Types, Morphologies and Distributions of Antennal Sensilla of Quadrastichus erythrinae (Hymenoptera: Eulophidae)

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TYPES, MORPHOLOGIES AND DISTRIBUTIONS OF ANTENNAL SENSILLA OF QUADRASTICHS ERYTHRINAE (HYMENPTERA: EULOPHIDAE)

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ABSTRACT

To uncover the relationship between chemical receptors and behaviors of the erythrina gall wasp (EGW), Quadrastichus erythrinae Kim (Hymenoptera: Eulophidae), and to elucidate the chemical connections between the parasite and the host plant, the present study focused on determining the types, morphologies and distributions of the various antennal sensilla of adult EGW. With scanning electron microscopy and 3-dimensional microscopy, we found that the antennae of EGW adults have 6 kinds of sensilla, namely, sensory pore sensilla, chaetica sensilla, multiporous plate sensilla, trichoid sensilla, basiconic capitate peg sensilla and uniporous trichoid sensilla. Both the male and female wasps have these 6 kinds of sensilla. However the types and numbers of sensilla on the funicle and clava differed between males and females, but such a difference was not seen on the scape and pedicel between the 2 sexual genders. We found one kind of sensillum located on the end of pedicel of Q. erythrinae Kim that has not been described previously. The results of our research may aid use of EGW in the biological control of undesirable Erythrina spp. trees.

Key Words: antennal scanning, Quadrastichus erythrinae Kim, sensilla, ultrastructure, morphology

Insects rely on the presence of chemical and physical factors to adapt to the environment during food selection, feeding, courtship, mating, breeding, inhabiting, defense and migration. Antennae of insects, in particular those of parasitic Hymenoptera, play a key role in perceiving external information (Weseloh 1972; Vinson et al. 1986; Bin et al. 1989; Isidoro et al. 1996). Haussner (1880) was the first to study the olfactory function of the antennae of insects, and he described the anatomical structures of orthopteran, neuropteran, hemipteran, dipteran, lepidopteran and hymenopteran antennae. Schneider (1964) used electrophysiological methods to success-
fully record in vitro the olfactory function of the antenna of *Bombyx mori* (L.) (Bombycidae), and to verify that the antennae of insects have an olfactory function; and this opened a way to investigate odor perception by antennae. Steinbrecht (1971) studied antennal morphology with scanning electron microscopy (SEM) and speculated that trichoid sensilla and basiconic sensilla had an olfactory function. Kaissling (1974) recorded the reactions of the single olfactory receptor cell of a trichoid sensillum by a method that later evolved into single cell recording (SCR) technology. Starting from the 1970s, several studies have characterized the antennal sensilla of various species of parasitic wasps using electron microscope techniques (Norton & Vinson 1974; Barlin & Vinson 1981; Barlin et al. 1981; Wibel et al. 1984; Navasar & Elzen 1991; Olson & Andow 1993; Isidoro et al. 1996; van Baaren et al. 2007; Amornsak et al. 1998; Ochieng et al. 2000; Pettersson et al. 2001; Bleeker et al. 2004; Das et al. 2011). Many researchers found that there are peculiar cuticular structures often located on variously modified antennomeres, associated with the pores (gland outlets) (Bin et al. 1999; Isidoro et al. 1996; Romani et al. 1999; Sacchetti et al. 1999; Guerrieri et al. 2001). Many of these studies also reported sexual dimorphism in the structures and types of antennal sensilla (Wibel et al. 1984;Navasaro & Elzen 1991;Amornsak et al. 1998;Bleeker et al. 2004).

Zhang et al. (2007) reported the ultrastructure of antennal sensilla of the erythrina gall wasp (EGW) (*Quadrastichus erythrinae* Kim (Hymenoptera: Eulophidae), but their work did not record the number of sensilla and their positions on each antennal segment, and they also missed 1 kind of sensillum. In order to explore habitat selection of EGW adults and their behavioral responses to the host plant, we conducted observations on the ultrastructure of the antennal sensilla of EGW adults with SEM and 3-dimensional microscopy, and sought to elucidate the types, morphological features, numbers and distribution characteristics of the different sensilla. We believe such information can help explain or clarify mating and oviposition behaviors of the parasitic wasp, and the functions of various sensilla. Moreover the roles of these sensilla in parasitoid behavior might be suggested after the functional characterization of the sensilla and successful completion of related behavioral studies.

