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Antennal Sensilla and Sexual Dimorphism of the Parasitoid *Trichospilus pupivorus* (Hymenoptera: Eulophidae)

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Abstract: Sensory structures (sensilla) of insects are present in high number in the antennae are important for perceiving environmental cues. Thus, sensilla play an important role in the localization, discrimination, and acceptance of a possible host by parasitoid insects. The sensilla, classified according to their shape, size, and distribution, may also show sexual dimorphism in insects. The types and distribution of antennal sensilla in female and male parasitoid *Trichospilus pupivorus* (Ferriere, 1930) (Hymenoptera: Eulophidae) were evaluated. *T. pupivorus* females had longer antennae than males. Both males and females have ten sensilla types with higher abundance of placoid sensilla in females, which suggest a possible functional dimorphism.

Key words: antennal sensilla, parasitoids, scanning electron microscopy, *Trichospilus pupivorus*

INTRODUCTION

Antennae are important appendices with sensory structures called sensilla (Norton & Vinson, 1974; Bleeker et al., 2004) that are found in higher concentration in this organ than in other insect body parts (Bleeker et al., 2004; Bruyne & Baker, 2008; Chen & Fadamiro, 2008). Sensilla are structures composed of neurons and the accessory thecogen, trichogen, and tormogen cells (Keil, 1997). Sensilla are characterized as mechano-, chemo-, thermo-, and hygroreceptors (Van Baaren et al., 2007; Zhou et al., 2011; Ahmed et al., 2013) distinguished by their morphology (Onagbola et al., 2009).

Sensilla have important specific functions in the selection, localization, discrimination, and acceptance of a host by parasitoids (Keil, 1997; Zhang et al., 2014). Moreover, sexual dimorphism of antennae by type, distribution, and abundance of sensilla has been reported for different insects (Norton & Vinson, 1974; Barlin & Vinson, 1981; Delvare & Lasalle, 1993; Chen & Fadamiro, 2008; Onagbola et al., 2009) because sensilla play an important role in recognizing partners for mating (Weseloh, 1972; Battaglia et al., 2002) and to localize hosts (Van Baaren et al., 2007).

The morphology of antennal sensilla has been described for several parasitoid species (Bleeker et al., 2004; Dweck & Gadallah, 2008; Zhou et al., 2013*a*, 2013*b*). These studies have provided important data on antennal sensilla of these insects, but detailed data of these structures for other species are still necessary. *Trichospilus pupivorus* (Ferriere, 1930) (Hymenoptera: Eulophidae) is an endoparasitoid from Southeast Asia (Bouček, 1976; Ubaidillah, 2006; Muralimohan & Srinivasa, 2008) with the potential to control insect pests (Tavares et al., 2011), such as *Opisina arenosella* Walker (Lepidoptera: Xyloryctidae) and *Thagona tibialis* Walker (Lepidoptera: Lymantriidae) pupae (Muralimohan & Srinivasa, 2008; Tavares et al., 2011).

The general habit of *T. pupivorus* may suggest its application to control Lepdoptera pest species, and, the knowledge of the antennal characteristics can help to understand the behavioral aspects of this natural enemy. This study provides the first description of the antennal sensilla of the parasitoid *T. pupivorus* males and females

MATERIALS AND METHODS

Insects

Females and males of *T. pupivorus* were obtained from a culture in the Laboratory of Biological Control of Insects at the Universidade Federal de Viçosa in Minas Gerais State, Brazil.

Scanning Electron Microscopy

Ten adults of both sexes of *T. pupivorus* newly emerged were cryo-anesthetized at −20°C for 5 min and subsequently decapitated with scissors. The antennae attached to the head

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were transferred to Zamboni fixative solution (Stefanini et al., 1967) for 24 h, dehydrated in a graded ethanol series (70, 80, 90, 95, and 100%), and transferred to hexamethyldisilazane for 10 min and air dried. Then the samples were gold covered (20 nm) and examined with a scanning electron microscope LEO 1430 VP (Carl Zeiss, Jena, Germany) at 15 kV and 15 mm working distance in the Nucleus of Microscopy and Microanalysis at the Federal University of Viçosa.

