensory neurons (Fig. 6: a, b), whose perikaryons lie close below the socket (Fig. 5b) or, more frequently, form a part of the above mentioned (see 3.1) «massive ring» of neuron cell bodies, and whose dendrites (Figs 5, 6), relatively short, proximally rich in mitochondria and neurotubules, and bundled together (although not
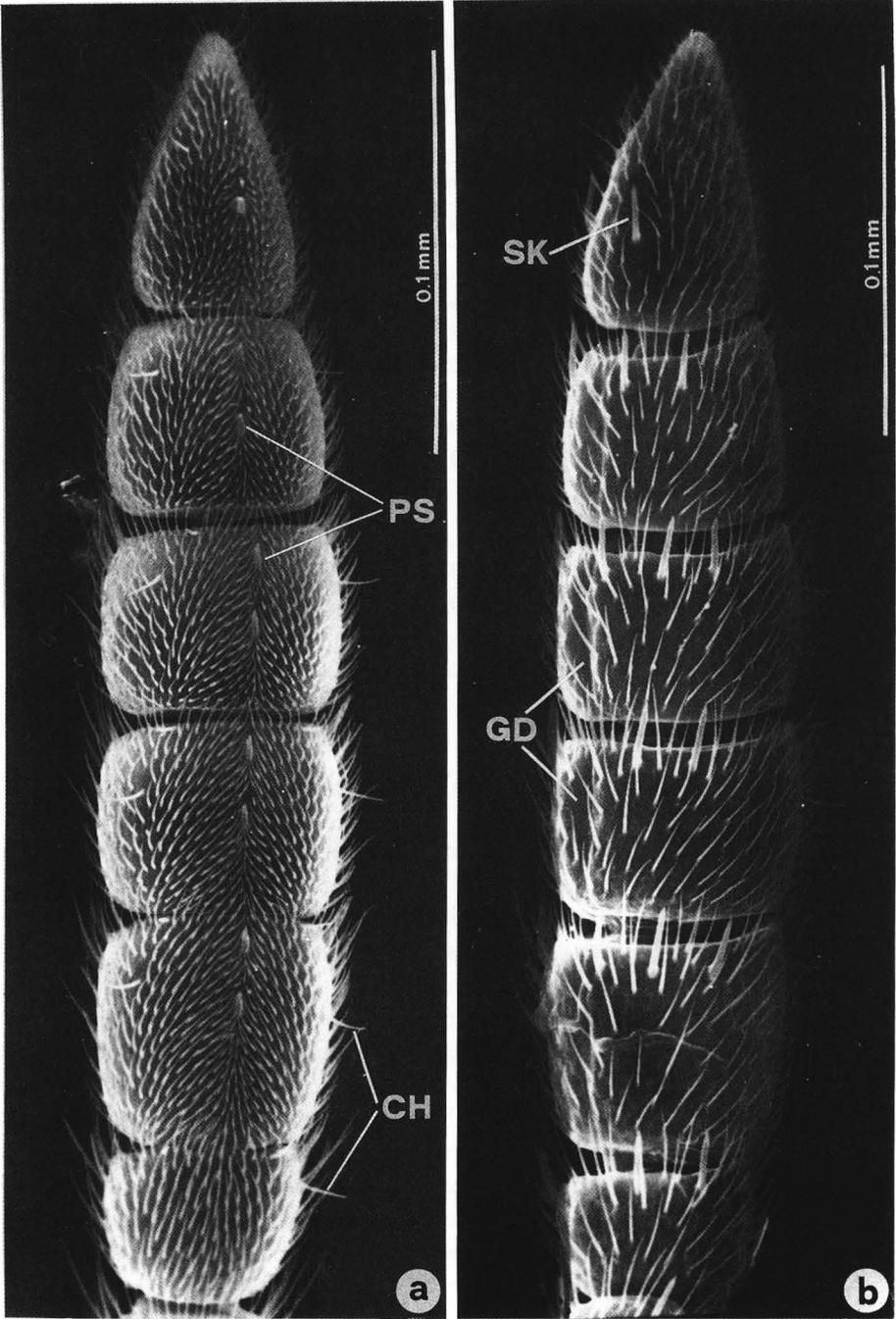
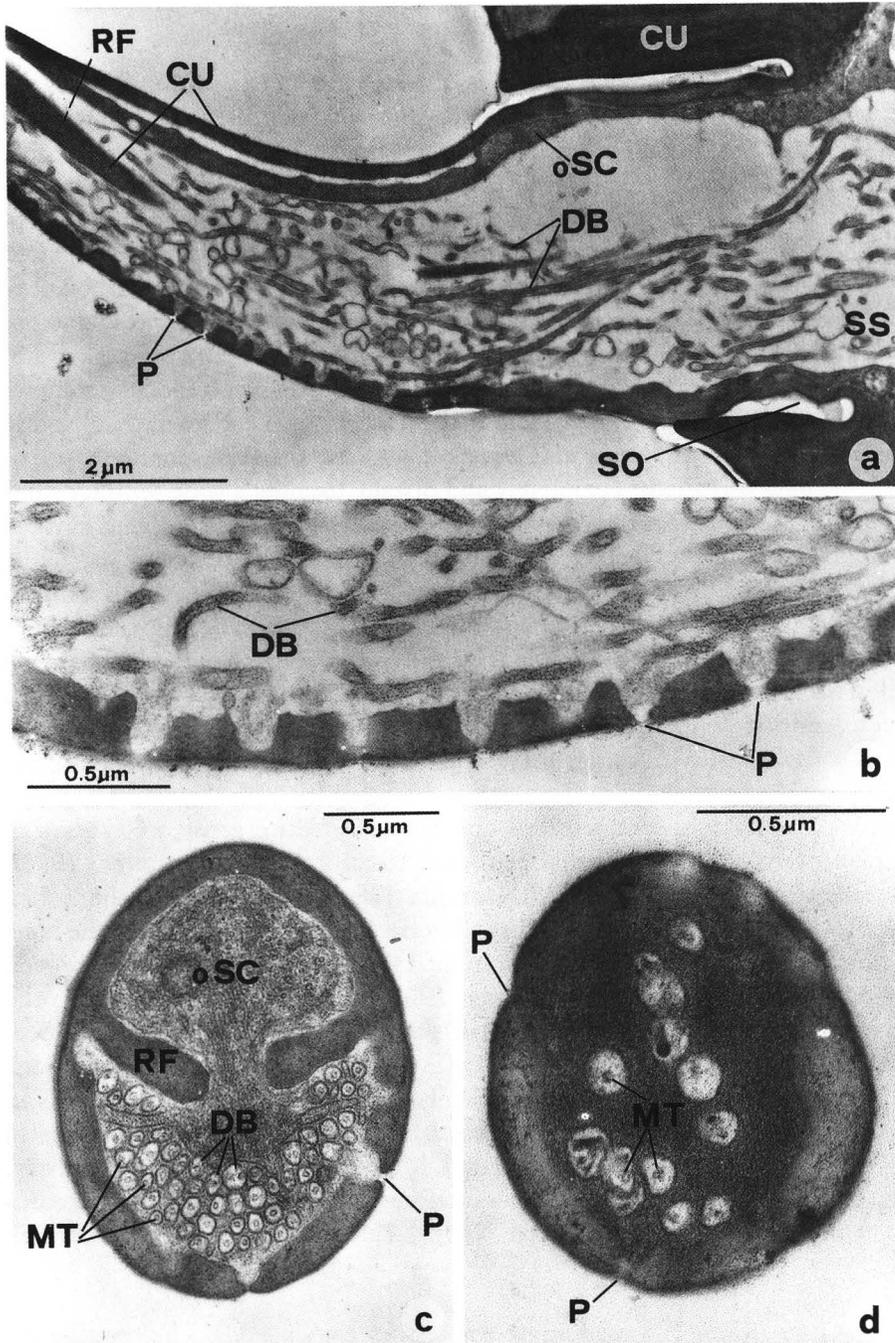Fig. 3 - Female antennomeres 6th to 11th, S.E.M. micrographs of ventral (a) and dorsolateral (b) aspects.

Fig. 4 - Female, «sickle-shaped sensillum»: a) longitudinal section of hair-shaft (proximal portion) and socket; b) detail of previous section; c) shaft intermediate cross section; d) subapical cross section of the same.

being enclosed in a discrete sheath) pass through the inner sheath cell, cross the ciliary and sensillar sinuses, enter the hair-shaft base and then divide into branches that fill the lateral (outer) lumen compartment to the shaft tip (DB, Fig. 4); b) three accessory cells (Figs 5, 6) relatively big and having a nucleus markedly larger than in the neurons, numerous mitochondria, short lengths of rough endoplasmic reticulum, scattered ribosomes and numerous microtubules longitudinally oriented: an inner sheath cell (iSC, Fig. 6) that encloses together (like a mesaxon) the inner segments of the above mentioned dendrites up to the ciliary constriction where it forms a ciliary sinus (CS) lined with packed microlamellae (ML, Fig. 6: a,b) and usually filled with free electrondense granules and secretion vesicles; and two outer sheath cells (oSC, Figs 4, 5, 6), quite similar between them, larger and less electrondense than the inner one, proximally lapping this almost completely and distally forming a wide sensillar sinus (SS), not separate from the ciliary sinus, made of numerous confluent cavities and lined with microvilli all around the bundle of the outer dendritic segments, and the distal cell (of the two) terminating within the shaft lumen with an extension (oSC, Fig. 4c) rich in microtubules. Septate junctions (SJ) are abundant along the boundaries between the sheath cells, they close the inner sheath cell in itself as a mesaxon and encircle like a collar the subdistal portion of each inner dendritic segment.

Morphologically speaking, these sensilla are typical olfactory-hairs. Comparing our observations with the descriptions reported in the literature, we may identify our «sickle-shaped sensilla» with SLIFER's «plate organs», well known to Hymenopterologists as «sensilla placodea» (SCHMIDT & KUHBANDNER, 1983), «sensilla sicula» (CALLAHAN, 1975), «sensilla trichodea curvata» and «horn- like sensilla» (CAVE, GAYLOR, 1987). These diverse names given to one and the same type of sensory organs, commonly presumed (and electrophysiologically proved for *Apis mellifica*: LACHER, SCHNEIDER, 1963) to be olfactory, are due to the outward appearance (posture) of the hair-shaft that runs completely free in Scelionidae (BIN, STRAND, VINSON, 1986; CAVE, GAYLOR, l.c.) and Formicoidea (CAVE, GAYLOR, l.c.), or lies longitudinally embedded in the antenna so as to leave free only the shaft lateral surface (the only porous in all cases) like in Ichneumonidae and Braconidae (BORDEN, MILLER, RICHERSON, 1973; NORTON, VINSON, 1974a, 1974b), or shows an intermediate position as in Chalcidoidea (BARLIN, VINSON, 1981; BOUCEK & NOYES, 1987; DAHMS, 1984; SLIFER, l.c.; WESELOH, 1972).

Papillary sensilla (PS) and relative accessory glands (AG). The sensillar cuticular parts form a coeloconic (sensu SCHNEIDER, 1964) structure consisting of a papilla-like peg (PA, Figs 7b, 8, 15a) set in a narrow, shallow pit (PT, Figs 7b, 14b), also interpretable as a trichoid one (sensu SCHNEIDER, l.c.) made of a

short, papillary hair inserted in a loose, relatively deep socket. The hair (from now on called «papilla», PA) is a stubby, flexible projection, roughly conical in frontal view, terminating with a discrete, peculiar «crypto- multiporous area» (Figs 7b, 15, 16) that shows 7-8 transverse rows of minute, flexible appendages, like hinged lids (5-6 per row: HL, Figs 15b, 16), each row covering a cross groove (GR, Figs 15b, 16) whose inner walls are extremely thin and multipo-rous (P, Figs 15b, 16). It is noteworthy that these cuticular ultrastructures are normally concealed by some material that most probably flows from the pores and condenses outside, as it appears in SEM observations with samples only gold sputtered. The pit (or socket; PT, Figs 7b, 14b) is actually a furrow en-circling the papilla base like an elliptic, loose, rigid collar having the outer edge somewhat projecting above the antennal surface, and at the bottom extremities (superior and inferior) the accessory glands' outlets (GO, Fig. 9b).

The cellular components of each sensillum consist of: a) very numerous (se-veral hundreds: 410, 406, 419 dendrites found in 3 samples, respectively) sen-sory neurons whose perikaryons (SN, Figs 10, 12, 13b, 25, 26) form most part of the «massive ring» (see 3.1) of neuron cell bodies, and whose inner dendritic segments (iD) possess a proximal portion unusually thin (and varied in length depending on the respective perikaryon position in the massive ring) but be-coming normally thick (0.4 μm in diameter) where all the dendrites converge into a bundle (Figs 10, 11, 13, 15c) for some length before the ciliary constri-ctions that give origin to the outer dendritic segments (D); these run naked, loose but almost parallel through the sensillar sinus (Figs 10, 13a, 26), gradually tapering (to 0.07 μm in diameter), sometimes forming «beads», and unbranched to the tips that enter and almost completely fill the papilla lumen (Figs 13b, 14b, 15); b) three quite large sheath cells (SC, Figs 10, 11, 13, 15a) having independent basal portions but the apical parts well connected with each other to form the sensillar sinus (see below), very similar to one another, and very characteristic: a big nucleus, cytoplasm most invaded by rough endoplasmic reticulum (RE, Fig. 17: a,b), with big Golgi apparati (G, Fig. 17: a,b) producing large amounts of very electrondense vesicles (Figs 10, 11, 17a), and having mitochondria especially crowded near the cell apical boundaries that form a very large sinus (SS, Figs 10, 11, 13, 15a, 26) including both ciliary and sen-sillar sinuses fused together (Fig. 15c) and having inner walls pluriconcave and lined with very abundant microvilli (MV, Fig. 14).

The accessory glands (AG, Figs 8, 10, 11, 12, 13) of an individual sensillum consist of two clusters (a superior/distal and an inferior/proximal; see GO, Fig. 9b), each composed of 2-3 independent secretory units, i.e. single-cell glands of the NOIROT-QUENNEDEY's (1974) 1st class, whose secretion directly flows into
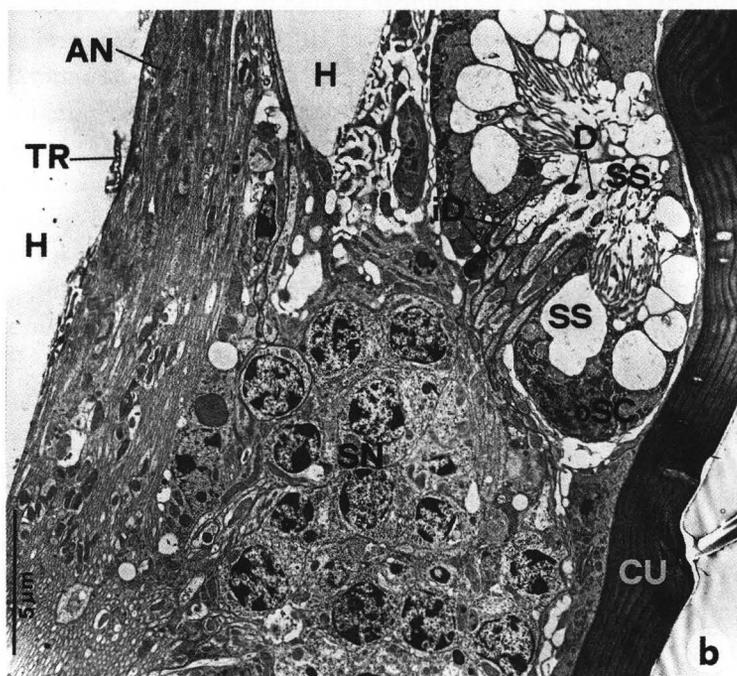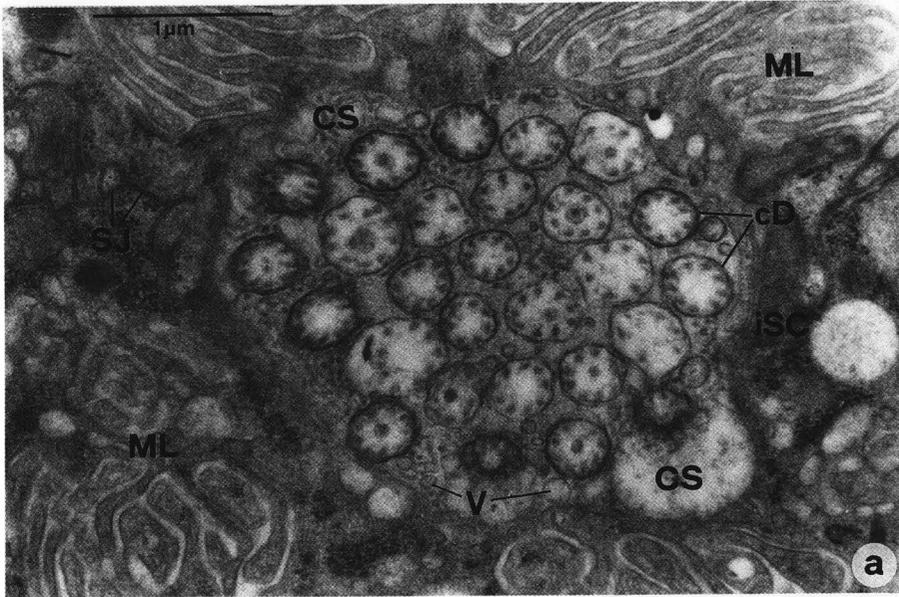
Fig. 5 - Female, «sickle-shaped sensillum»: longitudinal (a) and oblique (b) sections.

Fig. 6 - Female, «sickle-shaped sensillum» cellular parts: a) cross section at ciliary sinus level; b) cross section at inner dendritic segments' level; c) longitudinal section.
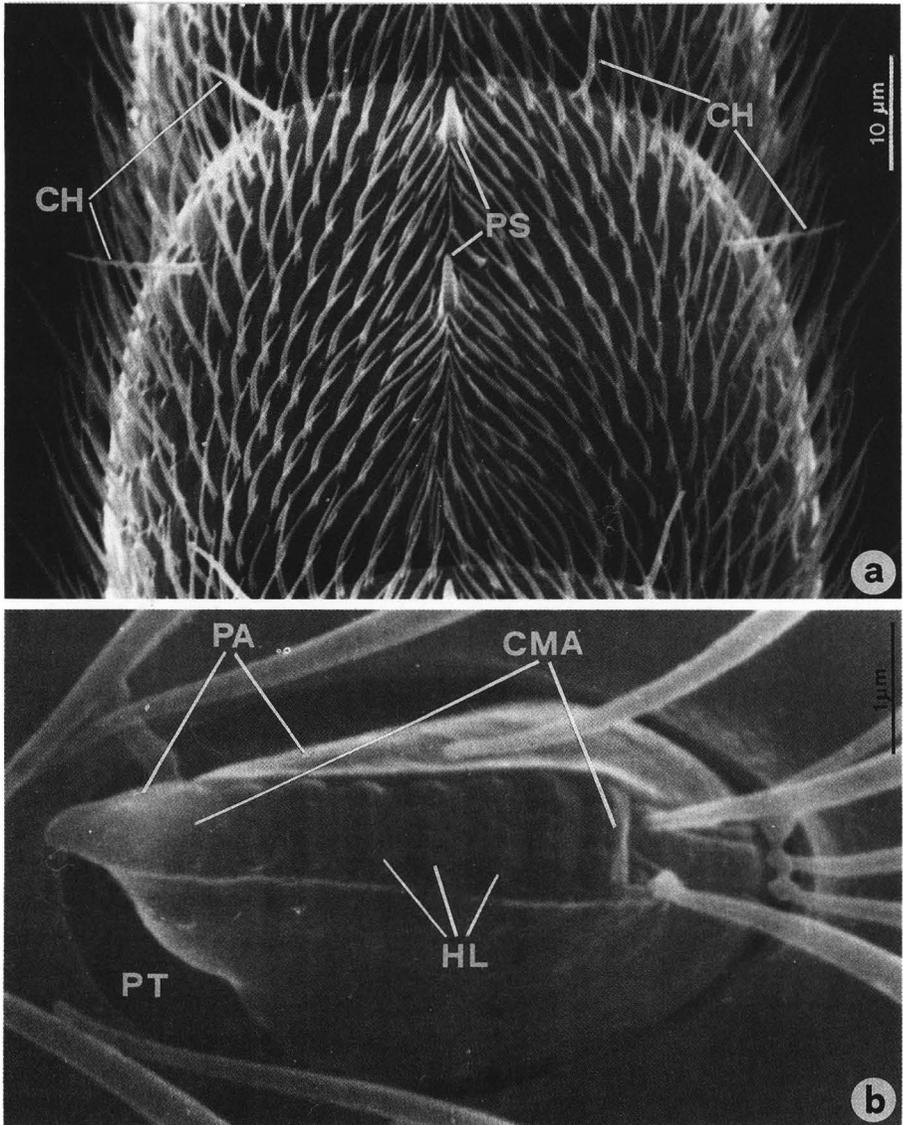
Fig. 7 - Female 10th antennomere, S.E.M. micrographs of ventral aspect (a) and a detail (b) showing a «papillary sensillum» (upper part on the left).
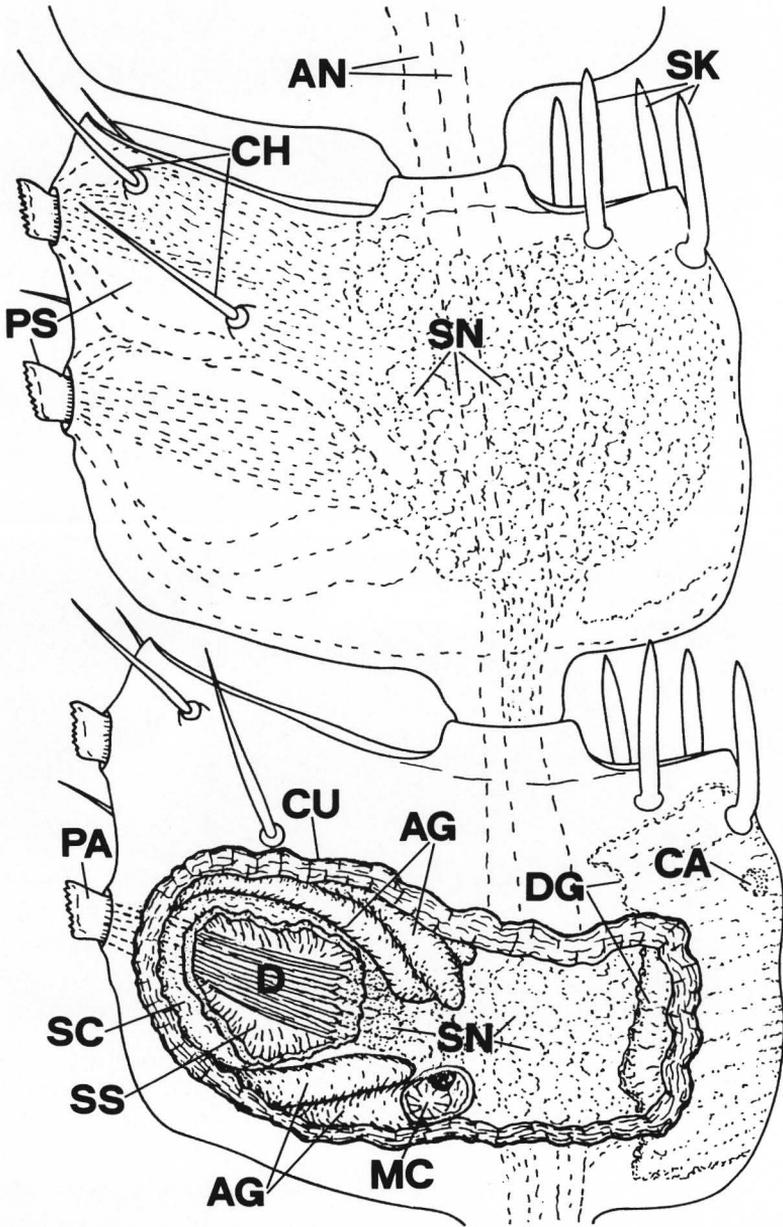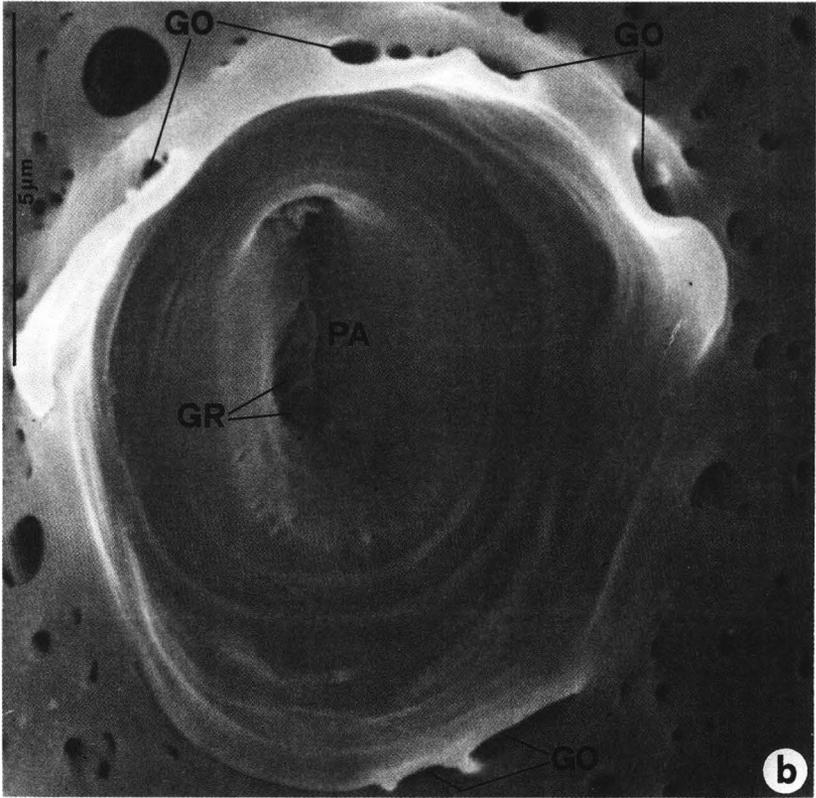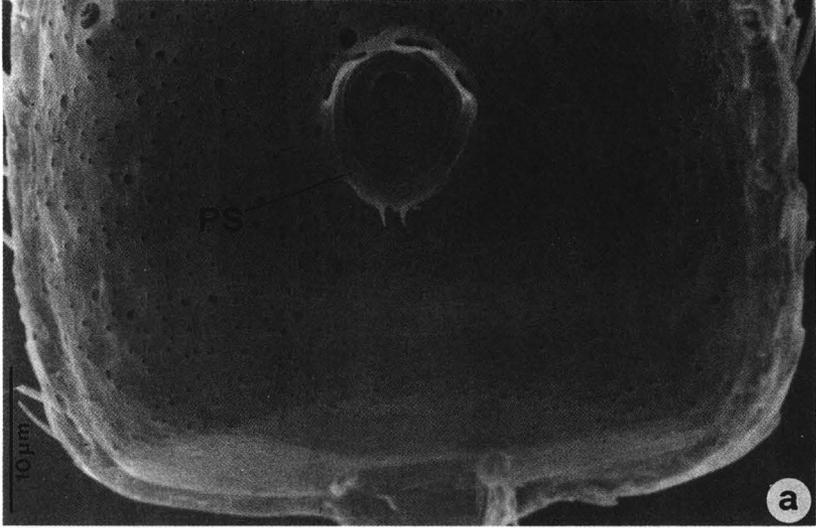
Fig. 8 - Female 9th + 10th antennomeres' tridimensional diagram showing topographical anatomy of chemosensilla and glands (10th antennomere) and an internal view of a «papillary sensillum» (9th antennomere).

