



ELSEVIER

Available online at [www.sciencedirect.com](http://www.sciencedirect.com)

Micron 39 (2008) 526–535

[www.elsevier.com/locate/micron](http://www.elsevier.com/locate/micron)

## Scanning electron microscopy studies of antennal sensilla of *Pteromalus cerealellae* (Hymenoptera: Pteromalidae)

Ebenezer O. Onagbola, Henry Y. Fadamiro \*

Department of Entomology and Plant Pathology, Auburn University, Auburn, AL 36849, USA

Received 23 May 2007; received in revised form 31 July 2007; accepted 1 August 2007

### Abstract

*Pteromalus cerealellae* (Ashmead) (Hymenoptera: Pteromalidae) is an ectoparasitoid of several insect pests of stored products. In order to provide requisite background information to support our ongoing research on its host location mechanisms, we examined the external morphology of the antennal sensilla of this parasitoid using scanning electron microscopy. Antennae of male and female *P. cerealellae* are geniculate in shape, ~1300 µm in length, and consist of 15 antennomeres. Eight morphological sensilla types were recorded in both sexes, including four types of the highly abundant and widely distributed sensilla trichodea (types I, II and IV are aporous while type III is multiporous), basiconic capitate peg sensilla, coeloconic sensilla, chaetica sensilla, and the most conspicuous plate-like placoid sensilla. Detailed examination of sensilla morphological features including pore presence and numbers suggest that the multiporous type III sensilla trichodea and the multiporous placoid sensilla may play a role in olfaction, whereas the uniporous chaetica sensilla may function as contact chemoreceptors. The types I and II sensilla trichodea are presumably mechanosensory, while the type IV sensilla trichodea may function as proprioceptors. The basiconic capitate peg sensilla and coeloconic sensilla probably function in thermo-hygro reception. Although the shape, structure, and size of antennae of males and female were basically similar, major differences were recorded between the sexes in the distribution of some sensilla types. The type II sensilla trichodea and the multiporous placoid sensilla are relatively more abundant in females, whereas males have greater number of the multiporous type III sensilla trichodea than females. These results are discussed in relation to the possible roles of the sensilla types in the host location behavior of *P. cerealellae*.

© 2007 Elsevier Ltd. All rights reserved.

**Keywords:** *Pteromalus cerealellae*; Parasitoids; Antennae; Sensilla; Scanning electron microscopy

### 1. Introduction

Antennae of insects, in particular parasitic Hymenoptera, are important sensory structures involved in various behaviors including habitat searching, host location, host examination, host recognition, host acceptance, oviposition, host discrimination and courtship and mating behavior (Weseloh, 1972; Vinson et al., 1986; Bin et al., 1989; Isidoro et al., 1996). Several studies have characterized the antennal sensilla of various species of parasitic wasps using electron microscopic techniques (Norton and Vinson, 1974; Barlin and Vinson, 1981; Barlin et al., 1981; Wibel et al., 1984; Navasaro and Elzen, 1991; Olson and Andow, 1993; van Baaren et al., 1996; Isidoro et al., 1996; Amornsak et al., 1998; Ochieng et al., 2000; Pettersson et al., 2001; Bleeker et al.,

2004). Many of these studies reported strong sexual dimorphism in structure and types of antennal sensilla (Wibel et al., 1984; Navasaro and Elzen, 1991; Amornsak et al., 1998; Bleeker et al., 2004), whereas other authors reported little or no distinct sexual differences in the antennal sensory system (Ochieng et al., 2000; Pettersson et al., 2001).

*Pteromalus cerealellae* (Ashmead) (Hymenoptera: Pteromalidae) is an ectoparasitoid of several insect pests of stored products including *Sitotroga cerealella* Olivier, *Callosobruchus maculatus* (Fab.), *Lasioderma serricornis* (Fab.), *Prostephanus truncatus* (Horn), and *Sitophilus* spp. (Ashmead, 1902; Brower, 1991). Females lay eggs in host larvae, which typically are concealed within seeds. Little is known about host location mechanisms in *P. cerealellae* or related wasps. To detect their concealed hosts, female *P. cerealellae* presumably use certain host location cues such as physical/mechanical cues (e.g., host vibration) and chemical cues, which could originate from the host insect or host environment (i.e. host-seed).

\* Corresponding author. Tel.: +1 334 844 5098; fax: +1 334 844 5005.  
E-mail address: [fadamhy@auburn.edu](mailto:fadamhy@auburn.edu) (H.Y. Fadamiro).

In an ongoing research on the host location mechanisms of *P. cerealellae*, we demonstrated antennal response of both sexes to host-related odor (unpublished results). To provide requisite background information to further this research, we investigated the external morphology of the antennal sensilla of the parasitoid using scanning electron microscopy (SEM). In this paper, we describe the morphology, location, abundance, and distribution of the different sensilla present on the antennae of male and female *P. cerealellae*. The possible roles of the sensilla types in the behavioral ecology of the parasitoid are also discussed.

## 2. Materials and methods

### 2.1. Insects

*Pteromalus cerealellae* was reared in our laboratory on the larvae of the cowpea bruchid, *C. maculatus*. The host insect was reared on cowpea seeds, *Vigna unguiculata* Walp (California Black Eyed variety) in 1 L wide-mouthed Mason glass jars. A fresh culture was started every 5 days by placing ~25 pairs of 3-day-old mated *C. maculatus* in a glass jar containing ~100 g of cowpea seeds held at  $30 \pm 1$  °C,  $70 \pm 5\%$  RH, and L12 h:D12 h (Mbata et al., 2005; Onagbola et al., 2007). The beetles were allowed to lay eggs on the seeds for 24 h after which they were removed with an aspirator. The infested seeds were incubated at the conditions specified above until the larvae had reached the fourth instar stage, which were then provided to *P. cerealellae* for parasitization. The parasitoid was maintained by transferring about 30 adult pairs onto a glass jar containing *C. maculatus*-infested cowpea seeds at a stage when most of the bruchid larvae were at the fourth larval instar (this occurred at ~15 days after infestation of cowpea seeds under our rearing conditions). The jars were held at the environmental conditions stated above for *C. maculatus*. Adult *P. cerealellae* were removed from the jars after 5 days of oviposition. Parasitized host larvae were incubated in a growth chamber at the above environmental conditions until the emergence of adult parasitoids.

### 2.2. Scanning electron microscopy (SEM)

Freshly emerged adult parasitoids were first anaesthetized in a freezer ( $-20$  °C) for 5 min after which the heads were removed. Antennae of *P. cerealellae* were carefully excised from the antennal sockets with fine forceps (Fisher Scientific) at  $20\times$  under a stereomicroscope (National Microscope, Model DC 3-420, Meiji, Japan). The antennae were first kept in 70% ethanol for 24 h and then dehydrated in a graded alcohol series of 75, 80, 85, 90 and 99.9% (van Baaren et al., 1996) in each case for 1 h. Antennae were individually mounted on aluminum stubs with double-sided sticky tapes. The antennae were mounted with ventral or dorsal sides on the sticky tape. The dehydration processes was followed by air drying in a drying cabinet conditioned to  $25 \pm 1$  °C and  $10 \pm 1\%$  RH for 5 days. The antennae were then sputter coated with gold/palladium (40:60) in a Polaron E 5400 high resolution sputter coater. The specimens were examined in a DSM 940 SEM (Zeiss, W. Germany) set at 10 kV and 15 mm working distance. Micrographs were taken of

the antennae, antennomeres, and sensilla. Abundance and the distribution of the sensilla on the antennae were compared between males and females. The length, width and the diameter of the pits in which sensilla are recessed (where applicable) were measured. A total of 12 antennae per sex were viewed under SEM.

### 2.3. Statistical analysis

Sensilla on the dorsal and ventral surfaces of the antennae of *P. cerealellae* were identified, counted and measured. Measurements ( $\mu\text{m}$ ) obtained from photomicrographs of at least 15 individual sensilla of the same type were used to calculate the means. Data obtained on the distribution and abundance of different types of sensilla on male and female antennae were analyzed using Student's *t*-test to determine any significant sexual differences ( $P < 0.05$ ).

