

Ultrastructure of antennal sensilla of an autoparasitoid *Encarsia sophia* (Hymenoptera: Aphelinidae)



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ABSTRACT

Encarsia sophia (Hymenoptera: Aphelinidae) is a parasitoid utilized for biological control of *Bemisia tabaci*, with selection of prey aided by chemoreceptor organs. The morphology and distribution of the antennal sensilla (chemoreceptors) of *E. sophia* were examined using Transmission electron micrographs. The total antennal length for *E. sophia* was $429.28 \pm 0.95 \mu\text{m}$ for females and 437.19 ± 8.21 for males, and each antennae was found to consist of seven sensilla of different types. Both sexes possessed sensilla chaetica, sensilla trichodea, basiconic capitate peg sensilla, multiporous grooved-surface placoid sensilla (MG-PS), uniporous rod-like sensilla, nonporous finger-like sensilla, and sensilla coeloconica. Transmission electron micrographs of longitudinal sections of female antennae showed that they were composed of fat body, cuticle, mesoscutello-metanotal muscles, neurons, and glandular tissue, and cross-sections of the basal MG-PS showed sensillar lymph cavities and dendrites. The MG-PSs were imbedded in an electron-dense mass with cuticular invaginations which acted as pores that connected to a central lumen. The possible function of each type of sensilla is discussed.

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1. Introduction

Chemoreceptors are found on the antennae and on a series of functional ultrastructures on the surface of insects. The ability of insects to detect environmental signals with these receptors has been well studied (Schneider, 1964). Chemoreceptors are involved in a variety of processes, such as searching for prey, courtship, and communication. Chemoreceptors detect volatile-chemical trails that are emitted by animals and plants, and aid in the selection of a suitable host via direct contact (Hays and Vinson, 1971; Vinson, 1984). The morphological differences among the sensilla of various

species of insects demonstrate significant variation in function and the types of environmental signals detected (Schneider, 1964).

Many studies of the ultrastructure of sensilla have focused on deducing function, and have revealed that the type and structure of sensilla located on the antenna greatly influence the type of information that insects are aware of (Schmidt and Smith, 1985; Zhou et al., 2013). Many hymenopteran species are parasitoids, including members of the genus *Encarsia*. Host specificity is common in these parasitoids; they preferentially parasitize specific hemipterans and lepidopterans, with host selection behaviors during oviposition of the male and female eggs (Hunter and Woolley, 2001). As a key environmental sensor, the sensillas of parasitoids are prime candidates for determining behavioral relationships between the parasitoid and the host.

Certain members of the genus *Encarsia*, which are quite small in size, are important obligate parasitic enemies of the globally distributed homopteran pest *Bemisia tabaci*, and are effective in controlling the spread of *B. tabaci* if introduced early during an outbreak. A member of the family Aphelinidae, *Encarsia sophia* is a parasitic wasp that is native to India, and has been shown to be an effective biological control species against *B. tabaci* (Antony et al., 2003). *E. sophia* exhibits arrhenotokous, heteronomous, and autoparasitoid reproduction. Female eggs are laid internally in whitefly nymphs and develop as primary parasitoids, whereas males develop as hyperparasitoids either on females of their own species or on other primary aphelinid parasitoids. Further, females

Abbreviations: SEM, scanning electron microscopy; TEM, transmission electron microscopy; SEMGs, scanning electron micrographs; TEMG, transmission electron micrographs; RA, radicle; SC, scape; PE, pedicel; F1–F6, the six flagellar segments; CH, sensilla chaetica; ST, sensilla trichodea; BCPS, basiconic capitate peg sensilla; MG-PS, grooved-surface placoid sensilla; CS, sensilla coeloconica; PO-UP, uniporous rod-like sensilla; FL-NP, nonporous finger-like sensilla; FG, flagellum; GL, glandular tissue; TB, tubular body; epd, epidermal cells; cut, cuticle; FB, fat body; MMM, mesoscutello-metanotal muscle; MC, molting channel; DE, dendrites; NE, neurons; mit, mitochondria; SL, sensillum lymph cavities; edm, electron-dense mass; OSL, outer sensillum lymph; SW, thick sensillar wall; ISL, inner sensillar lymph.

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develop as primary endoparasitoids in whitefly nymphs, and males develop as secondary ectoparasitoids on female *E. sophia* or other primary aphelinid parasitoids (Antony et al., 2003). Thus, host selection is very important for *E. sophia*, both for reproduction and for controlling the sex ratio of their offspring (Kochetova, 1977). Parasitoid species display behavioral adaptations for the following four aspects of oviposition selection: habitat selection, host tracking, host acceptance, and host suitability (Viggiani, 1984). It is likely that the antennal sensilla play an important role in these behaviors.

E. sophia was recently imported to the northern, central, and southeastern regions of mainland China for biological control applications. Despite its widespread use, basic research on the host-selection behavior of *E. sophia* remains in its infancy. Studies of the microstructure of *Encarsia* sensilla are scarce, and are limited primarily to those of *E. amicola* (Wang and Huang, 2007) and *E. guadeloupae* (Zhou et al., 2013). *Encarsia* have abundant mechanosensory and olfactory antennal sensilla, including sensilla chaetica, sensilla trichodea, multiporous sensilla placoid, uniporous rod-like sensilla, and nonporous finger-like sensilla, which they use to locate whitefly nymphs. Studies of the microstructure of the sensilla of *E. sophia* might identify structural variations that influence detection efficiency of *B. tabaci* through variable uptake of chemical messengers. We examined the distribution and structure of the various antennal sensilla and the internal structure of the antennae of *E. sophia* using scanning electron microscopy (SEM) and transmission electron microscopy (TEM) to gain insight into functions, and to further our understanding of the chemical basis of their host-selection behavior.

2. Materials and methods

2.1. Insects

The jiyou-768 transgenic strain of *Gossypium hirsutum* (cabbage), which expresses a toxin derived from *Bacillus thuringiensis* (BT-cotton), was used as the host plant for *E. sophia*, and was kindly provided by the Texas AgriLife Research, Texas A&M University System at Weslaco. *E. sophia* were reared on *B. tabaci* nymphs in a greenhouse at 25–28 °C at the Institute of Plant and Environment Protection, Beijing Academy of Agriculture and Forestry Sciences, China. Cotton leaves with parasitized nymphs were kept in 9-cm petri dishes. The newly enclosed male and female adult parasitoids were maintained in separate petri dishes, and were fed 10% aqueous solution of honey.