the sensillar pit through irregular outlets (Figs 9b, 14b). Each glandular cell, running tortuously from the antennal center (Figs 11, 12, 26) to the pit wall, is very elongate, has its nucleus (NU, Fig. 17d) situated near the cell base and surrounded by a moderate amount of cytoplasm possessing short lengths of rough endoplasmic reticulum, abundant scattered ribosomes (R, Fig. 17d), several Golgi apparati (G), and mitochondria as numerous as these are everywhere in the cell (M, Fig. 17: c,d), while the apical cell membrane, lined with abundant microvilli, is invaginated to form a sort of canal, or «microvillar cavity» (MC, Fig. 17: c,d), running through most of the cell length and easy to detect (even at low magnification) because of the presence in it of an electrondense secretion (S, Figs 14b, 17: c,d).
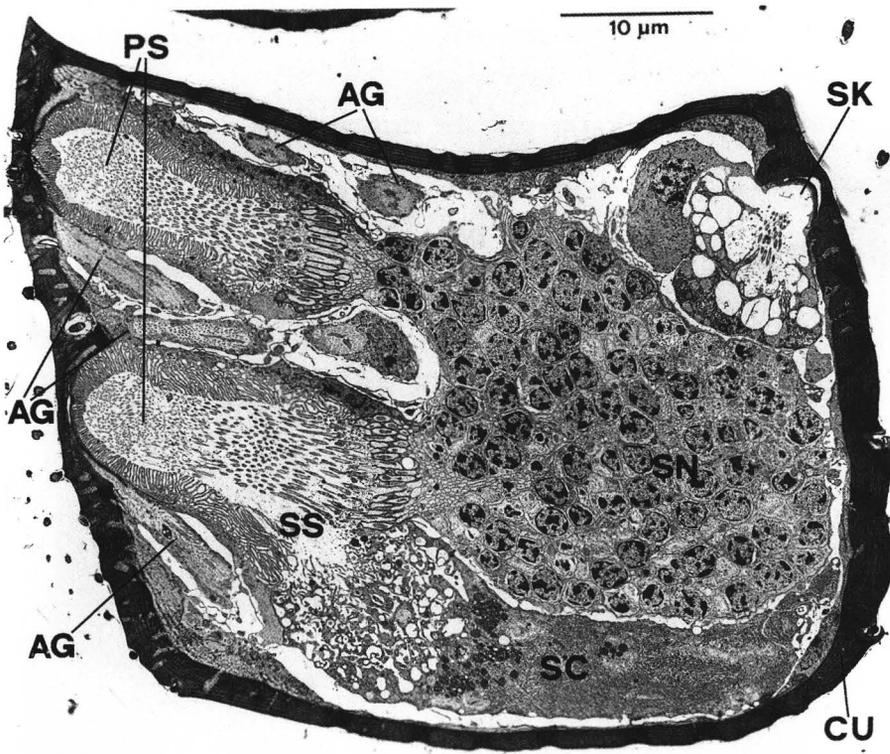
Fig. 10 - Female 8th antennomere, submedian sagittal section.

Fig. 9 - Female 8th antennomere, S.E.M. micrographs of the inner ventral wall proximal half (a) and a «papillary sensillum» inner view (b) (from another specimen).

On morphological basis, these sensilla are typical chemoreceptors but their cuticular components let them be considered either olfactory (being thin-walled and multiporous) or gustatory (pores present on the peg tip only). However, the general outward configuration of these sensilla, the peculiar ultrastructure and position of the peg openings, and especially the presence of such accessory glands producing a secretion that must work as a proper solvent/carrier (what else ?) for the stimulant molecules, strongly suggest a gustatory function. Furthermore, the presence of so many sensory neurons must be indicative of a great versatility of response (CHAPMAN, 1982) to various and/or multicomponent semiochemicals, as well as for a prompt detection of the same.

Comparing our observations with the literature, we may identify our «papillary sensilla» with BIN's (1981) «plate sensilla», BIN- STRAND-VINSON'S (1986) «placoid sensilla» and CAVE-GAYLOR's (1987) «sensilla basiconica», all concerning Hymenoptera, Scelionidae only.

Sensilla chaetica (CH). The cuticular elements form a typical «sensillum
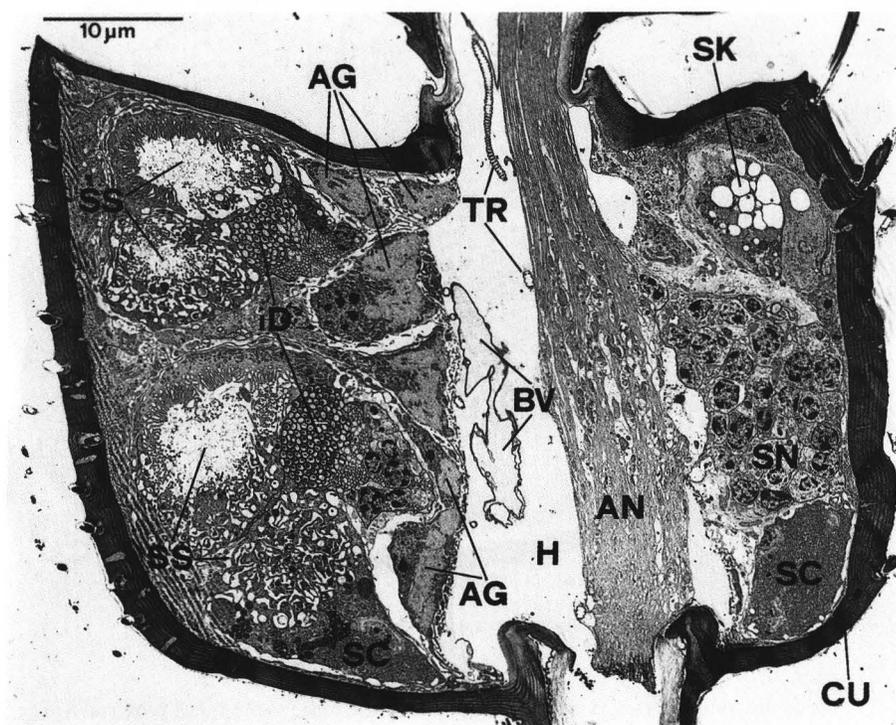
Fig. 11 - Female 7th antennomere, median longitudinal (about 45° rotated sagittal, see Fig. 12, arrow heads) section showing cellular parts of «papillary sensilla» and relative «accessory glands».

chaeticum» (sensu SCHNEIDER, l.c.) having an outstanding hair-shaft (Figs 3a, 7a), almost perpendicular to the antennal surface, slightly bent proximad (posterad), ranging 11- 13.5 μm in length and 0.8-1 μm in diameter at base, rather rigid, fluted, thick walled (Fig. 19: a,b), gradually tapering from the base to a roundish, uniporous tip, inserted in a specialized, flexible socket (Fig. 18: a,b).
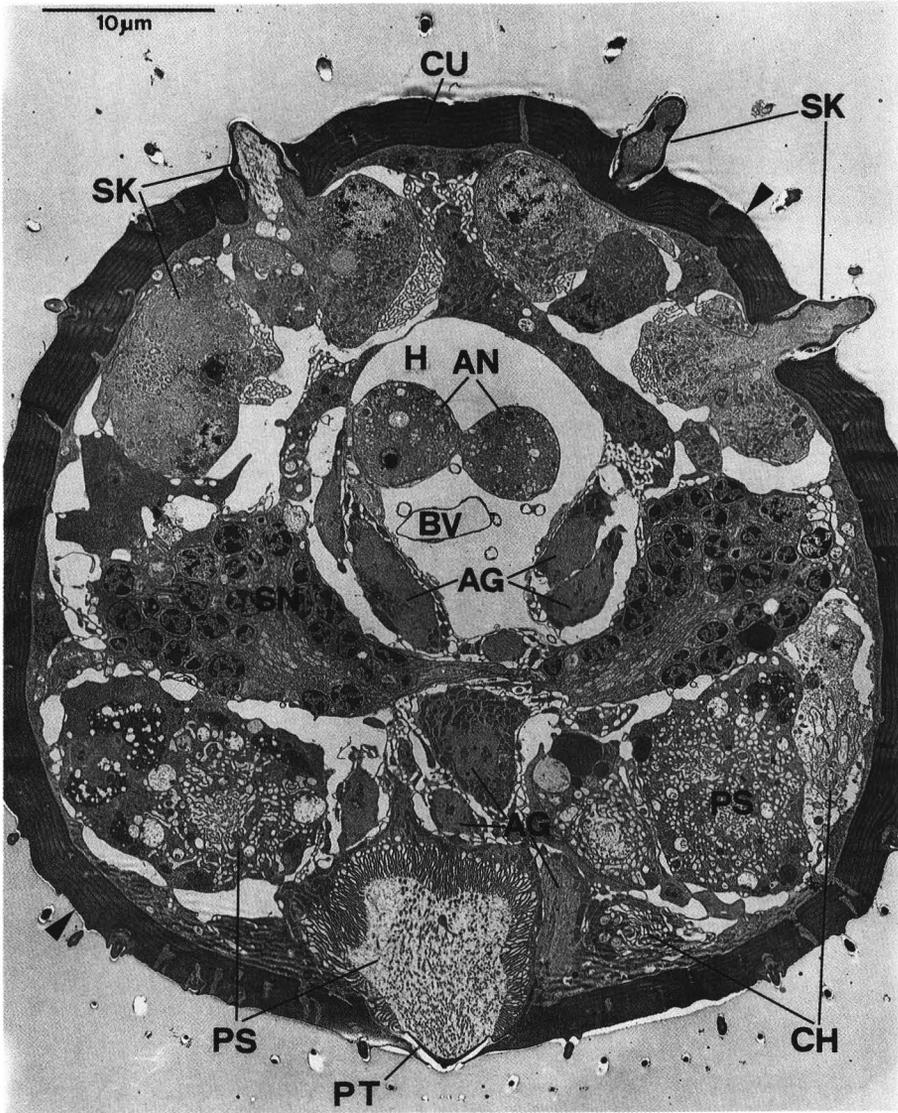
Fig. 12 - Female 10th antennomere, cross section at distal «papillary sensillum» level, through papilla base.
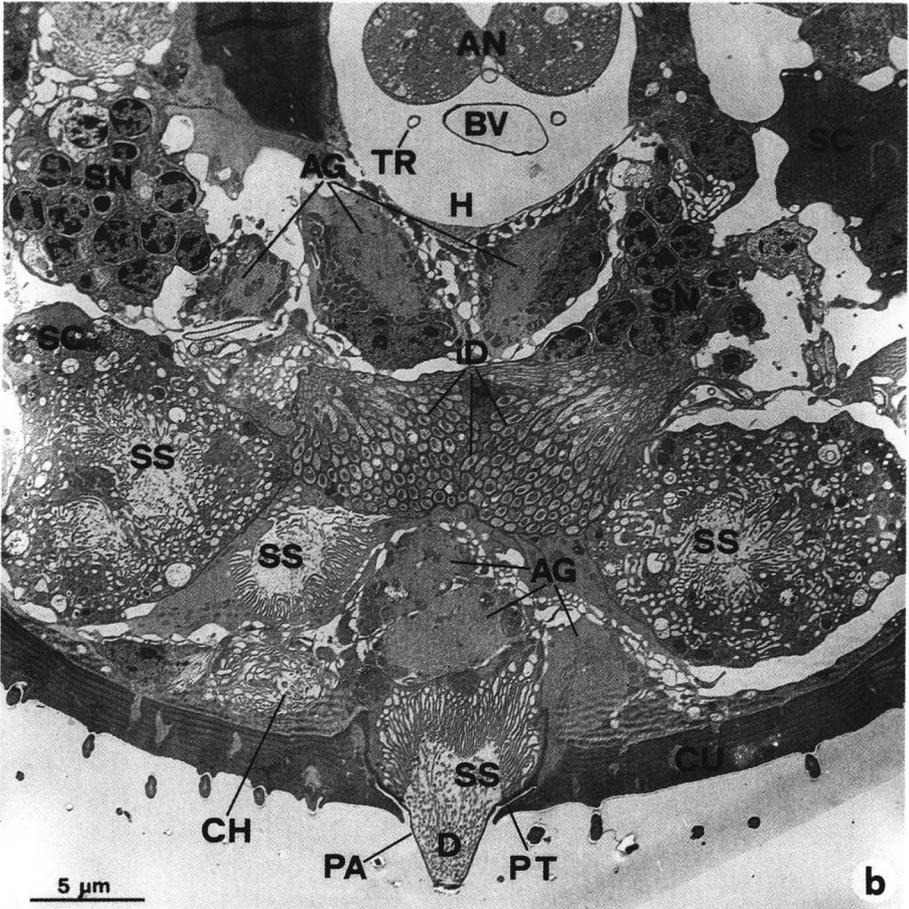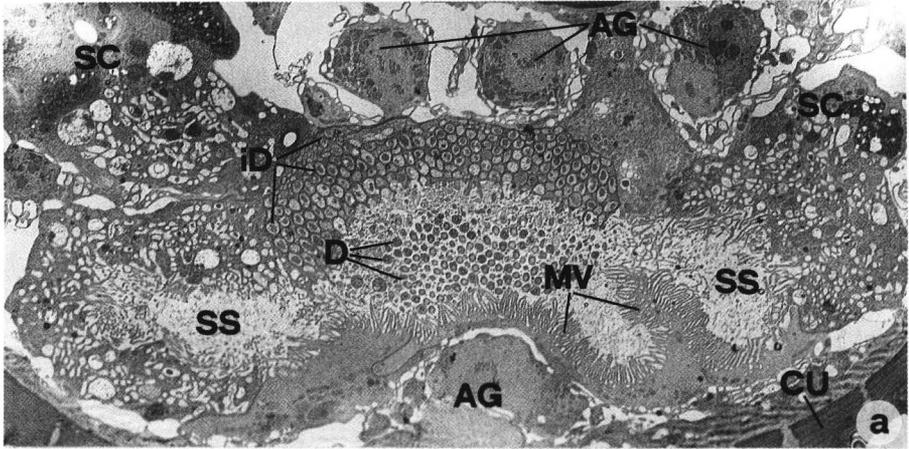
Fig. 13 - Female 10th antennomere, successive cross sections (a little more distal than in Fig. 14) displaying details of «papillary sensillum»: (a) more distal than (b), both at the same magnification.
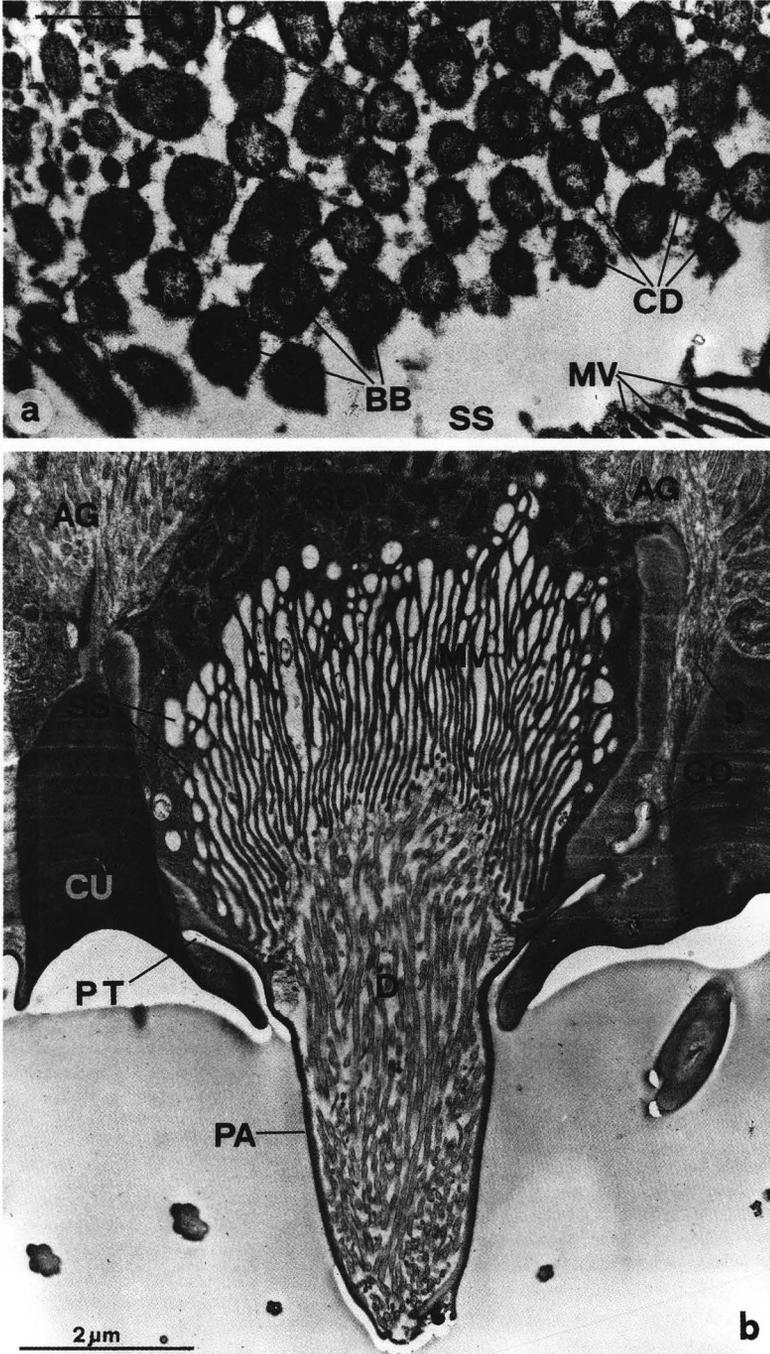
Fig. 14 - «Papillary sensillum», cross section details through: a) sensillar sinus; b) papilla.
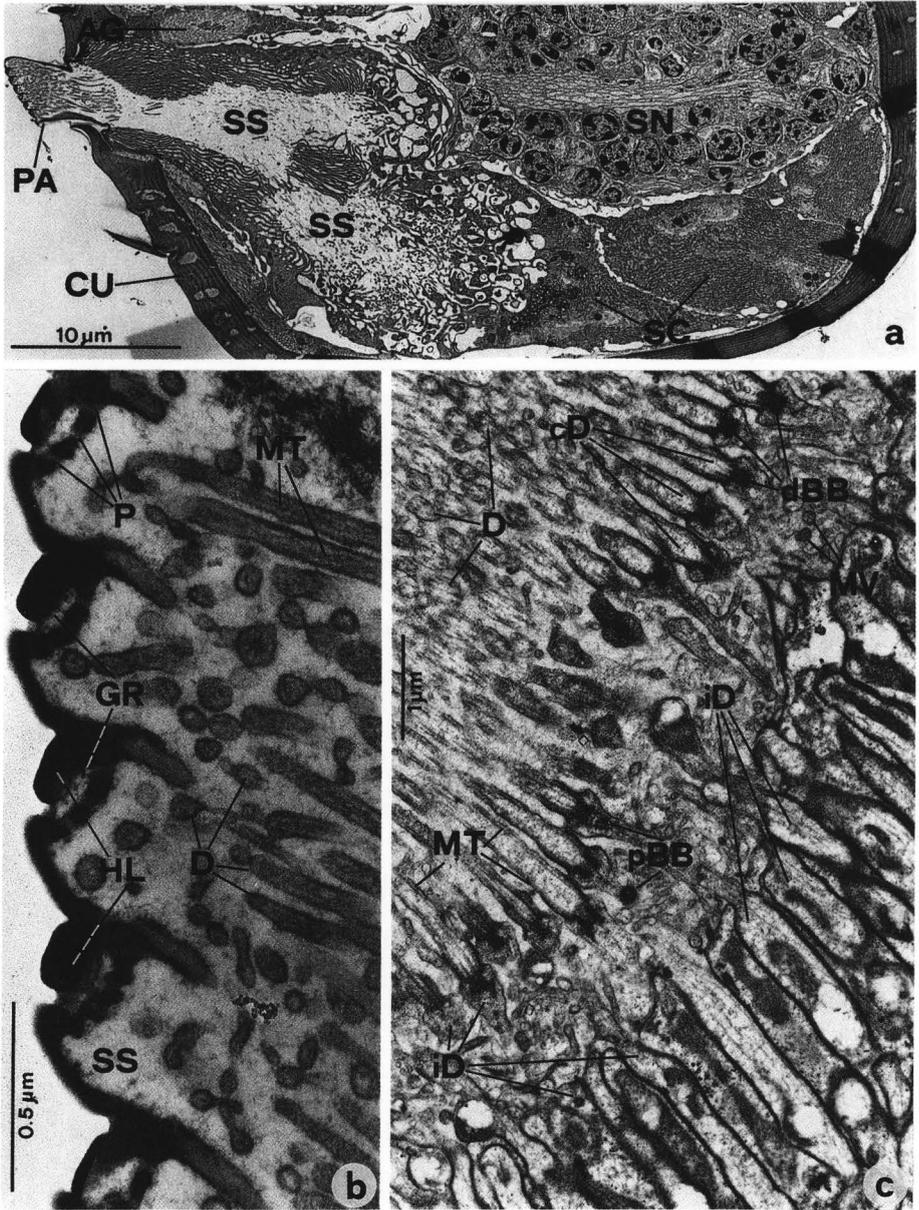
Fig. 15 - Female 7th antennomere, longitudinal section of proximal «papillary sensillum»: a) general view; b) detail of papilla «crypto-multiporous area»; c) detail of cellular components.