## 3. Results

### 3.1. Terminology

The literature on morphology of insect antennae is somewhat inconsistent and confusing with different names and terminologies assigned to sensilla types despite similarity in form and distribution. To overcome this inconsistency in terminology, we define and classify antennal sensilla in this study on the basis of their external appearance when viewed under a scanning electron microscope (SEM) and followed the nomenclature of Chapman (1982, 1998), Wibel et al. (1984), Isidoro et al. (1996); Amornsak et al. (1998), Pettersson et al. (2001), Ryan (2002), and Bleeker et al. (2004). The description of sensilla types is based largely on our inference from the published photomicrographs, using morphological characters such as presence and positions of pores as bases for identification.

### 3.2. General description of antennae of *P. cerealellae*

The antennae of *P. cerealellae* are geniculate in shape and consist of the basic segments: scape with radicula, pedicel, and flagellum. The radicula (Rd) is completely separated from the scape, has a different type of sensilla, and thus may be considered as a separate segment. The radicula fits into the antennal socket where it functions as the fulcrum to the antenna. It constitutes ~4% of the total antennal length and is  $50 \pm 0.8$   $\mu\text{m}$  (mean  $\pm$  S.E.) and  $55 \pm 0.6$   $\mu\text{m}$  long in males and females, respectively (Table 1). The cylindrical scape (Sc) is about 5 times as long as

Table 1  
Mean length of antennal segments in male and female *P. cerealellae* ( $n = 12$ )

Antennal segments	Male	Female
Radicula <sup>a</sup>	$50 \pm 0.8$	$55 \pm 0.6$
Scape	$355 \pm 6.0$	$386 \pm 4.4$
Pedicel	$104 \pm 1.8$	$106 \pm 1.2$
Flagellum	$798 \pm 13.4$	$780 \pm 9.0$
Total	$1308 \pm 21.9$	$1328 \pm 15.2$

<sup>a</sup> Further studies are necessary to confirm the radicula as a separate segment. Values show mean length ( $\mu\text{m} \pm$  S.E.).

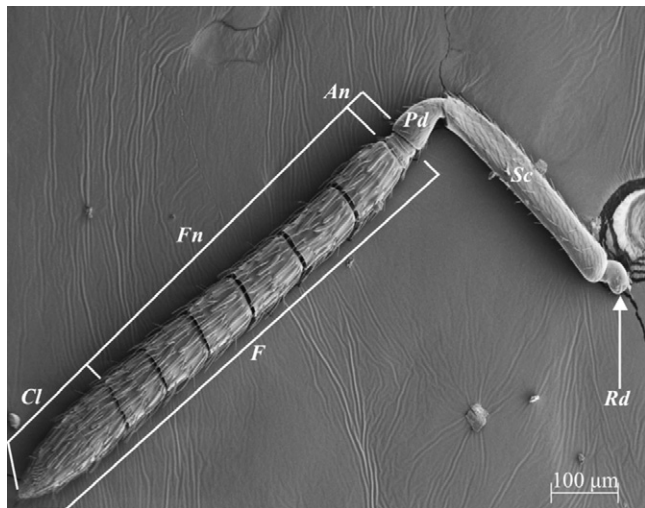


Fig. 1. Antenna of *P. cerealellae*. Figure shows the scanning electron micrograph of an excised geniculate antenna of *P. cerealellae* male showing the radicle (Rd), scape (Sc), pedicel (Pd), anelli (An), funicle (F) and the clava (Cl). The female antenna is similar in shape and morphology.

wide (length:  $355 \pm 6.0 \mu\text{m}$  in males and  $355 \pm 6.0 \mu\text{m}$  in females) constituting  $\sim 30\%$  of the total antennal length. The pedicel (Pd) is a short, barrel-shaped segment measuring  $14 \pm 1.8 \mu\text{m}$  long in males and  $106 \pm 1.2 \mu\text{m}$  long in females and constitutes  $\sim 8\%$  of the total antennal length. The radicle, scape and pedicel is each composed of one antennomere. In this

study, we define antennomeres as individual separate segments or sub-segments and number them consecutively from the radicle (1st antennomere = A1) to the last claval antennomere (15th antennomere = A15). The elongate flagellum (F) constitutes  $\sim 60\%$  of the total antennal length and measures  $798 \pm 13.4 \mu\text{m}$  and  $780 \pm 9 \mu\text{m}$  long in males and females, respectively (Table 1). The flagellum is differentiated into the basal ring-like sub-segments, anelli (An), mesal funicle (Fn) and distal club-shaped clava (Cl) (Fig. 1). The anelli, funicle, and clava consist of two, six, and four antennomeres, respectively, making the whole antenna of *P. cerealellae* to be composed of 15 antennomeres. The anelli antennomeres are small and ring-like while the funicular antennomeres are cylindrical. The first three claval antennomeres are barrel-shaped, whereas the last forms a flattened plate that covered the preceding barrel-shaped antennomere (Fig. 2; Cl). Each of the anelli antennomere is about twice as wide as long (Fig. 2; An), whereas each funicular antennomere (e.g., Fn<sub>6</sub>, Fig. 2) is nearly twice as long as wide. The enlarged antennal clava tapers to a circular, flattened point (the last antennomere) which faces ventrally down on the antennal tip. The surfaces of the antennae of both sexes appear similar, but the abundance and distribution of the different sensilla differ.

### 3.3. Sensilla types

Eight morphologically different types of sensilla were recorded on the antennae of male and female *P. cerealellae*.

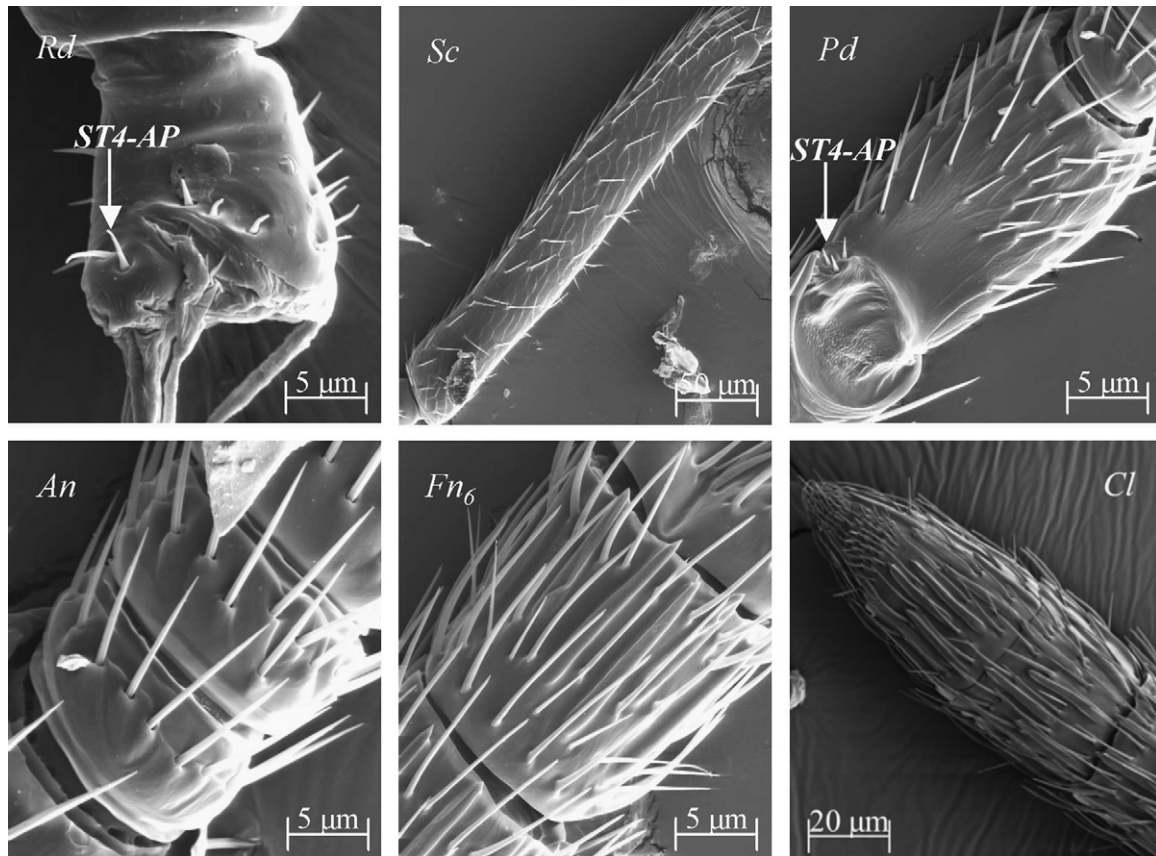


Fig. 2. Scanning electron micrographs of the antennal segments and antennomeres of *P. cerealellae*. Figure shows the basal radicle (Rd), elongate scape (Sc), barrel-shaped pedicel (Pd), the ring-like anelli (An), the 6th antennomere of the antennal funicle (Fn<sub>6</sub>) and the club-shaped clava (Cl).