2.2. Scanning and TEMGs methods

For SEM, 30 adult *E. sophia* were placed in a 1.5-mL centrifuge tube, and rinsed three times with phosphate-buffered saline (PBS) at pH 7.0. The insects were fixed in 2.5% glutaraldehyde for 24 h at 4 °C, and washed three times for 15 min with 0.1 M phosphate buffer, pH 7.0. The specimens were dehydrated in a graded ethanol series by incubation in 30%, 50%, 70%, 80%, 90%, and 95% ethanol for 10 min each. The dehydrated specimens were incubated in isoamyl acetate for 15 min, and critical point dried for 1.5 h in an HPC-2 oven (Hitachi, Tokyo, Japan), generally following Zhou et al. (2013). The antennae were removed using an insect needle, and examined using an MZ205 stereomicroscope (Leica, Wetzlar, Germany). The antennae were coated with gold using an E-1010 ion sputter coater (Hitachi Ltd., Tokyo, Japan), and observed using an S-3000N scanning electron microscope (Hitachi Ltd., Tokyo, Japan).

We used TEM to examine the antennae of female insects only. For TEM, female insects were washed in PBS and fixed as described above for SEM. The fixed specimens were dehydrated in 100%

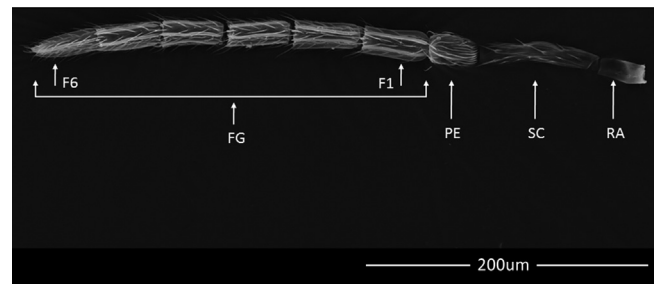


Fig. 1. Scanning electron micrographs (SEMGS) of the antennae of a male *E. sophia*. Radicle (RA), scape (SC), pedicel (PE), flagellum (FG), six flagellar segments (F1–F6).

ethanol for 20 min, and postfixed in 2% osmium tetroxide for 1.5 h. The postfixed specimens were incubated in acetone for 20 min, and embedded in Epon-812 at 70 °C for 24 h. Ultrathin sections were prepared using an EM UC7 microtome (Leica, Germany). The sections were stained with lead citrate and uranyl acetate, and observed using an H-7650 transmission electron microscope (Hitachi Ltd., Tokyo, Japan).

2.3. Statistical analysis

The number and sizes of 30 pairs of antennal sensilla of the antennal segments were measured using the Photoshop CS3 software (Adobe System, Mountain View, CA, USA), and lengths were measured by CAMSONAR Images MP 1.0 software, based on the SEM photomicrographs of the dorsal and ventral surfaces of the antennae.

3. Results

3.1. Gross morphology of the antenna of *E. sophia*

The SEM analysis showed that the antennae of *E. sophia* consisted of nine segments, which included a radicle, an elongated scape, a thick pedicel, and a six-segmented flagellum (Fig. 1). Many sensilla were found on the antennae of *E. sophia* in which host choice was sex-dependent. The types of sensilla identified were sensilla chaetica, sensilla trichodea, basiconic capitate peg sensilla, multiporous, grooved-surface placoid sensilla (MG-PS), uniporous rod-like sensilla, nonporous finger-like sensilla, and sensilla coeloconica. The mean total length of the antennae of females and males was $429.28 \pm 0.95 \mu\text{m}$ and $437.19 \pm 8.21 \mu\text{m}$, respectively. The radicle had a smooth surface (Fig. 2A). The mean length of the radicle in females ($41.25 \pm 1.23 \mu\text{m}$) was longer than that of the males ($32.44 \pm 0.73 \mu\text{m}$), comprising 9% and 7.4% of the total length of each antenna in females and males, respectively. The SC was approximately two times longer than the radicle, measuring $91.14 \pm 1.92 \mu\text{m}$ in females and $86.98 \pm 4.43 \mu\text{m}$ in males, and comprising 21% and 19.9% of the total length of the antenna in females and male, respectively. The PE was relatively short and was conical in shape. The mean length of the PE was $39.94 \pm 0.73 \mu\text{m}$ in females and $38.15 \pm 2.17 \mu\text{m}$ in males, comprising 9.3% and 8.7% of the total length of the antenna in females and males, respectively. The mean total length of the flagellum was $256.81 \pm 1.09 \mu\text{m}$ in females and $279.59 \pm 3.01 \mu\text{m}$ in males, comprising 59.8% and 64% of the total length of the antenna in females and males, respectively.

The TEM analysis showed that the antennae of females contained fat body (FB) (Fig. 3D), cuticle, mesoscutello-metanotal muscle (MMM), and neurons (NE). A transverse cross-section of the region containing multiporous grooved-surface placoid sensilla (MG-PS) showed outer sensilla lymph cavities (OSL), inner sensillum lymph (ISL) and dendrites (DE) (Fig. 4.1F). In a TEM image of a longitudinal section of an MG-PS, the pore, which contained