The cellular constituents are represented by: a) five sensory neurons lying in the «massive ring» and sending their inner dendritic segments (Fig 20: b,c) into a bundle through the inner sheath cell (Fig. 20c) and the ciliary sinus (CS, Fig. 20: a,b), while the outer (ciliary) dendritic segments (D), enclosed in a thick common sheath (DS, Figs 18, 19c) cross the sensillar sinus (SS) and then four of them enter the hair-shaft lumen running it (Fig. 19: a, b) almost to its tip, whereas the fifth dendrite (the same that constricts at a higher level than the others: iD, Fig. 20: b,c; hence easily recognizable also in its inner segment), being enclosed in a distinct sheath, terminates at the shaft base with a conspicuous tubular body (TB, Fig. 18); b) three accessory cells: one inner sheath cell (iSC, Figs 19c, 20), showing outstanding microlamellae (ML, Fig. 20), microvilli, longitudinally oriented microtubules, numerous mitochondria and scattered ribosomes, laps the inner dendritic segments, forms a narrow ciliary sinus (filled with electrondense, granulous material) and produces a dendritic sheath (DS, Figs 18, 19c, 20) that encases the outer dendritic segments to the hair
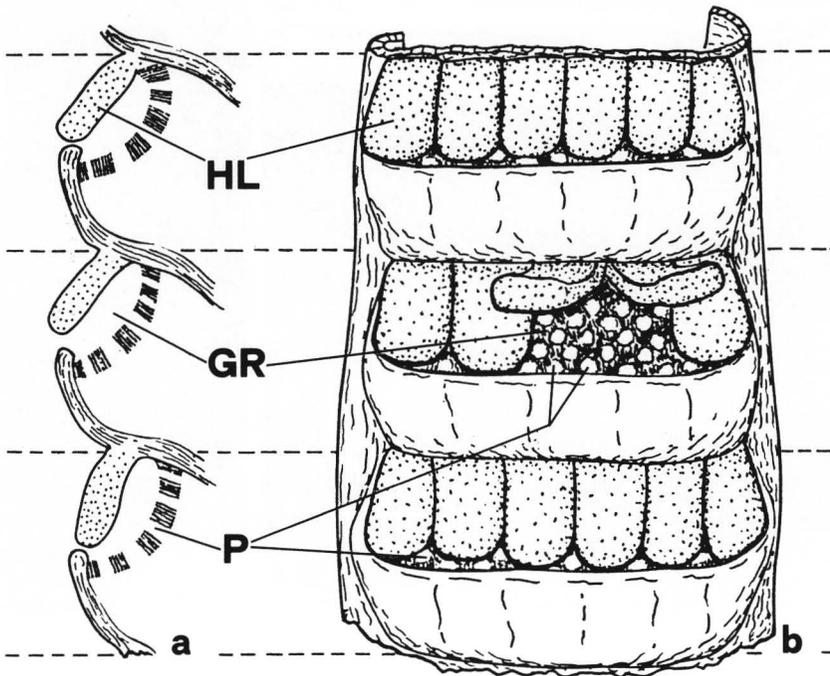
Fig. 16 - Diagram of «papillary sensillum» cuticular fine structures: a) detail of papilla «cryptomultiporous area», longitudinal section; b) frontal aspect of ditto. Two of the hinged lids (HL) of the median row are artificially lifted up to let the pores in the groove be seen.
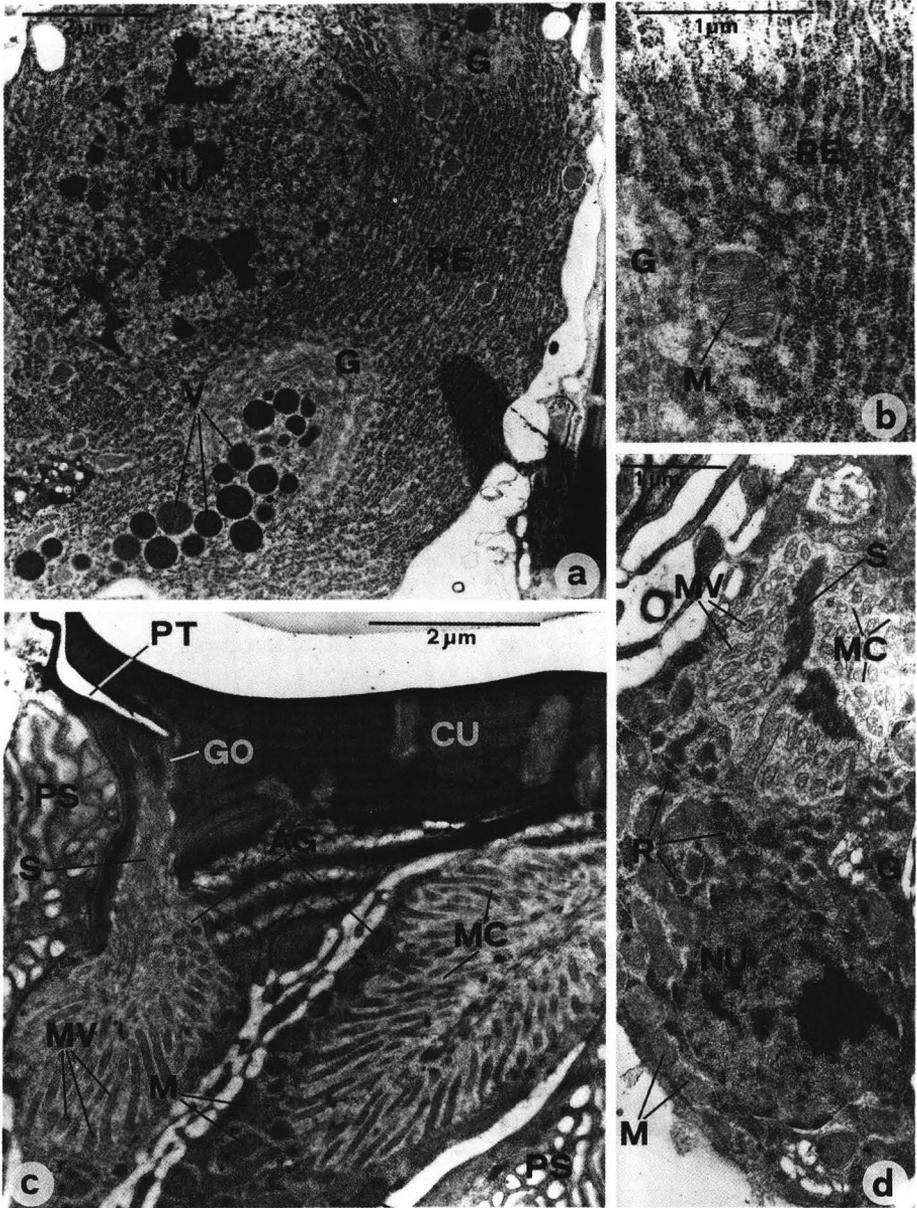
Fig. 17 - «Papillary sensillum»: a) sheath cell basal part; b) detail of the same; c) and d) accessory glands' details.

base; and two outer sheath cells (oSC, Figs 18: a,b; 19c, 20a), quite similar to each other, having cytoplasm relatively rich in rough endoplasmic reticulum and mitochondria, wide covering the inner sheath cell, and distally forming a large sensillar sinus (SS, Figs 18, 19c) lined with abundant, quite long microvilli (MV, Fig. 18b).

As for morphology, both external and internal, these sensilla are typical gustatory hairs. From the literature on the topic, we may easily identify our «sensilla chaetica» with CAVE-GAYLOR's (l.c.) homonimous sensilla and Bin's (l.c.) «hair sensilla»; but also NORTON-VINSON's (l.c.) «fluted basiconic sensilla» found in Braconidae and Ichneumonidae, SLIFER's (l.c.) «thick-walled pegs» from a Pteromalide and VOEGELÉ-CALS-PIHAN-DAUMAL's (l.c.) sensilla of the «sole chercheuse» of Trichogrammes are most probably all of the same type as ours.

Grooved peg sensilla (GP). The cuticular parts form a typical «sensillum coeloconicum» (sensu SCHNEIDER, l.c.), having a small (3μm long), clavate peg (Fig. 21) with walls proximally smooth, distally grooved and multiporous along the grooves (Fig. 22: c,d) except on the tip (Fig. 22e), and set in a round, shallow pit wider at the bottom than at its opening (Fig. 22b).

The cellular components consist of: a) four sensory neurons whose perikaryons lie in the «massive ring» and whose dendrites run together in a bundle on (Fig. 23) to near the peg base where one of them (the same whose inner segment -iD, Fig. 23f- constricts at a higher level than the others) tapers and terminates (Fig. 23b), while the other three enter the peg lumen (Fig. 22b) and, still enclosed in a thick dendritic sheath (DS, Fig. 22: b,c) originating at ciliary constrictions' level (Fig. 23: e, f) and terminating where the peg grooves and porosity begin (Fig. 22: c,d), run the peg lumen up to almost the tip, without branching; b) three accessory cells: an inner sheath cell, characterized by having plenty of microlamellae (ML, Fig. 23f), that forms a ciliary sinus (CS, Fig. 23f) filled with electrondense material, and produces the above described dendritic sheath; and two outer sheath cells, quite similar to each other, proximally enclosing the previous described cell, and distally forming a large sensillar sinus (SS, Figs 22b, 23a) lined with packed microlamellae (ML) and almost completely filled with electronlucid vesicles apparently produced by these cells (Fig. 23: d,e).

Morphologically speaking, these sensilla might be considered olfactory for having a multiporous peg, but their internal components and general configuration strongly suggest a gustatory function. Comparing our observations with those reported in the literature, our «grooved peg sensilla» may be easily identified with BIN-STRAND-VINSON's (l.c.) «bulb sensilla» of the same insect, CAVE-GAYLOR's (l.c.) «multiporous grooved sensillum» of another Telenomine, BARLIN-VINSON-PIPER's (1981) «short basiconic capitate sensilla» both found in
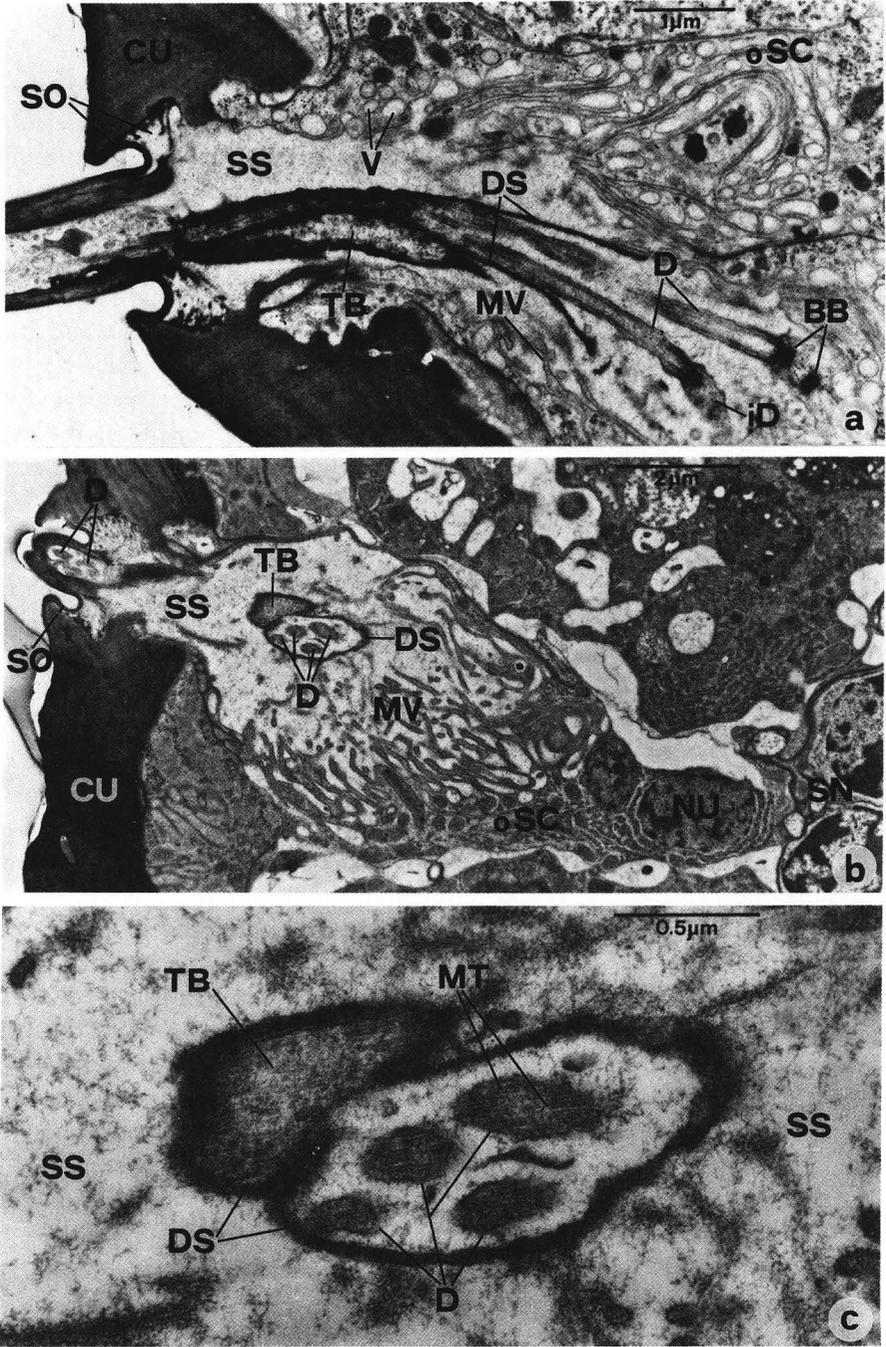
Fig. 18 - Female antennomere, details of sections showing cuticular and cellular parts of a «sensillum chaeticum»: a) longitudinal section; b) cross section; c) detail of the previous section.
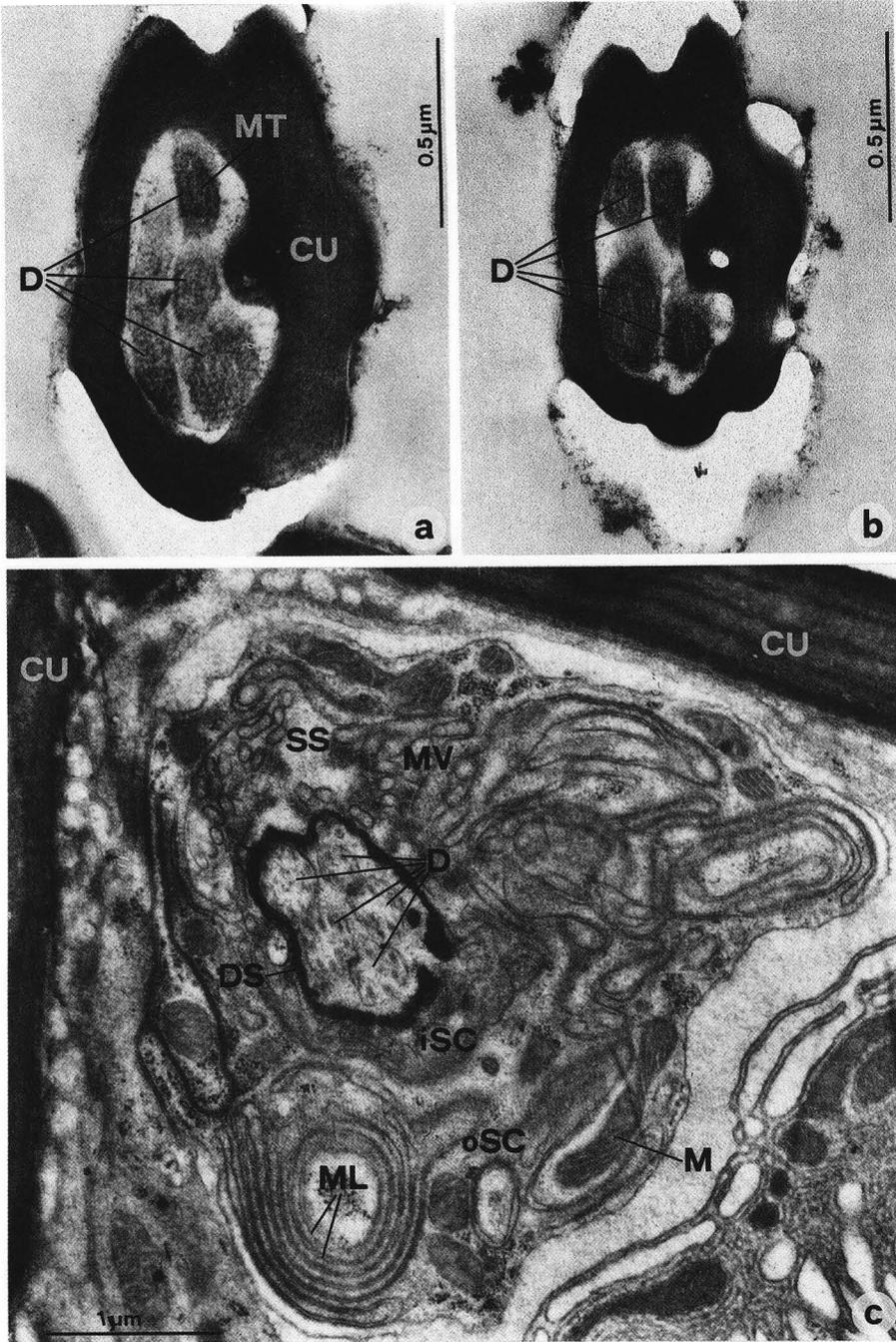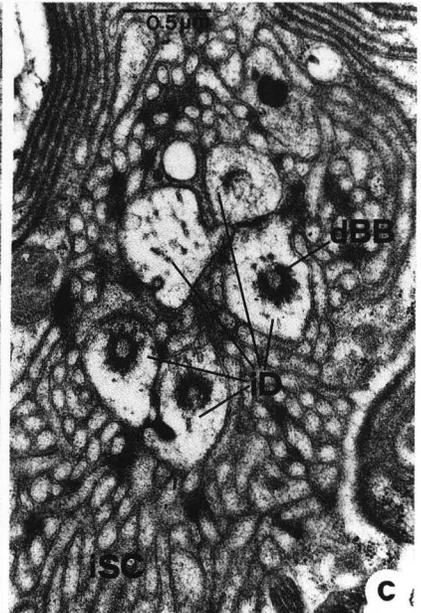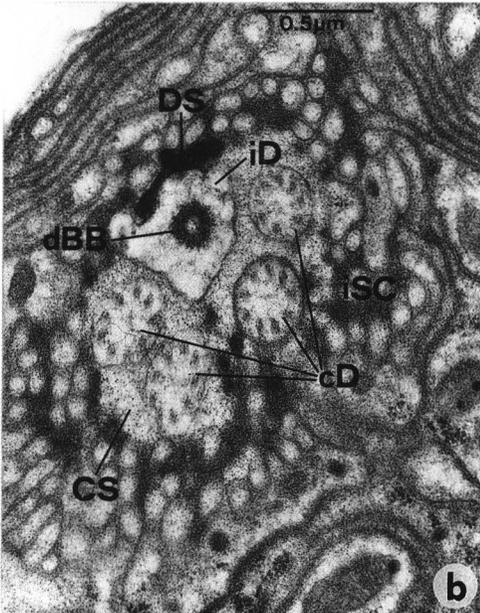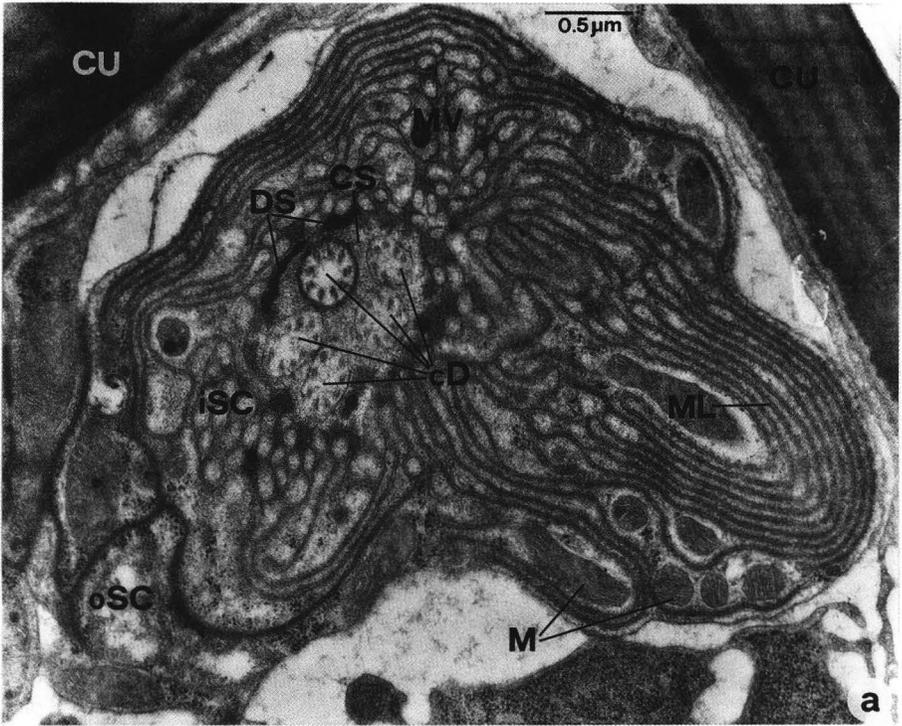
Fig. 19 - Female, «sensillum chaeticum»: shaft oblique sections, subproximal (a) and intermediate (b) ; c) cellular parts cross section.