Table 2  
Abundance and distribution of different sensilla on the antennae of male and female *P. cerealellae*

Sensilla	Sex	Antennal segment				Total
		Radicula	Scape	Pedicel	Flagellum	
ST1-AP	Male	–	–	–	56 ± 1.4	56b
	Female	–	–	–	69 ± 0.5	69a
ST2-AP	Male	–	159 ± 1.2	51 ± 0.8	47 ± 1.6	257b
	Female	–	228 ± 1.5	68 ± 1.6	193 ± 1.2	489a
ST3-MP	Male	–	–	–	709 ± 1.4	709a
	Female	–	–	–	373 ± 1.5	373b
ST4-AP	Male	20 ± 0.0	–	3 ± 0.0	0 ± 0.0	23
	Female	20 ± 0.0	–	3 ± 0.0	0 ± 0.0	23
MPS	Male	–	–	–	44 ± 0.3	44b
	Female	–	–	–	96 ± 0.4	96a
ChS-UP	Male	–	–	–	18 ± 0.3	18
	Female	–	–	–	15 ± 0.3	16
BCPS	Male	–	–	–	6 ± 0.0	6
	Female	–	–	–	9 ± 0.0	9
CS	Male	–	–	–	2 ± 0.0	2
	Female	–	–	–	1 ± 0.0	1

Values are mean (±S.E.) number of different types of sensilla on each antennal segment ( $n = 12$  antennae per sex). ST1-AP: aporous type I sensilla trichodea; ST2-AP: aporous type II sensilla trichodea; ST3-MP: multiporous type III sensilla trichodea; ST4-AP: aporous type IV sensilla trichodea; MPS: multiporous placoid sensilla; ChS-UP: uniporous chaetica sensilla; BCPS: basiconic capitate peg sensilla and CS: coeloconic sensilla. Total numbers for each sensilla type having different letters are significantly different between male and female ( $t$  test,  $P < 0.05$ ).

These include four types of sensilla trichodea (types I, II and IV are aporous while type III is multiporous), uniporous chaetica sensilla, multiporous placoid sensilla, basiconic capitate peg sensilla, and coeloconic sensilla. Sensilla trichodea are long, slender and hair-like with or without pores on the shaft, and have been categorized on the basis of external structure and size. They are distinguished from chaetica sensilla on the basis of presence of grooves on the surface of the thick-walled shaft which tapers to a blunt tip (Ryan, 2002). Basiconic capitate peg sensilla have longitudinal ridges and are recessed in shallow pits differentiating them from coeloconic sensilla, which are recessed in deep cuticular pits (Ryan, 2002). The multiporous placoid sensilla are the largest and most distinct sensilla type on the antennae of parasitic wasps (e.g., Isidoro et al., 1996; Pettersson et al., 2001). The distribution of the different sensilla types on each antennal segment is shown in Table 2.

### 3.3.1. Aporous type 1 sensilla trichodea (ST1-AP)

Sensilla trichodea type I occur on the distal ends (on the last antennomere in males and on the last two antennomeres in females) of the antennal flagellum. They have small conical basal sockets with slender and strongly bent shafts (Fig. 3A; ST1-AP). The number and distribution of the ST1-AP is shown in Table 2 (whole antennae) and Table 3 (focus on the flagellum). The ST1-AP range from  $29.5 \pm 0.2 \mu\text{m}$  to  $48.0 \pm 0.4 \mu\text{m}$  in length and  $3.0 \pm 0.1 \mu\text{m}$  and  $3.5 \pm 0.1 \mu\text{m}$  in basal width, depending upon their location on the antennae (Table 4). Female *P. cerealellae* have greater number of ST1-AP than males (Table 2).

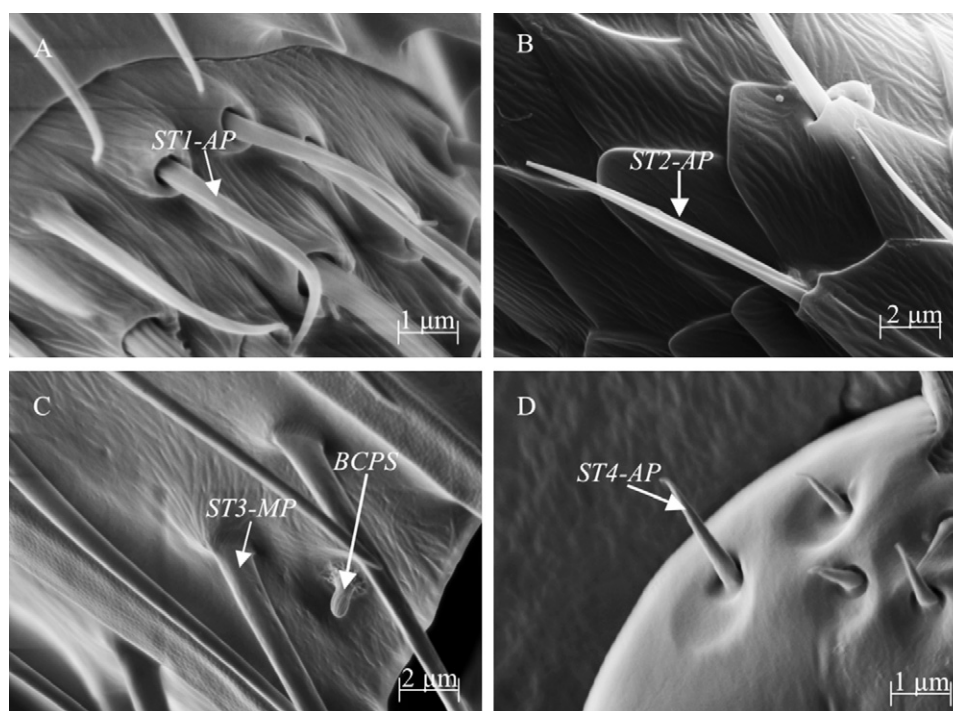


Fig. 3. Sensilla trichodea types recorded on the antennae of *P. cerealellae*. Figure shows scanning electron micrograph of type I (ST1-AP) on the last claval antennomere (A); type II (ST2-AP) on pedicel (B); type III (ST3-WP) on funicle antennomere (C), and type IV (ST4-AP) on radicula (D).