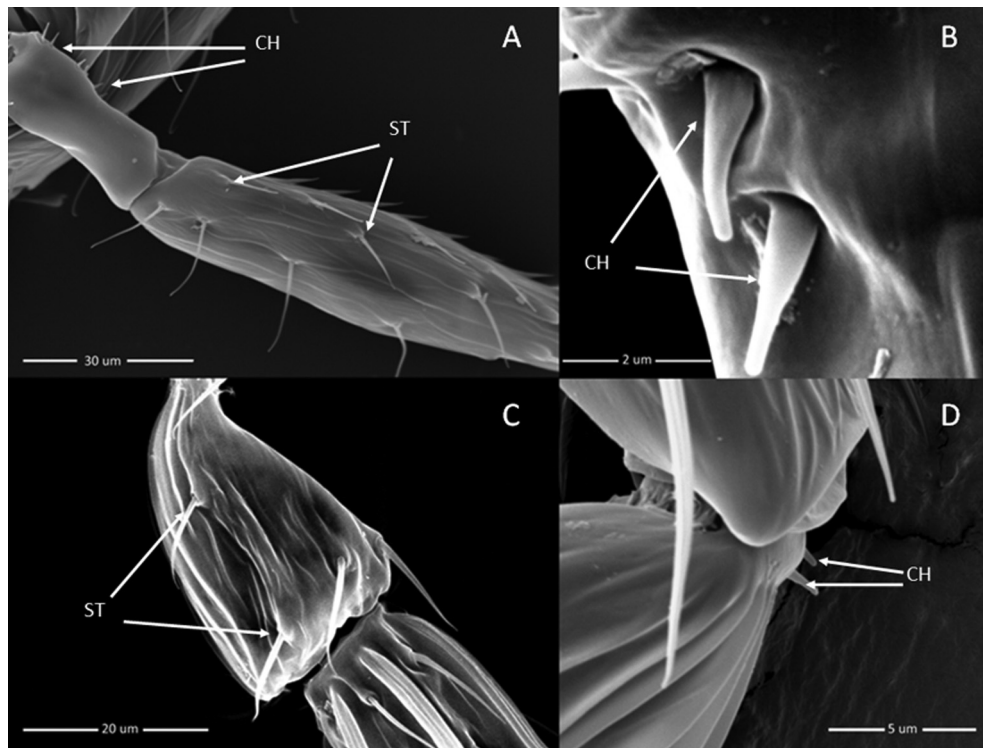


Fig. 2. Antennal sensilla of a female *E. sophia*. SEMGs show sensilla of radicle, scape and pedicel: (panel A) a sensillum chaetica (CH) on the base of the radicle and a sensillum trichodea (ST) on the scape; (panel B) a smooth CH; (panel C) an ST on the pedicel; and (panel D) a CH on the pedicel.

dendrites, was visible through to the lumen of MG-PS (Fig. 4.1E), and the base of the MG-PS was located within an electron-dense mass (edm) (Fig. 4.1E).

In the TEM images of the antennae of female *E. sophia*, a layer of epidermis was located beneath the cuticle (Fig. 3C and F), both of which spanned the entire length of the antenna. Dead epidermal cells were present at the interface with the cuticle, leaving a thick waxy layer that prevented body-water evaporation, resembling a layer of tissue surrounding the muscle (Fig. 3F). The cross section and longitudinal section of the female antennae showed that MMM and FB were evenly distributed inside each antenna (Fig. 4.1D and G, 4.2A). The longitudinal section clearly showed the neurons and dendrites (Fig. 4.2A), and the tubular body which consisted of glandular tissue (GL) with microtubules, which laid perpendicular to the surface of the cuticle (Fig. 3C). The longitudinal section of the tip of the antenna of females revealed GL (Fig. 3C) and clusters of unicellular secretory units that extended beneath the cuticle. The cross sections and longitudinal sections of an MG-PS revealed a multiporous surface, numerous neurons, and pores that were connected through cuticular invaginations to a central lumen that contained dendrites and SL (Fig. 4.1E and F).

3.2. Characterization of sensillas

3.2.1. Types of sensilla

Seven different types of sensilla were identified on the antennae of female and male *E. sophia*: sensilla chaetica (CH), sensilla trichodea (ST), basiconic capitate peg sensilla (BCPS), MG-PS, sensilla coeloconica (CS) (Figs 4.2C and 5F), uniporous rod-like sensilla (PO-UP), and nonporous finger-like sensilla (FL-NP). Both females and males had the same types of sensilla, but the number of each type of sensilla per segment was different. The MG-PS was the longest sensillum and had numerous pores in its grooves (Figs. 4.1C and 6C). The TEM images also showed multiple pores on the MG-PS surfaces that connected to the lumen. The BCPS of females had a rough

surface, whereas the males had a stump-like peg with multiple pores in the distal region. The CHs were found on the radicle and pedicel. Two types of ST were observed, one with a smooth surface (Fig. 6B) and another with a grooved surface (Fig. 4.1B). Uniporous rod-like sensilla (RO-UP) and grooved surfaced apical-pore nonporous finger-like sensilla (FL-NP) were present on the tip of the antennae. CS (Figs 4.2C and 5F) were present on the fourth flagellar segment (Fig. 1) of both females and males.

3.2.2. Sensilla chaetica

The CHs were found on the radicle and pedicel only. The short, tapered CH had smooth cuticle and a blunt apex, with a thick base that inserted into a pit (Figs. 2B and D, 5A, B and D). Numerous CH were present in females, with six CH aligned in a row on the base of the radicle, nine CH located near the head of the radicle, and two pairs measuring $3.04 \pm 0.35 \mu\text{m}$ in length and $0.62 \pm 0.06 \mu\text{m}$ in diameter were observed on the pedicel. In males, the number of CHs were similar to that in females, except for those aligned on the radicle, which included five that were shorter in length ($2.67 \pm 0.43 \mu\text{m}$) and smaller in diameter ($0.58 \pm 0.05 \mu\text{m}$) relative to those of the females.

3.2.3. Sensilla trichodea

In both males and females, STs were abundant on all of the antennal segments except for the radicle (Fig. 1). The STs were elongated hair-like structures that tapered to an apex (Fig. 4.2B). The TEM images revealed that most of the ST projected from a conical socket that was elevated above the cuticle (Fig. 4.1A), and that the molting channel was $0.37 \mu\text{m}$ deep and $0.50 \mu\text{m}$ wide (Fig. 3F). The surface of the ST shaft had longitudinally aligned grooves (Fig. 4.1B and 4.2B) that were $12.25 \pm 0.35 \mu\text{m}$ in length and $0.66 \pm 0.05 \mu\text{m}$ in width at the base of the ST. The males displayed two types of ST. One type was similar to that observed in females. The other type had a smooth surface (Fig. 6B), and a mean length and diameter of $13.52 \pm 1.16 \mu\text{m}$ and $0.94 \pm 0.08 \mu\text{m}$, respectively.