Terminology of Sensilla

Sensilla were identified and named based on their external morphology according to the nomenclature proposed by Zhou et al. (2013*a*), previously based on the terminologies of Amornsak et al. (1998).

Data Analysis

The antennal size and the sensilla morphology were analyzed at the dorsal and ventral antennal surfaces for both sexes of *T. pupivorus*. Antennae were measured from images obtained in the scanning electron microscope using Image-Pro Plus and data submitted to nonparametric Mann–Whitney *U* statistical tests at 5% significance level using SPSS software (version 22.0).

RESULTS

Antennae of both male and female *T. pupivorus* were located frontally on the head between the compound eyes and were of the geniculate type, with eight antennal segments. They had a radicula, a long scape, a pedicel, and a flagellum with a funicle with two antennomers and a terminal clava with three antennomers.

Antennae of *T. pupivorus* were longer in females (473 ± 6.39 μm) than in males (338 ± 6.26 μm) (Table 1). The scape was the largest antennal segment in both sexes of *T. pupivorus*. Females had a longer scape length (167 ± 2.64 μm) than males (119 ± 88 μm). However, the scape width was smaller in females (29.49 ± 0.74 μm) compared with males (52.83 ± 1.51 μm) (Table 1; Figs. 1a, 1b). Females had a longer pedicel (74.66 ± 1.83 μm) than males (58.67 ± 1.98 μm), although their pedicel was narrower (32.93 ± 0.40 μm) than in males (35.83 ± 0.52 μm) (Table 1; Figs. 1a, 1b).

The antennal flagellum in *T. pupivorus* was divided in a funicle (F1 and F2) and a terminal clava (three antennomers, C1, C2, and C3). Females had longer flagella (235.28 ± 4.77 μm) than males (154.17 ± 3.04 μm) (Table 1; Fig. 1). Similar results were found for the clava of females (142.34 ± 0.88 μm) compared with males (94 ± 1.79 μm). The size (length and width) of the three antennomers in the antennal clava decreased from C1 to C3 in both sexes (Table 1; Figs. 1a, 1b). However, all antennomers were longer in females (Table 1; Fig. 2).

Ten types of sensilla were distributed on antennae of *T. pupivorus* males and females: three types of trichodea sensilla (TS-1, TS-2, TS-3), four types of basiconic sensilla (BS-1, BS-2, BS-3, and BS-4), finger-like sensilla (FL), *sensilla chaetica (CH), and sensilla placoid (PS).*

Trichodea sensilla were the most abundant and found in all antennal segments of both sexes of *T. pupivorus* (Fig. 3). These sensilla were long, with sharp tips and widely distributed in the scape, pedicel, and flagellum. Based on morphology, the trichodea sensilla were classified into three types. The TS-1 was found in the flagellum and was characterized by a smooth and slightly bent tip. The TS-2 type was found in all antennal segments and was long and curved with a tapered tip without curvature. The TS-3 was short with a tapered end and a strong curvature at the apex and was found in the pedicel and in some segments of the antennal flagellum of *T. pupivorus*.

Four types of BS were found distributed on the flagellum of both sexes of *T. pupivorus* (Fig. 4*). The* BS-1 was characterized by small pouches, inserted around the base of a depression in the cuticle (Figs. 4a, 4b). The BS-2 was similar to a long cuticular finger with a curved tip (Fig. 4a). The BS-3 was smaller than the BS-2 and located in a cuticular depression, narrower in the base than in the tip (Figs. 4a, 4c). The BS-4 were similar to BS-2, but with a mild curved tip (Fig. 4a).

