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ANTENNAL SENSILLA AND SEXUAL DIMORPHISM OF THE ADULT LADYBIRD BEETLE *SEMIADALIA UNDECIMNOTATA* SCHN. (COLEOPTERA : COCCINELLIDAE)

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Abstract—The antennal receptors of the adult male and female ladybird beetle, *Semiadalia undecimnotata* (Coleoptera : Coccinellidae), were examined by scanning and transmission electron microscopy. Twelve types of receptors were characterized and grouped into 5 morphological classes: Böhm, trichoid, coeloconic, basiconic, and chetiform sensilla. Sensory function was determined on the basis of sensillar ultrastructure and electrophysiological response. Olfactory sensilla are confined in both sexes to the 2 terminal antennal segments. In contrast, gustatory and mechanosensitive organs are present along the entire length of the antennae. Sexual dimorphism of antennal receptors is limited to the latter 2 functional classes. The principal characteristics of this dimorphism are the following: a) males possess 540 sensilla (all types), while females possess only 500; b) males exhibit 2 types of taste receptors not present in females; c) females exhibit one type of mechanoreceptor absent in males; d) the 3 sex-specific types of sensilla, which occupy the same position in males and females, are confined to the inner side of the antennae. The possible role of male-specific sensilla in intersexual communication is discussed.

Index descriptors (in addition to those in title): Functional morphology, insect predators, SEM, TEM.

INTRODUCTION

The use of ladybird beetles for the biological control of insect pests such as: aphids (Ferran, 1983; Ferran and Larroque, 1984) and coccids (Fabres and Kiyindou, 1985; Kiyindou and Fabres, 1987; Kiyindou, 1993) has led to extensive research of their bio-ecology and predatory behaviour.

Various authors (Stubbs, 1980; Nakamuta, 1983, 1985; Le Strat, 1985; Obata, 1986, 1987, 1988) have suggested a possible role of sensory stimuli (olfactory, gustatory or mechanical) in prey, or mate detection. Nevertheless, with the exception of previous studies on the labial and maxillary palps of *Coccinella septempunctata* (Yan *et al.*, 1982, 1987) and the maxillary palps of *S. undecimnotata* (Barbier *et al.*, 1989), very little research has been carried out on the ultrastructure of coccinellid sensory receptors. Likewise, apparently no previous electrophysiological study of these receptors has been

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undertaken. In this study, we examined the antennal sensory apparatus of males and females of the aphidophagous coccinellid, *Semiadalia undecimnotata*, information critical for eventual further experimental studies on coccinellid sensory capabilities and pheromones. This study follows previous work on the integumentary exocrine glands of this species (Barbier *et al.*, 1992). This basic research into the functional morphology of the predacious coccinellid provides the groundwork for applied research on its efficient mass rearing and manipulation for biological control purposes.

MATERIALS AND METHODS

S. undecimnotata were reared under standardized conditions which do not induce a diapause of adults: 27°C and 60–70% R.H., with a photoperiod of 16 hr daylight. Larvae and adults were fed on populations of the aphid, *Acyrtosiphon pisum* (Harris), consisting mainly of apterous parthenogenetic females. These prey were reared on young (2–3 cm) shoots of the pea, *Pisum sativum*, in a temperature-controlled cage at 12°C with a photoperiod of 12 hr daylight. Under these conditions, the aphid population grew only by thelytogous parthenogenesis.

Scanning electron microscopy (SEM)
  Anatomical samples obtained from newly emerged adults were dehydrated with successive ethanol and acetone baths. They were either air-dried or critical-point dried, gold coated with a J.F.C. 1100 sputter coater and examined by scanning electron microscope (JEOL, J.S.M. 35).

Transmission electron microscopy (TEM)
  Antennal samples were fixed in 2.5% glutaraldehyde in 0.1 M sodium phosphate buffer (pH 7.4), then transferred to a 2% osmium tetroxide solution in the same buffer. The samples were dehydrated in acetone, embedded in epon-araldite resin, and prepared in 50–100-nm slices by microtome. These ultrathin sections were contrasted with uranyl acetate and lead citrate, and examined by transmission electron microscope (Phillips CM 12).

Electrophysiological sampling methods
  To record single units from sensilla, we employed the methods described in the sources listed below. In all cases, the recording electrode consisted of a chloride-treated silver wire within a glass micro-capillary tube with opening diameter <0.3 mm at its tip.

  "Tip recording method." The recording electrode "sleeve" is placed over the sensillum tip (Hodgson *et al.*, 1955). Recording microelectrode is inserted into the sensillum base (Boeckh, 1962). Recording microelectrode "sleeve" is slipped over the severed extremity of the sensillum (Kaissling and Thorson, 1980).

Data acquisition
  The responses were filtered and amplified as needed with a high gain amplifier (TM 503 Tecktronix), then sent in parallel to both a storage oscilloscope (502 A Tecktronik) and a microcomputer (9816 Hewlett Packard) via an A/D converter. The analogue signal was then digitized with a digitizer apparatus (DL 902 Datalab) for 20 sec and saved in a data file.

RESULTS

General sensory apparatus of antennae
  Male and female antennae are filiform, 1200 μm long and composed of 11 distinct segments: the scape, the pedicel and the 9 segments of the flagellum (Fig. 1A, B). The total sensory apparatus is comprised of about 540 receptors in the male and 500 in the female (Table 1), belonging to 5 principal categories: Böhm, trichoid, coeloconic, basiconic, and chetiform sensilla. Our typology of receptors includes 3 types of basiconic and 6 types of chetiform sensilla. To these 12 different types of sensillar receptors may be added the Johnston organ, which appears as 2 small depressions at the distal extremity of the pedicel.