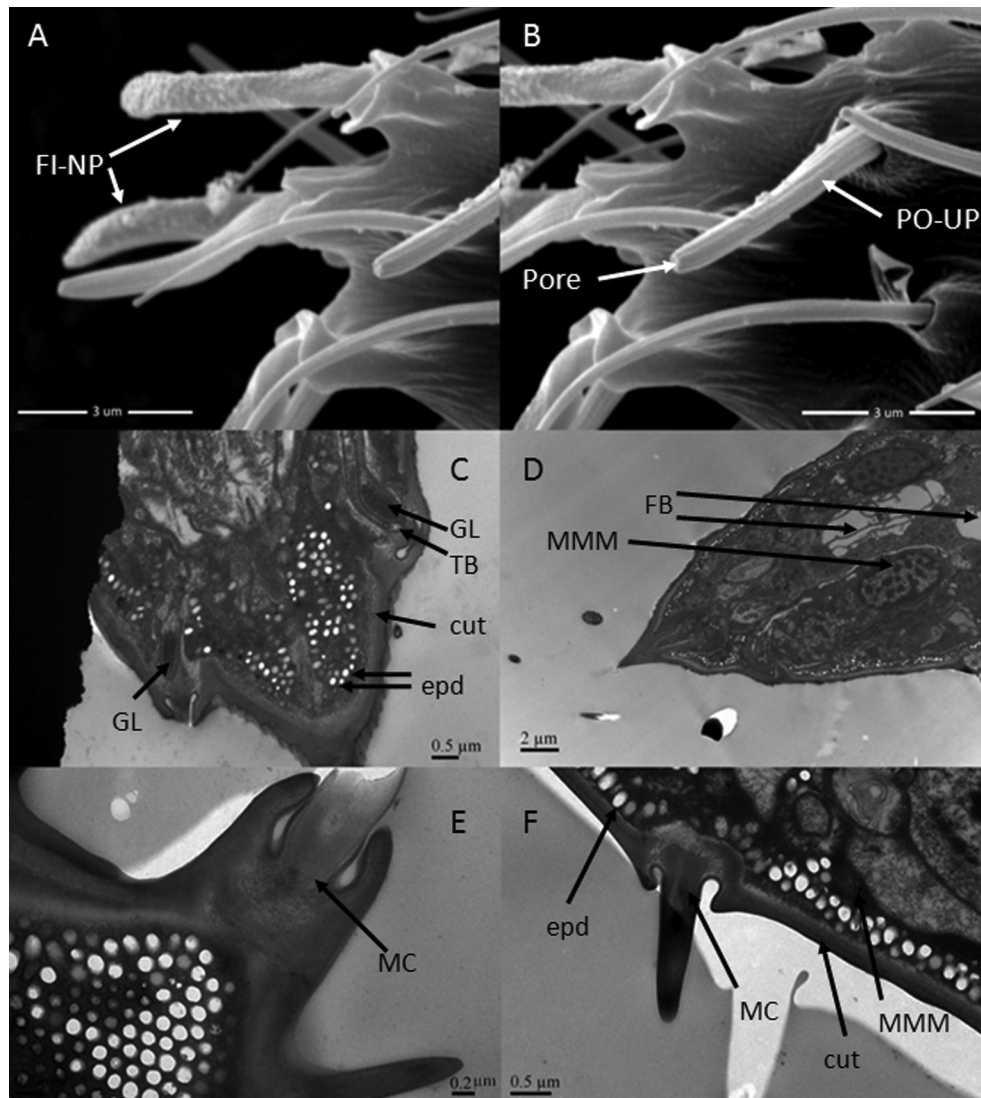


Fig. 3. Micrographs of the antennal sensilla of a female *E. sophia*. Scanning and transmission electron micrographs show sensillum of flagellum: (panel A) a nonporous finger-like sensillum (FI-NP) on the F6 flagellar segment and (panel B) the grooved surface and apical pore of a uniporous rod-like sensillum (PO-UP) on the sixth flagellar segment. Transmission electron micrographs (TEMs) show the following: (panel C) glandular tissue (GL), a tubular body (TB), and epidermal cells (epd); (panels C and F) the cuticle (cut); (panel D) the fat body (FB); (panels D and F) mesoscutello-metanotal muscle (MMM); and (panels E and F) the molting channel (MC) of the antennal sensilla of a female *E. sophia*.

3.2.4. Basiconic capitates peg sensilla

The BCPS of males were stump-like pegs. The BCPS of females had a rough surface (Fig. 4.1B), whereas those of the males had pores and a grooved surface (Fig. 6D). The BCPS projected from a shallow cuticular pit. The mean diameter of the neck of the BCPS was $0.89 \pm 0.04 \mu\text{m}$ in females and $1.02 \pm 0.05 \mu\text{m}$ in males. The capitae-like body had a slim neck that broadened to a blunt tip. The BCPS occurred over the entire flagellum, with one or two BCPS per flagellar segment (Fig. 4.1B). Most BCPS were clustered over the distal region of the flagellum, except for the terminus flagellar segments. The length of the BCPS was $3.54 \pm 0.17 \mu\text{m}$ in females and $3.76 \pm 1.12 \mu\text{m}$ in males, but the width was similar between females ($1.37 \pm 0.04 \mu\text{m}$) and males ($1.39 \pm 0.03 \mu\text{m}$).

3.2.5. Multiporous grooved-surface placoid sensilla

The MG-PS was present over most of the flagellum, and were generally aligned parallel with the antennal axis and porous plate. The MG-PS projected from non-socketed plates, and was slightly elevated above the antennal surface along their entire length (Figs. 4.1A and 5E). The MG-PS was the longest type of sensillum

observed on the *E. sophia* antennae, and lay between two rows of ST (Fig. 5E). They were placoid-like shaped, and had longitudinal grooves, in the furrow between which were located pores (Figs. 4.1C and 6C). The mean length of the MG-PS was $39.99 \pm 0.66 \mu\text{m}$ in females and $42.67 \pm 0.65 \mu\text{m}$ in males, and the mean diameter was $2.08 \pm 0.08 \mu\text{m}$ in females and $1.86 \pm 0.12 \mu\text{m}$ in males. The TEM images showed that the MG-PS had thin cuticular walls, with multiple pores that were continuous with the internal lumen (Fig. 4.1E). Branched dendrites were present in the lumen, surrounded by a thick sensillar wall (Fig. 4.1F).