Eulophides; but also Norton- Vinson's (l.c.) «smooth basiconic sensilla» from two Braconides and an Ichneumonidae, Voegelé-Cals- Pihan-Daumal's (l.c.) «sensilla ampullacea» of Trichogrammes and Weseloh's (l.c.) «small subterminal basiconic sensilla» from an Encyrtide seem to be of same type as ours.

Dorsal glands (DG) and associated sensilla campaniformia (CA). The «dorsal depression» of female *T. basalis* previously indicated by Bin, Strand, Vinson (l.c.) as antennal structures possibly involved in sex recognition, are actually the outward appearance (GD, Figs 3b, 24) of a series of extensive antennal glands, here called «dorsal glands». Each of these (DG, Figs 8, 25, 26) is formed by a longitudinally elongate cluster of approximately 20 unicellular secretory units of Noirot- Quennedey's (l.c.) 1st class, varied in size and shape, almost completely filling the backward space of the antennomeral haemocoele (Figs 25, 26) and adhering to the inner wall of the «dorsal depression» whose porosity actually consists of the numerous, irregular outlets of the gland (GO, Fig. 27).

The ultrastructural features of these secretory cells are somewhat similar to those of the papillary sensilla accessory glands (cf. Fig. 17: c,d with Fig. 28), for having a great abundance of mitochondria everywhere, the ribosomes mainly scattered in the perinuclear region, and especially for the apical cell membrane being very rich in microvilli and invaginated to form a very large extracellular cavity (MC, Figs 27, 28: a,d) functioning as a simple, subcuticular reservoir open to the dorsal depression. It is remarkable that the secretion appearance strikingly resembles that illustrated by Stuart and Satir (1968) from the sternal gland of a termite and presumed to be a trail-following pheromone.

The sensillum campaniforme associated to each dorsal gland (except for the distalmost antennomere, see 3.1) is a typical Schneider's (l.c.) «sensory cupola». The cuticular parts form a roughly hemispherical, nonporous cap, almost completely embedded (CA, Fig. 24) in the antennal cuticle and showing two distinct components: an outer one (oCU, Fig. 29b) looking solid and darker than the surrounding cuticle (but removable like a plug with boiling 10% KOH water solution), and an inner part (iCU, Fig. 29: b, c, e) apparently fibrous and elastic (most probably rich in resilin). The cellular components are represented by: a) one sensory neuron whose perikaryon lies close beneath the cuticle (Fig. 29a) and sends a short but relatively thick inner dendritic segment (iD, Fig. 29e) followed by an even shorter ciliary segment running tortuously (Fig. 29: b,c, e) and enclosed in a thick dendritic sheath (DS, Fig. 29) on to a relatively

Fig. 20 - Female, «sensillum chaeticum» cellular parts: a), b) and c) serial cross sections, going inwardly.
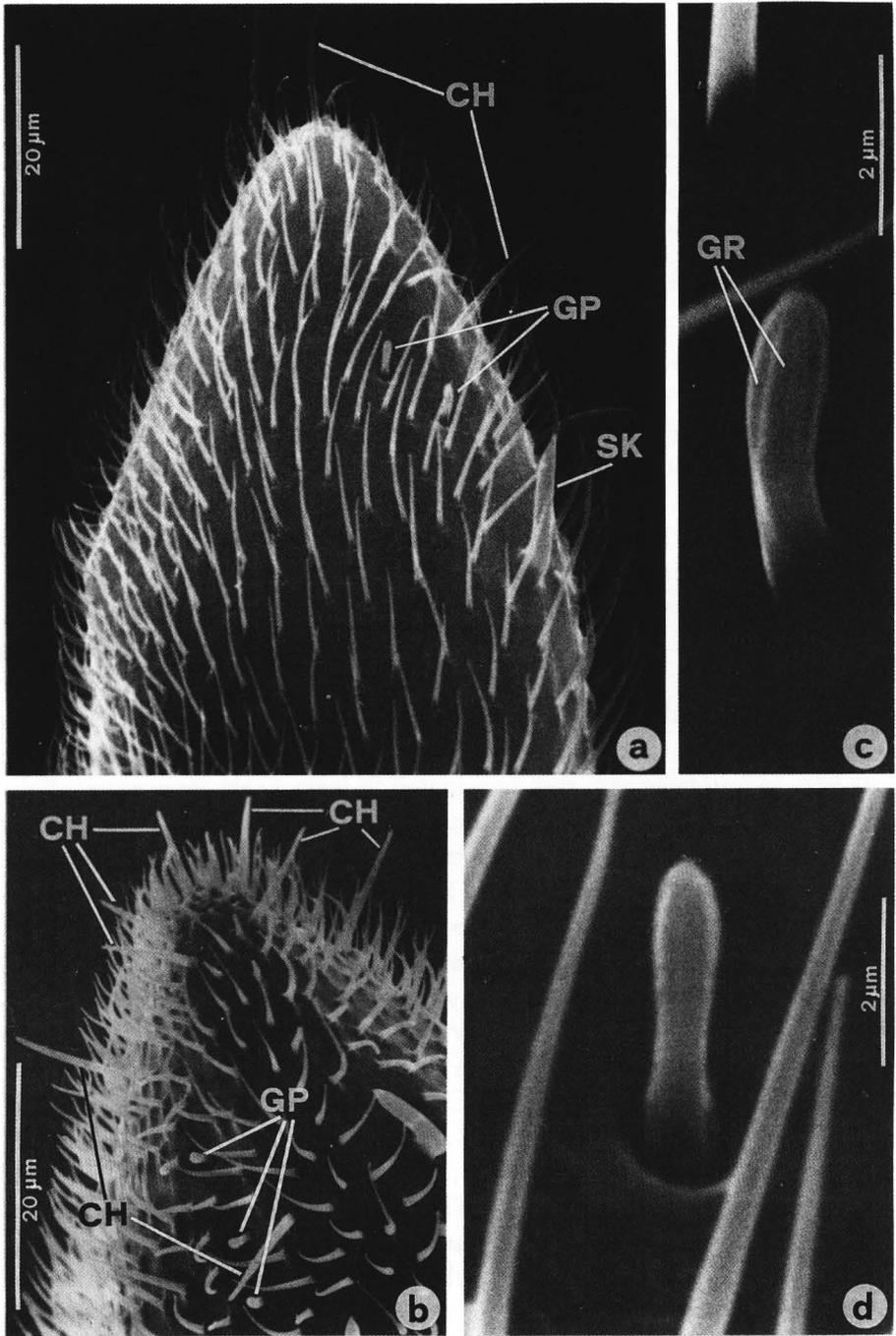
Fig. 21 - Female apical antennomere details, S.E.M. micrographs of: a) dorsolateral view; b) apicodorsal aspect; c) grooved peg (grooves in focus); d) the same as in (c) (socket in focus).
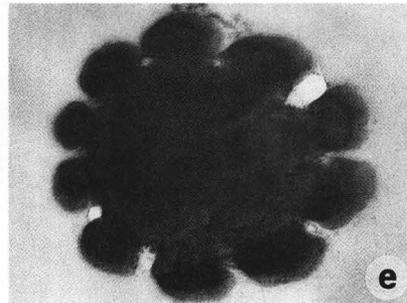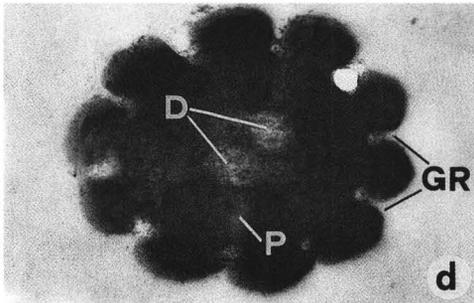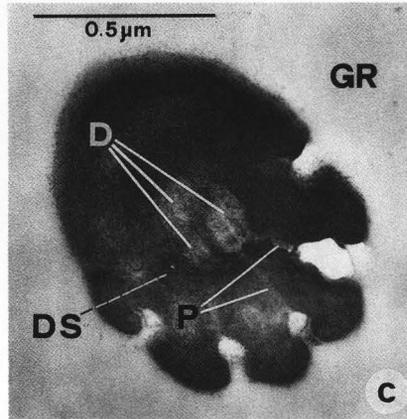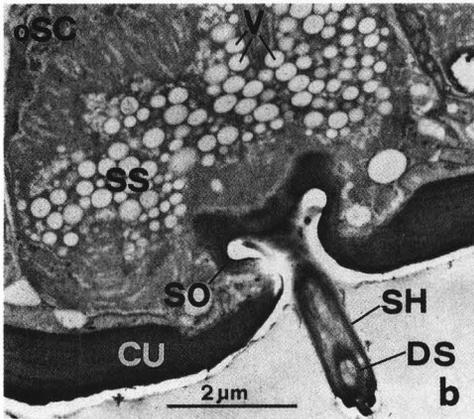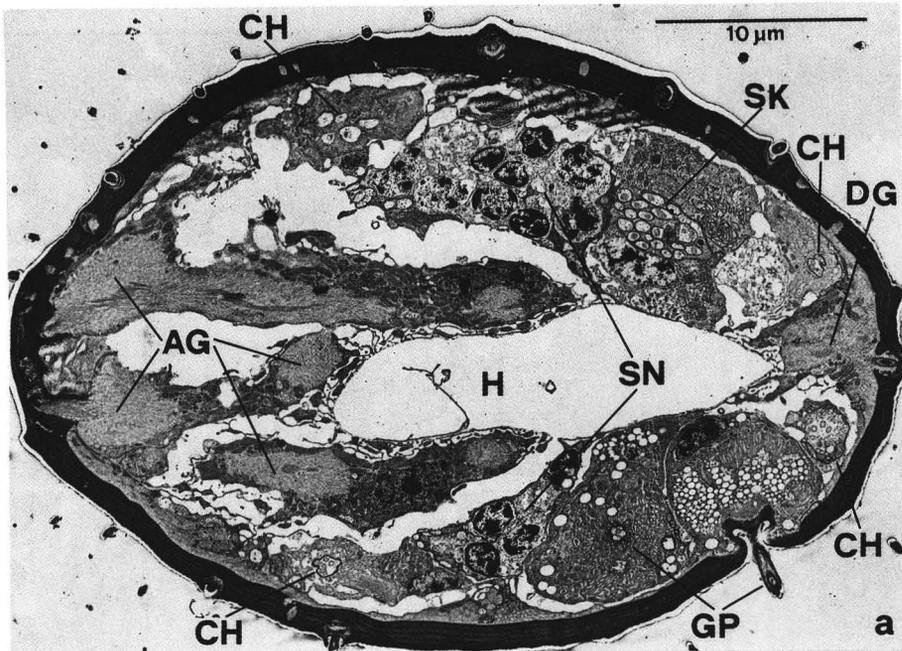
Fig. 22 - Female apical antennomere: a) cross section at the proximal grooved peg level (Fig. 21,a); b) detail of ditto showing the proximal «grooved peg sensillum»; c) oblique section of the peg at about half length; d) subapical cross section of ditto; e) apical cross section of ditto. (c, d and e at the same magnification).
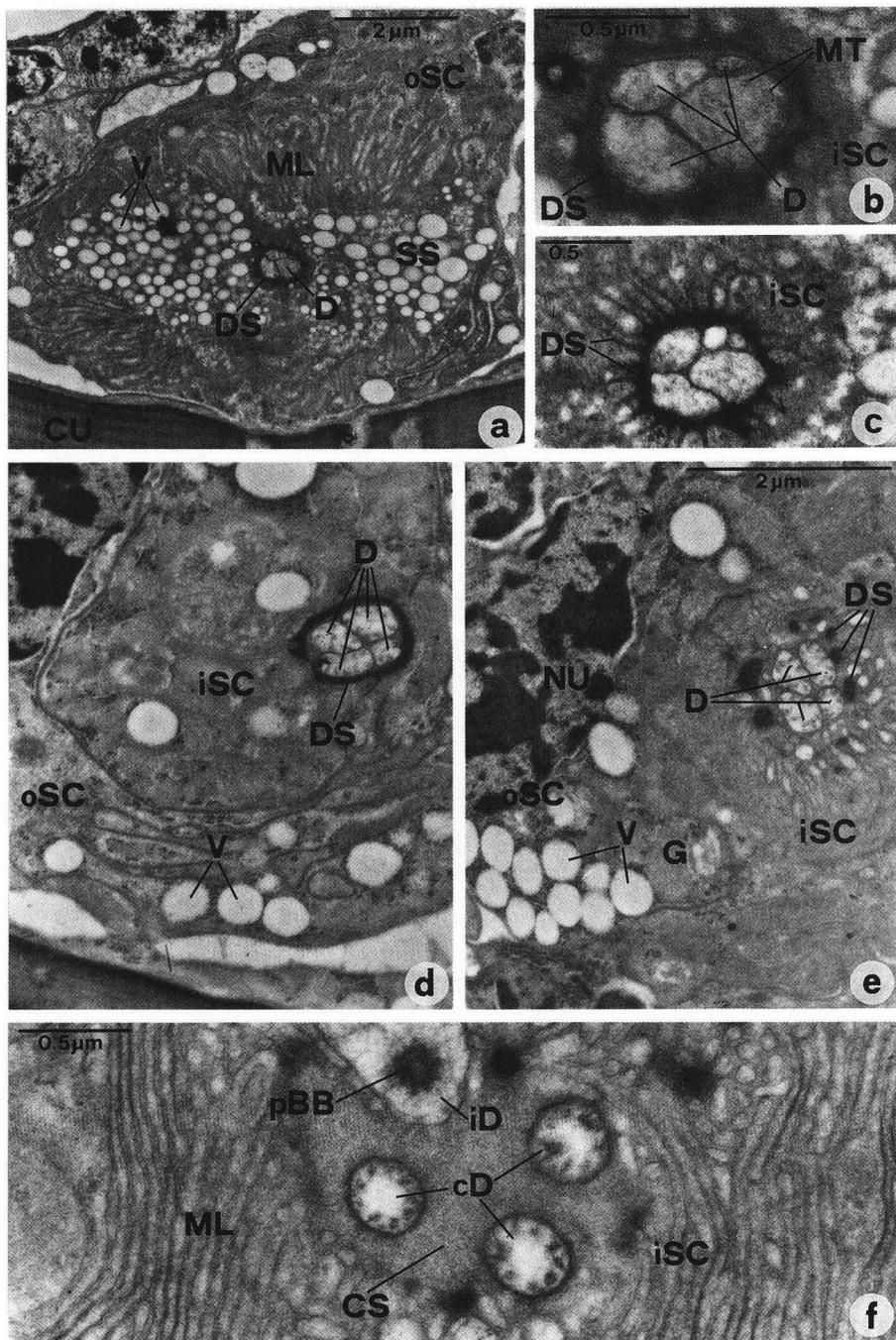
Fig. 23 - Female apical antennomere, «grooved peg sensillum» cellular components, details of serial cross sections: a) just beneath the socket; b) detail of ditto; c) the same as (b), a little deeper; d) near basal end of dendritic sheath; e) at basal end of dendritic sheath; f) the same as in (e), a little deeper. (d and e at the same magnification).
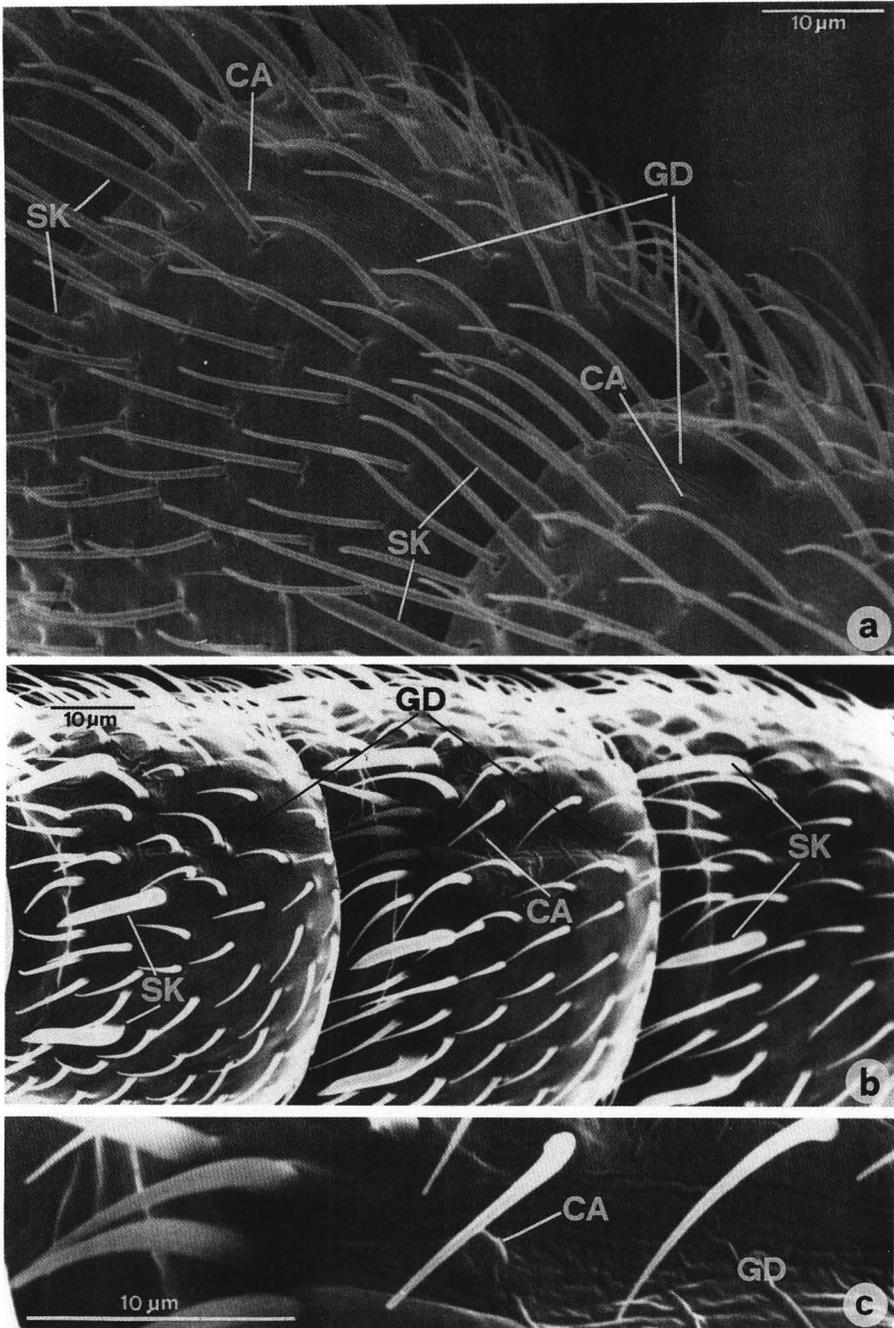
Fig. 24 - Female 8th-10th antennomeres, S.E.M. micrographs, subdorsal aspect: (a) and (b) from different specimens; c) detail of (b).

big tubular body (TB, Fig. 29b) apparently attached to both inner and outer cuticular parts through its dendritic sheath; b) only one sheath cell (SC, Fig. 29), relatively rich in microlamellae, mitochondria and longitudinally oriented microtubules, proximally enclosing the inner dendritic segment, like a mesaxon, with septate junctions all around it (SJ, Fig. 29 d), and distally forming a single, wide sinus (SS, Fig. 29: c, e) lined with numerous microvilli; extensive septate junctions characterize the boundaries between the sheath cell and the adjacent gland cells, as well as between these cells (SJ, Fig. 27a). These sensilla strongly resemble the sensilla campaniformia associated with the above mentioned termite pheromone-gland, and interpreted (STUART, 1964; STUART & SATIR, l.c.) as part of a feedback control system controlling the amount of pheromone released.
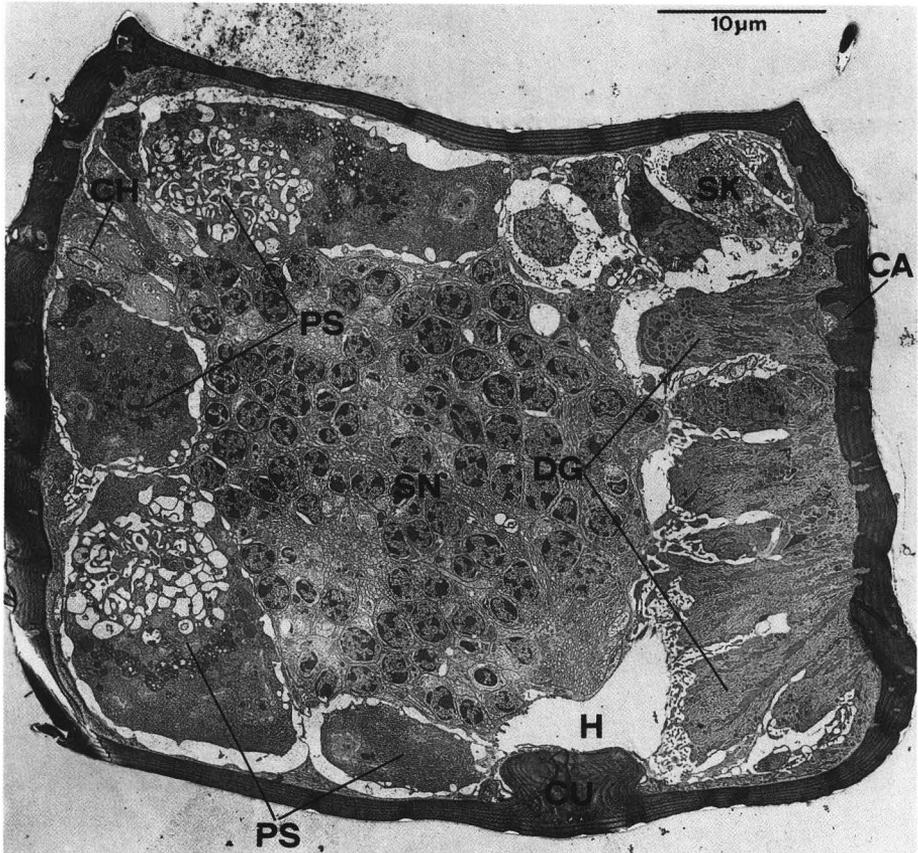

Fig. 25 - Female 9th antennomere, submedian sagittal section ventrally shifted (see Fig. 26, arrow heads) to intersect lateral end of both papillary sensilla sinuses (PS).