**Materials and Methods**

Galls containing EGW were collected from *Erythrinavariegata* L. var. *orientalis* (L.) Merr. (Fabales: Fabaceae) trees planted along the pavement in University Town of Guangzhou. The collected galls were taken to the laboratory and kept in a growth cabinet at 25 °C, 75% RH and 12:12 h L:D. The antennae were removed from newly eclosed wasps and dried in the air. Then they were mounted on the objective table using conductive adhesive tape, coated with rhotanium by ion beam sputtering (BAL-TEC SCD500 ion sputter, Leica Company, Switzerland), and observed with a XL 30 environmental scanning electron microscope (FEI Company, USA). For observation in three-dimensional microscopy, the whole wasps were preserved in 75% ethanol and directly observed with a 3D super depth microscopic system (Keyence Corp., Japan).

The sensilla were classified according to the nomenclature systems of Schneider (1964) and Zacharuk (1985). The micrographs were taken from different angles and the numbers of sensilla were counted based on the micrographs. Mean numbers of sensilla were calculated from 3 specimens. The images were processed by Photoshop 7.0 and statistical analysis was performed by SPSS 13.0 software (SPSS Inc., Chicago, Illinois, USA).

**Results**

The antennae of the EGW adults were geniculate and inserted on the head at the lower middle part of the face. Each antenna was comprised of a scape, a pedicel and a flagellum (Fig. 1A).

The antenna of the EGW adult female had 9 segments and it had a light brown color; the number of flagellomeres in the anellus, funicle and clava were 1, 3 and 3, respectively; the scape presented a slightly flattened column; the length of pedicel was 2 to 2.5 times its width; the funicular segments were equal in length and width; the 3rd clava was thicker than the funicle, with the length being equal to the sum of the 2nd and 3rd funicles; the length and width of the 1st claval segment were equal; the transverse section of the 2nd claval segment was wider than the longitudinal section; the 3rd claval segment was contracted into a circular cone and a bent chaetica sensillum was located at its tip (Fig. 4A).

The antennae of the EGW adult male had 10 segments, which were white in color. The funicle had 4 segments and its 1st segment was shorter than the other segments; the clava had 3 segments that were thicker than those of the funicle, and with the length of the clava equaled the sum of the 2nd and 3rd funicular segments; the length and the width of 1st claval segment were equal; the transverse section of the 2nd claval segment was broader and the 3rd claval segment was contracted into a circular cone; there was 1 chaetica sensillum (Fig. 3L) at the tip of the 3rd segment.

The antenna of an adult EGW had 6 kinds of sensilla, namely, sensory pore (SP), chaetica sensilla (CS), multiporous plate sensilla (MPS), trichoid sensilla (TS), basiconic capitate peg sensilla
Sensory Pores (SP)

Sensory pores occurred on the longitudinal distal surface of the pedicel near its connection with the anellus. Eleven to 14 sensory pores were regularly arranged in a circle around the main axis of the pedicel. The distance between adjacent pores varied from 1.25-2.5 μm and the diam of each pore varied from 1-1.25 μm (Fig. 2C and Fig. 3E).

Chaetica Sensilla (CS)

Each chaetica sensillum was a “thorn-shaped”, more rigid than a trichoid sensillum (TS), and with an acute apex. Chaetica sensilla had longitudinal stripes and were set in a hollow base. CS were divided into CS I and CS II. CS I (Fig. 2A-D, Fig. 3A-D, and Fig. 4B) were...
thick and short; with bearing angles that varied greatly, and some projected from the antennal surface at a vertical angle of about 90 degrees, while others lay horizontally along the antennal surface, such as those on the scape and on the pedicel. In comparison with a CS I, the CS II sensillum (Fig. 2E; Fig. 3F, H and J) was longer, and the bearing site was raised above the surface of antenna; most of CS II lay horizontally along the antennal surface; the root diam varied from 1.25-1.87 μm; the CS II sensillum was twice as long as the CS I; there were many CS II sensilla distributed on the antenna with more proximally than distally.