Table 1. The mean number of the sensory receptors on each segment of the antenna.

| | Sensilla number ± SE | | Student's *t*-test | |
	Male	Female	(df = 3)	
Segment 1 (scape)	63 ± 1.71	63 ± 1.58	0.24	NS
Segment 2 (pedicel)	23 ± 1.08	16 ± 1.19	3.70	*
Segment 3	25 ± 1.55	12 ± 1.37	6.79	**
Segment 4	13 ± 0.25	13 ± 1.66	0.13	NS
Segment 5	13 ± 1.03	11 ± 1.31	1.19	NS
Segment 6	14 ± 0.29	9 ± 0.87	6.12	**
Segment 7	11 ± 0.85	8 ± 0.41	2.66	NS
Segment 8	11 ± 0.63	8 ± 0.87	2.18	NS
Segment 9	16 ± 0.71	13 ± 0.85	4.33	*
Segment 10	44 ± 1.25	42 ± 1.18	2.83	NS
Segment 11	306 ± 4.90	306 ± 1.87	0.07	NS
Total/antenna	539 ± 3.50	500 ± 7.65	4.07	*

Means were calculated from 4 male and 4 female antennae (the number of Böhm sensilla was not calculated)

NS = insignificant difference; SE = Standard error; * and ** indicate differences significant at 0.05 and 0.005, respectively.

The greatest receptor density is observed on the terminal 2 segments (306 receptors on segments 10 and 11) in both sexes. The central segments of the antennae have the fewest receptors, particularly in the female (Table 1).

In both sexes, there is a decrease in the number of receptors from the scape to the 8th segment, then an increase in receptor morphological diversity and number from segments 9 to 11. In addition, the 11th segment presents a distinct form: its ventral and dorsal surfaces widen toward the tip, conferring a triangular shape with an increased surface distally, and joining to form a chisel-like edge at the tip of the segment. The ventral surface, which has the larger surface area, also offers the greatest diversity of receptors. We first describe the receptors common to both sexes, then those related to sexual dimorphism.

Ultrastructure of antennal receptor types found in both sexes

Among the 12 types of receptors, 9 are common to both sexes (Figs. 1–3). They belong to the following 5 main classes.

Böhm sensilla (S.bo). About 40 of these classic mechanoreceptory organs are located on the scape and pedicel. On the scape, they are localized on the dorsal proximal side, part of which is articulated with the cephalic capsule. On the pedicel, these sensilla occupy the ventral and dorsal proximal sides, which are articulated with the scape (Fig. 2E). This placement suggests a role in proprioception of antennal position and movement.