Table 1. Length and Width (Mean ± SE, $n = 10$) of Antennal Segments in Males and Females of *Trichospilus pupivorus* (Hymenoptera: Eulophidae).

	Length		Width	
Antennal Segments	Female	Male	Female	Male
Whole antennae	473.73 ± 6.39a	338.18 ± 6.26b	–	–
Scape	167.33 ± 2.64a	119.88 ± 3.42b	29.49 ± 0.74b	52.83 ± 1.51a
Pedicel	74.66 ± 1.83a	58.67 ± 1.98b	32.93 ± 0.40b	35.83 ± 0.52a
Flagellum	235.28 ± 4.77a	154.17 ± 3.04b	–	–
Clava	142.34 ± 2.50a	94.72 ± 1.79b	–	–
Funicle 1	40.78 ± 0.88a	32.76 ± 1.65b	37.36 ± 1.01a	36.51 ± 0.59a
Funicle 2	40.84 ± 1.27a	25.86 ± 0.64b	39.21 ± 0.82a	38.52 ± 0.56a
Clava 1	36.42 ± 1.32a	27.03 ± 0.62b	40.90 ± 0.55a	36.66 ± 0.57b
Clava 2	31.19 ± 0.67a	22.49 ± 0.84b	33.37 ± 0.77a	33.92 ± 1.34a
Clava 3	75.10 ± 1.41a	45.27 ± 0.98b	25.68 ± 0.54a	26.24 ± 0.86a

Means followed by different letters in the same line are significantly different by the nonparametric Mann–Whitney *U* test ($p < 0.05$).