3.2.2 Male chemosensilla and glands

Sickle-shaped sensilla (SK). Except for having bigger hair-shafts which vary in length from 20 to 33 μm, and fewer sensory neurons (medially 18 per sensillum), these sensilla are very much the same as in the female (cf. Figs 3b, 4: c,d, 5a, 6, 24: a,b with Figs 30, 32, 33, 34, 35, 37).
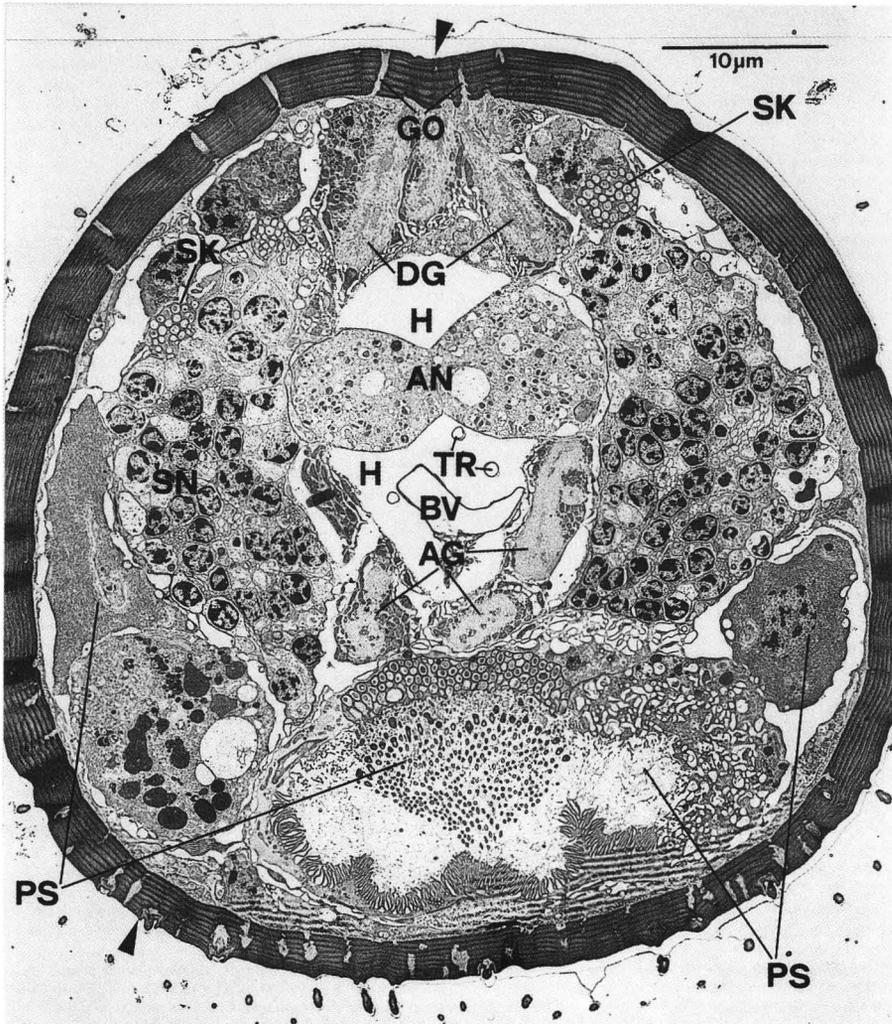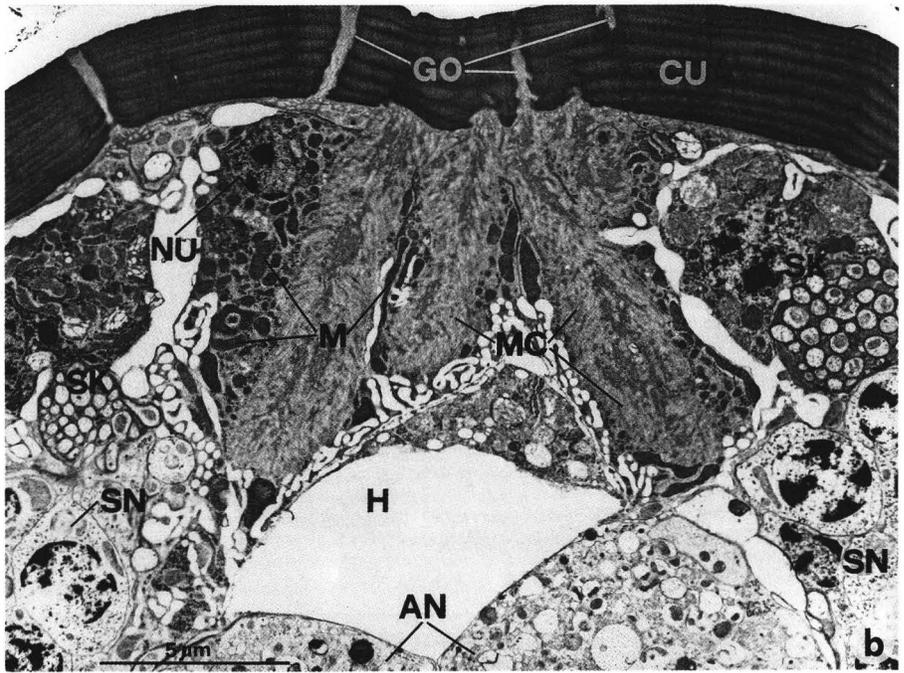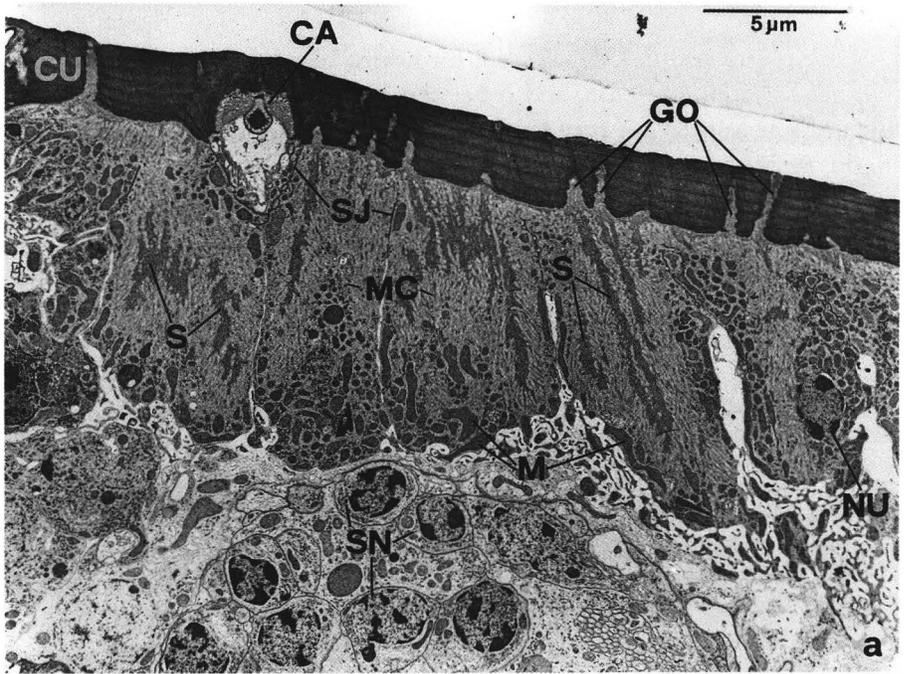

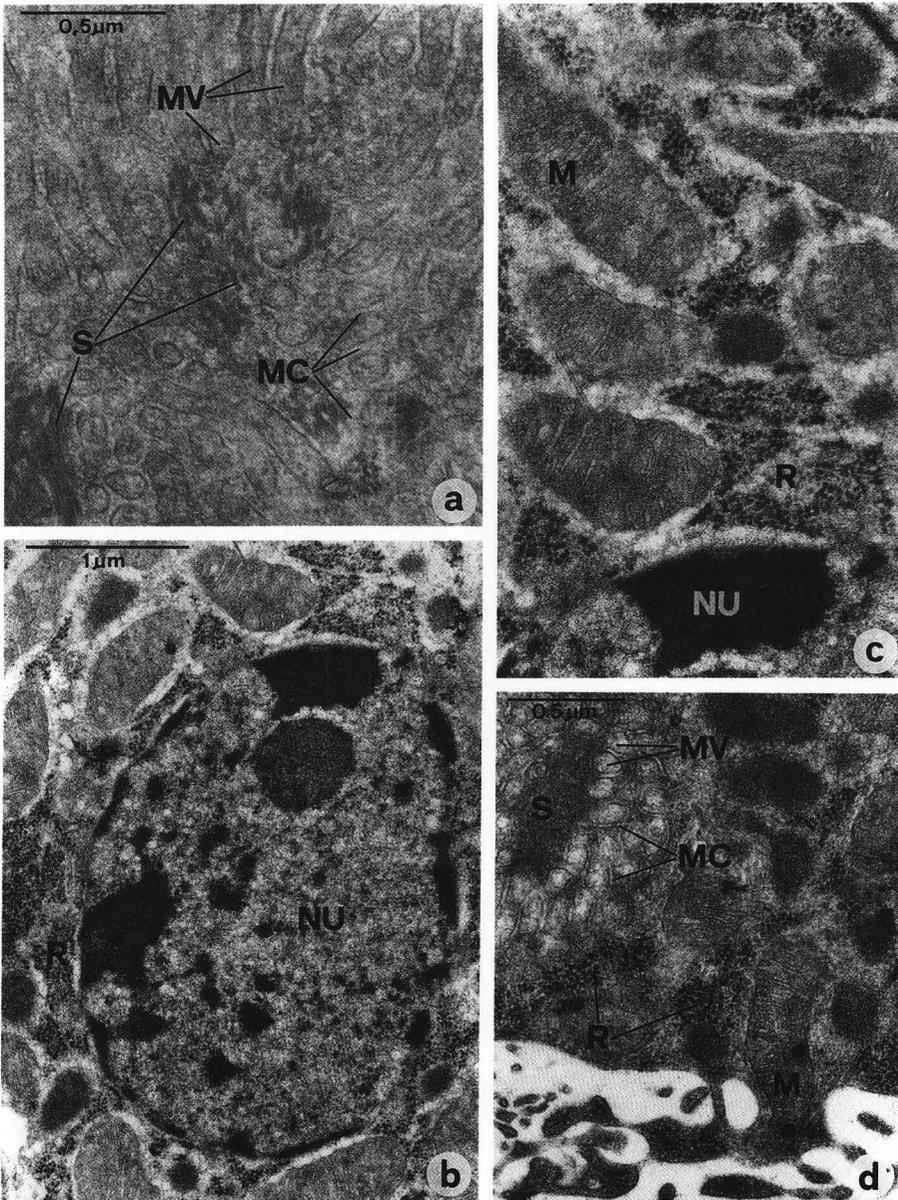Fig. 26 - Female 10th antennomere cross section at distal papillary sensillum level, just below papilla.

Fig. 28 - Female, «dorsal gland» cell details: a) morphologically apical part; b) and c) perinuclear portions; d) basal part showing the bottom of the apical invagination (MC). (a and c at the same magnification).

Fig. 27 - Female 9th antennomere, longitudinal (a) and cross (b) section details showing «dorsal gland» maximal extension in length and breadth, respectively.
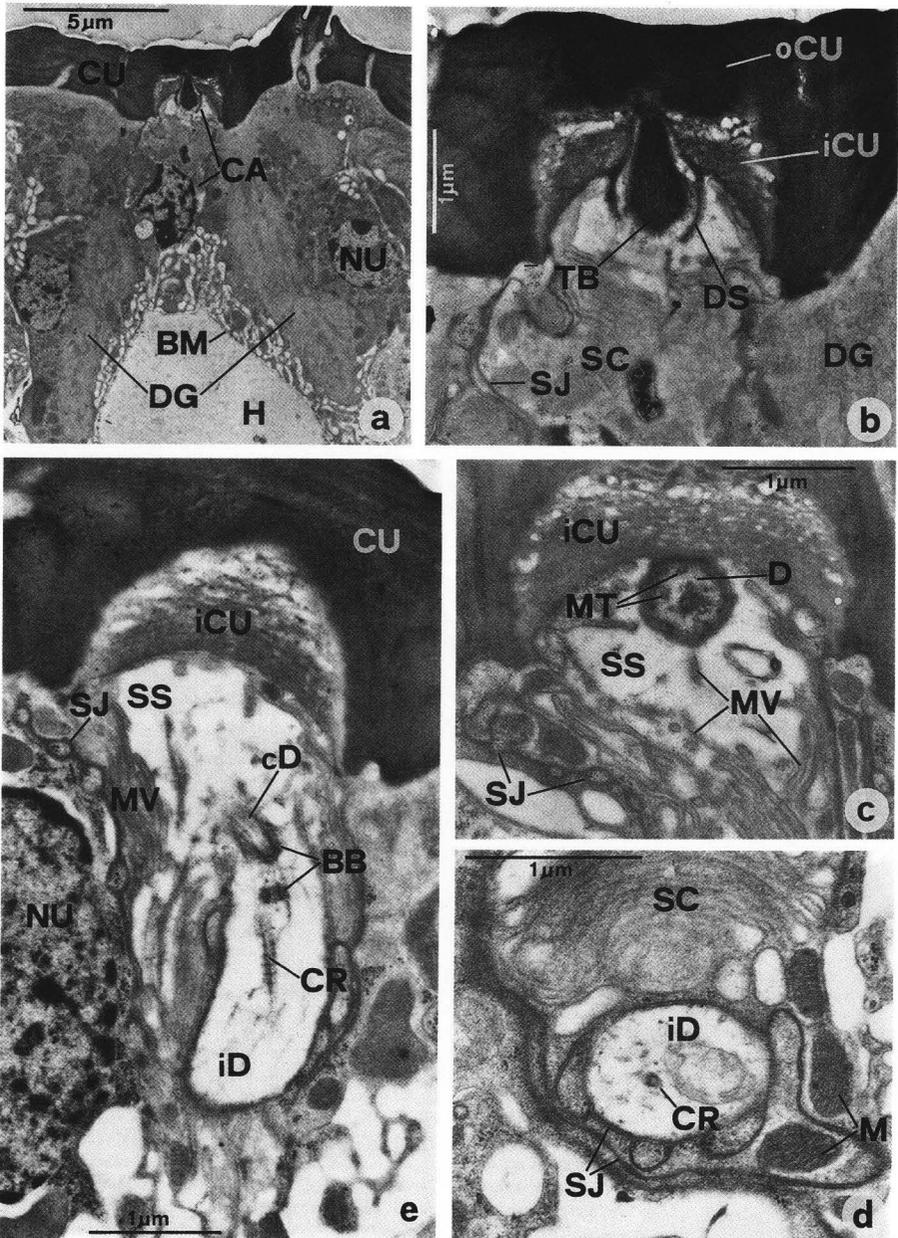
Fig. 29 - Female 10th antennomere, «dorsal gland» (DG) and «sensillum campaniforme» (CA): a) gland cross section, general view; b) longitudinal section of sensillum cuticular parts and dendrite tip (tubular body); c) sensillum cellular parts exhibiting subapical cross section of the outer dendritic segment; d) cross section of the inner dendritic segment; e) longitudinal section of the ciliary and inner dendritic segments.

Sensilla conica (SCO). This kind of sensillum, both for location and some of the internal features, seems to be homologous with the female's «papillary». The cuticular parts consist of a conical, rather elastic (thus looking varied in shape: Figs 30, 36a, 41a), smooth, blunt tipped, non-porous hair- shaft, approximately 12 µm in length and 1.5 µm in diameter near the base, inserted in a wide, round, rather rigid socket.

The cellular components are represented by: a) two or three sensory neurons whose perikaryons lie in the «massive ring» (Fig. 31) and whose inner dendritic segments, rich in mitochondria and neurotubules (Fig. 39: b,d), run through the inner sheath cell, while the outer dendritic segments run, parallel and naked, through the large single sinus (SS, Fig. 39: a,c) and enter the shaft lumen (Fig. 38: a,b) up to its tip, without branching (Fig. 38c); b) and two sheath cells: an inner one enclosing the inner dendritic segments like a mesaxon (Fig. 39: b,d), adhering to them with septate junctions all around; and an outer sheath cell, rich in mitochondria, scattered ribosomes and longitudinally oriented microtubules, that proximally encircles the previous one in the same way (oSC, Fig. 39: b,d) as this encloses the inner dendritic segments, and distally forms a large sensillar sinus (SS, Figs 38a, 39: a,c), lined with numerous microvilli and not distinguished from a ciliary sinus. On ultrastructural basis, these sensilla might be considered aporous gustatory hairs (sensu ZACHARUK, 1985).

Sensilla chaetica (CH, Figs 30, 31, 36, 41). They are structurally identical to those of the female (compare Figs 33b, 37, 40 with 18, 19), but much longer, being 18-20 µm long.

Grooved peg sensilla (GP, Figs 30, 31, 41). These sensilla are identical with those of the female (compare Figs 37, 42 with 22, 23), in structure and size as well.

Dorsal glands (DG) and associated sensilla campaniformia (CA). The glands (Figs 31, 32b, 37, 43a) are identical in structure but much smaller than in the female (see 3.1), while the sensilla campaniformia are just the same (compare Figs 43 with 29).

Ventral gland (Fig. 44: a, PG, and b, VG). It has already been described by BIN and VINSON (1986) and considered to be a male sex gland. Here we may confirm the previous description, adding some cytological details (Figs 45, 46) such as the abundance of scattered ribosomes and of Golgi apparati, and the presence of lysosomes.
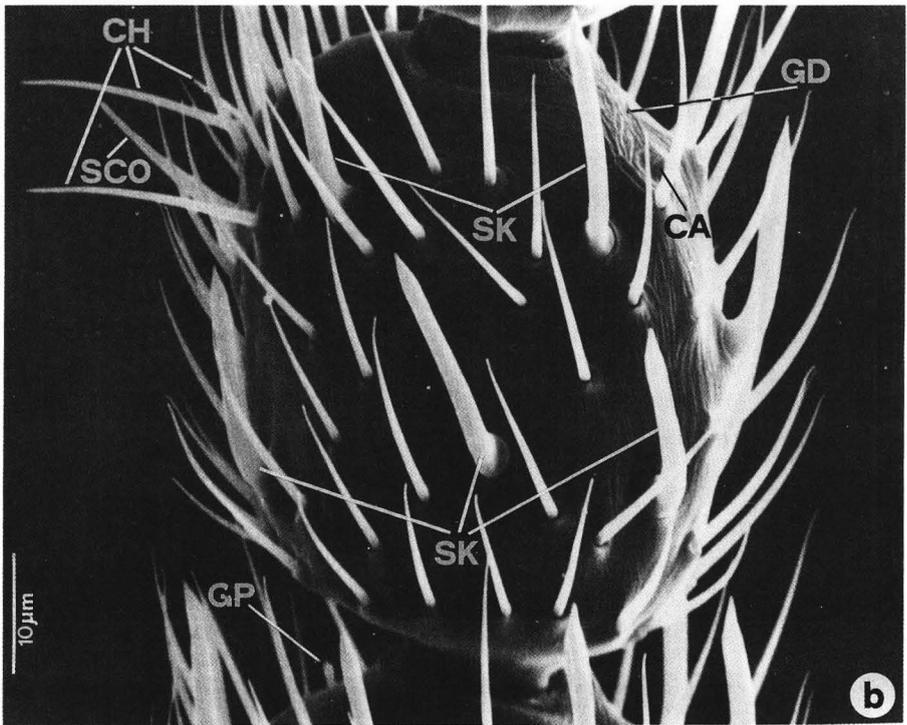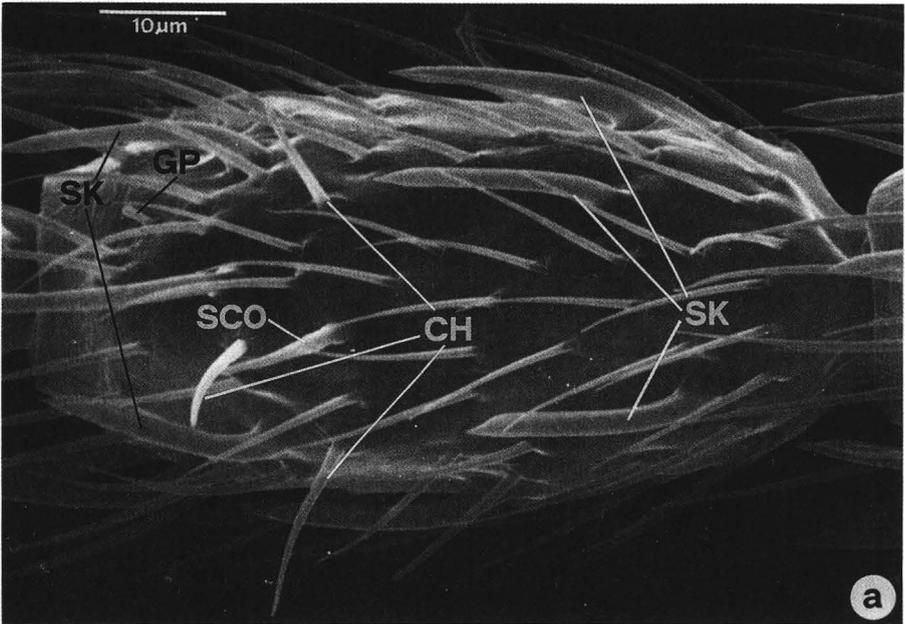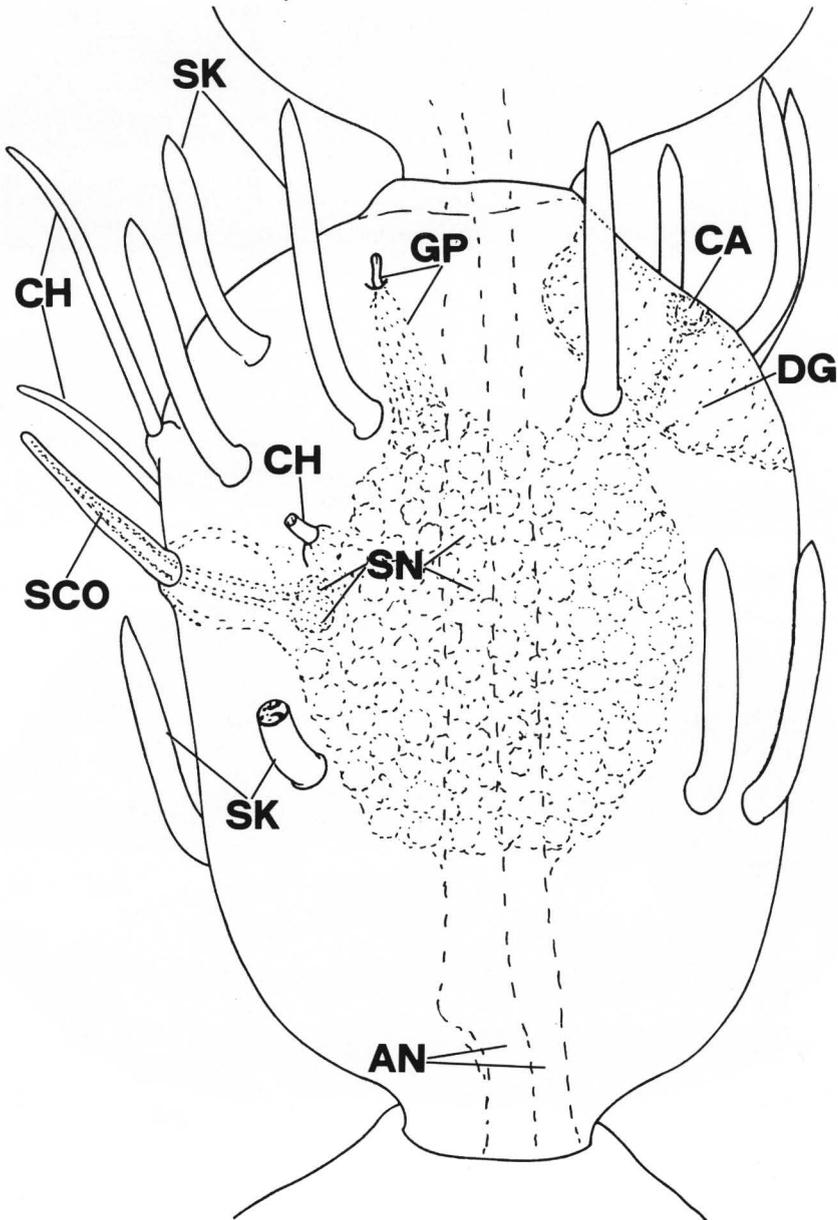
Fig. 31 - Tridimensional diagram of male (6th-11th, lateral view) antennomere topographical ana-tomy regarding chemosensilla and dorsal gland.