3.2.6. Nonporous finger-like sensilla

The FL-NP occurred on the distal region of the antenna in females, appearing as pimple-like structures on the surface (Fig. 3A), whereas the same region was relatively smooth in males, with some shallow pitting (Fig. 6E). The FL-NP was the most sparsely distributed sensilla, with only three present per antenna in females and two per antenna in males. The mean length of the FL-NP was $4.75 \pm 0.15 \mu\text{m}$ in females and $4.51 \pm 0.17 \mu\text{m}$ in males. The

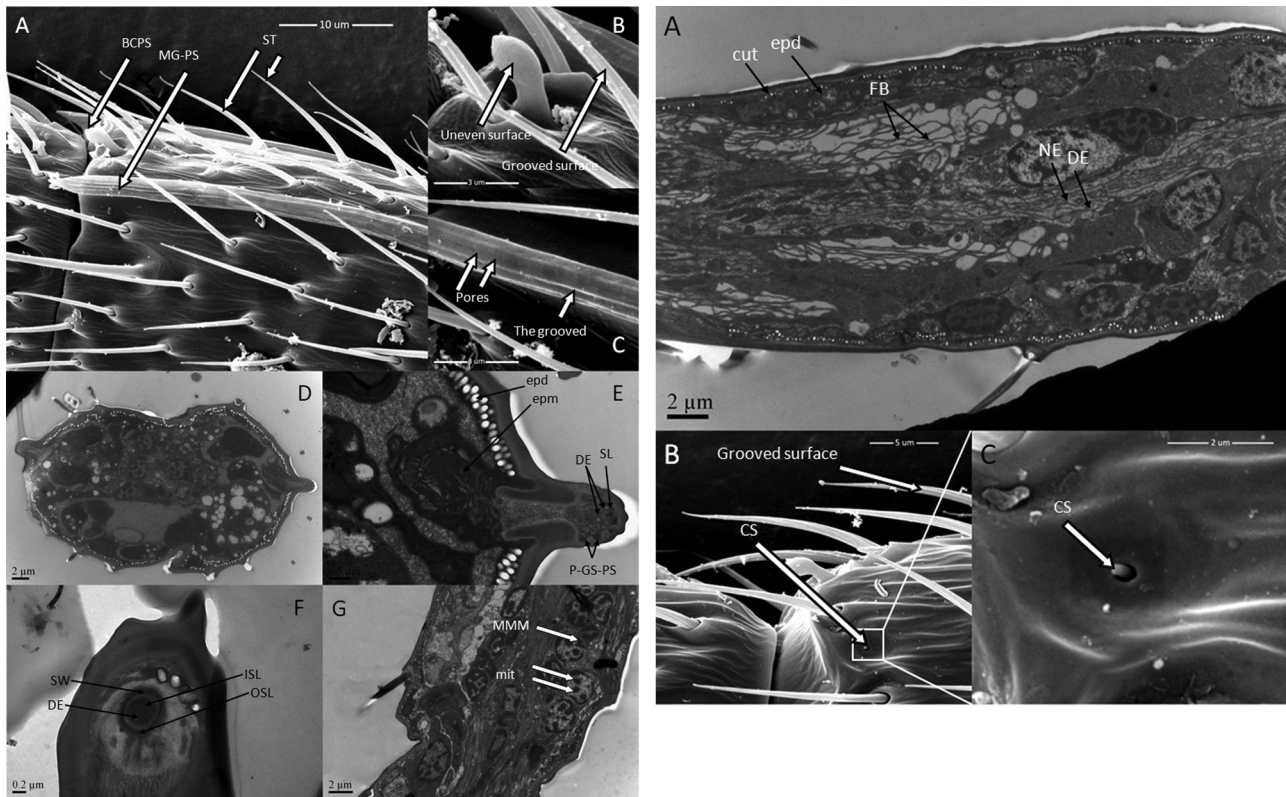


Fig. 4. (1) Antennal sensilla of a female *E. sophia*. SEMs show MG-PS and BCPS, and TEMs show cross section and longitudinal section of antenna and MG-PS: (panel A) multiporous grooved-surface placoid sensillum (MG-PS), a basiconic capitate peg sensillum (BCPS), and a sensillum trichodea (ST); (panel B) the rough surface of a BCPS; and (panel C) the pores on a MG-PS. TEMs of the following are shown: (panel D) a cross-section of an antenna of a female; (panel E) the epidermal cells (epd), dendrites (DE), sensillum lymph cavities (SL), electron-dense mass (edm), and the pores (P-GS-PS) of an MG-PS; (panel F) a cross-section of an MG-PS of a female *E. sophia* revealing the outer sensillum lymph (OSL), thick sensillar wall (SW), inner sensillar lymph (ISL), and dendrites (DE); (panel G) a longitudinal section of an antenna from a female *E. sophia* revealing mitochondria (mit) and mesoscutello-metanotal muscle (MMM). (2) Antennal sensilla of a female *E. sophia*. SEMs show CS, and TEMs show longitudinal section of antenna: (panel A) a longitudinal section of an antenna from a female *E. sophia* revealing dendrites (DE) and neurons (NE). SEMs of the first flagellar segment showing the following: (panel B) the grooved surface of an ST and (panels B and C) a sensilla coeloconica (CS) and coxacava.

mean basal diameter of the FL-NP was $0.90 \pm 0.16 \mu\text{m}$ in females and $0.89 \pm 0.08 \mu\text{m}$ in males.

3.2.7. Uniporous rod-like sensilla

The PO-UP were distributed over the distal end of the antennae. These sensilla had parallel, longitudinal grooves and a large apical pore, and projected from a large cuticular socket (Fig. 3B). The TEM images showed that the socket was $1.56 \mu\text{m}$ wide (Fig. 3E) and $0.75 \mu\text{m}$ deep, which was twice the depth of the ST socket ($0.37 \mu\text{m}$; Fig. 3F). The mean length and diameter of the PO-UP were $5.39 \pm 0.58 \mu\text{m}$ and $0.71 \pm 0.04 \mu\text{m}$, respectively, whereas those in males were longer and slimmer, with a mean length and diameter of $7.46 \pm 0.60 \mu\text{m}$ and $0.69 \pm 0.05 \mu\text{m}$, respectively (Figs. 3B and 6F).