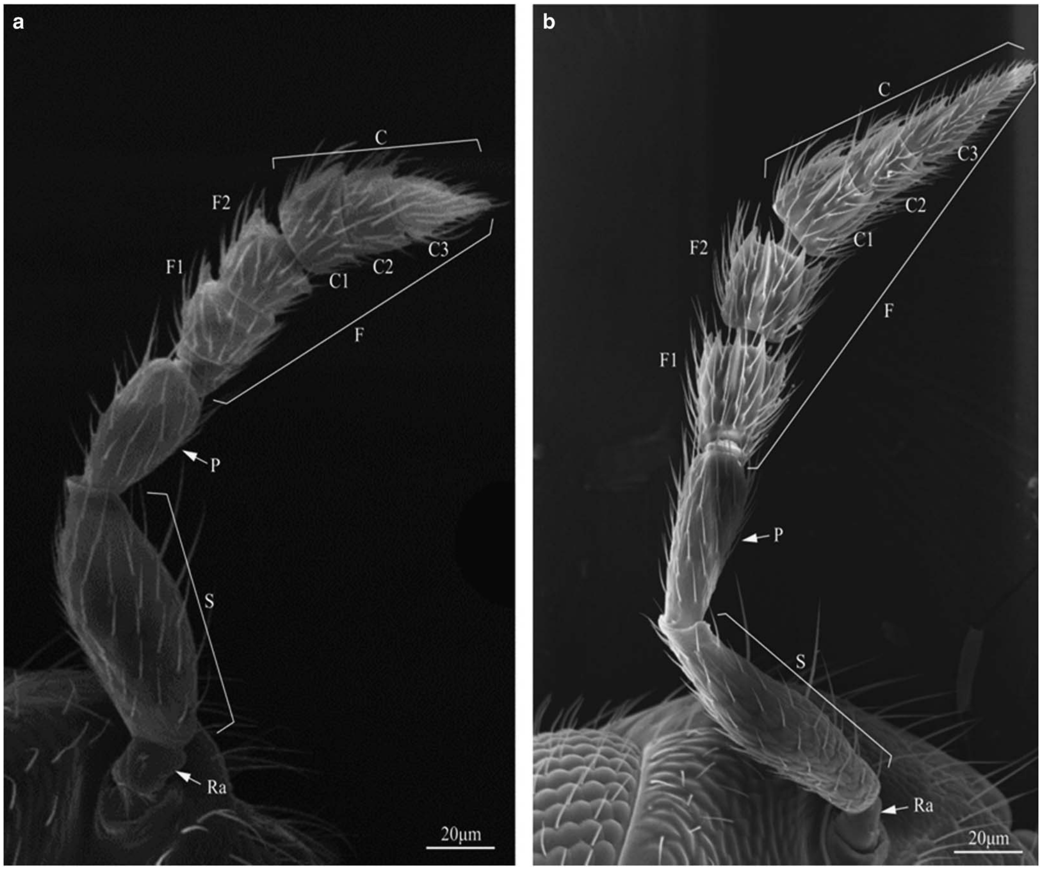

Figure 1. Scanning electron micrographs of the antenna of *Trichospilus pupivorus* (Hymenoptera: Eulophidae). **a:** Male antenna showing radicula (Ra), scape (S), pedicel (P) and flagellum (F) with funicle (F1 and F2) and clava (C) segmented (C1, C2 and C3). **b:** Female antenna with narrow scape, pedicel and a long clava.

The finger-like sensilla were found at the apex of the antennae of both males and females of *T. pupivorus* with two distinct parts, a wide and robust base connected to a tapered tip (Fig. 4a).

Sensilla chaetica were found only in the antennal radicula of both sexes of *T. pupivorus* and in fewer numbers than the other sensilla. These sensilla were characterized with thick and short hair-like structures with smooth surface, similar to TS, but shorter, with a tapered tip and inserted in cuticular depressions (Fig. 2).

Placoid sensilla were characterized as longer and more robust than other sensilla Figs. 2, 5). They were found in the flagellum and clava antennomers of both sexes of *T. pupivorus*, although with a higher concentration in the clava of females.

Discussion

Geniculate antennae, with a long scape, a basal radicula, a barrel-shaped pedicel, and a long flagellum, divided into a funicle and a clava, are typical for Hymenoptera (Olson & Andow, 1993; Onagbola & Fadamiro, 2008). The larger size and width of the pedicel in *T. pupivorus* may be due to the occurrence of the Johnston's organ, a chordotonal organ responsible for the transduction of antennal vibrations into nerve impulses (Sivan-Loukianova & Eberl, 2005; Dieudonne et al., 2014). Johnston's organ has a multi-functional nature serving as an air speed indicator, perception of wing vibration, and orientation in relation with Earth gravity (Chapman, 2013). In Diptera, this organ is used for courtship during mating due to wing vibration (Matsuo et al., 2014), whereas in the honeybee *Apis mellifera* (Hymenoptera) in the perception of air speed during flight (Taylor et al., 2013). However, the role of a well-developed Johnston's organ in *T. pupivorus* needs further electro-physiological and behavioral studies.

The different antennal sizes in *T. pupivorus* males and females is related to sexual dimorphism such as reported for the parasitoid *Metaphycus parasaissetiae* Zhang & Huang (Hymenoptera: Encyrtidae) (Zhou et al., 2013*a*). However, in *Rhopalicus tutela* (Walker) (Hymenoptera: Pteromalidae) and *Cotesia glomerata* (Marshall) (Hymenoptera: Braconidae), the antennae in males were found to be longer than in females (Pettersson et al., 2001; Bleeker et al., 2004). Similar numbers of antennomers were found in both sexes of *T. pupivorus*, however, this differed from those found in *Palmistichus elaeisis* (Delvare & Lasalle, 1993) and