Fig. 30 - Male 9th (a) and 10th (b) antennomeres, subventral and dorsomedial (oblique) views respectively. (S.E.M. micrographs).
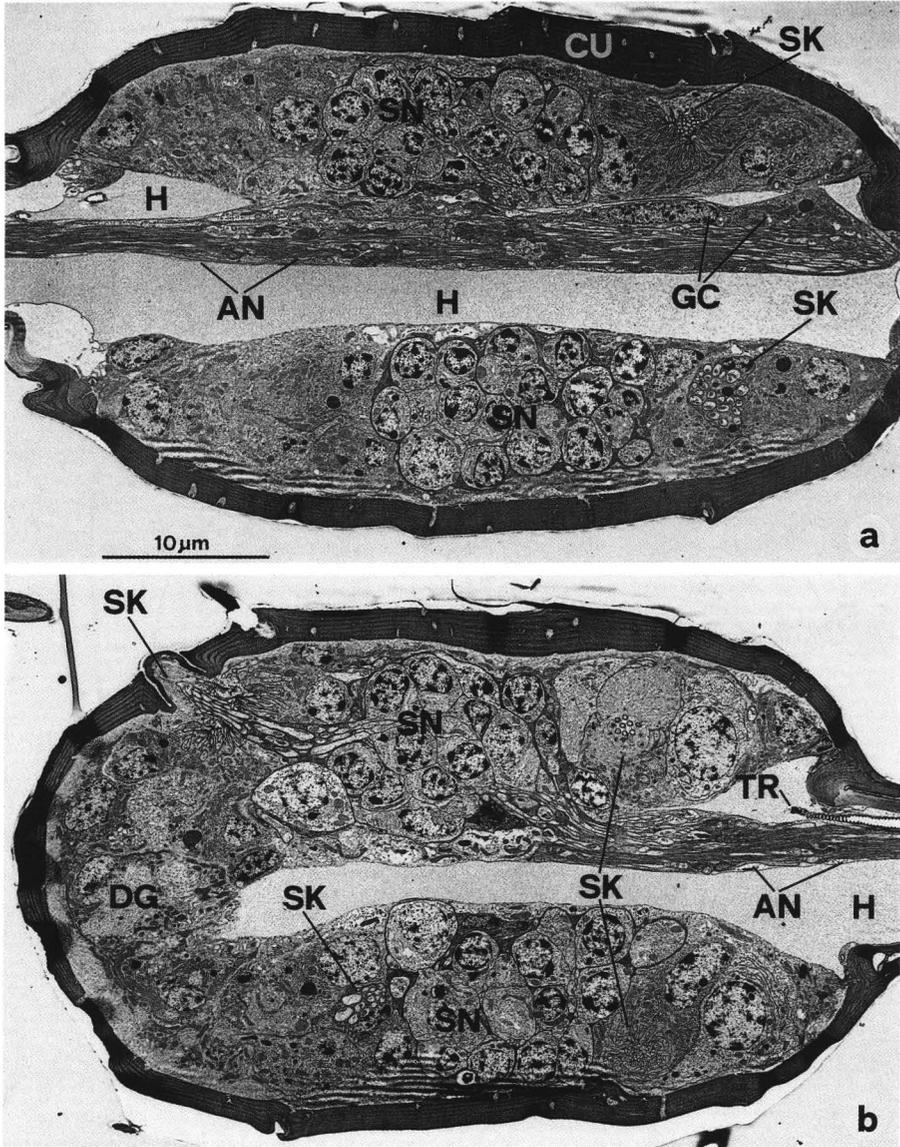
Fig. 32 - Male 10th (a) and 11th (b) antennomeres, longitudinal (as indicated in Fig. 37 by arrow heads) and oblique-longitudinal sections, respectively. (a and b, at the same magnification).
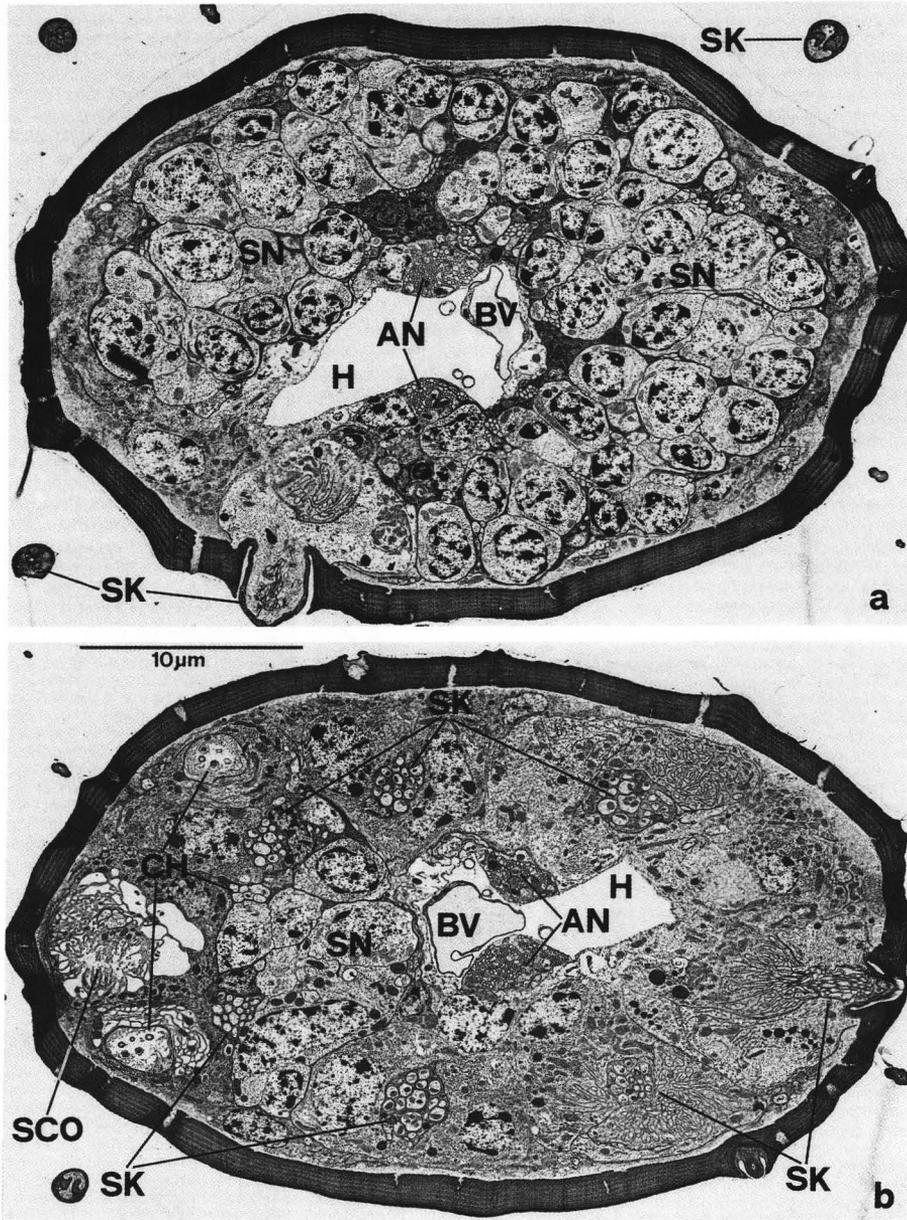
Fig. 33 - Male 11th antennomere, submedian (a) and a little more distal (b) cross sections. (a and b, at the same magnification).
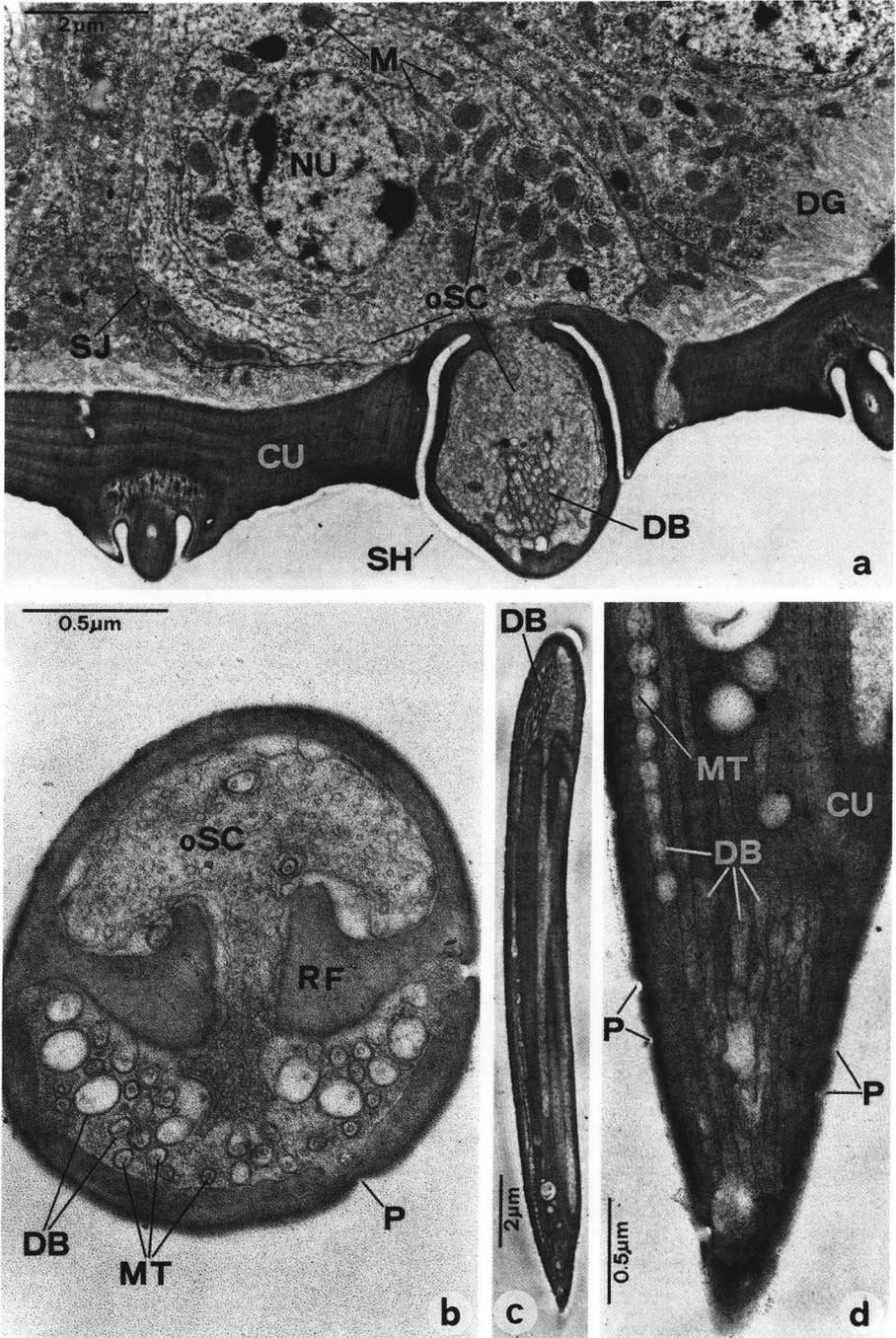
Fig. 34 - Male, «sickle-shaped sensillum»: a) cross section at socket level; b) shaft intermediate cross section; c) shaft longitudinal section; d) apical detail of (c).
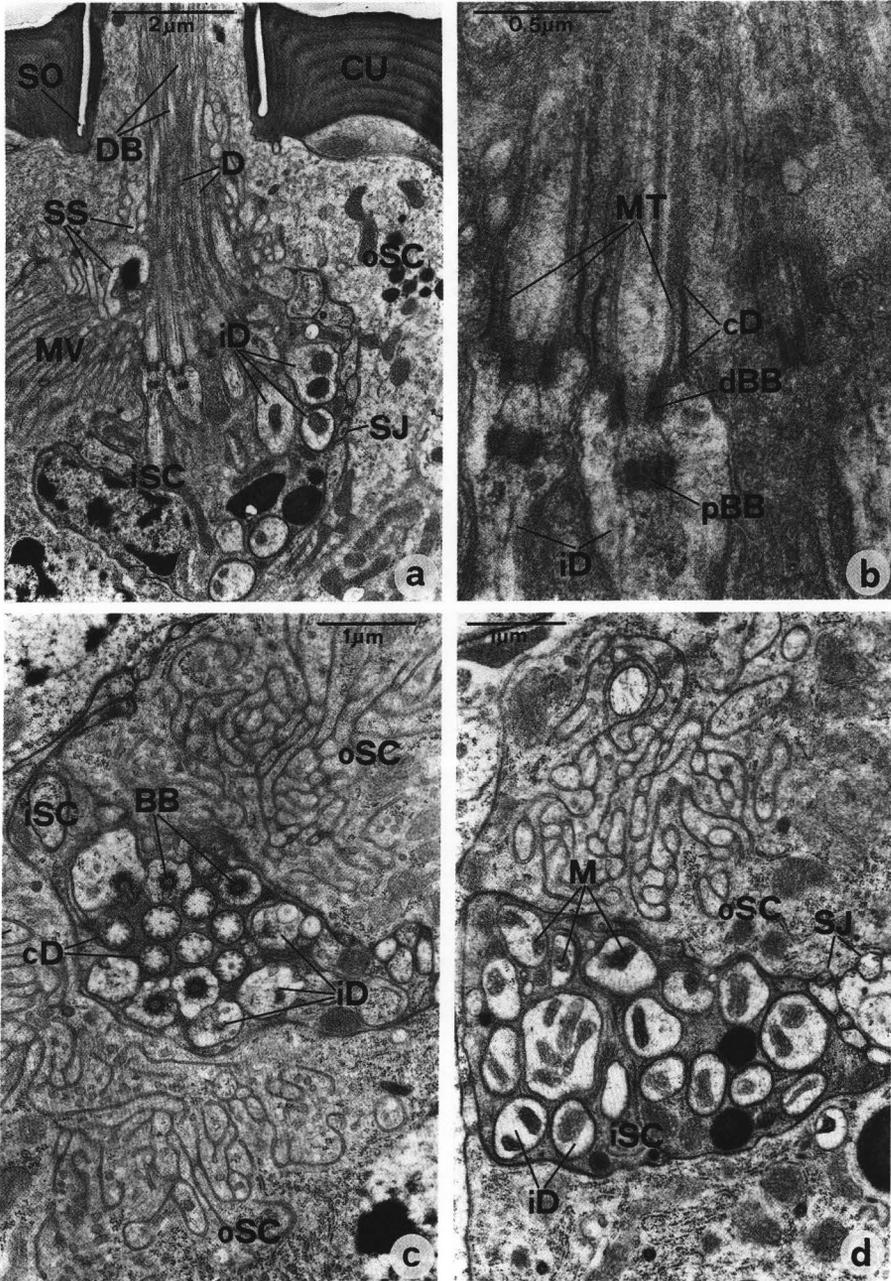
Fig. 35 - Male, «sickle-shaped sensillum», cellular parts' details: a) oblique section; b) detail of (a); cross sections through dendritic ciliary constrictions (c) and inner dendritic segments.
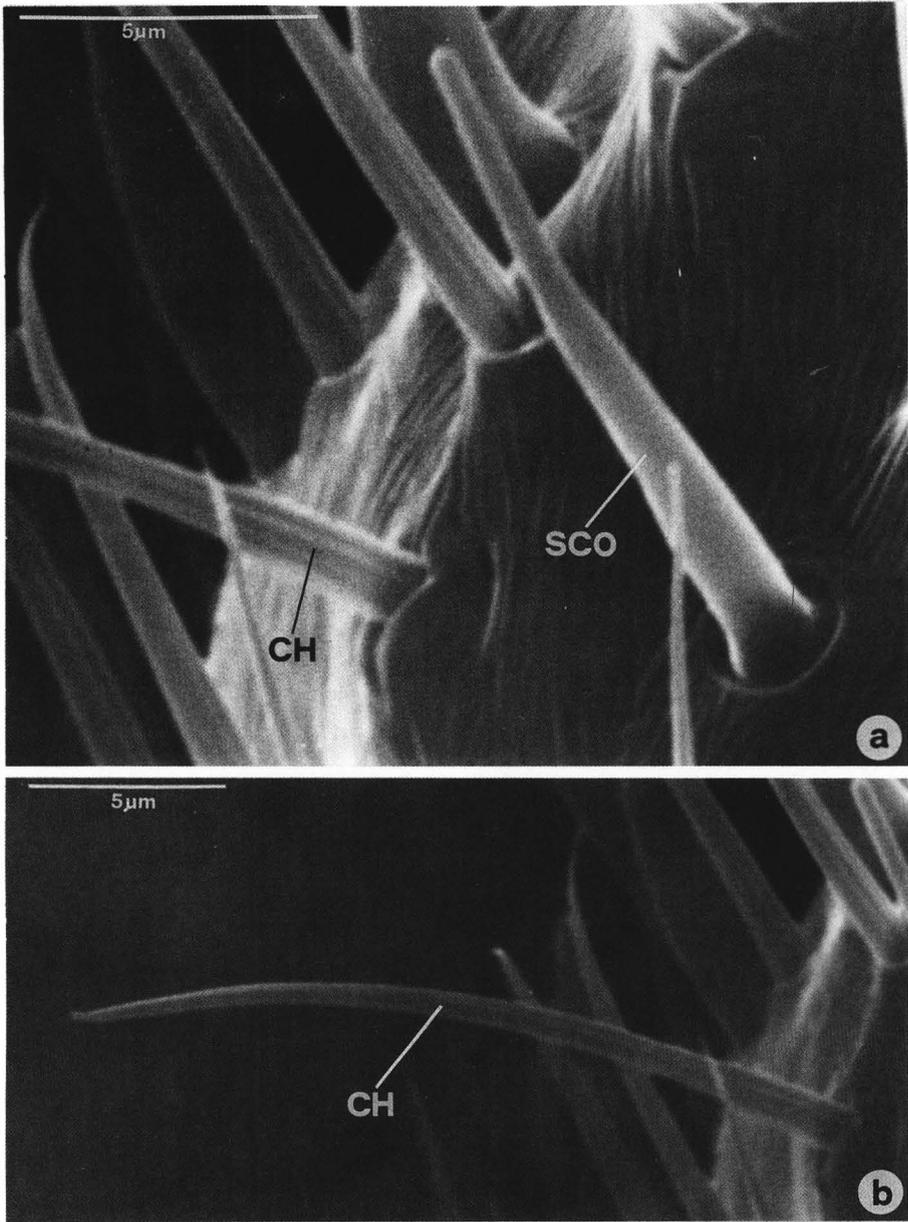
Fig. 36 - Male 11th antennomere subdistal ventral details, S.E.M. micrographs showing: «sensillum conicum» (a, SCO) and a «sensillum chaeticum» (a and b, CH).
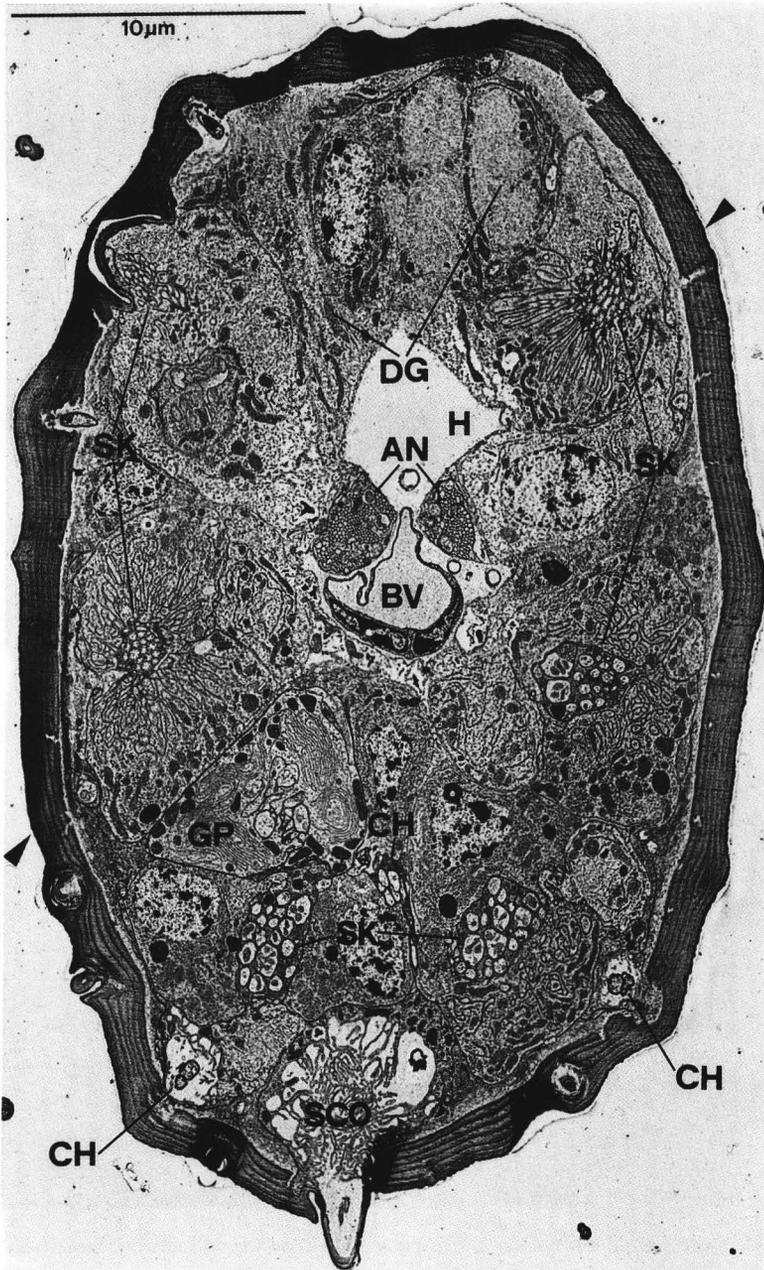
Fig. 37 - Male 11th antennomere, cross section at the level of «sensillum conicum» (SCO) socket.
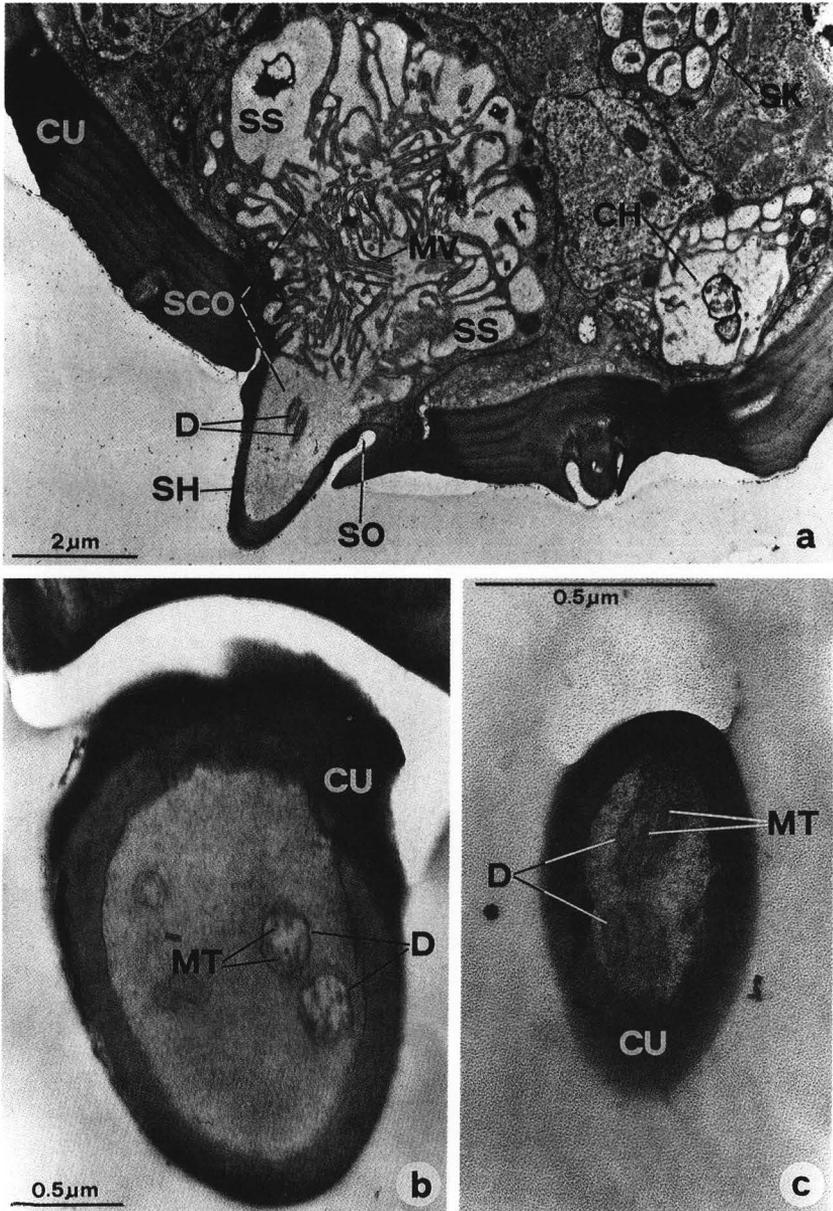
Fig. 38 - «Sensillum conicum» details: a) oblique section of socket and just underneath laying cellular parts; shaft subproximal (b) and subdistal (c) oblique sections.