Table 3  
Approximate number and distribution of sensilla on flagella of antennae of male and female *P. cerealellae*

Sensilla	Sex	Antennomeres (A)												Total	
		4	5	6	7	8	9	10	11	12	13	14	15		
ST1-AP	Male	–	–	–	–	–	–	–	–	–	–	–	–	56	56
	Female	–	–	–	–	–	–	–	–	–	–	–	22	47	69
ST2-AP	Male	9	17	18	–	1	–	1	–	1	–	–	–	–	47
	Female	15	18	39	21	14	21	19	17	15	14	–	–	–	193
ST3-MP	Male	–	–	85	88	87	90	83	88	88	65	35	–	–	709
	Female	–	–	29	59	59	70	63	58	22	13	–	–	–	373
ST4-AP	Male	–	–	–	–	–	–	–	–	–	–	–	–	–	0
	Female	–	–	–	–	–	–	–	–	–	–	–	–	–	0
MPS	Male	–	–	2	5	4	6	4	4	6	8	5	–	–	44
	Female	–	–	8	1-	1-	14	11	13	13	13	4	–	–	96
ChS-UP	Male	–	–	–	–	–	–	–	–	–	–	–	18	18	
	Female	–	–	–	–	–	–	–	–	–	–	7	9	16	
BCPS	Male	–	–	–	–	1	–	1	1	1	1	1	–	–	6
	Female	–	–	2	3	2	2	–	–	–	–	–	–	–	9
CS	Male	–	–	–	–	1	–	–	–	–	–	–	–	–	1
	Female	–	–	–	–	1	–	1	–	–	–	–	–	–	2

Values are approximate number of different types of sensilla on each flagellar antennomere. ST1-AP: aporous type I sensilla trichodea; ST2-AP: aporous type II sensilla trichodea; ST3-MP: multiporous type III sensilla trichodea; ST4-AP: aporous type IV sensilla trichodea; MPS: multiporous placoid sensilla; ChS-UP: uniporous chaetica sensilla; BCPS: basiconic capitate peg sensilla and CS: coeloconic sensilla.

### 3.3.2. Aporous type 2 sensilla trichodea (ST2-AP)

The ST2-AP are elongated and widely distributed on the scape, pedicel, anelli, funicle (F1–F5) and the first two claval (C11–C12) antennomeres of male and female antennae. They are tapered and show deep basal insertion into sockets terminating in pointed apices (Fig. 3B; ST2-AP). The length and basal socket characteristics of ST2-AP vary according to location, but the morphology of the shafts does not vary; the shafts have fluted surfaces (Fig. 3B). The ST2-AP is the most abundant sensilla type on the female antennae numbering about 489 on each antenna, with relatively fewer numbers on the male antennae (Table 2). The ST2-AP is morphologically similar to

the ST1-AP in external appearance and cuticular insertion into sockets but differs in the shape of the shafts. ST1-AP tapers to a fine tip on a bent shaft (Fig. 3A), whereas the shaft of ST2-AP is straight (Fig. 3A and B).

### 3.3.3. Multiporous type 3 sensilla trichodea (ST3-MP)

The ST3-MP are long and tapering and distributed on all the funicular antennomeres and on the first three claval antennomeres of male and female antennae. They are the most abundant sensilla on the antennae of male *P. cerealellae* (Tables 2 and 3). Each sensillum gradually curves distally arising directly from the cuticle (no socket is present). They have smooth cuticle covered by small pores (Fig. 3C; ST3-MP). The ST3-MP is slightly bulbous at the base (Fig. 5a and c; ST3-MP) with a mean length and basal diameter of  $88.9 \pm 0.4 \mu\text{m}$  and  $4.6 \pm 0.3 \mu\text{m}$ , respectively (Table 4). Multiple pores can be seen on the walls of the ST3-MP occurring at a density of  $2.8 \pm 0.12$  per  $\mu\text{m}^2$  (mean  $\pm$  S.E.,  $n = 5$ ) at half length.

### 3.3.4. Aporous type 4 sensilla trichodea (ST4-AP)

The aporous sensilla trichodea type IV (ST4-AP) occur at two locations: on the basal portion of the radicle (Fig. 2, Rd; Fig. 3D; ST4-AP) and on the pedicel (Fig. 2, Pd; ST4-AP). Each sensillum is a triangular peg-like structure with smooth cuticle that tapers to a blunt apex. The ST4-AP are short measuring  $16.7 \pm 0.9 \mu\text{m}$  in length and a basal width of  $3.5 \pm 0.1 \mu\text{m}$  (Table 4). They are inserted into large pits of  $8.3 \pm 0.3 \mu\text{m}$  in diameter. Twenty ST4-AP sensilla occur on the radicle of male and female *P. cerealellae* arranged in groups of three to five, whereas only one cluster of three sensilla occurs on the basal part of the pedicel (Table 2; Fig. 2, Pd).

Table 4  
Sizes of the antennal sensilla of *P. cerealellae*

Sensilla	Length ( $\mu\text{m}$ )	Basal width ( $\mu\text{m}$ )	Pit diameter ( $\mu\text{m}$ )
ST1-AP	$29.5 \pm 0.2$	$3.0 \pm 0.1$	NA
ST2-AP	$48.0 \pm 0.3$	$3.5 \pm 0.1$	NA
ST3-WP	$88.9 \pm 0.4$	$4.6 \pm 0.3$	NA
ST4-AP	$16.7 \pm 0.9$	$3.5 \pm 0.1$	$8.3 \pm 0.3$
MPL	$112.8 \pm 0.4$	$11.6 \pm 0.0$	NA
ChS-UP	$39.6 \pm 1.6$	$3.5 \pm 0.1$	NA
BCPS	$8.4 \pm 0.2$	$4.5 \pm 0.2$	$13.2 \pm 0.1$
CLCN	$2.9 \pm 0.1$	$2.9 \pm 0.4$	$5.3 \pm 0.1$

Values are mean ( $\mu\text{m} \pm$  S.E.). Measurements obtained from a total of 30 sensilla per type from antennae of males and females (15 per sex). ST1-AP: aporous type I sensilla trichodea; ST2-AP: aporous type II sensilla trichodea; ST3-MP: multiporous type III sensilla trichodea; ST4-AP: aporous type IV sensilla trichodea; MPS: multiporous placoid sensilla; ChS-UP: uniporous chaetica sensilla; BCPS: basiconic capitate peg sensilla; CS: coeloconic sensilla; NA: not applicable (i.e. the sensilla are not recessed in pits).

### 3.3.5. Uniporous chaetica sensilla (ChS-UP)

Uniporous chaetica sensilla occur on the distal ends of the antennae of both sexes. This type of sensilla is characterized by grooved surfaces (Fig. 4A; ChS-UP) and project slightly more perpendicularly with respect to the axis of the antennal surface than does the ST1-AP type. The ChS-UP measures  $39.6 \pm 1.6 \mu\text{m}$  and  $3.5 \pm 0.1 \mu\text{m}$  in length and basal diameter, respectively (Table 4). The length, orientation, and the blunt tip with apical pore of the ChS-UP (Fig. 4A; ChS-UP) may suggest a contact chemoreception function (Ryan, 2002).

### 3.3.6. Multiporous placoid sensilla (MPS)

Multiporous placoid sensilla are the largest and the most conspicuous sensilla type on the antennae of *P. cerealellae*. Each sensillum arose from an elevated cuticular rim and it tapers apically. The MPS occur on all funicular (A6-A11) and claval (A12-A15) antennomeres forming a ring-like distribution. They have a mean length and width of  $112.8 \pm 0.4 \mu\text{m}$

and  $11.6 \pm 0.0 \mu\text{m}$ , respectively (Table 4), and are more numerous on the antennae of females (Tables 2 and 3). Multiporous placoid sensilla are generally aligned parallel with the antennal axis. They are sausage-shaped and are located between the rows of ST2-AP and ST3-MP. MPS sensilla are elongate, plate-like sensory organs with shafts containing numerous pores (Fig. 4B; MPS). As estimated at half-length, multiple pores occur on the walls of the MPS at a density of  $31.6 \pm 1.61$  per  $\mu\text{m}^2$  (mean  $\pm$  S.E.,  $n = 5$ ).