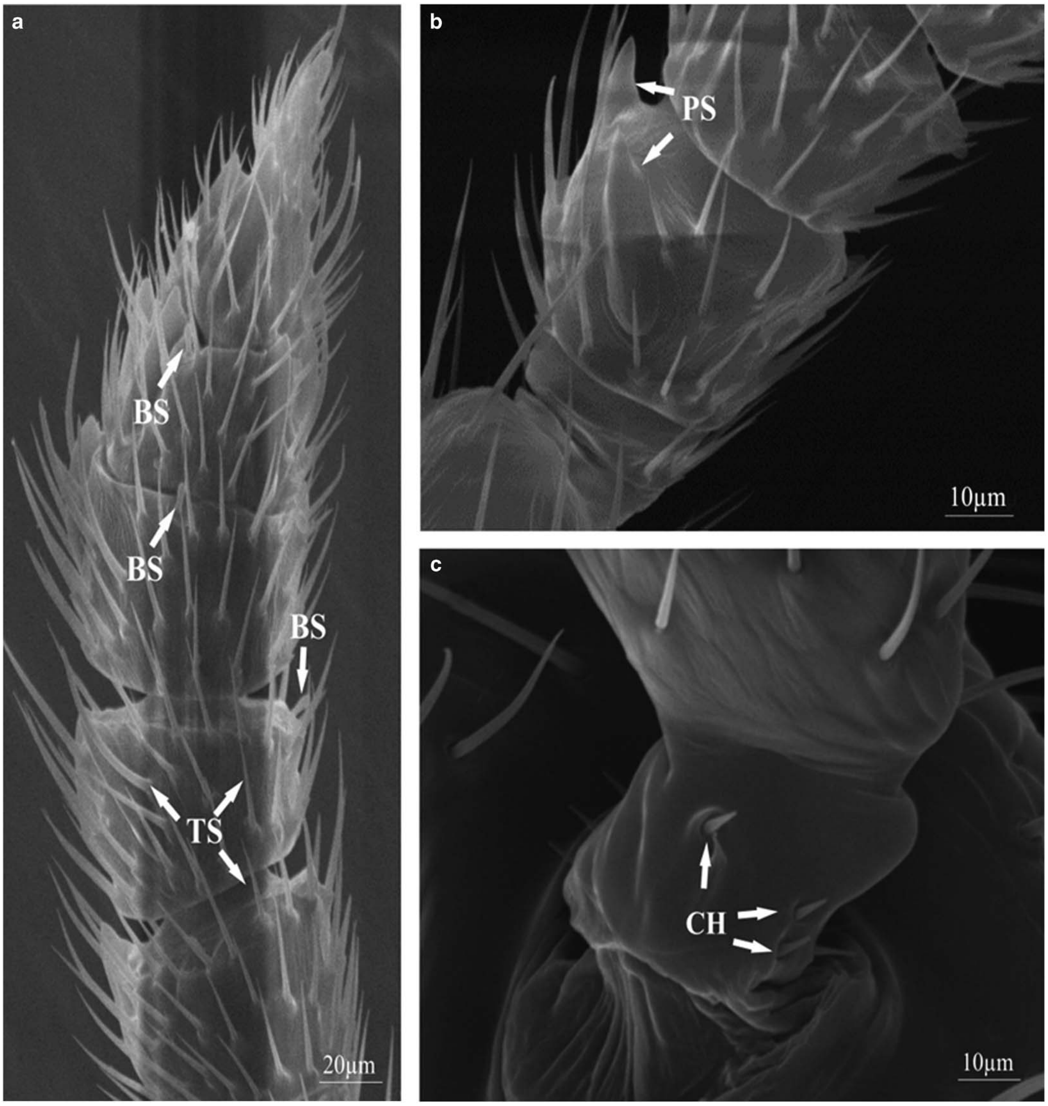

Figure 2. Scanning electron micrographs of the antenna of *Trichospilus pupivorus* (Hymenoptera: Eulophidae) male. **a:** Flagellum with basiconic (BS) and trichodea sensilla (TS). **b:** Placoid sensilla (PS). **c:** Sensilla chaetica (CH) in the antennal radicula.