Fig. 39 - «Sensillum conicu.n», cellular parts' cross sections: a) and c) through dendritic ciliary constrictions; b) and d) at inner dendritic segment level. Both possible conditions, i.e. with two (a and b) or three (c and d) sensory neurons, are here illustrated.
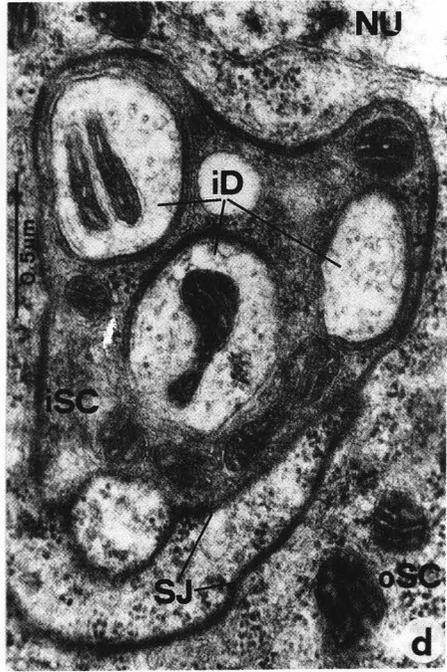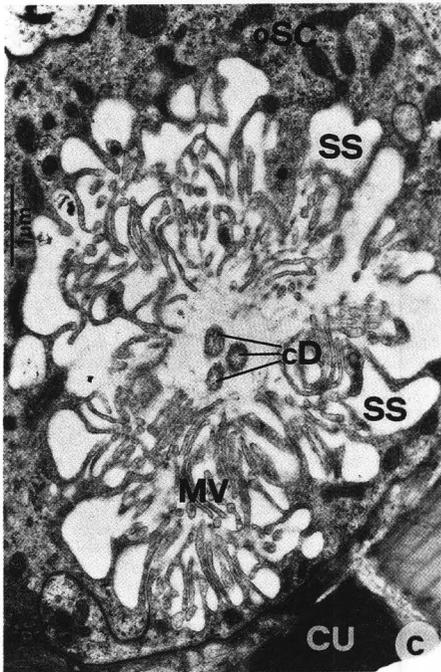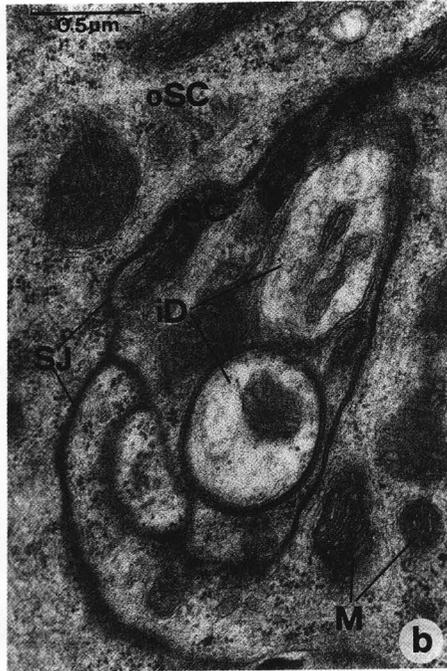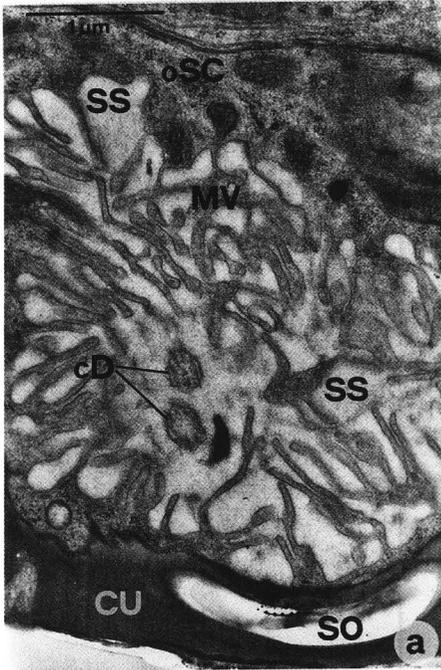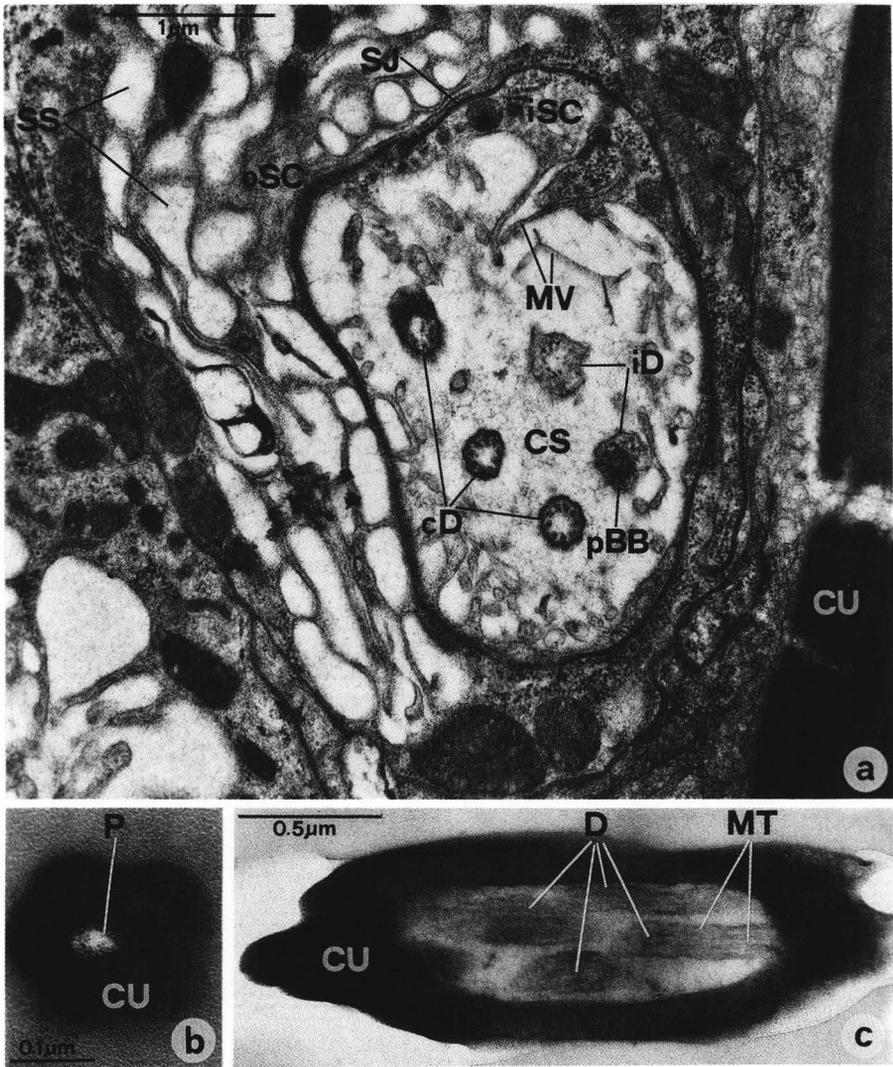
Fig. 40 - Male, «sensillum chaeticum»: a) cellular parts subtransversal section; b) shaft apical cross section; c) shaft oblique section at about half length.

Fig. 41 - Male 11th antennomere distal portion, S.E.M. micrographs: a) lateroventral aspect; b) «grooved peg sensillum» (GP) (base in focus); c) the same (grooves in focus).
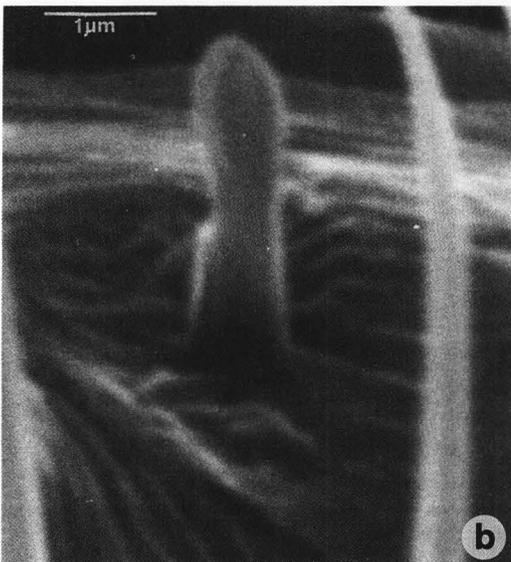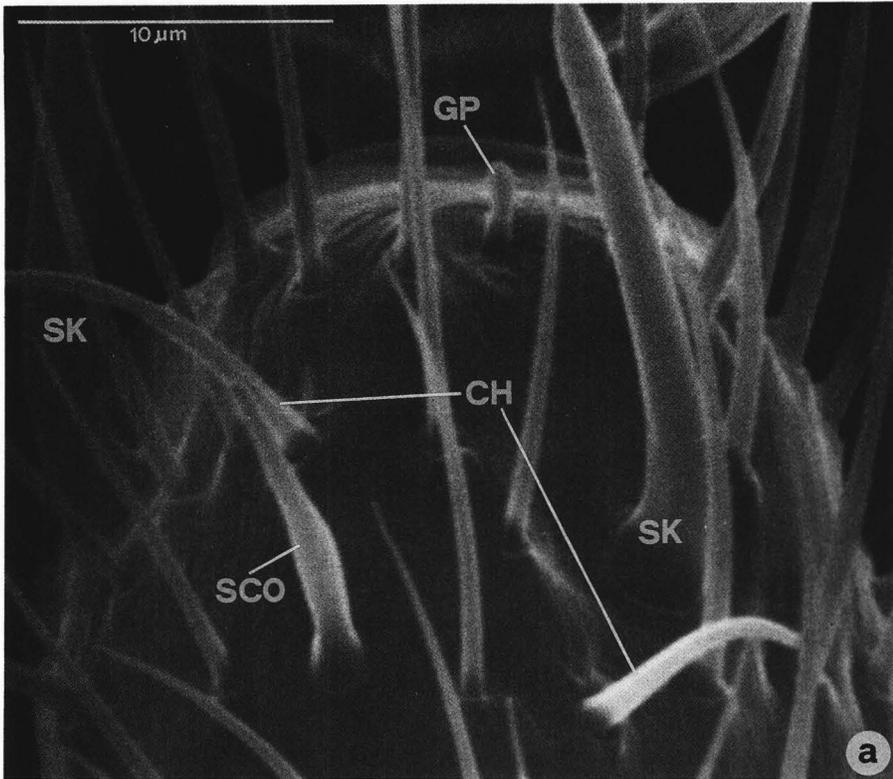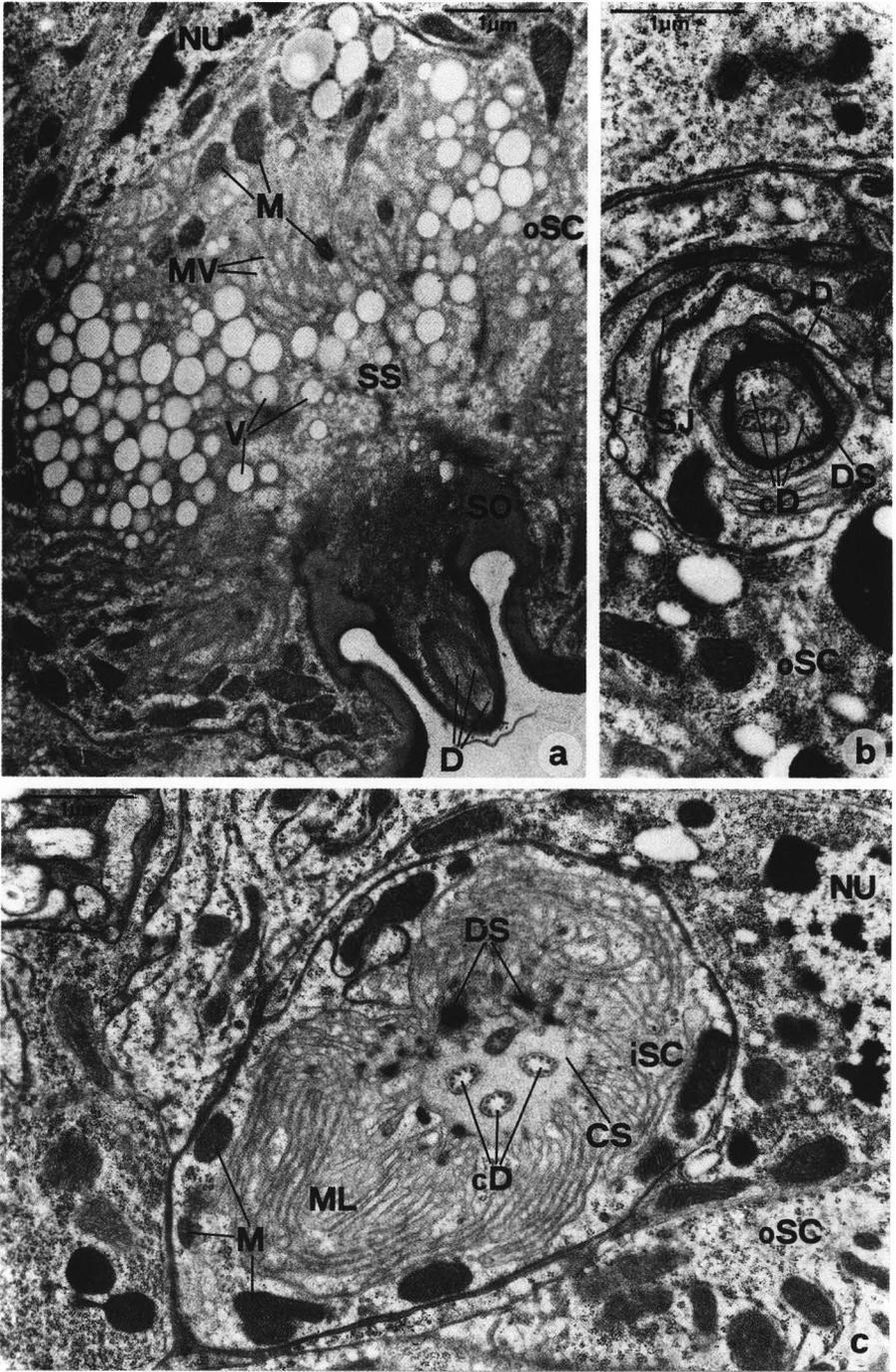
Fig. 42 - Male, «grooved peg sensillum» details: a) oblique section; b) cellular parts' cross section through the ciliary constrictions of three dendrites (cD) and near the tip of the fourth dendrite (D); c) same subject, cross section at the level of common dentritic sheath origin.
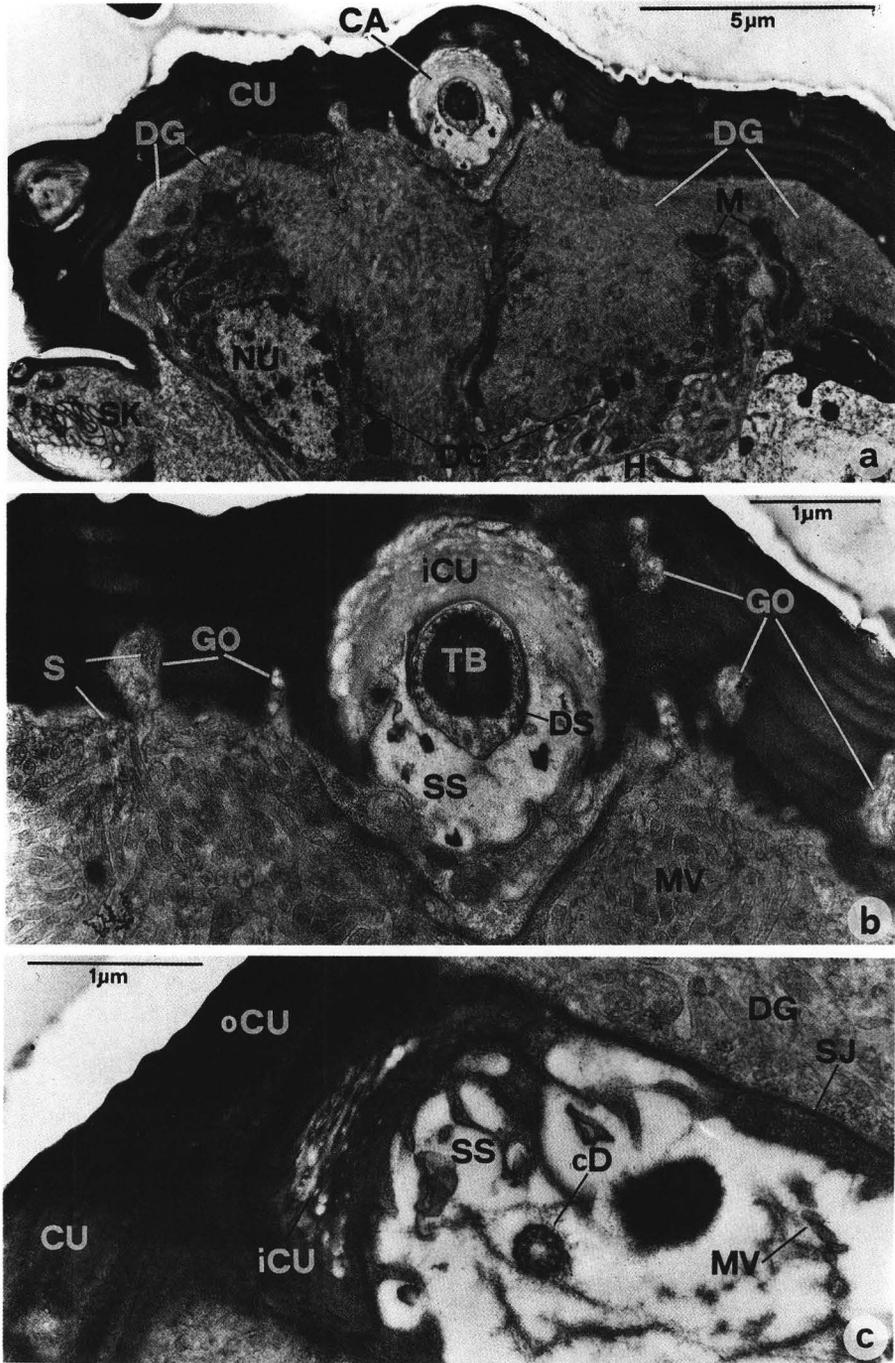
Fig. 43 - Male «dorsal gland» (DG) and relative «sensillum campaniforme» (CA): a) gland cross section through sensillum dendritic tip (tubular body); b) detail of (a); c) more proximal section through dendritic ciliary constriction (cD) of the same sensory neuron.
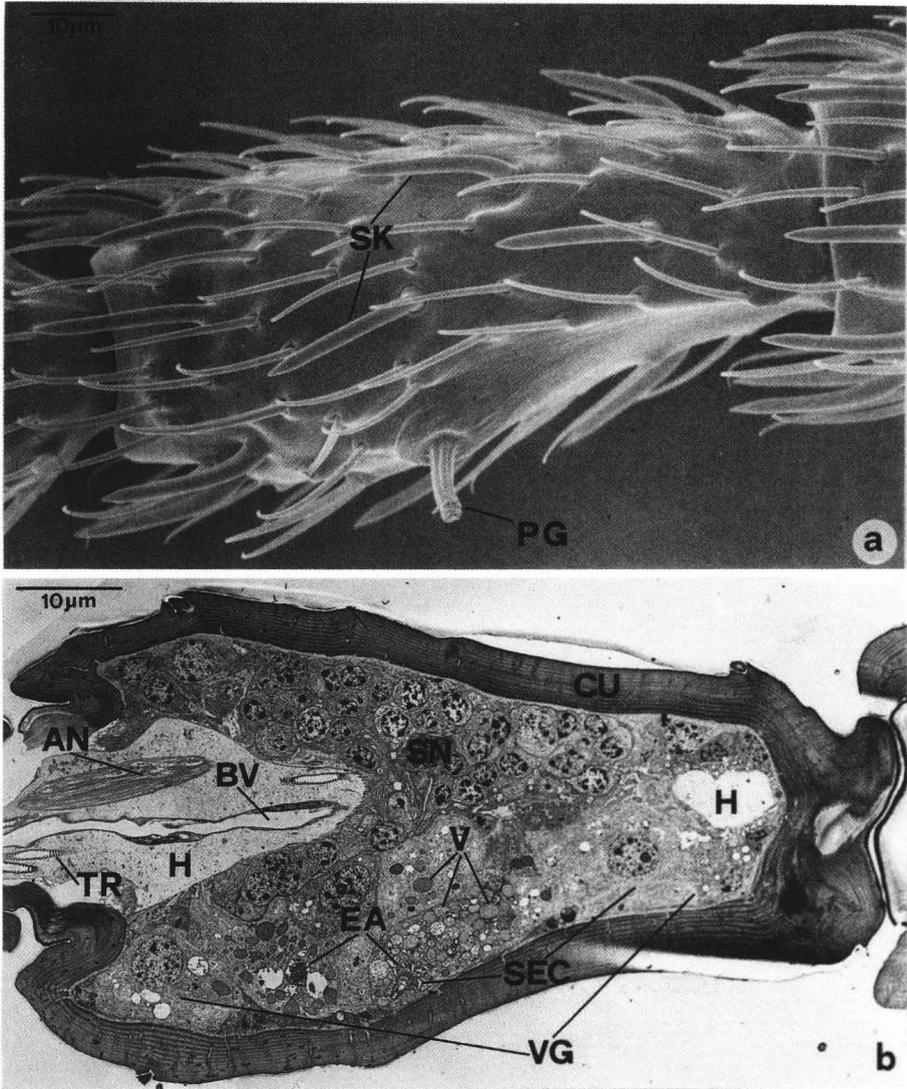
Fig. 44 - Male 5th antennomere: a) S.E.M. micrograph, medial-ventral aspect; b) submedian sagittal section showing longitudinal full extension of the «ventral gland» (VG).