### 3.3.7. Basiconic capitate peg sensilla (BCPS)

Basiconic capitate peg sensilla (BCPS) are distinguished by their external structure, shape and distribution (Figs. 4C and D; BCPS). BCPS are bulb-like structures, each set into a shallow cuticular depression of  $13.2 \pm 0.1 \mu\text{m}$  in width. Each BCPS measures  $8.4 \pm 0.2 \mu\text{m}$  in length and  $4.5 \pm 0.2 \mu\text{m}$  in width (Table 4). They possess a rounded capitate peg on a distinct stalk. An obvious ring of wrinkled cuticle (Fig. 4D; WC)

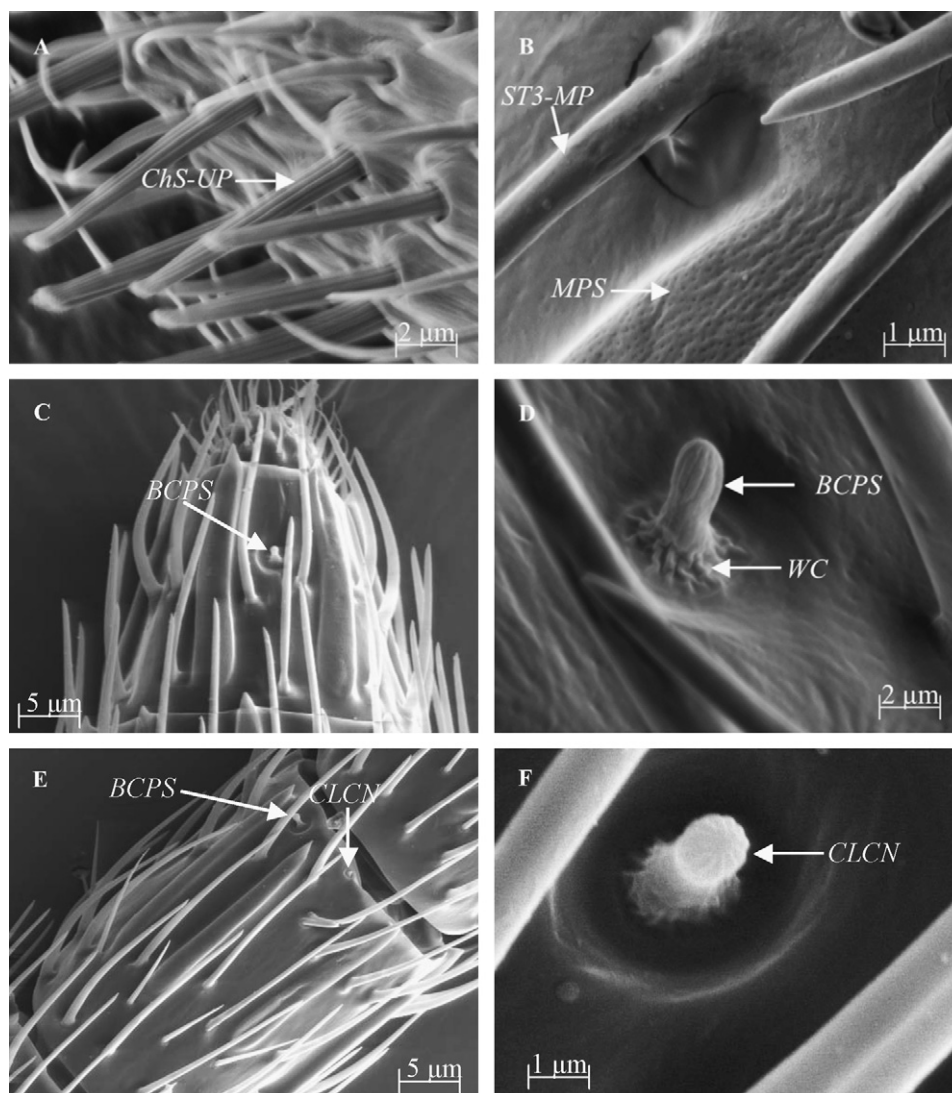


Fig. 4. Other sensilla types recorded on antennae of *P. cerealellae*. Figure shows scanning electron micrographs of the uniporous chaetica (ChS-UP) (A); multiporous placoid (MPL) (B); basiconic capitate peg (BCPS) (C) and (D, showing wrinkled cuticle, WC); and coeloconic (CS) sensilla (E and F) on different antennomeres of *P. cerealellae*.

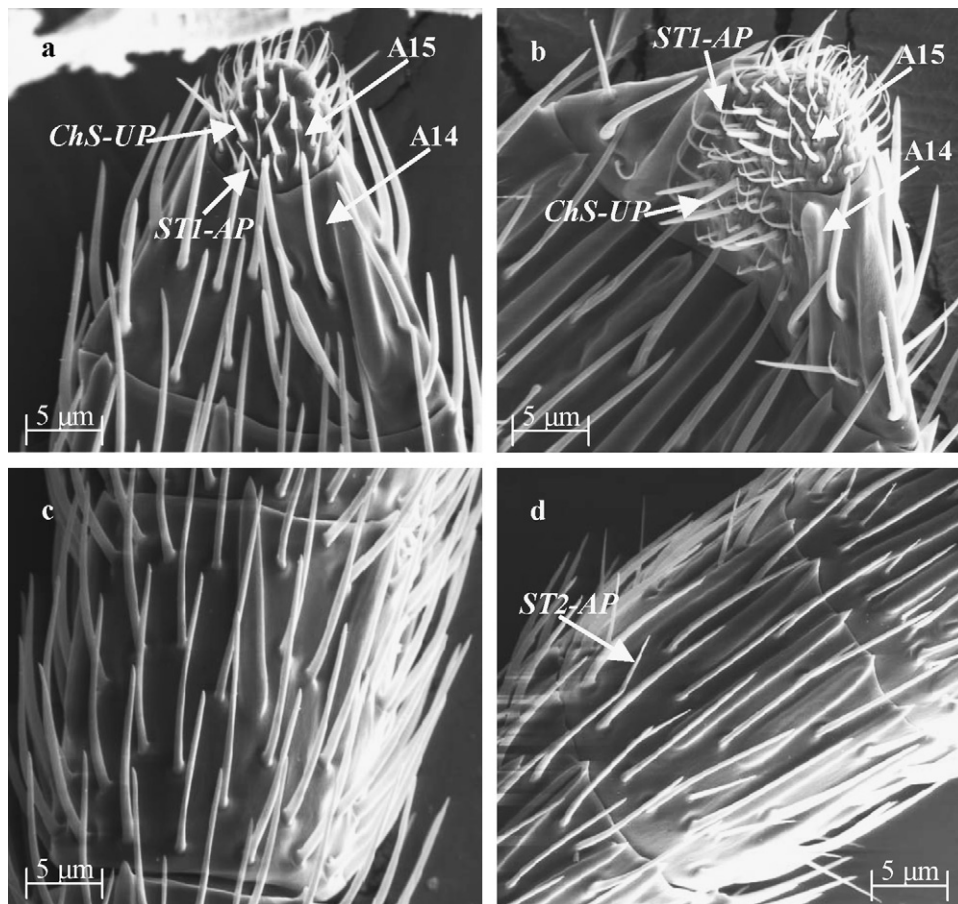


Fig. 5. Sexual differences in the abundance and distribution of some key sensilla types on the antennae of *P. cerealellae*. Figure shows scanning electron micrographs of the ventral surfaces of tips of antennae of male (a) and female (b) and the dorsal surfaces of the sixth funicular antennomeres (A11) of male (c) and female (d). The ST1-AP and ChS-UP which are distributed on the last two antennomeres (A14 and A15) on the female antennae (a) are only found on the terminal antennomere (A15) in the males (b). The ST2-AP is present on the sixth funicular antennomere (A11) of females (d), but absent on the same antennomere in males (c). ST1-AP: aporous type I sensilla trichodea; ST2-AP: aporous type II sensilla trichodea; ChS-UP: uniporous chaetica sensilla.

surrounds the stalk, which is set in a distinct cuticular depression. A total of six BCPS occur on the flagellar antennomeres A8, and A10–A14 on the male antenna and nine on flagellar antennomeres A6–A9 on the female antenna (Table 3). On both male and female antennomeres, the BCPS are located on the distal portions of the flagellar antennomeres (Fig. 4C and E; BCPS).

### 3.3.8. Coeloconic sensilla (CS)

Coeloconic sensilla are recessed in deep pits (Ryan, 2002). They are stump-like pegs with no grooved trunk, and nearly as long as wide with blunt but ridged tip (Fig. 4E and F; CS). Male *P. cerealellae* have two CS located on the 3rd (A8) and 5th (A10) funicular antennomeres, whereas females have only one on the 3rd funicular antennomere.