Trichoid sensilla (t.s.). These sensilla are present only on the 2 terminal segments in equal numbers in both sexes (Table 2). This is the dominant type on the terminal (11th) segment (Fig. 1D). The t.s. are small both in length (10–12 μm) and diameter (2.5 μm at the base, tapering to 1 μm apically), and have no articulatory socket (Fig. 2A). Several features suggest a long-range chemoreceptive (olfactory) function: they are
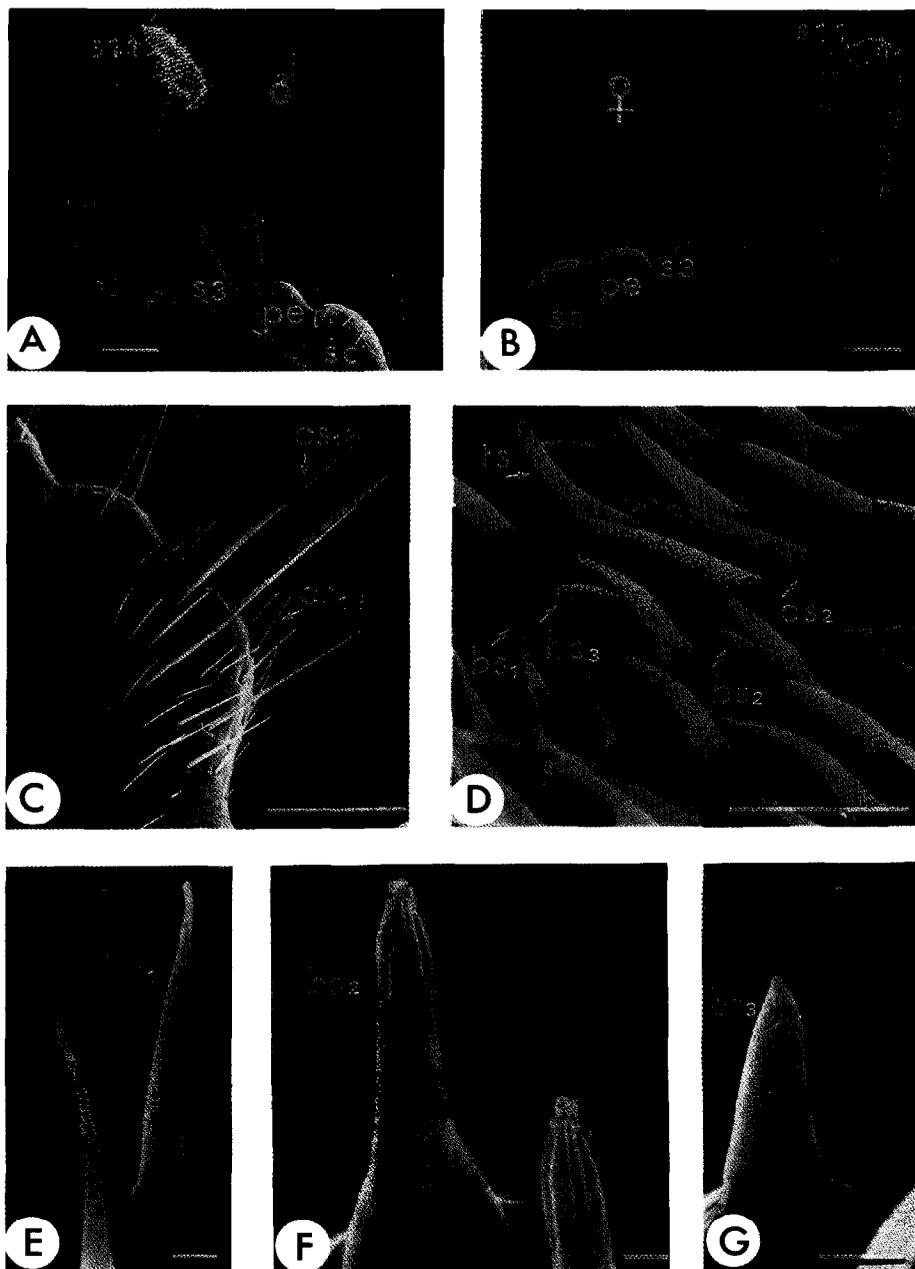
Fig. 1. (A) Male antenna (ventral face), (sc) scape, (pe) pedicel, (s3) 3rd segment, (s11) terminal segment (Scale bar = 100 μm). (B) Female antenna (ventral face) (Scale bar = 100 μm). (C) Dorsal face of scape: (cs1a) chetiform sensillum type 1a; (cs1b) chetiform sensillum type 1b (Scale bar = 10 μm). (D) Ventral face of the tip of the 11th segment: t.s., trichoid sensillum; cs2, chetiform sensillum type 2; bs1, bs2 and bs3, basiconic sensilla types 1, 2 and 3 (Scale bar = 10 μm). (E–G) High magnification of basiconic sensilla types 1, 2 and 3 (Scale bars = 1 μm).
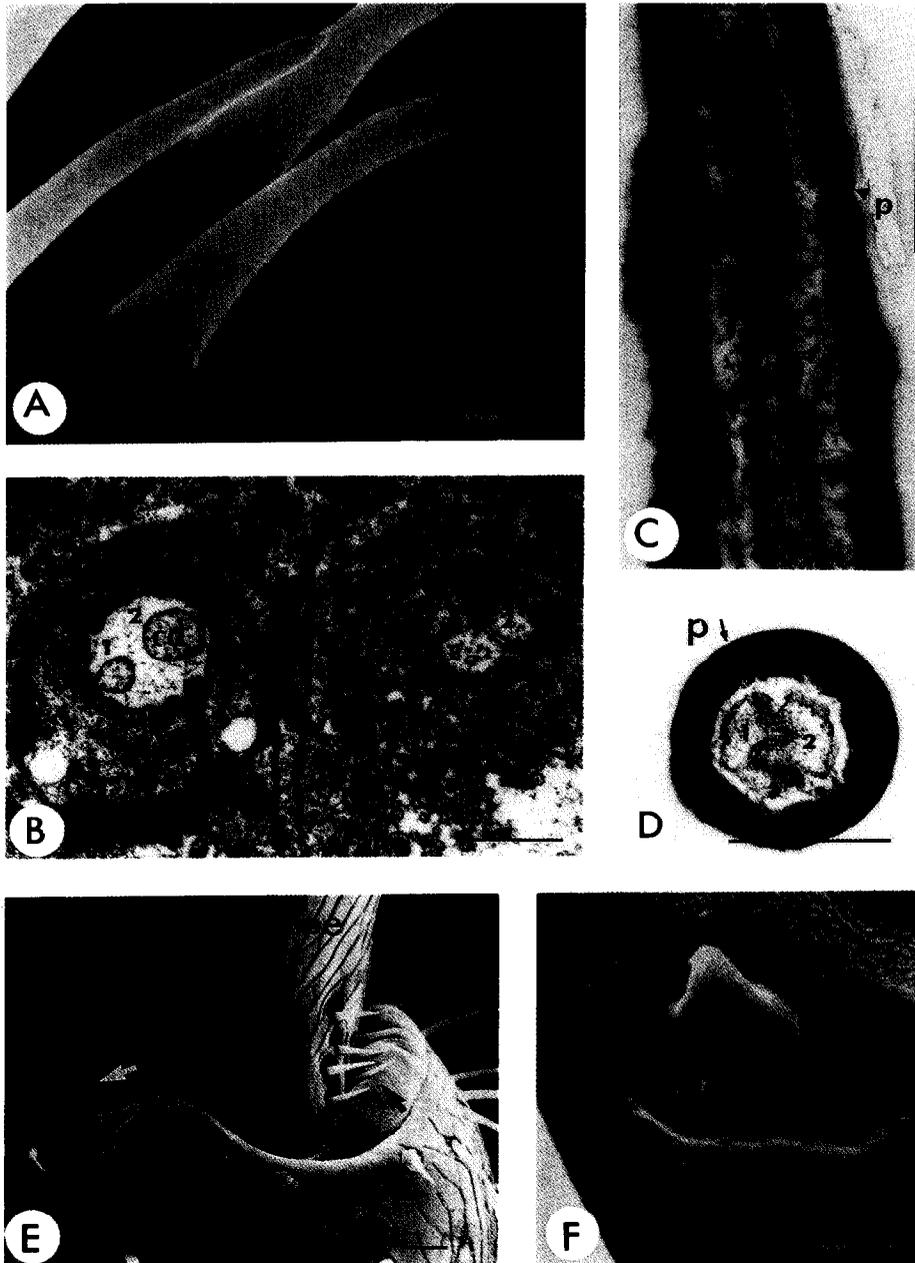
Fig. 2. (A) SEM of trichoid sensillum (ts) found in both sexes (Scale bar = 1 μm). (B–D) TEM of the same sensillum (Scale bars = 1 μm). (B) Cross-section through 2 chemoreceptive dendrites (cd) with their dendritic sheath (ds). (C, D) Longitudinal- and cross-sections through the 2 chemoreceptive dendrites (cd) without their dendritic sheath and extending toward the apex of the external process with pores (p) in its wall. (E) SEM, scape (sc) and pedicel (pe) with ventral (white arrow) and dorsal (black arrow) Böhm sensilla (Scale bar = 10 μm). (F) SEM, cœloconic sensillum (cœ.s.) (Scale bar = 1 μm).
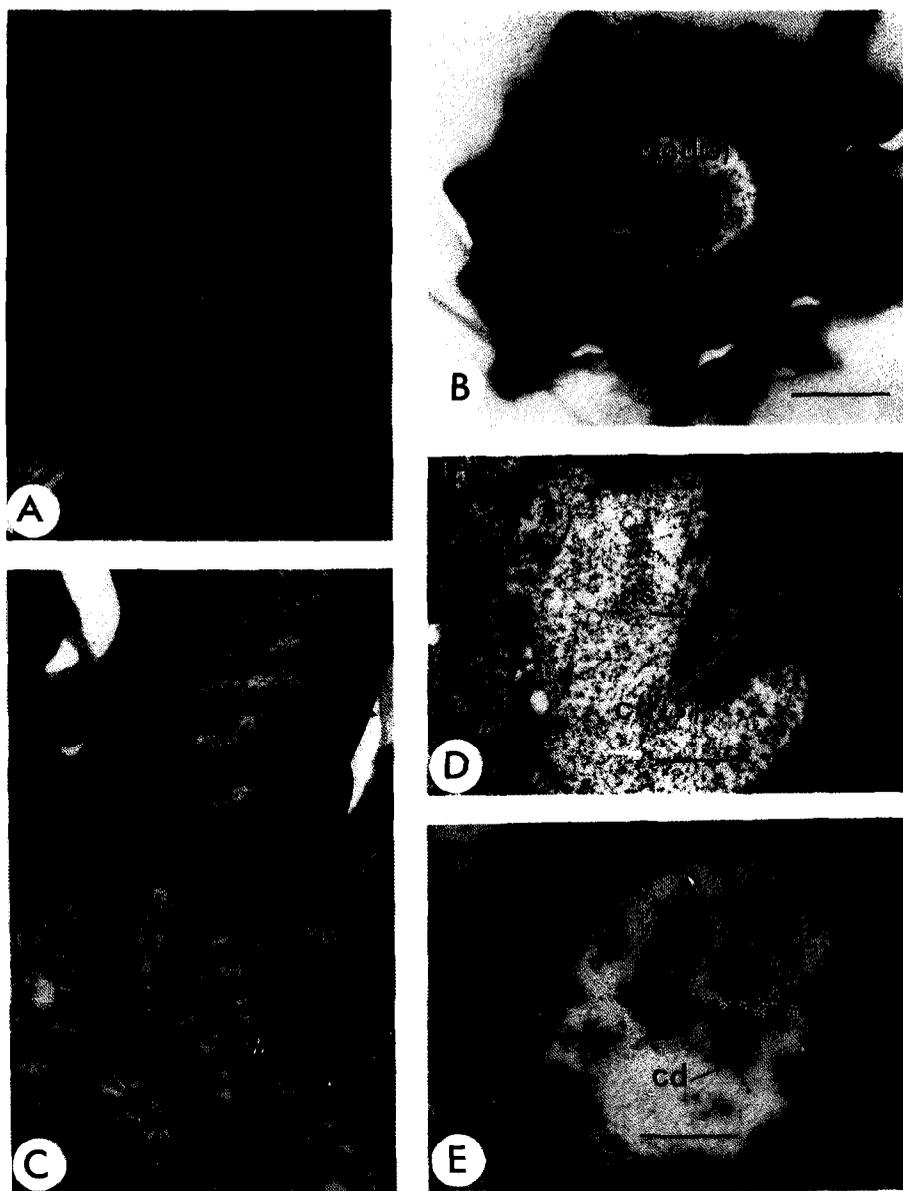
Fig. 3. Ultrastructure of chetiform sensillum type 3 (cs3) found in both sexes. (A), SEM of cs3 showing deep grooves (Scale bar = 10 μm). (B–E) TEM of the same sensillum (Scale bars = 1 μm). (B) Cross-section of the external process with deep grooves and 5 chemoreceptive dendrites (cd) in their common dendritic sheath (ds). (C) Longitudinal section showing the flexible cuticle (fc) at the base of the external process, one of its fine chemoreceptive dendrites (cd), the tubular body (tb) of the mechanoreceptive dendrite (md) and the dendritic sheath (ds). (D) Cross-section through the tubular body (tb) and the 5 chemoreceptive dendrites (cd) and their dendritic sheath (ds). (E) Cross-section through the five chemoreceptive (cd) and the one mechanoreceptive (md) dendrites.