Fig. 45 - Male 5th antennomere sagittal section, «ventral gland» secretory cell details: a) perinuclear aspect; b) detail of the same.
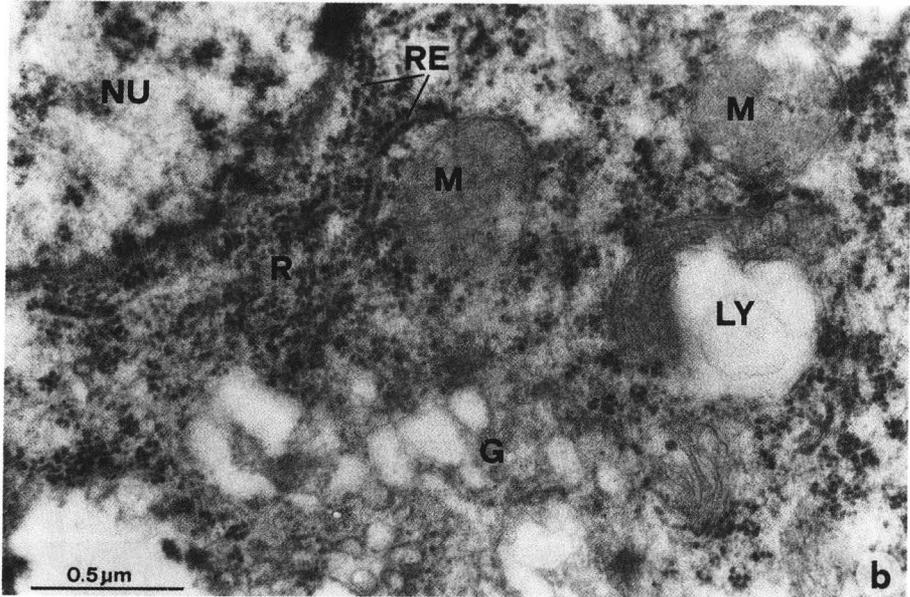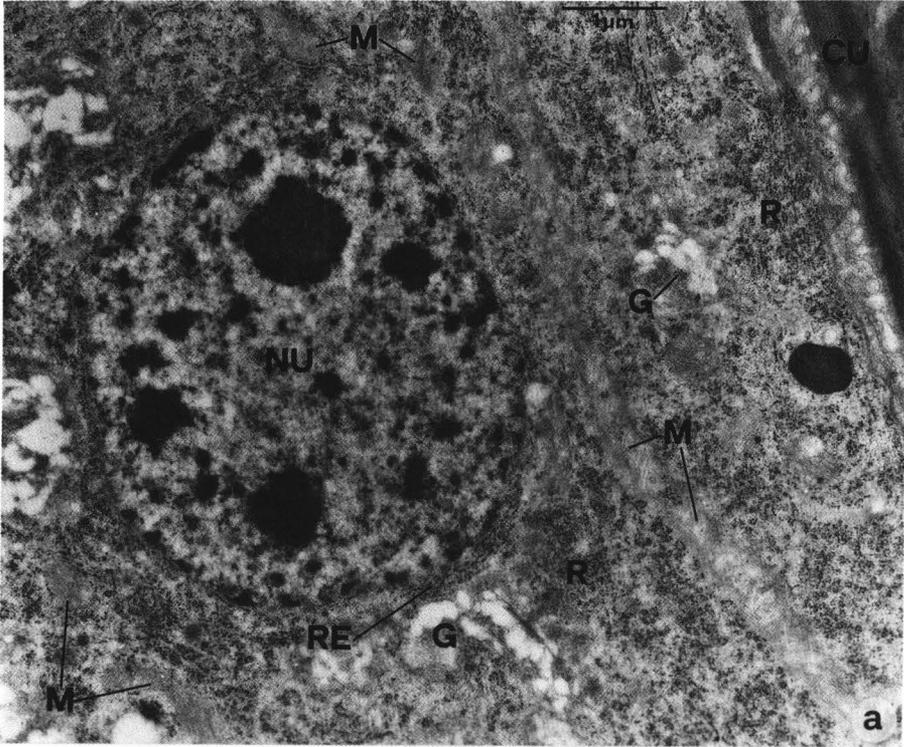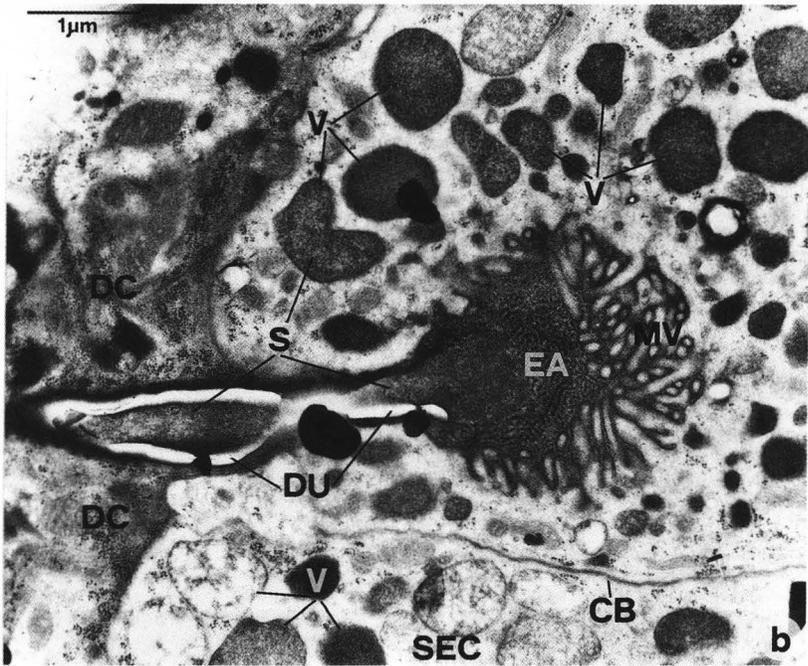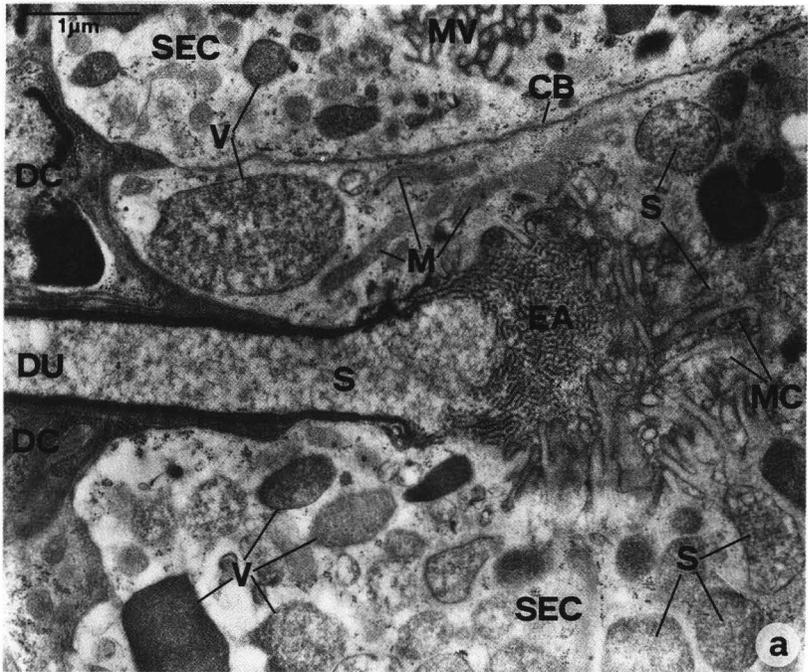
3.3 Role of antennae in reproductive behaviour

We speculate on the functional significance of the chemosensilla and glands reported on part of the antennae of *T. basalis*. These speculations are based on previously published behavioural data or unpublished information.

3.3.1 Mating behaviour

About 24 h before the females emerge males begin patrolling the host egg masses and sometimes battle with competitors which have emerged from the same egg mass (BIN *et al.*, 1986) or arrived from another (JONES, submitted). Next, the male stands above an egg from which a female is going to emerge vibrating his antennae. This presumed detection of females within the host is likely mediated by a volatile sex-pheromone as reported for other parasitoids (SCHWARTZ & GERLING, 1974; TAGAWA, 1977). Of the various receptors, the sickle-shaped sensilla (A3-A12) are most likely involved in this detection.

As soon as the female emerges the mating behaviour begins. The male vibrates his antennae rapidly and approaches the emerging female. After touching the female he mounts and continues to vibrate the antennae orienting them to those of the female. He then brushes the dorsal side of her antennae with the tips of his. This activity probably places the male sensilla chetica (A12) in proximity to the female dorsal glands (A6- A11). Next, he touches the lateral and ventral sides of the female antennae entwining his around hers and repeatedly sweeping her antennae from the base to the tip using his entire flagella. At this step there is repeated contact and possible interchange involving the male sex-glands (A5), the female dorsal glands (A6-A11) and the (still unknown) respective sensilla. For the male we suspect the sensilla chetica (A6-A12), the sensilla conica (A7-A11) and grooved peg sensilla (A6-A11) are involved and for the female, papillary sensilla (A7-A11), sensilla chetica (A6-A11), and the grooved peg sensilla (A3-A11). During antennal contact some signs must be transmitted to the male because he begins to move backwards to initiate copulation. As he moves backward he continues vibrating the antennae and extrudes the penis.

The following tables (Tables 2,3) are complementary to our previous studies (BIN et al., 1986) with added qualitative and quantitative information on spe-

Fig. 46 - Male, «ventral gland» sagittal section, glandular unit terminal portion details showing the end apparatus (EA) and relative ductule containing secretion more (b) or less (a) packed, just like it looks within the various secretion vesicles (v).

TAB. 2 - Chemosensilla and glands in relation to Female Recognition Time (FRT) by an intact (A12-A1) or antennoectomized (A11-A1, etc.) male. Female is intact. Time in seconds.

Chemosensilla/Glands		Male antennomeres present					Comments
Type	Number	A12-A1	A11-A1	A9-A1	A6-A1	A5-A1	
OLFACTORY S.							
Sickle-shaped	total	340	306	254	172	146	unlikely
	%	100	90	74.7	50.5	42.9	involved
GUSTATORY S.							
Conica	total	10	10	6			
	%	100	100	60			
Chaetica	total	54	34	22	4		apparently
	%	100	62.9	49.7	7.4		involved
Grooved Peg	total	12	12	8	2		unlikely
	%	100	100	66.6	16.6		involved
GLANDS							
Dorsal	total	12	12	8	2		
	%	100	100	66.6	16.6		
Ventral	total	1	1	1	1	1	
	%	100	100	100	100	100	
FRT	total	64.8	135	331.8	553.2		
	%	100	208.3	512.0	853.7	no response	

TAB. 3 - Chemosensilla and glands in relation to Male Recognition Time (MRT) by an intact (A11-A1) or antennoectomized (A8-A1, A6-A1) female. Male is intact. Time in seconds.

Chemosensilla/Glands		Female antennomeres present			Comments
Type	Number	A11-A1	A8-A1	A6-A1	
OLFACTORY S.					
Sickle-shaped	total	72	48	16	unlikely involved
	%	100	66.6	22.2	
GUSTATORY S.					
Papillary	total	18	8	0	possibly involved
	%	100	44.4		
Chaetica	total	54	22	6	apparently involved
	%	100	40.7	11.1	
Grooved Peg	total	12	6	6	unlikely involved
	%	100	50	50	
GLANDS					
Dorsal	total	12	6	2	
	%	100	50	16.6	
MRT	total	64.2	390		
	%	100	607.4	no response	

cifically involved sensilla. The recognition time of an intact female (FRT) by an intact (A12) and antenno-ectomized male (Table 2) is expressed in actual time and in percent and shows how recognition time increases with progressive reduction (by amputation) of antennomeres until no response occurs. The recognition time of an intact male (MRT) by an intact (A11) or antenno-ectomized female is given in Table 3.

3.3.2 Host location

In addition to the female antennae in mating behaviour, the antennae play a major role in host finding and acceptance. We presume that females must respond to plant and host odors during the host finding process (VINSON, 1985). Whether it is plants or host the sickle-shaped sensilla on A3-A11 are the most likely involved due to the numerous thin wall pores and numerous neurons probably giving a great deal of flexibility in volatile chemical responses.

3.3.3 Host acceptance

Once a host is located there is evidence that the recognition and acceptance response are mediated by a non-volatile compound on the host egg (COLAZZA et al., in preparation). Upon contacting an egg mass the T. basalis female first explores the egg-mass by drumming and/or rubbing the side or edge of the mass with the ventral part of the clava. The papillary sensilla on A7-A11 and associated accessory glands are likely involved in host recognition. The possible role of the secretion, if any, is intriguing. The sensilla chaetica may also be involved in host acceptance but may also play a role in detecting the marking pheromone contaminating the host egg.

4. CONCLUSIONS

Our aim was. a morpho-functional identification of the antennal sensory and secretory structures involved in *Trissolcus basalis* chemical comunication between the sexes and in host location- acceptance as well, in order to understand more fully the complex behavioural mechanisms involved in the reproduction. Now, from the above reported and discussed results, both morphological and behavioural, the following conclusions may be drawn:

a) There are 5 kinds of chemosensilla, three of which present in both sexes, namely «sickle-shaped sensilla», «sensilla chaetica» and «grooved peg sensilla»,

one kind only in the female, «papillary sensilla», and another one only in the male, «sensilla conica»; and 3 kinds of glands, one of which, «dorsal glands», present in both sexes, another one, papillary sensillum «accessory glands», only in the female, and a third one, «ventral gland», only in the male.

b) Sickle-shaped sensilla, are the sole olfactory organs in either sex; they are sexually dimorphic, being as a whole much more efficient in the male (ca. 170, instead of ca. 36, sensilla and ca. 3000, instead of ca. 1000, sensory neurons per antenna, also with bigger and broader distributed hair-shafts), while (most probably) more versatile in the female for having many more (ca. 28 instead of ca. 18) sensory neurons per sensillum. These morphological considerations together with behavioural observations (see 3.3.1) may suggest for the male a necessity for a most efficient sex pheromone receptor system, and for the female a need for a more versatile (broader-spectrum) olfaction detecting probable more complex odorants such as air-borne kairomones and synomones, which are conceivably less diluted than the sex pheromone(s) in the environment, thus requiring a relatively less sensitive olfactory system.

c) Papillary sensilla are atypical gustatory organs, most versatile given the enormous number of ca. 400 sensory neurons per sensillum. They are probably involved in host recognition (see 3.3.3) and possibly in male recognition (see 3.3.1) as well.

d) Sensilla conica seem to be homologous with papillary sensilla, although being much less versatile (only 2 or 3 sensory neurons per sensillum) and having a quite different cuticular parts. Their function is uncertain.

e) Sensilla chaetica are typical gustatory hairs, having identical ultrastructure, numbers and virtually the same distribution in both sexes. They seem to be involved in reciprocal sex recognition and host acceptance.

f) Grooved peg sensilla are atypical gustatory organs, ultrastructurally identical in both sexes. They seem to come into contact with mate's antennal surface during the reciprocal antennal entwining (see 3.3.1).

g) Dorsal glands are ultrastructurally identical in both sexes, but much more developed in the female; most probably they are controlled by the associated sensilla campaniformia. The glands may play some role in mate recognition.

h) Accessory glands of papillary sensilla produce a secretion that fills the pit of these. The secretion might mediate the perception of the contact kairomone.

i) Ventral gland, present only on the 5th antennomere (the sex segment) of the male, produce a secretion that is necessary for him to be recognized by the female.

For further elucidation of this complex system it is necessary to combine electrophysiological, chemical and behavioural investigations.

Another perspective offered by this study is that some of the structures

illustrated also occur in Parasitic Hymenoptera other than Scelionidae, e.g. Platygastridae (MASNER & HUGGERT, 1989; BIN *et al.*, unpublished) and Diapriidae (BIN et al., unpublished) and therefore could be useful morphological characters for the biotaxonomy of other groups.

5. ACKNOWLEDGEMENTS

6. RIASSUNTO

SENSILLI CHEMIORECETTORI E GHIANDOLE ANTENNALI E LORO POSSIBILE SIGNIFICATO
NEL COMPORTAMENTO RIPRODUTTIVO DI *TRISSOLCUS BASALIS* (WOLL.) (HYMENOPTERA, SCELIONIDAE)

Il *Trissolcus basalis* è un parassitoide solitario delle uova di *Nezara viridula* L. Dalle ovature parassitizzate sfarfallano per primi i Trissolcus maschi, i quali, essendo capaci di individuare la presenza delle proprie femmine (per via di un feromone sessuale volatile) all'interno delle uova dell'ospite, si fermano singolarmente davanti all'uovo parassitizzato, in attesa che sfarfalli l'individuata compagna. Alla fuoriuscita di questa seguono speditamente un rapido corteggiamento da parte del maschio, il riconoscimento e la reciproca accettazione del partner e quindi la copula: il tutto in poche decine di secondi. La femmina fecondata va subito in cerca di un'ovatura idonea di Nezara per ovideporre lasciando infine un feromone di marcatura sulle singole uova da essa parassitizzate. Detto comportamento riproduttivo risulta chiaramente e necessariamente mediato dalle antenne di ambo i sessi nella prima parte, e della femmina, ovviamente, nella seconda parte. Attraverso uno studio in stretta collaborazione tra etologi (Bin, Colazza, Vinson) e morfologi (Isidoro, Solinas) vengono identificati sensilli chemiorecettori e ghiandole antennali implicati nei meccanismi comportamentali sopra menzionati. In particolare, sono stati individuati, descritti e più o meno ampiamente interpretati: a) un solo tipo di sensilli olfattivi («sickle-shaped sensilla»), presente in ambo i sessi, ma assai più rappresentato e potente nei maschi (recettori del feromone sessuale?) e più versatile nelle femmine (recettore di kairomone e sinomoni?); b) quattro tipi di sensilli gustativi, due dei quali sono presenti in ambo i sessi («sensilla chaetica», chiaramente implicati nel reciproco riconoscimento tra i sessi; e «grooved peg sensilla», di difficile interpretazione), mentre un terzo tipo, del tutto particolare, è presente solo nelle femmine, («papillary sensilla» chiaramente implicati nel riconoscimento- accettazione dell'ospite), ed un quarto, pure particolare, ma meno facilmente interpretabile, è presente solo nei maschi («sensilla conica»); c) tre tipi di ghiandole di cui uno è presente in ambo i sessi («dorsal glands», chiaramente implicato nel reciproco — ma soprattutto da parte del maschio — riconoscimento tra i sessi), mentre degli altri due tipi, uno è associato ai «papillary sensilla» della femmina e dunque strettamente legato al funzionamento dei medesimi e l'altro, tipico del maschio, era già noto e qui se ne conferma la funzione di ghiandola a feromone sessuale maschile.

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