### 3.4. Abundance and distribution of sensilla on antennae of male and female *P. cerealellae*

Major differences were recorded in the distribution and abundance of some sensilla types on the antennae of male and female *P. cerealellae* (Table 2). The ST1-AP occur on the antennal apices of both sexes and are significantly more

abundant on the female than on the male antennae ( $F = 75.9$ , d.f. = 1,  $P < 0.0001$ ; Tables 2 and 3). Similarly, the long, hair-like ST2-AP occur in significantly greater numbers on the female antennae ( $F = 5398$ , d.f. = 1,  $P < 0.0001$ ; Tables 2 and 3). The ST2-AP occur on the scape (A1), pedicel (A2), anelli (A3–A4), funicle (A5–A11) and on the first two claval antennomeres (A12–A13). In contrast, the ST3-MP are absent on the scape, pedicel and anelli but widely distributed on the funicular (A6–A11) and the first three claval antennomeres (A12–A14) (Tables 2 and 3). The ST3-MP are significantly more abundant on the antennae of males compared to females ( $F = 25259$ , d.f. = 1,  $P < 0.0001$ ; Tables 2 and 3). The distribution of the ST4-AP is restricted to the cavities of the antennal socket (on the radicula) and the ventral surface of pedicel at the scape-pedicel elbow joint (Table 2; Fig. 2, A; Pd), and no differences were recorded between the sexes on the abundance and distribution of this sensilla type. The distribution of the MPS is also similar on the antennae of the two sexes. However, Student's *t*-test analysis revealed significant difference in the abundance of these sensilla on the antennae of male and female wasps ( $F = 10057$ , d.f. = 1,  $P < 0.0001$ ; Tables 2 and 3) with the females having approximately twice the number recorded in the males (Tables 2 and 3). The abundance of the

ChS-UP, BCPS and CS are not significantly different between the sexes (Tables 2 and 3). The ChS-UP, like the ST4-AP, occur together with the ST1-AP, and like the ST4-AP are distributed only on the distal ends of the antennal flagellum in males (A15) and in females (A14–A15) (Table 3; Fig. 5a and b). The BCPS occur on the proximal and distal antennomeres of the antennal flagellum of the females and males respectively (Table 3). The abundance of the ST2-AP, ST3-MP and MPS and the distribution of the BCPS may indicate the existence of sexual dimorphism in the antennae of *P. cerealellae*.

#### 4. Discussion

The external morphology, types and distribution of sensilla on the antennae of male and female *P. cerealellae* recorded in this study are largely in conformity with those reported for other parasitoid species (Wibel et al., 1984; Olson and Andow, 1993; Isidoro et al., 1996; Pettersson et al., 2001; Bleeker et al., 2004). The antennae of insects have been typically described as consisting of basic three segments, scape with radicula, pedicel, and flagellum (e.g., Chapman, 1998; Isidoro et al., 1996). The radicula of *P. cerealellae* antennae can actually be considered as a separate segment since it is completely separated from the scape and has a different type of sensilla. However, since the term “segment” is usually reserved for parts with their own musculature (Chapman, 1998), further studies are necessary to confirm the radicula of *P. cerealellae* as a separate segment.

Our study revealed eight morphologically different types of sensilla on the antennae of male and female *P. cerealellae*, similar to those described for other hymenopteran wasps including pteromalid species, such as *Nasonia vitripennis* (Walker) (Slifer, 1969; Wibel et al., 1984), *Rhopalicus tutela* (Walker) (Pettersson et al., 2001) and non-pteromalid wasps like *Trichogramma nubilale* (Ertle and Davis) (Hymenoptera: Trichogrammatidae) (Olson and Andow, 1993). It should be noted that different nomenclatures were used in some of these studies to describe the antennal sensilla.

Major sexual differences were recorded in the distribution and abundance of five sensilla types on the antennae of *P. cerealellae*, similar to the report on another pteromalid, *N. vitripennis* (Wibel et al., 1984). In general, a greater number of antennal sensilla occur on the males compared to the females. For instance, the aporous type II sensilla trichodea (ST2-AP) occur in greater numbers (almost twice) in females than in males. The ST2-AP appear similar to the “aporous sensilla trichodea B” described on the antennae of *T. nubilale* (Olson and Andow, 1993) and to the tactile sensilla (mechanosensory bristles) described on *R. tutela* antennae (Pettersson et al., 2001). The ST2-AP have been described in many Hymenoptera belonging to different families as having putative mechanoreceptive functions, such as in the perception of mechanosensory stimuli (Amornsak et al., 1998; Olson and Andow, 1993; Isidoro et al., 1996; van Baaren et al., 1996, 1999; Pettersson et al., 2001; Roux et al., 2005; Marques-Silva et al., 2006). Isidoro et al. (1996) suggested that these sensilla may be involved in host examination and host discrimination because most parasitoids usually examine the hosts by drumming its

surface with the apicoventral part of the antennal club which bears these sensilla. It is probable that the ST2-AP play a similar role in the behavior of *P. cerealellae* given that the parasitoid has been observed to exhibit antennal drumming behavior (unpublished data).

The multiporous type III sensilla trichodea (ST3-MP) have previously been described with different names including multiporous sensilla trichodea with wall pores (Wibel et al., 1984; Pettersson et al., 2001; Ryan, 2002; Bleeker et al., 2004), s. basiconica type B in *M. croceipes* (Navasaro and Elzen, 1991), multiporous pitted (MPP) sensilla trichodea C in *T. nubilale* (Olson and Andow, 1993), and basiconica type I sensilla (Ochieng et al., 2000). The ST3-MP are also similar in morphology and distribution to the “thin-walled chemoreceptors” described on the antennae of *N. vitripennis* (Wibel et al., 1984), the “sensilla trichodea” on the antennae of *R. tutela* (Pettersson et al., 2001), and to the “sensilla trichodea C” of *T. nubilale* (Olson and Andow, 1993). In general, antennal sensilla trichodea are presumed to function as olfactory receptors in many insects (Steinbrecht, 1987, 1997; Bleeker et al., 2004), and electrophysiological studies have confirmed a sex pheromone receptor function for the trichoid sensilla of *Neodiprion sertifer* Geoffroy (Hymenoptera: Diprionidae) (Hansson et al., 1991). Also, Pettersson et al. (2001) proposed a pheromone receptor function for the sensilla trichodea of *R. tutela*. The greater abundance of the ST3-MP on the antennae of male *P. cerealellae* relative to the females may indicate a probable role in mate location, possibly for detection of female sex pheromones, as reported for some other parasitoids (Barlin et al., 1981; Chapman, 1982; Bleeker et al., 2004). Since ST3-MP are found in large numbers and have an elongated shaft, they may also provide a large surface area to receive the stimuli from the females of this species.

The type IV sensilla trichodea (ST4-AP) described in the current study are similar to the trichoid sensilla described on the antennae of the scelionid *Gryon boselli* Mineo and Szabo (Villa and Mineo, 1990) and *Trichogramma australicum* (Schmidt and Smith, 1987; Amornsak et al., 1998). These authors proposed that this sensilla type may play a role in the measurement of the antennal curved surface and act as proprioceptors. Chapman (1998) also described the hairs which occur at the joints between segments or on sclerites as trichoid sensilla because they taper from base to tip and also due to lack of pores. The author suggested that these hairs monitor the position of one cuticular element relative to another and that they are positioned so that the flexing of one part of the cuticle with respect to another will cause the hairs to bend. Our scanning electron micrographs of the ST4-AP revealed no obvious pores suggesting that the sensilla may be aporous. The occurrence of the ST4-AP only on the radicula, which fits into the antennal socket, and at the scape-pedicel elbow joint in *P. cerealellae* may also suggest their role as proprioceptors, such as in the measurements of the antennal curved surface and the position of one cuticular element relative to another.