Table 2. The mean number of each type of sensilla on the antenna *S. 11-notata*

Sensilla		Sensilla number ± SE		Student's *t*-test		
		Male	Female	df		
Trichoïd sensilla		§236 ± 2.49	§233 ± 1.43	3	0.99	NS
Cœloconic sensilla		†1 ± 0.25	†1 ± 0.21	9	0.36	NS
Basiconic sensilla	type 1	†9 ± 0.55	†10 ± 0.42	9	2.25	NS
	type 2	†14 ± 0.45	†15 ± 0.52	9	3.35	**
	type 3	†3 ± 0.13	†3 ± 0.13	9	0	NS
Chætiform sensilla	type 1	§210 ± 2.38	§185 ± 3.68	3	5.26	*
	type 2	§18 ± 0.48	§18 ± 0.41	3	0.29	NS
	type 3	†8 ± 0.31	†8 ± 0.20	9	0.80	NS
	type 4	‡12 ± 0.32	‡—	19	22.90	**
	type 5	‡28 ± 0.47	‡—	19	53.23	**
	type 6	†—	†28 ± 0.52	9	37.11	**
Total of sensilla		539 ± 3.50	500 ± 7.65	3	4.07	*

†: Means were calculated from 10 antennae; ‡: from 20 antennae; §: from 4 antennae. (The number of Böhm sensilla was not calculated.)
NS = insignificant difference; SE = Standard error; * and ** indicates differences significant at 0.05 and 0.005, respectively.

innervated by 2 dendrites, which divide as they extend toward the apex of the external process, and the wall is thick and multiporous (Fig. 2B–D).