3.2.8. Sensilla coeloconica

The CS were located on the third flagellar segment only (Figs. 4.2C and 5F), with only one CS per antenna. The CS projected from a pit in the cuticle. The diameter of the CS was $0.38 \mu\text{m}$ in females and $0.4 \mu\text{m}$ in males.

4. Discussion

Chalcidoidea species are very small, ranging in length from the smallest known insect (0.11 mm) to relatively large wasps (45 mm) (Heraty et al., 2003). *Encarsia* species are minute. There are 344 *Encarsia* species that have been described (Heraty et al., 2007; Noyes, 2000). These include primarily parasites of aphids, scale insects and lepidopterans (Polaszek, 1991; Williams and Polaszek,

1996), with some species used in biological control of their insect hosts. Certain *Encarsia* species, including *E. tricolor* (Huang and Loomans, 2009), *E. bimaculata* (Antony et al., 2004), *E. pergandiella* (Hunter, 1991), and *E. sophia* (Antony et al., 2003; Chen et al., 2013), are autoparasitoid insects, meaning immature stages develop as females (primary endoparasitoids) or males (secondary ectoparasitoids) on different hosts. Male *E. sophia* are thus rare, with males difficult to obtain in the wild. In our current study, we examined the antennae of both male and females.

Previous studies have been performed on the development (Antony et al., 2003, 2004) and ecology (Luo and Liu, 2011; Zang and Liu, 2007; Zang et al., 2011a, b) of *Encarsia* species. The reproductive cycles of hymenopteran parasitoids are highly host-specific (Karamaouna and Copland, 2000), with antennal sensilla aiding host-seeking behaviors. However, SEM studies of the ultrastructure of these sensilla in *Encarsia* are scarce (Wang and Huang, 2007; Zhou et al., 2013), and no TEM studies have been reported. In the current study, we used SEM to examine the antennal sensilla of male and female *E. sophia*, and TEM was used to examine the internal structure of the antennae of female *E. sophia*.

Scutellar sensilla of chalcidoideans were first examined using TEM by Romero and Heraty (2010), although such examinations of the antennae of *Encarsia* were not included. TEM analysis of cross- and longitudinal sections of female *E. sophia* antennae revealed MMM and FB that were similar to those observed in sections of the scutellar sensilla of *Aphytis melinus* (Romero and Heraty, 2010). The location of the glandular tissue beneath the cuticle in the antennae of *E. sophia* was similar to that in *Encyrtidae*, which have been

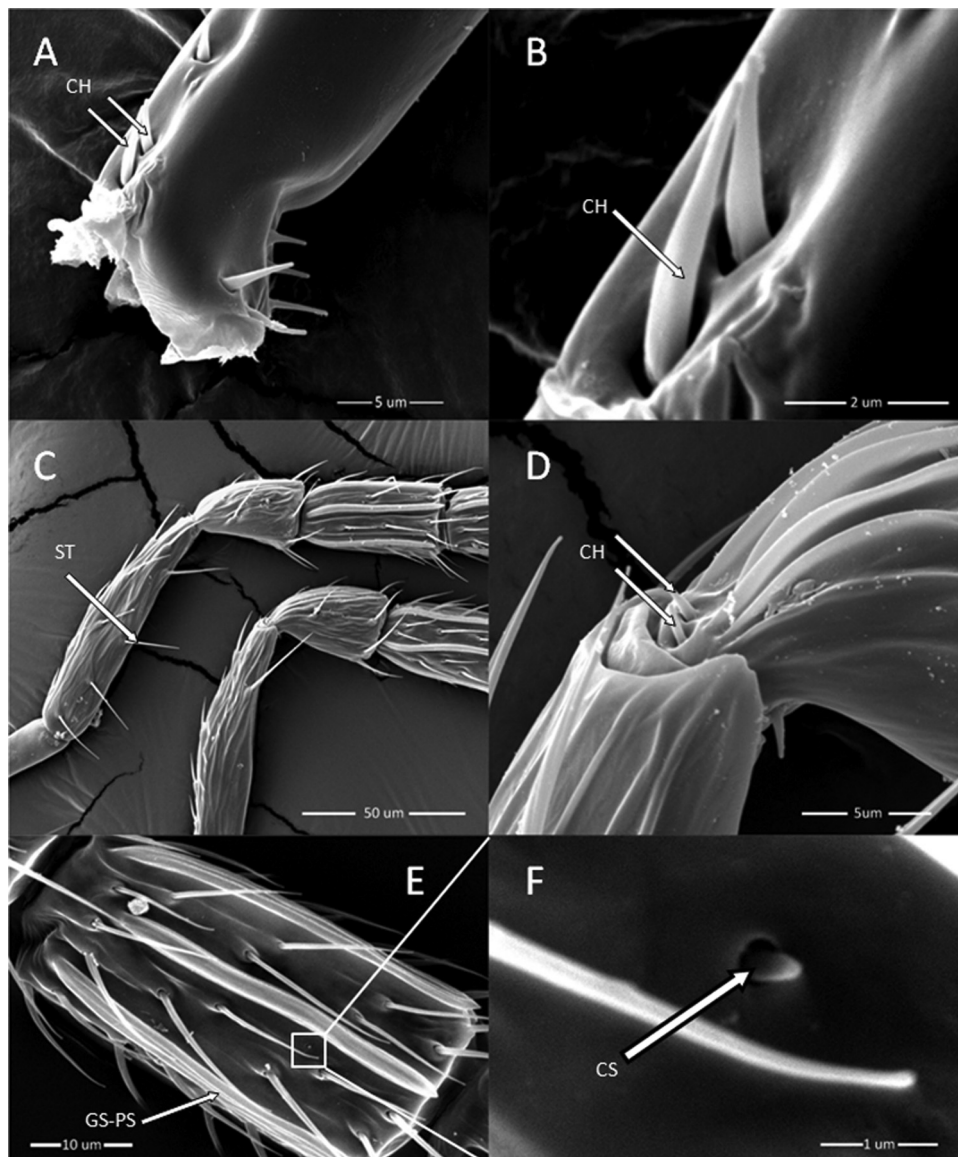


Fig. 5. SEMGs of antennal sensilla of a male *E. sophia*. SEMGs show sensilla of radicle, scape, pedicel and CS of flagellum: (panel A) a sensillum chaetica (CH) on the base of the radicle; (panel B) a smooth CH; (panel C) a sensillum trichodea (ST) on the scape; (panel D) a CH on the pedicel; and (panel E) a multiporous grooved-surface placoid sensillum (MG-PS), (panels E and F) a sensillum coeloconica (CS), and (panel F) a coxacava on the third flagellar segment. GS-PS

shown to play an important role in courtship behavior (Guerrieri et al., 2001). In addition, the pores, internal structure, and innervation of the MG-PS in *E. sophia* were similar to those of the MG-PS of other chalcidoideans, which have been shown to function in nerve conduction (Barlin and Bradleigh Vinson, 1981a).