The elongate multiporous placoid sensilla (MPS) are widely distributed on the antennae of parasitic wasps (Richerson et al., 1972; Barlin and Vinson, 1981; Wibel et al., 1984; Olson and



Andow, 1993; Amornsak et al., 1998; Hallberg and Hansson, 1999; Pettersson et al., 2001). The MPS are generally arranged in alternate rings around the funicular antennomeres (Barlin and Vinson, 1981; Pettersson et al., 2001). Their multiple pores suggest an olfactory function (Barlin and Vinson, 1981; Ochieng et al., 2000; Bleeker et al., 2004; Roux et al., 2005; Marques-Silva et al., 2006). The greater abundance of the MPS in female *P. cerealellae* than in males is in contrast to the reports for several other Hymenopteran species (van Baaren et al., 1999; Navasaro and Elzen, 1991; Ochieng et al., 2000; Bleeker et al., 2004), and may indicate their role in host location, possibly in the detection of host-related semiochemicals.

The uniporous chaetica sensilla (ChS-UP) are remarkably different from the other sensilla types observed in *P. cerealellae*, being characterized by their grooved surfaces. Their morphology and location is similar to some previously described sensilla in many insects including the “thick-walled chemoreceptors” of the pteromalid, *N. vitripennis* (Slifer, 1969; Wibel et al., 1984), the “uniporous pit pore sensilla trichodea D” in *T. nubilale* (Olson and Andow, 1993), the “uniporous gustatory sensilla” described on the antennae of many parasitic wasps (Isidoro et al., 1996), and the “curved trichoid formation with an apical pore” described in *Opius concolor* by Barbarossa et al. (1998). The ChS-UP have also been described as “fluted basiconic sensilla” in the braconid *Cardiochiles nigriceps* Vireck (Norton and Vinson, 1974) “aporous, socketed hairs” in the eulophid *T. hagenowii* (Barlin et al., 1981), and as “tapering fluted setae” in the eulophid *Melittobia australica* Girault (Dahms, 1984). The ChS-UP have also been described in other wasps as having a terminal pore suggesting that they may be involved in contact chemoreception (Altner and Prillinger, 1980; Olson and Andow, 1993; Pettersson et al., 2001), including gustatory function (Isidoro et al., 1996; Barbarossa et al., 1998). The ChS-UP are confined to the apices of the antennae of *P. cerealellae* and many other pteromalids, further suggesting their role as contact chemoreceptors (Slifer, 1969; Wibel et al., 1984; Pettersson et al., 2001) and probable involvement in host recognition and host acceptance (Weseloh, 1972; Borden et al., 1973).

The basiconic capitate peg sensilla (BCPS) described in the current study resemble the “multiporous pegs sensilla” on the eulophid *T. hagenowii* (Barlin et al., 1981), “basiconic capitate peg” on antennae of the pteromalid *N. vitripennis* (Wibel et al., 1984), “peg-like sensillum” or “sensillum coeloconicum” in the eulophid *Sympiesis sericeicornis* Nees (Hymenoptera: Eulophidae) (Meyhofer et al., 1997), and the type I coeloconic sensillum on antennae of *Cotesia* spp. (Bleeker et al., 2004). Studies by van Baaren et al. (1996) and Olson and Andow (1993) revealed that pores are present in the furrows on the bulbous distal end of BCPS, suggesting that they may play a role in olfaction (van Baaren et al., 1996; Steinbrecht, 1997; Keil, 1999; Bleeker et al., 2004) or as hygro-, thermo- and mechanoreceptors (Wibel et al., 1984; Wcislo, 1995; Pettersson et al., 2001). In contrast, Meyhofer et al. (1997) reported no evidence of pores on this antennal sensilla type in *S. sericeicornis*, similar to our results for *P. cerealellae*. The BCPS are proximally distributed on the flagellum of the female

*P. cerealellae*, whereas they are more distally distributed on the flagellum of the antennae of males. The grooves on bulbous tips of the BCPS on the antennae of *P. cerealellae* are without punctations suggestive of thermo- or hygroreceptive functions (Hallberg, 1979; Altner et al., 1983; Wibel et al., 1984).

Coeloconic sensilla (CS) is the least abundant sensilla type on *P. cerealellae*, and have been previously described as “pit organs” because they are recessed into deep pits (Wcislo, 1995), and as coeloconic sensilla type II (Bleeker et al., 2004). The specific function of the CS sensilla is difficult to assess. Altner et al. (1983) and Bleeker et al. (2004) suggested that the CS, like the BCPS, may be involved in thermo-hygro perception. The CS may play a similar role in *P. cerealellae* given the absence of sexual differences in their abundance and absence of pores on them.

Female *P. cerealellae* may use both mechanosensory and olfactory cues to locate concealed stored product larval hosts. In addition to identifying key mechanosensory sensilla trichodea types I and II, this study has identified and characterized the distribution of two sensilla types, the multiporous type III sensilla trichodea (ST3-MP) and the multiporous placoid sensilla (MPS) which are likely involved in olfactory communication in *P. cerealellae*, providing necessary background information for our ongoing studies of host location mechanisms in this species, including behavioral and electrophysiological studies of olfaction. Although the density of MPS on the flagellum of *P. cerealellae* is much less than that of the ST3-MP, the relatively greater pore density of the MPS may suggest its equal importance in olfaction in *P. cerealellae*. Future studies on the functional morphology of the antennal sensilla of *P. cerealellae* using transmission electron microscopy coupled with electrophysiological recordings will likely confirm the functions of the different sensilla identified in this study.

## Acknowledgements

We gratefully acknowledge Dr. Samuel A. Ochieng (Tennessee State University, Institute of Agricultural and Environmental Research, McMinnville, Tennessee, USA) for technical assistance. We also thank Dr. Michael Miller (Auburn University, Auburn, Alabama) for assistance with the use of the electron microscopes. This research was supported in part by the Alabama Agricultural Experiment Station and an Auburn University Competitive Research grant to H.Y.F.

## References

- Altner, H., Prillinger, L., 1980. Ultrastructure of invertebrate chemo-, thermo-, and hygroreceptors and its functional significance. *Inter. Rev. Cytol.* 67, 69–139.
- Altner, H., Schaller-Selzer, L., Stetter, H., Wohlrab, I., 1983. Poreless sensilla with inflexible sockets: A comparative study of a fundamental type of insect sensilla probably comprising thermo- and hygroreceptors. *Cell Tiss. Res.* 234, 279–307.
- Amornsak, W., Cribb, B., Gordh, G., 1998. External morphology of antennal sensilla of *Trichogramma australicum* Girault (Hymenoptera: Trichogrammatidae). *Int. J. Insect Morphol. Embryol.* 27 (2), 67–82.