Coeloconic sensilla (coe. s.). In both sexes, only one receptor is present per antenna (Table 2), located in the junction between the ventral and dorsal faces at the apex of the terminal antennal segment. The (coe. s.) are short (2.5 µm) and conical, tapering from 2 µm at the base to 0.5 µm at the tip. They are found within a depression on the cuticular surface (Fig. 2F).

Basiconic sensilla
Basiconic sensilla, type 1 (b.s.1). About 10 of these sensilla are spread over the 10th and 11th segments in both sexes. They are present on a small zone at the distal extremity of the 10th segment, just below its articulation with the terminal segment, and on very restricted areas on the ventral face of the 11th segment (Fig. 1D, E). The b.s.1 are short (9–10 µm). They taper from 2 µm diameter at the base to 0.25 µm at the tip, giving them a needle-like appearance. Their surface is smooth and poreless and tip of the hair does not show the presumed pore.

Basiconic sensilla type 2 (b.s.2). More numerous than b.s.1 (Table 2), the b.s.2 are also located on the last 2 segments. They are present in approximately equal numbers in males and females. They are typically inserted on a small dome without an articulatory socket, and oriented perpendicularly to the antennal surface. They are short (about 7–8 µm), with a conical base, their diameter decreasing progressively from 2 to 0.7 µm from the base to the apex. The external surface is smooth at the base, with grooves midway along the process which, toward the apical extremity, become digitations that seem to surround a terminal pore (Fig. 1D, F).

Basiconic sensilla, type 3 (b.s.3). A maximum of 3 b.s.3 receptors is present per antenna (Table 2). They occupy a small zone on the ventral face of the 11th segment. These elements are short (3–6 µm), conical and thick set, with a smooth external surface. Their diameter decreases from 2.7 to 0.3 µm from the base to the tip. They are rigid and stand perpendicular to the antennal surface (Fig. 1D, G).

Chetiform sensilla

Chetiform sensilla, type 1 (c.s.1). The c.s.1, present in large numbers, are slightly more common in the male than in the female (Table 2). They are distributed over the entire antenna, though generally preponderant on the external side. Two subtypes of c.s.1 were distinguishable on the basis of their difference in size on the scape, where they co-occur (Fig. 1C). The c.s.1.a, the shorter type, vary from 15 to 50 µm, and taper from 2.5 to 1 µm in diameter. The c.s.1.b are longer (120–170 µm) and of greater diameter (tapering from 5 to 3 µm). They are located only on the internal side of the scape. Subtype a is more common than b over the entire antenna. Both subtypes are characterized by a tapered form and simple extremities. Their surfaces are without pores, and their base appears to be articulated (Fig. 1C). Their morphology suggests a mechanosensitive function, but additional functions are possible.

Chetiform sensilla, type 2 (c.s.2). Less common than the c.s.1 (Table 2), the c.s.2 are limited to the tip of the 11th segment. They are similar in appearance to the c.s.1, but are shorter (10–25 µm long) and somewhat curved. They are tapered, with diameters diminishing from 2 to 0.4 µm from the base to the apex. Grooves are present, but less marked than in the c.s.1 (Fig. 1D).

Chetiform sensilla, type 3 (c.s.3). Less numerous than the c.s.1 or 2 (Table 2), these are found only on the periphery of the ventral and dorsal faces of the terminal portion of the 11th segment. They are clearly distinguishable by their orientation, practically perpendicular to the cuticular surface (Fig. 3A), and by their size. Being 80 µm long, they are longer than all other sensilla on this segment. They taper from 5 µm diameter at the base to 1 µm at the apex. Their cuticle, thick and poreless, is marked by deep longitudinal grooves. Innervation is provided by 6 dendrites. One terminates by a tubular body at the base of the external process, a morphology characteristic of mechanosensory neurons. The other 5 dendrites extend within the external process without dividing, and are enclosed in a common sheath (Fig. 3B–E). The bases of the sensilla seem to be articulated with the antennal surface. These ultrastructural details indicate dual mechanosensitive and contact chemosensitive (gustatory) functions.

Antennal sexual dimorphism

The last 3 types of chetiform sensilla, located on the inner side of the antennae, constitute the principal elements of antennal sexual dimorphism. Two types are present only in male antennae, while one is specific to female antennae.

Male-specific antennal receptors.

Chetiform sensilla, type 4 (c.s.4). The approximately 12 tightly clumped c.s.4 (Table 2) are found on the inner distal part of the 3rd segment. They form a clump of bristles

very characteristic of this sex. Because the external process of each receptor is quite long (105 μm), and the receptors are inserted on a protuberance on the distal part of the 3rd segment, the c.s.4 receptors stand out above surrounding antennal sensilla (Figs. 1A, 4A). The rather large diameter (7 μm at the base) gives them a stocky appearance. Cuticular grooves develop distally into digitations, which surround a terminal pore (Fig. 4B). Longitudinal cross-sections reveal a thick wall (Fig. 4C, D) and innervation by 3 dendrites. A large tubular body (about 200 microtubules) is present at the distal extremity of one of these dendrites, at the base of external process (Fig. 4C). These microtubules are attached to the dendritic sheath (Fig. 4E). At least 2 other dendrites seem to be present in the external process (Fig. 4D). These observations suggest that these sensilla have dual gustatory and mechanosensitive functions.

Chetiform sensilla, type 5 (c.s.5). These numerous sensilla (Table 2) are located on the distal part of the inner side of all segments from the pedicel to the 10th, except for the 3rd (Figs. 1A, 5A, B). In size (about 140 μm), they resemble the long chetiform sensilla type 1a. However, they are clearly differentiated by their circular cross-section, constant diameter (5 μm), regular curvature, deep grooves and a terminal pore surrounded by short distal digitations (Fig. 5C). The concavity of the inner side of the antenna brings the c.s.5 terminal pores into close proximity, despite their insertion on 8 different antennal segments. These ultrastructural details suggest dual chemosensory and mechanosensory functions.