Tamarixia radiata (Waterston, 1922) (Hymenoptera: Eulophidae), with a higher number of antennomers on the male antennae (Onagbola et al., 2009). Although, the reason for this morphological dimorphism is unclear in parasitoids, it might be related to the functional complexity of antennae between sexes in different species. Nonetheless, regarding Eulophidae, funicular segment size was different in holotypes of *P. elaeisis* from different countries in South America (Delvare & Lasalle, 1993), and relevant differences in number of funicular segments and antenna size of males were found in population of *T. radiata* (Peña-Carrillo et al., 2015) suggesting that the size and/or number of antennomers may also vary according to geographic position in populations from the same species. Furthermore, the antennal size may be associated with sensilla number and size to enlarge the surface area of sensory receptors. Placoidea sensilla size has been correlated to the antennal size in parasitoids (Borden et al., 1978; Amornsak et al., 1998; Zhou et al., 2013*a*).

Trichodea sensilla are distributed in higher quantity in females than in males of *T. pupivorus*, with higher density on the flagellum and increasing concentration on the clava. TS-1 was the most abundant sensilla type covering the whole surface of the antennae of *T. pupivorus* as found for other parasitoids (Norton & Vinson, 1974; Ochieng et al., 2000; Zhou et al., 2013*a*). TS-1 has a mechanoreceptor function (Roux et al., 2005; Marques-Silva et al., 2006; Dweck, 2009). Similar to TS-1, TS-3 occurs in both sexes of *T. pupivorus* and in other Eulophidae (Onagbola & Fadamiro, 2008; Onagbola et al., 2009), also with mechanosensory function (Zhou et al., 2013*a*). The higher concentration of mechanoreceptors such as TS-1 and TS-3 may be due to several functions that they perform, such as detecting air currents and vibration signals, important for searching in females. Mechanoreceptors