Multiporous Plate Sensilla (MPS)

There were 2 types of MPS on the antenna of adult EGW: MPS I (Fig. 2F, H, J-L; Fig. 3I, K; Fig. 4C) and MPS II (Fig. 2F, H, J-L; Fig. 4D; Fig. 1B). The MPS I was wider than the MPS II; almost all MPS I were attached to the surfaces of the funicle and the clava, and only the tips of MPS I sensilla were detached with the surfaces of their areas of distribution; the tip was round, blunt and thick with a smooth surface, and varied from 47.5-57.5 μm and 7.5-5 μm in length and width, respectively. MPS I sensilla were found distributed on the funicle and clava of the EGW adult female. On the funicle of the antenna of the EGW adult female, there was only 1 MPS I on each segment of the funicle, and on the lateral surface of funicle they were parallel to the longitudinal axis of antenna; on the clava of the EGW adult female, there was at least 1 MPS I on each segment. Only 1 MPS I occurred on each segment of the funicle of the EGW adult male at an angle with the longitudinal axis of antenna of the funicle, i.e., with tip of the MPS I extending obliquely outward, but no MPS I was seen on the clava of the adult male. In comparison with the MPS I, the section of the MPS II sensillum rising above the antennal surface accounts for a large proportion of the whole sensillum, i.e., about three fourth or one half of whole sensillum, and the tip was sharper than the tip of the MPS I.

The MPS II sensillum was more slender and longer than the MPS I sensillum, slightly curved, with a smooth surface; and the average length and width of various MPS II sensilla varied from 37.5-49.45 μm and 4.50-3 μm, respectively. MPS II sensilla were distributed on the funicle and clava of the antenna of the adult female, but only on the clava of the adult male, and 1-3 MPS II were found spread over the back of the clava of the adult male.

As for the MPS distribution on each segment of the clava of the adult female, there was 1 MPS I and 2 MPS II on the back of the 1st claval segment. There was no MPS sensillum on the ventral side of clava. One or 2 MPS II sensilla were found on the back of the 2nd claval segment and 1 MPS I was found on the ventral side. There were 2-3
MPS II sensilla on the 3rd clava. No MPS II was seen on the front side, while 2 MPS II were borne on both sides. On the funicle there was 1 MPS I and 1 or 2 MPS II borne laterally on the back of each funicular segment of the adult female.

The number of MPS sensilla distributed on the antenna of the female was greater than on the male. The number of MPS I sensilla on the antenna of female was fewer than the MPS II, while the numbers of MPS I and MPS II on the antenna of male were equal.

Trichoid Sensilla (TS)

Trichoid sensilla were mainly distributed on the clava of the antenna of adult males and females, and some were spread over the 3rd and 4th funicular segments both of the adult male and the adult female. No TS was seen on the scape, the pedicel, nor on the 1st and 2nd funicular segments. The characteristics of TS were as follows: smooth surface, flexible, slender, 30°-45° tilting from the antennal axis, blunt end, pointing...
toward the tip of the antenna. The length of TS varied from 24.5-45 μm (Figs. 2J, 2L; and Figs. 3H, 3J and 3L).

Basiciconic Capitate Peg Sensilla (BCPS)

Basiciconic capitate peg sensilla are each comprised of a spherical head and a short peg. The base of short peg was inserted in a round depression of the cuticle. No BCPS sensilla were seen on the back of antenna, they were distributed only on the funicular segments and ventral side of claval tip of the female. They were also distributed on all the funicular segments in addition to the 1st segment of the funicle and on the tip and ventrolateral surface of the clava of the male. There were 3-5 BCPS sensilla on each segment where they occurred (Fig. 2E, G, I and K; Fig. 3G; Fig. 4E).

Uniporous Trichoid Sensilla (UTS)

The uniporous trichoid sensillum lies on the central protuberance of the extreme end of the antenna of adult males and females. Only 1 UTS sensillum was present on each antenna, bending over the ventral side of antenna. The UTS on the antenna of the adult female was longer than on the adult male (Fig. 2K, Fig. 3L and Fig. 4A).