Female-specific antennal receptors: chetiform sensilla, type 6 (c.s.6). The c.s.6, the only sensillar type specific to female antennae, number fewer than 30 (Table 2). Though the general appearance of these sensilla is quite similar to that of the c.s.1.b, they can be clearly distinguished by their placement, in precisely the same locations as the male-specific sensilla. They are observed on the internal distal faces of all segments from the 2nd (pedicel) to the 10th segment, including the 3rd. In the female, in contrast to the male, the 3rd segment is of the same width as the other antennal segments. The c.s.6 were also distinguishable from the c.s.1.b by their shorter process (80–100 μm), smaller diameter (from 5 μm at the base to 1.25 μm at the tip), and less pronounced grooving (Fig. 5D). The fact that the c.s.6 are inserted within an articulatory cavity, providing mobility, suggests that its functions include mechanoreception.

Electrophysiological readings

Because of technical difficulties in applying electrophysiological techniques to smaller and more sparsely distributed sensillar types, we tested only the c.s.4 and c.s.5 (specific to males) and the c.s.6 (specific to females). Particular attention was given to the c.s.4, whose position and dense clumping facilitated application of our sampling methods. The 3 techniques employed allowed us very easily to observe electrophysiological activity of a phasicotonic mechanosensory unit for each of the 3 receptor types tested (Fig. 6). In contrast, trials with test solutions (NaCl, saccharose, distilled water) or with extracts of entire beetles or organs (head, elytra) in water or lipid solvents such as hexane, have not allowed us to identify contact chemosensitive neural activity for any of the tested sensillar categories. Aphid extracts also produced inconclusive results.
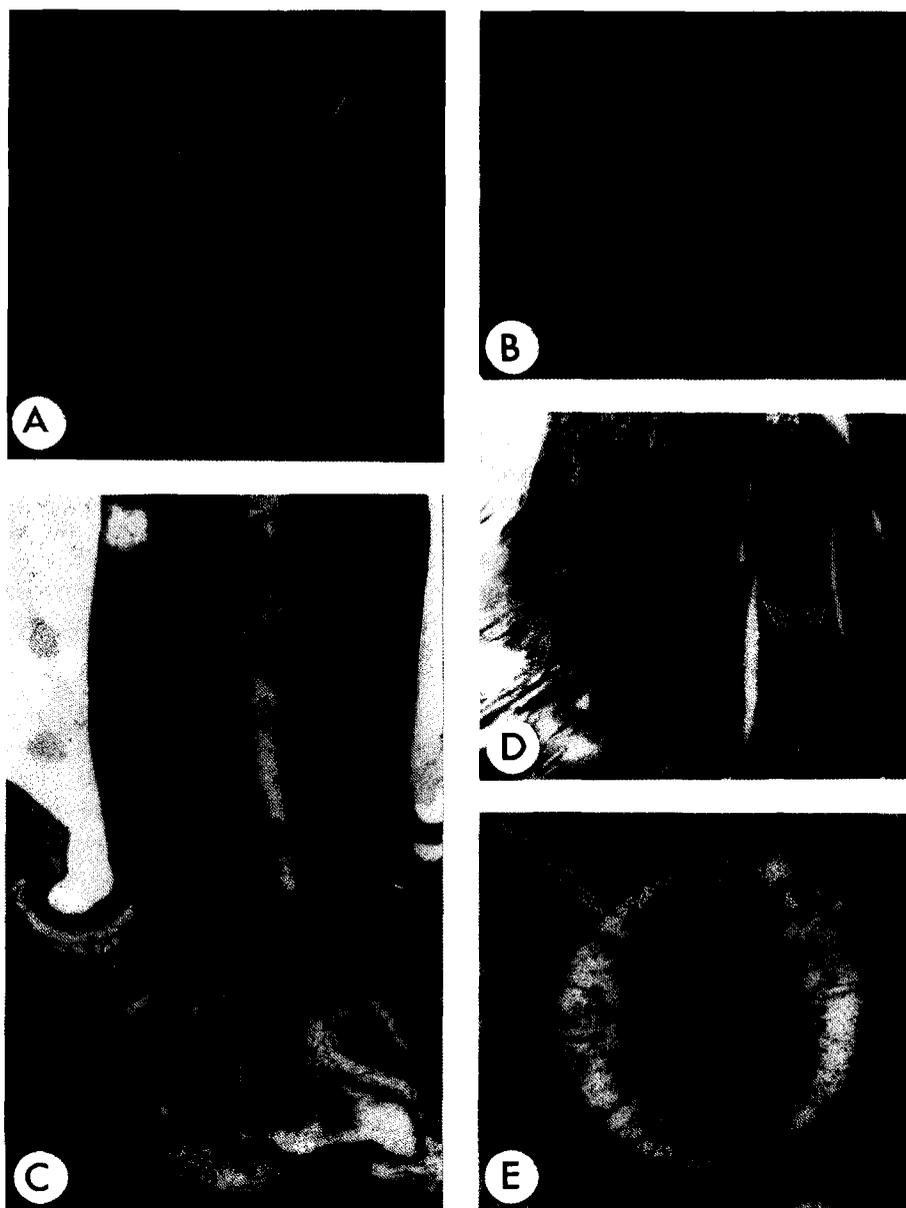
Fig. 4. Antennal sexual dimorphism. (A) and (B) SEM of the male chetiform sensillum type 4 (cs4). (A) Numerous c.s.4 clumped on the 3rd segment (s3) (Scale bar = 10 μm). (B) Apex of c.s.4 with its terminal pore (tp) (Scale bar = 1 μm). (C–E) TEM of the same sensillum. (C) Longitudinal section through the base of c.s.4 showing the flexible cuticle (fc), the dendritic sheath (ds) and the tubular body (tb) (Scale bar = 1 μm). (D) Axial section through 2 chemoreceptive dendrites, (cd) inside the external process (Scale bar = 1 μm). (E) High magnification showing the numerous microtubules (mt) connected to the dendritic sheath (ds) of the tubular body (Scale bar = 0.5 μm).
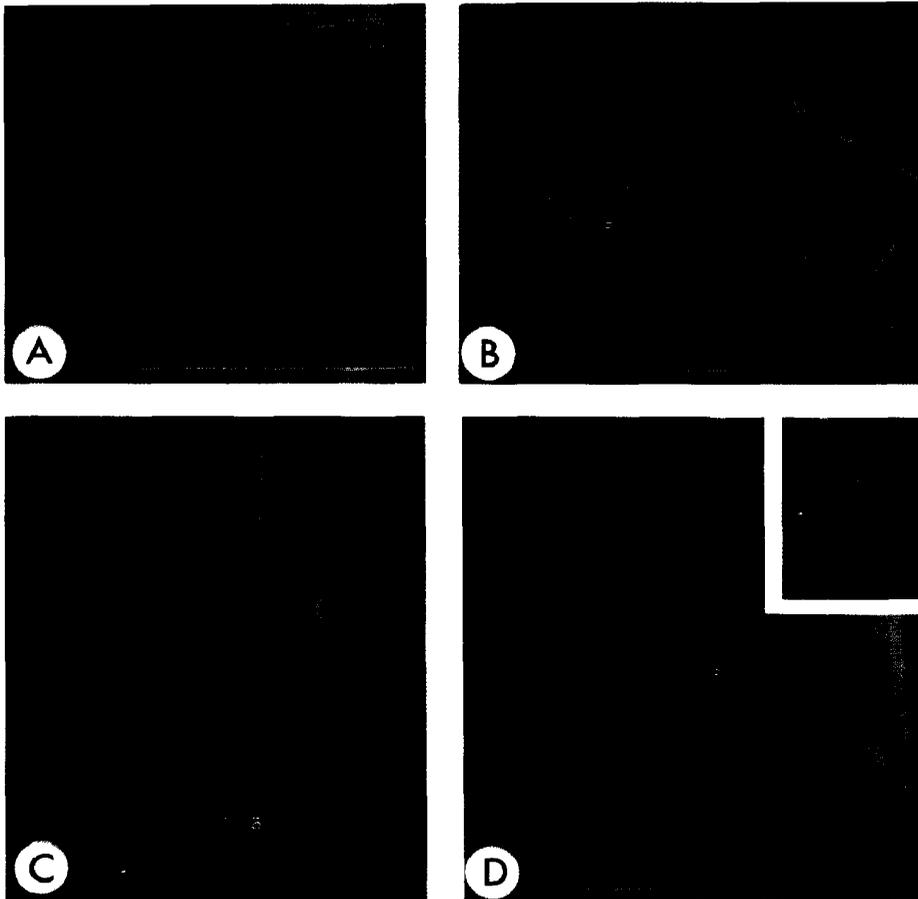
Fig. 5. Antennal sexual dimorphism (SEM). (A–C) Morphology of the male chetiform sensillum type 5 (cs5). (A) c.s.5 are located on the internal side of segments (Scale bar = 100 μm). (B) c.s.5 are convergent when segments are in concave position (Scale bar = 10 μm). (C) Distal digitations surrounding the terminal pore (tp) (Scale bar = 1 μm). (D) Morphology of the female chetiform sensillum type 6 (cs6) (Scale bar = 10 μm), and magnified (cs6) (Scale bar = 10 μm).