The morphological types and distribution of the antennal sensilla of *E. sophia* were similar to those of *E. guadeloupae* (Zhou et al., 2013) and *E. amacula* (Wang and Huang, 2007). However, the MG-PS and CS differed from those of *E. guadeloupae*, which may reflect differences in the reproductive strategies used by these species and the role that sensillas play in reproductive behavior. Most insect antennae contain a basal scape, a pedicel and a flagellum; described by Chapman (Chapman, 1998) as the three basic components. The antennae of *E. sophia* contained a radicle in addition to these, and the flagellum consisted of six segments similar to those of *E. mineoi* (Viggiani and Mazzone, 1980). Previous SEM studies of the antennal sensilla of *E. asterobemisiae*, *E. olivine*, and *E. sophia* revealed similarities to those of other parasitic hymenopterans such as *Pteromalus cerealellae* (Onagbola and Fadamiro, 2008), *P. puparum*

(Dweck, 2009), *Scleroderma guani* (Li et al., 2011), *Phenacoccus manihoti* (Le Rü et al., 1995), and *Trichogramma nubilale* (Olson and Andow, 1993) Table 1.

Each sensilla reported in previous SEM studies of *E. sophia* was also identified in our study, with eight types on the antennae both of male and female. The CH were similar to those described as nonporous sensilla chaetica in *E. guadeloupae* (Zhou et al., 2013) and aporous type 4 sensilla trichodea in *P. cerealellae* (Onagbola and Fadamiro, 2008). The CH of other hymenopterans have been described as putative mechanoreceptors involved in perceiving vibrational stimuli (Romani et al., 2009). The ST identified in *E. sophia* herein lacked a pore, which suggests a mechanoreceptor function. Because STs are often the most abundant antennal sensilla, they have been assigned a variety of names. The absence of pores, the sharply pointed shape, and the longitudinally grooved shaft of the ST observed in the current study were consistent with the previously described structures of the nonporous sensilla trichodea type 1 in *P. puparum* (Dweck, 2009), the nonporous sensilla trichodea in *E. guadeloupae* (Zhou et al., 2013), and the aporous

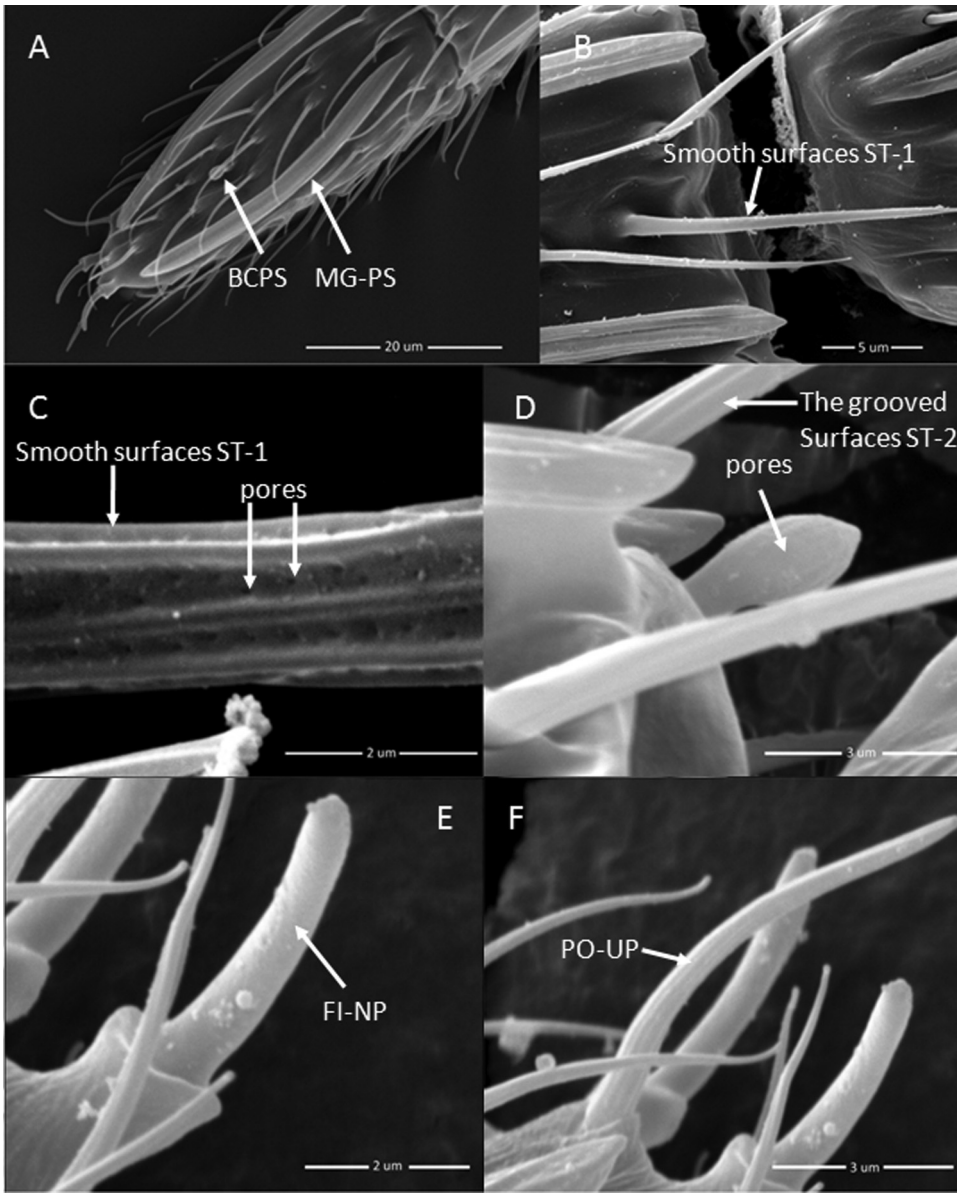


Fig. 6. SEMGs of antennal sensilla of male *E. sophia*. SEMGs show sensilla of flagellum: (panel A) a multiporous grooved-surface placoid sensillum (MG-PS) and a basiconic capitates peg sensillum (BCPS); (panel B) a smooth sensillum trichodea (ST); (panel C) the pores and grooved surface of an MG-PS; (panel D) the pores of a BCPS and the grooved surface of an ST; (panel E) a nonporous finger-like sensillum (FL-NP); and (panel F) the grooved surface and apical pore of a uniporous rod-like sensillum (PO-UP) on the sixth flagellar segment.