Distribution and Numbers of Antennal Sensilla of Adult Males and Females

As seen from Table 2, the types and numbers of sensilla on the scape and pedicel were similar, but the numbers were different in the various segments of flagellum.

On the clava, the CS II sensilla were distributed similarly on the antenna of adult females and adult males. The numbers of CS II on the 1st claval segment of the female and the male were equal. The last 2 segments of the clava did not have CS II.

On the funicle, the number of CS II on the 1st segment of antenna of adult females was equal to the number on the 2nd segment of the male. The numbers of CS II on the last 2 segments of antenna of female were found to be 2 times greater than on the antenna of male. The numbers of MPS I on the funicular segments of adult males and females were similar, and only 1 MPS I was present on each segment. The distribution of MPS I on the clava differed greatly between the sexes. There was more than one MPS I on the clava of the female, but there was no MPS I on the clava of the male. The numbers of MPS II on the antennae of adult males and females differed greatly. On the funicle, there was no MPS II on the antenna of the male, while there was at least 1 MPS II on each of the funicular segments of the female.
TABLE 2. MEAN ± SE OF NUMBER AND DISTRIBUTION OF EACH OF THE VARIOUS SENSILLA ON THE ANTENNA OF ERYTHRINA GALL WASP FEMALES AND MALES.

<table>
<thead>
<tr>
<th>Types of sensilla</th>
<th>Sex</th>
<th>Scape</th>
<th>Pedicel</th>
<th>Funicullar segment</th>
<th>Claval segment</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1st</td>
<td>2nd</td>
</tr>
<tr>
<td>Sensory Pore</td>
<td>F</td>
<td>10-17 (12.7)</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Sensory Pore</td>
<td>M</td>
<td>9-16 (12.7)</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Chaetic Sensilla I</td>
<td>F</td>
<td>33-36 (34.7)</td>
<td>19-22 (20.7)</td>
<td>1-2 (1.7)</td>
<td>—</td>
</tr>
<tr>
<td>Chaetic Sensilla II</td>
<td>M</td>
<td>28-49 (39.0)</td>
<td>22-24 (23.3)</td>
<td>14-18 (16.3)</td>
<td>18-22 (20.3)</td>
</tr>
<tr>
<td>Chaetic Sensilla I</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td>Chaetic Sensilla II</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Chaetic Sensilla II</td>
<td>F</td>
<td>12-14 (13.0)</td>
<td>18-21 (19.7)</td>
<td>8-12 (10.0)</td>
<td>9-17 (13.0)</td>
</tr>
<tr>
<td>Chaetic Sensilla II</td>
<td>M</td>
<td>12-14 (13.0)</td>
<td>18-21 (19.7)</td>
<td>8-12 (10.0)</td>
<td>9-17 (13.0)</td>
</tr>
<tr>
<td>Multiporous Plate Sensilla I</td>
<td>F</td>
<td>1-2 (1.7)</td>
<td>0-2 (1.3)</td>
<td>1</td>
<td>0-2 (1.3)</td>
</tr>
<tr>
<td>Multiporous Plate Sensilla I</td>
<td>M</td>
<td>1-2 (1.7)</td>
<td>0-2 (1.3)</td>
<td>1</td>
<td>0-2 (1.3)</td>
</tr>
<tr>
<td>Multiporous Plate Sensilla II</td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Multiporous Plate Sensilla II</td>
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<td>1</td>
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<tr>
<td>Multiporous Plate Sensilla II</td>
<td>F</td>
<td></td>
<td></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Multiporous Plate Sensilla II</td>
<td>M</td>
<td></td>
<td></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Trichoid Sensilla</td>
<td>F</td>
<td>4</td>
<td>4</td>
<td>—</td>
<td>1-2 (1.7)</td>
</tr>
<tr>
<td>Trichoid Sensilla</td>
<td>M</td>
<td>4</td>
<td>4</td>
<td>—</td>
<td>1-2 (1.7)</td>
</tr>
<tr>
<td>Basiconic Capitate Peg Sensilla</td>
<td>F</td>
<td>2-3 (2.7)</td>
<td>1-5 (3.3)</td>
<td>3</td>
<td>1-3 (2.3)</td>
</tr>
<tr>
<td>Basiconic Capitate Peg Sensilla</td>
<td>M</td>
<td>2-3 (2.7)</td>
<td>1-5 (3.3)</td>
<td>3</td>
<td>1-3 (2.3)</td>
</tr>
<tr>
<td>Uniporous Trichoid Sensilla</td>
<td>F</td>
<td></td>
<td></td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Uniporous Trichoid Sensilla</td>
<td>M</td>
<td></td>
<td></td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