50 m sec

Fig. 6. Typical spike response recorded from a chetiform sensillum type 4 (cs4), on male antenna subject to a continuous mechanical stimulation.

DISCUSSION AND CONCLUSION

S. undecimnotata antennae have few sensory receptors (540 for the male, 500 for the female) in relation to other Coleoptera. Even the Alticinae, which, among coleopterans, are considered to have very few receptors (Ritcey and McIver, 1990), have over twice as many sensilla per antenna (about 1000). We discuss below the probable roles of olfactory-gustatory- and mechanoreceptors in *S. undecimnotata* behaviour and ecology.

Olfactory function Long-range chemosensory perception seems to be provided essentially by the trichoid sensilla which comprise nearly half of all antennal receptors. The ultrastructure of the trichoid sensilla is typical of olfactory receptors, described variously by Altner (1977) and Zacharuk (1980) as "wall-pore sensilla" or "multiporous chemosensilla". The coccinellid's olfactory organs are clustered on the 2 distal segments, and particularly on the terminal segment. Their number and location are the same in the 2 sexes, which suggests that they have little or no role in intersexual communications. Nevertheless, olfactory sensilla are unusually common in *S. undecimnotata* in relation to other receptor categories. Several roles for olfactory function may be hypothesized: habitat selection, oviposition site search, prey search, or intersexual communication. Olfactory sensilla with structure similar to that of the trichoid sensilla in *S. undecimnotata*, have been observed in the Scolytidae (Dickens and Payne, 1978; Hallberg, 1982), while olfactory organs with shape similar to that of the c.s.2 were described in the Curculionidae (Hatfield *et al.*, 1976; Smith *et al.*, 1976). In these analogous cases, olfactory sensilla are involved in the detection of the plant host, and perform this same function in *S. 11-notata*. In a study by Iperti (1965), *S. 11-notata* was restricted to vegetational formations below 50 cm and which included plants of particular families (Papillonaceae, Compositae, Euphorbiaceae). A plant detection role for olfactory sensilla is further suggested by the small absolute number of olfactory receptors in *S. 11-notata* (235), when compared with Lepidoptera. According to Chapman (1982), insect olfactory systems detecting abundant volatiles (e.g., from large plants), require fewer sensilla than those detecting rare volatiles (such as pheromones).

Trichoid-like sensilla are also observed in tineid moths, where they play a role in oviposition site search (Faucheux, 1987). Such a function seems unlikely in coccinellids, which oviposit on widely varying substrates. Details of coccinellid biology suggest other possible roles for olfactory function: it could allow coccinellids, newly emerged from diapause at the end of the spring, to locate aphid prey rapidly, using odour trails deposited by ants searching for aphid honeydew (Bhatkar, 1982). It may also allow them to recognize and avoid leaves, which they have already visited (Marks, 1977) or to detect their prey (Le Strat, 1985; Obata, 1986), as in predacious Cleridae [where similar olfactory sensilla have been characterized electrophysiologically (Hansen, 1983)]. These olfactory receptors may also detect chemical signals that mediate intraspecific interactions for aggregation and migration at the beginning of diapause (Iperti, 1986).