- Ashmead, W.H., 1902. A new *Cataloccus* on *Sitotroga cerealellae* Oliv. *Psyche* 9, 345.
- Barbarossa, I.T., Muroi, P., Dardani, M., Casula, P., Angioy, A.M., 1998. New insight into the antennal chemosensory function of *Opius concolor* (Hymenoptera: Braconidae). *Int. J. Zool.* 65, 367–370.
- Barlin, M.R., Vinson, S.B., 1981. Multiporous plate sensilla in antennae of *Chalcidoidea* (Hymenoptera). *Int. J. Insect Morphol. Embryol.* 10 (1), 29–42.
- Barlin, M.R., Vinson, S.B., Piper, G.L., 1981. Ultrastructure of the antennal sensilla of the cockroach-egg parasitoid *Tetrastichus hagenowii* (Hymenoptera: Eulophidae). *J. Morphol.* 168, 97–108.
- Bin, F., Colazza, S., Isidoro, N., Solinas, M., Vinson, S.B., 1989. Antennal chemosensilla and glands, and their possible meaning in the reproductive behaviour of *Trissolcus basalis* (Woll) (Hymenoptera: Scelionidae). *Entomologica* 30, 33–97.
- Bleeker, M.A.K., Smid, H.M., Aelst, A.C., van Loon, J.J.A., Vet, L.E.M., 2004. Antennal sensilla of two parasitoid wasps: a comparative scanning electron microscopy study. *Micros. Res. Tech.* 63, 266–273.
- Borden, J.H., Miller, G.E., Richerson, J.V., 1973. A possible new sensillum on the antennae of *Itopectis conquisitor* (Hymenoptera: Ichneumonidae). *Can. Entomol.* 105, 1363–1367.
- Brower, J.H., 1991. Potential host range and performance of a reportedly monophagous parasitoid. *Pteromalus cerealellae* (Hymenoptera: Pteromalidae). *Entomol. News* 102, 231–235.
- Chapman, R.F., 1982. Chemoreception: the significance of receptor number. In: Berridge, M.J., Treherne, J.E. (Eds.), *Advances in Insect Physiology*, vol. 16. Academic Press Inc., London, pp. 247–357.
- Chapman, R.F., 1998. *The Insects Structure and Function*, fourth ed. Cambridge University Press, p. 770.
- Dahms, E.C., 1984. An interpretation of the structure and function of the antennal sense organs of *Melittobia australica* (Hymenoptera: Eulophidae) with the discovery of a large dermal gland in the male scape. *Mem. Queensl. Mus.* 21, 361–385.
- Hallberg, E., 1979. The fine structure of the antennal sensilla of the pine saw fly *Neodiprion sertifer* (Insecta: Hymenoptera). *Protoplasma* 101, 111–126.
- Hallberg, E., Hansson, B.S., 1999. Arthropod sensilla: Morphology and phylogenetic considerations. *Micros. Res. Tech.* 47, 428–439.
- Hansson, B.S., Van Der Pers, J.N.C., Högberg, H.E., Hedenström, E., Anderbrant, O., Löfqvist, J., 1991. Sex pheromone perception in male pine sawflies. *Neodiprion sertifer* (Hymenoptera; Diprionidae). *J. Comp. Physiol.* 168, 533–538.
- Isidoro, N., Bin, F., Colazza, S., Vinson, S.B., 1996. Morphology of antennal gustatory sensilla and glands in some parasitoid hymenoptera with hypothesis on their role in sex and host recognition. *J. Hymen. Res.* 5, 206–239.
- Keil, T.A., 1999. Morphology and development of the peripheral olfactory organs. In: Hansson, B.S. (Ed.), *Insect Olfaction*. Springer, Heidelberg, pp. 5–47.
- Marques-Silva, S., Matiello-Guss, C.P., Delabie, J.H.C., Mariano, C.S.F., Zanuncio, J.C., Serrão, J.E., 2006. Sensilla and secretory glands in the antennae of a primitive ant: *Dinoponera lucida* (Formicidae: Ponerinae). *Micros. Res. Tech.* 69, 885–890.
- Mbata, G.N., Thomas, A., Fadamiro, H.Y., 2005. Parasitism by *Pteromalus cerealellae* (Hymenoptera: Pteromalidae) on the cowpea weevil, *Callosobruchus maculatus* (Coleoptera: Bruchidae): host density, temperature effects, and host finding ability. *Biol. Control* 33, 286–292.
- Meyhofer, R., Casas, J., Dorn, S., 1997. Mechano- and chemoreceptors and their possible role in host location behavior of *Sympiesis sericeicornis* (Hymenoptera: Eulophidae). *Ann. Entomol. Soc. Am.* 90, 208–219.
- Navasaro, R.C., Elzen, G.W., 1991. Sensilla on the antennae, foretarsi and palpi of *Microplitis croceipes* (Cresson) (Hymenoptera: Braconidae). *Proc. Entomol. Soc. Wash.* 93, 737–747.
- Norton, W.N., Vinson, S.B., 1974. Antennal sensilla of three parasitic hymenoptera. *Int. J. Insect Morphol. Embryol.* 3, 305–316.
- Ochieng, S.A., Park, K.C., Zhu, J.W., Baker, T.C., 2000. Functional morphology of antennal chemoreceptors of the parasitoid *Microplitis croceipes* (Hymenoptera: Braconidae). *Arthropod Struct. Dev.* 29, 231–240.
- Olson, D.M., Andow, D.A., 1993. Antennal sensilla of female *Trichogramma nubilale* (Ertle and Davis) (Hymenoptera: Trichogrammatidae) and comparisons with other parasitic hymenoptera. *Int. J. Insect Morphol. Embryol.* 22, 507–520.
- Onagbola, E.O., Fadamiro, H.Y., Mbata, G.N., 2007. Longevity, fecundity and progeny sex ratio of *Pteromalus cerealellae* in relation to diet, host provision, and mating. *Biol. Control* 40 (2), 222–229.
- Pettersson, E.M., Hallberg, E., Biggersson, G., 2001. Evidence for the importance of odour-reception in the parasitoid *Rhopalicus tutela* (Walker) (Hymenoptera: Pteromalidae). *J. Appl. Entomol.* 1, 125, 293–301.
- Richerson, J.V., Borden, J.H., Hollingdale, J., 1972. Morphology of a unique sensillum placodeum on the antenna of *Coeloides brunneri* (Hymenoptera: Braconidae). *Can. J. Zool.* 104, 1235–1250.
- Roux, O., van Baaren, J., Gers, C., Arvanitakis, L., Legal, L., 2005. Antennal structure and oviposition behavior of the *Plutella xylostella* specialist parasitoid *Cotesia plutellae*. *Micros. Res. Tech.* 68, 36–44.
- Ryan, M.F., 2002. *Insect Chemoreception: Fundamental and Applied*. Kluwer Academic Publishers, The Netherlands, p. 303.
- Schmidt, J.M., Smith, J.J.B., 1987. The external sensory morphology of the legs and hairplate system of female *Trichogramma minutum* Riley (Hymenoptera: Trichogrammatidae). *Proc. R. Soc. Lond. Ser. B. Biol. Sci.* 232, 323–366.
- Slifer, E.H., 1969. Sense organs on the antenna of a parasitic wasp, *Nasonia vitripennis* (Hymenoptera, Pteromalidae). *Biol. Bull.* 136, 253–263.
- Steinbrecht, R.A., 1987. Functional morphology of pheromone-sensitive sensilla. In: Prestwich, G.D., Blomquist, G.J. (Eds.), *Pheromone Biochemistry*. Academic Press, Orlando, pp. 353–383.
- Steinbrecht, R.A., 1997. Pore structures in insect olfactory sensilla: a review of data and concepts. *Int. J. Insect Morphol. Embryol.* 26, 229–245.
- van Baaren, J., Barbier, R., Nénon, J.P., 1996. Females antennal sensilla of *Epidinocarsis lopezi* and *Leptomastix dactylopii* (Hymenoptera: Encyrtidae), parasitoids of pseudococcid mealybugs. *Can. J. Zool.* 74, 710–720.
- van Baaren, J., Boivin, G., Lannic, J.L., Nénon, J.P., 1999. Comparison of antennal sensilla of *Anaphes victus* and *A. listronoti* (Hymenoptera: Mymaridae), egg parasitoids of Curculionidae). *Zoomorphology* 119, 1–8.
- Villa, L., Mineo, G., 1990. Morphology of antennal structures of *Gryon boselli* Mineo et Szabo (Hymenoptera: Scelionidae): A scanning electron microscope study. *Frustrula Entomol.* XIII, 9–17.
- Vinson, S.B., Bin, F., Strand, M.R., 1986. The role of the antennae and host factors in host selection behavior of *Trissolcus basalis* (Wall.) (Hymenoptera: Scelionidae). *Les Colloq. de l'INRA* 43, 267–273.
- Weislo, W.T., 1995. Sensilla numbers and antennal morphology of parasitic and non-parasitic bees (Hymenoptera: Apoidea). *Int. J. Insect Morphol. Embryol.* 24, 63–81.
- Weseloh, R.M., 1972. Sense organs of the hyperparasite *Cheiloneurus noxius* (Hymenoptera: Encyrtidae) important in host selection processes. *Ann. Entomol. Soc. Am.* 65, 41–46.
- Wibel, R.G., Cassidy, J.D., Buhse Jr., H.E., Cummings, M.R., Bindokas, V.P., Charlesworth, J., Buumgartner, D.L., 1984. Scanning electron microscopy of antennal sense organs of *Nasonia vitripennis* (Hymenoptera: Pteromalidae). *Trans. Am. Micros. Soc.* 103 (4), 329–340.