Note: By carefully examining 3 antennae of females, we calculated the mean number of sensilla of each kind, and then we statistically analyzed the data of antennal sensilla on the flagellae of both EGW adult females and male.

“—” indicates that there is no such sensillum.
There was more than one MPS II on each of the claval segments of the female, and 2 were located on the 3rd segment, but only 1 was seen on each claval segment of the male. The numbers of TS and BCPS on the flagellomeres of the antennae of the male and the female were similar, and the numbers of TS increased progressively with each successive flagellomere. In contrast the numbers of BCPS decreased progressively with each successive flagellomere in both the male and the female.

**DISCUSSION**

The antennae of EGW adults bear 6 types of sensilla that are common on the antennae of other hymenopteran species (Wang et al. 2007; Bleecker et al. 2004; Cônsoli et al. 1999; Xu et al. 2000), but different authors have used different names to describe the various sensilla. The types and numbers of sensilla on the scape and pedicel were equal, but they differed among the segments of the flagellum. For instance, the trichoid sensillum mentioned in our study is called the thick-walled chemical sensillum (Zou et al. 2009).

We found 11-14 circular holes situated where the pedicel connects to the anellus. The morphology of the hole was similar to that on the antenna of *D. isaea* females found by Zou et al. (2009). We observed that there are such sensilla in the antennal pedicel of both adult EGW males and females. Dai (1988) mentioned that the pedicel surface of antenna of oophagous *Trichogramma* had obvious longitudinal reticulated mottles and form a circular fossa at the end. Zou et al. (2009) speculated that the fossa might be connected with a structure inside the sensory pore, which was able to perceive air flow and sound. This sensory pore, found between the antennal pedicel and the anellus, is difficult to observe. Since no special study has been done on this sensory pore, its functions need further in-depth study.

Except for the anellus and the last 2 segments of clava, chaetica sensilla are widely distributed on the antennae of EGW adult males and females. The CS sensilla on the various segments have different forms, which may indicate that different segments have different functions. The CS I sensillum is a typical mechanical sensillum, mainly distributed on the scape and pedicel. Possibly it detects changes of antennal position. A similar sensillum also exists on the antenna of *Semialalia undecimnotata* Schneider (Isidoro et al. 1996) and *Monochamus alternatus* Hope (Dai et al. 1990). CS II resembles the CS of *Aprostocetus prolixus* and *Aprostocetus fukutai* (Wang et al. 2007), which is borne on the antennal flagellum. The wall of the CS sensillum is thin, has no hole, and thus it likely is a mechanical sensillum (Wang et al. 2007).

The multiporous plate sensilla on the antenna of EGW were similar to those of female *D. sisaea*; the MPS I sensillum of EGW was similar to that of female *T. hagenowii* (Schneider 1964) and female *T. schoenobii* (He 1984); and the MPS II of EGW was similar to that of female *Torymus warreni* (Barlin & Vinson 1981). Cônsoli et al. (1999) named such sensilla as MPS. Some authors have described these structures as olfactory sensilla (Barlin & Vinson 1981; Dai et al. 1990). Doutt (1964) believed that parasitic wasps utilized MPS to check long-distance information and substances from the host. Not only was the number of MPS on the antenna of female EGW larger than on the male, but also their types and positions were different. Whether such differences pertain to host specificity requires a broader study.