The 2 olfactory neurons of the trichoid sensilla do not seem to be accompanied by a 3rd hygroreceptive or thermoreceptive neuron, as is the case in some insects (Bernard, 1974; Altner and Prillinger, 1980). Micro-climatic conditions play a role in site-selection and release from diapause in *S. 11-notata*. The morphological characteristics of the basiconic sensilla 3 and the single coeloconic sensillum suggest that they function in hygroreception and thermoreception (Altner and Prillinger, 1980; Zacharuk, 1985).

For b.s.1 and 2, we have only external morphological observations and a terminal pore is not described. Organs in *Epilachna varivestris*, with an external morphology similar to that of b.s.1, were thought to have an olfactory function (Fisher and Kogan, 1986). Fluted sensilla similar to b.s.2, present in *Dendroctonus* (Dickens and Payne, 1978), are generally considered as olfactory chemosensilla. Sensilla b.s.2 also resemble sensilla of *Ips typographus* which possess a lamellate dendritic outer segment (Hallberg, 1982), which is similar to that of sensilla in which thermoreception has been demonstrated (Altner, 1977). Without additional ultrastructural data, their specific function in *S. undecimnotata* cannot be determined with certainty.

Gustatory function contact chemosensory perception, appears to be assured by c.s.3, c.s.4 and perhaps c.s.5. These receptors are spread over the entire antenna, in marked distinction to olfactory receptors, present only on the 2 apical segments.

The c.s.3 and c.s.4 have ultrastructure similar to that of the gustatory receptors labelled "terminal pore sensilla" and "uniporous chemosensilla" by Altner (1977) and Zacharuk (1980). They have a single pore through which chemical communication may occur between the dendrites and the external environment. The tubular body observed at the base of their external process, indicates a supplementary mechanosensitive neuron. The mechanosensitive function suggested by these morphological characteristics was confirmed by electrophysiological records. The c.s.3 are present in both sexes and appear to be the first to come in contact with stimuli, given their location on the last segment, their large size, and their perpendicular insertion in the cuticle. These characteristics are similar to those of the mixed receptors, which are the first to contact stimuli in the curculionid beetles *Hypera meles* (Smith et al., 1976) and *Conotrachelus nenuphar* (Alm and Hall, 1986).

We note that the distinction made between the gustatory and olfactory receptors is not absolute; certain gustatory receptors, or clumps of receptors, may detect olfactory stimuli over short distances (Städler and Hanson, 1975). The apparently weak olfactory capabilities of *S. undecimnotata* may be reinforced in this way.

Mechanoreceptive function is also well represented on *S. undecimnotata* antennae. In both sexes, mechanoreception is ensured both by classical mechanoreceptors on the scape and pedicel (Böhm sensilla), and by c.s.1 over the entire antennae (demonstrated electrophysiologically). Moreover, analysis of ultrastructure showed mixed functions for several classes of sensilla: in c.s.3 one mechanoreceptive neuron is associated with 5 gustatory neurons; in males, c.s.4 and c.s.5 were shown to have one mechanoreceptive neuron. Likewise, neurons of the female-specific sensilla, c.s.6, were shown to have mechanoreceptive electrophysiological activity.

The importance of antennal mechanoreception has been highlighted for other predacious insects, such as the Carabidae *Nebria brevicollis* (Daly and Ryan, 1979). Similarly, tarsal mechanoreceptors play an important role in prey detection by larvae of *Coccinella transverguttata* (Storch, 1976). These examples allow us to hypothesize a link between antennal mechanoreception and predatory behaviour in *S. 11-notata*. Antennal mechanoreceptors may enable *S. undecimnotata* to detect the weak vibrations produced by aphid movement on nearby vegetation. They may also allow these coccinellids to detect the morphological differences between the virginiparous and gynoparous aphids on which they feed: the presence of apterous aphids is associated with high ovogenesis, while that of alate aphids tends to trigger diapause (Wipperfurth et al., 1987).

Sex pheromone detection is generally attributed to sensillar classes disproportionately present in males, for example, the olfactory basiconic sensilla of the beetle, *Lasioderma serricorne* (Okada *et al.*, 1992). Sexual dimorphism in *S. undecimnotata* is characterized by additional gustatory receptors in males (c.s.4 and c.s.5). This trait suggests a possible role of antennal gustatory reception in male sexual behaviour. Both the c.s.4 and the c.s.5 are located on the inner face of the antennae, and the curvature of the antennae focuses the terminal pores of these sensilla into a relatively small spatial region, facilitating spatial summations and simultaneous perception of multiple stimuli. During mating, males are observed to sweep their antennae rhythmically directly above female elytra. Ultrastructure of the integumentary glands located on the elytra suggest that they may produce pheromones (Barbier *et al.*, 1992). Moreover, Obata (1987) has inferred that mating behaviour in coccinellids is induced by chemical signals.

Electrophysiological examination of male gustatory receptors was thus undertaken in order to elucidate their possible role in mating behaviour. Though our initial results confirmed a mechanosensory function for c.s.4 and c.s.5, our methods could not confirm the contact chemosensory function indicated by our observations of ultrastructure. Several possible factors may account for the absence of reproducible results from experiments on the male-specific receptors: the signal from chemoreceptors may be insufficient to distinguish it from background noise (problems of signal amplification), or chemoreceptory function may be limited to certain short periods of the insect's sexual cycle. In the latter case, a maturation period might be necessary to observe a maximal reaction (diapause is suppressed in *S. 11-notata* populations mass reared under laboratory conditions). In order to deal with these factors, we will re-examine the effects of the female elytral glandular secretions on male chemosensitive organs, employing insects from natural populations sampled from various periods of their sexual cycle.

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