Table 1
The prevalence of antennal sensilla in male and female *Encarsia sophia*.

Sensilla ^a	Sex	Antennal segment ^a									Total
		RA	SC	PE	F1	F2	F3	F4	F5	F6	
CH	Female	15		4							19
	Male	14		4							18
ST	Female		26	18	33	44	49	53	71	102	396
	Male		23	25	27	43	49	57	79	89	392
BCPS	Female				1	1	1	1	1	1	6
	Male				2	2	2	2	1	1	10
MG-PS	Female				0	1	1	2	3	3	10
	Male				3	3	4	4	3	3	20
CS	Female						1				1
	Male						1				1
PO-UP	Female									6	6
	Male									2	2
FL-NP	Female									3	3
	Male									2	2

^a Abbreviations: RA, radicle; SC, scape; PE, pedicel; F1–F6, the six flagellar segments; CH, sensilla chaetica; ST, sensilla trichodea; BCPS, basiconic capitates peg sensilla; MG-PS, grooved-surface placoid sensilla; CS, sensilla coeloconica; PO-UP, uniporous rod-like sensilla; FL-NP, and nonporous finger-like sensilla.

type 2 sensilla trichodea in *P. cerealellae* (Onagbola and Fadamiro, 2008). ST are considered to be mechanoreceptors that supply information on size and shape when drumming on the surface of a host (Schmidt and Smith, 1985).

The BCPS of female *E. sophia* had a rough surface, whereas those of males had a grooved surface with pores. The male BCPS is similar to the multiporous grooved sensilla basiconica C and type I coeloconic sensilla described in *Trichogramma nubilale* (Olson and Andow, 1993) and *Cotesia* spp. (Bleeker et al., 2004), and the BCPS1 of *trichogramma australicum* girault (Amornsak et al., 1998). The presence of pores in the BCPS of male *E. sophia* suggests that they function either as olfactory receptors (Baaren et al., 1996; Bleeker et al., 2004), hygroreceptors, thermoreceptors, or mechanoreceptors (Pettersson et al., 2001). The function of the BCPS of female *E. sophia* may be similar to that of nonpunctate BCPS, such as those of *P. cerealellae*, which are thought to function as thermoreceptors or hygroreceptors (Onagbola and Fadamiro, 2008).

MG-PS have been identified on the antennae of various hymenopterans (Dweck, 2009; Dweck and Gadallah, 2008; Olson and Andow, 1993; Richerson et al., 1972; Zhou et al., 2013). In our study, the MG-PS of the male and female *E. sophia* possessed many grooves, each of which contained pores similar to those described for *Tetrastichus hagenowii* (Hymenoptera: Eulophidae) (Barlin et al., 1981b). In contrast, the MG-PS of *E. guadeloupae* lacked grooves, while functioning in olfaction, (Barlin and Bradleigh Vinson, 1981a; Bleeker et al., 2004; Steinbrecht, 1984). We also observed that the number of MG-PS in female *E. sophia* was less than that observed in males. This sex-biased prevalence of MG-PS was not observed in *P. cerealellae* (Onagbola and Fadamiro, 2008), where this structure has been suggested to play an important role in host location and the detection of host-related semiochemicals (Bleeker et al., 2004; Dweck, 2009; Onagbola and Fadamiro, 2008; Zhou et al., 2013).

The FL-NP in *E. sophia* exhibited a morphology characterized by a nonporous surface with pimple-like structures. These were more abundant in females than in males, and differed from the surface of the PO-UP. Previous studies have suggested that FL-NP may be mechanoreceptors (Altner et al., 1981; Hunger and Steinbrecht, 1998; Romani et al., 2009). The PO-UP are located at the tip of the antennae in *E. sophia*, suggesting that they might be mechanoreceptors that operate in direct contact with the host during feeding or oviposition (Altner et al., 1981; Romani et al., 2009). Similar mechanoreceptors are thought to function in host recognition and host acceptance in other hymenopterans (Weseloh, 1972; Zhou et al., 2013). In addition, the pore in the tip of the PO-UP of *E. sophia* suggests a gustatory function (Barbarossa et al., 1998; Isidoro et al., 1996).

Only one type of CS was identified on the antennae of *E. sophia*, and were located on the third flagellar segment in both males and females. CS have been described as “pit organs” because they are recessed in deep cuticular depressions (Wcislo, 1995). The low abundance of CS in *E. sophia* confounded our efforts to assess their function, and no function has been assigned to CS in other *Encarsia* species. However, there are suggestions these might function as thermoreceptors or hygroreceptors (Altner et al., 1983; Bleeker et al., 2004). Hygroreceptor function would indicate that the CS is instrumental in determining infections in the host, and therefore whether the host would be suitable for spawning eggs. In general, antennal sensilla can be said to function as various types of chemoreceptor or mechanoreceptor (Li et al., 2009). The MG-PSs in male outnumbered those in female *E. sophia*, perhaps aiding mate selection particularly in males. The pores of the MG-PS of *E. sophia* may play an important role in chemoreception from the inner and outer structures, and the CH and ST might function more as mechanoreceptor. Sensillum aid the wasp in finding and parasitizing a host; the host most likely to give successful incubation of eggs. The findings of our study of the antennal sensilla of

E. sophia furthers efforts to understand the host-selection behaviors and reproductive strategies of this important parasitoid of crop pests.

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