We observed that the TS of the antennae of EGW adults resembled the thick-walled chemical sensilla of *D. sisaea* (Zou et al. 2009), except for being longer than the thick-walled chemical sensilla. It also resembled the 2 kinds TS II of *Aprostocetus prolixus* described by Wang et al. (2007). The TS are the most numerous on the clava of the EGW. In particular, the TS take up the largest proportion of all sensilla on the clava of male EGW, and we found that the TS on the 2nd and 3rd claval segments of EGW males were longer than on other parts. We observed that the surface of the TS sensillum was smooth and had no notch, hole and hair, thus it was not like the 3 types summarized by Wang et al. (2007). Research has proven that the TS sensillum has many functions in the Cerambycidae and is an important organelle for insects to perceive sex pheromones (Wang et al. 2007). Therefore, whether the TS on the antenna of EGW has other functions requires further elaborate study.

The basiconic capitate peg sensillum is also called sensillum ampullaceum and capitate sensillum (Wang et al. 2007). BCPS probably have many kinds of olfactory functions. Olfactory functions are dependent upon the thickness of the sensillum wall and the presence of pores in the wall (Wang et al. 2007). In comparison with a thin-walled sensillum, the thick-walled sensillum is more selective to special chemical substances, such as a pheromone (Cônsoli et al. 1999). A thick-walled sensillum has holes, is sensitive to odor and carbon dioxide, and is able to perceive temperature and humidity (Miller 1972). Different from the situation in other chalcids, we found that the BCPS were only distributed on the distal part of the segments of the funicle and the clava of EGW females, while they were distributed in the ventral side and lateral surface of segments of the funicle and clava except for the first funicular segment of the EGW male. Therefore, whether BCPS has certain specific functions needs further study.
The UTS of EGW were similar to those of *D. isaea* (Zou 2009) and oophagous *Trichogramma* spp. (Gong et al. 2004), and were distributed on the antennae of both EGW adult males and females. The UTS in EGW females were thinner and longer than those of EGW males. Both had a base diam of approximately 1.25 μm and a length of approximately 12.5 μm, resembling CS I sensillum, but with a larger curve than the CS I sensillum. The UTS on the antenna of EGW males were short, with a diam of approximately 1.3 μm and a length of approximately 5 μm. Each UTS was surrounded by other sensilla in both females and males. On the antenna of the EGW female, each UTS was bracketed by 2 MPS II – one at each side; on the antenna of EGW male, each UTS was bracketed by TS. The UTS has a taste function (Zou et al. 2009), but in our study we didn’t find holes in the UTS and each antenna had only one UTS. Therefore, the precise function of UTS still needs further study.

The antennae of EGW play important roles in habitat positioning, host orientation, mating, oviposition and courtship and in the defense against parasitic hymenopterans (Miller 1972). Some researchers have researched and exploited the morphology, distribution and functions of the sensilla on the antennae of parasitic wasps, and have utilized electrophysiological results to gain in-depth understanding and to uncover the relations between chemical receptors and behaviors of parasitic wasps. Likewise they have elucidated chemical connections between insects and plants. All of these discoveries are providing a theoretical basis for improving biological control programs.

Compared with parasitic wasps, the phytophagous EGW has fewer sensilla and the positions of some sensilla are different. The reason is that EGW is strongly host-specific, being parasitic on harmful *Erythrina* spp. trees, and EGW moves around on its host after eclosion, so that it has no need to seek extensively for its host. Therefore, EGW has few sensilla specialized to perceive the host at long distance. We observed that there are few MPS II on the antenna of the EGW male, which has only 1 MPS I on the funicle; although, this study cannot directly confirm the functions of MPS I and MPS II without physiological characterization of the different sensilla types, we may deduce—based on the differences of the MPS on EGW males and females, and on the biological characteristics of EGW—that the MPS II may sense the sex pheromone, and the MPS I may sense plant volatiles. Therefore, since, the EGW female needs to select a suitable site to oviposit, the sensilla are needed to seek and receive those volatiles of the host that emanate especially from sites suitable for oviposition. The task of the EGW male is to locate the female to mate, and therefore the male needs sensilla to perceive the sex pheromone. Because EGW males are in close proximity to females, the capacities of sensilla of the male to seek for the places sought by the female may be modest. The structures and functions of the sensilla of EGW adults still need to be further investigated by immuno-electron microscopy and by single-cell receptor potentiometry. The functions of the different sensilla still need to be better elucidated and verified.

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