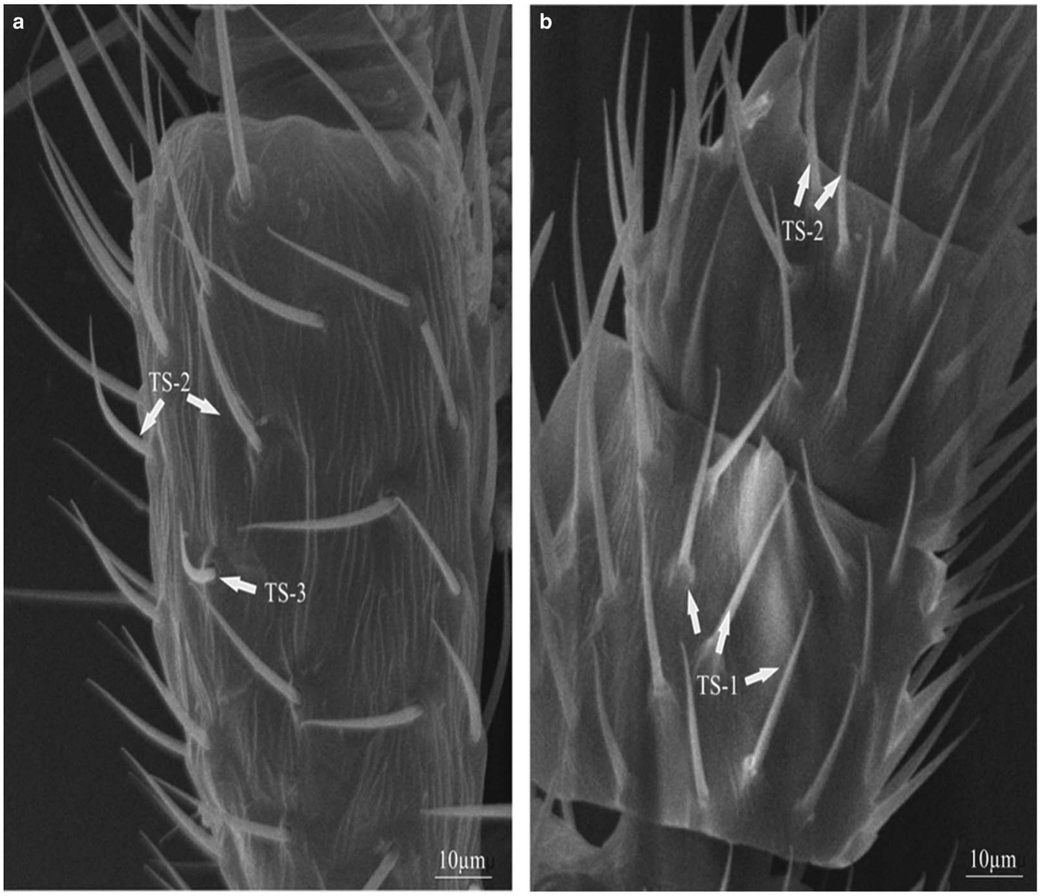

Figure 3. Scanning electron micrographs of the antenna of *Trichospilus pupivorus* (Hymenoptera: Eulophidae) female. **a:** Trichodea sensilla-2 (TS-2) and trichodea sensilla-3 (TS-3) on the pedicel. **b:** Trichodea sensilla-1 (TS-1) and TS-2 in antennal clava.

also play an important role before and during oviposition as they are used by females when probing the host surface (Van Baaren et al., 2007; Onagbola & Fadamiro, 2008; Onagbola et al., 2009; Wenninger et al., 2009). This is important because parasitoids select different host sizes and control the number of eggs laid according to host size (Klomp & Teerink, 1962).

In parasitoids, TS-2 previously reported as "trichoidea sensilla 4" in *Trichogramma australicum* (Hymenoptera: Trichogrammatidae) (Amornsak et al., 1998) and "multiporous sensilla trichoidea" in *Trichogramma galloi* Zucchi and in *Trichogramma pretiosum* Riley (Hymenoptera: Trichogrammatidae) (Cônsoli et al., 1999), has chemoreceptor function and may be related to cue perception during mating (Zhou et al., 2013*a*). Trichodea sensilla of type 2 occur in higher concentration in males of *M. parasaissetiae*, suggesting that these individuals find females using chemical stimuli (Zhou et al., 2013*a*). Nonetheless, the abundance of this sensillum was similar in the antennae of both sexes of *T. pupivorus*. Number of TS-2 were consistently different in females of *Trichogramma* species (Voegelé et al., 1975; Cônsoli et al., 1999) and some authors have also suggested they may be involved with host exploitation (Olson & Andow, 1993), as this sensillum has gustatory function (Isidoro et al., 1996) enabling the host recognition or acceptance process by female parasitoids (Cônsoli et al., 1999). For instance, the indifference in number of TS-2 in both sexes of *T. pupivorus* may be related to host recognition, as this parasitoid as some other Eulophidae species do not discriminate between host qualities such as age or parasitized host, as previously observed in the laboratory (unpublished data).

BS-1 have commonly been found in Hymenoptera and described in Eulophidae as "basiconic capitate peg sensilla" in *T. radiata* (Waterston) (Onagbola et al., 2009) and in *Quadrastichus erythrinae* Kim (Li et al., 2013), "peg-like sensilla" or "sensilla coeloconica" in *Sympiesis sericeicornis* Nees (Meyhöfer et al., 1997) and function as thermo-hygro receptors (Wibel et al., 1984; Pettersson et al., 2001; Onagbola & Fadamiro, 2008).

BS-2 have been described as "sensilla trichoid tip pore (TP)" (Bleeker et al., 2004), "basiconic type I" (Ochieng et al., 2000), fluted BS (Norton & Vinson, 1974), and "uniporous chaetic sensilla" (Onagbola & Fadamiro, 2008). This sensillum has a pore at its apex (Altner & Prillinger, 1980; Olson & Andow, 1993; Zhou et al., 2013*a*), playing a role as a contact chemoreceptor (Altner & Prillinger, 1980; Olson & Andow,

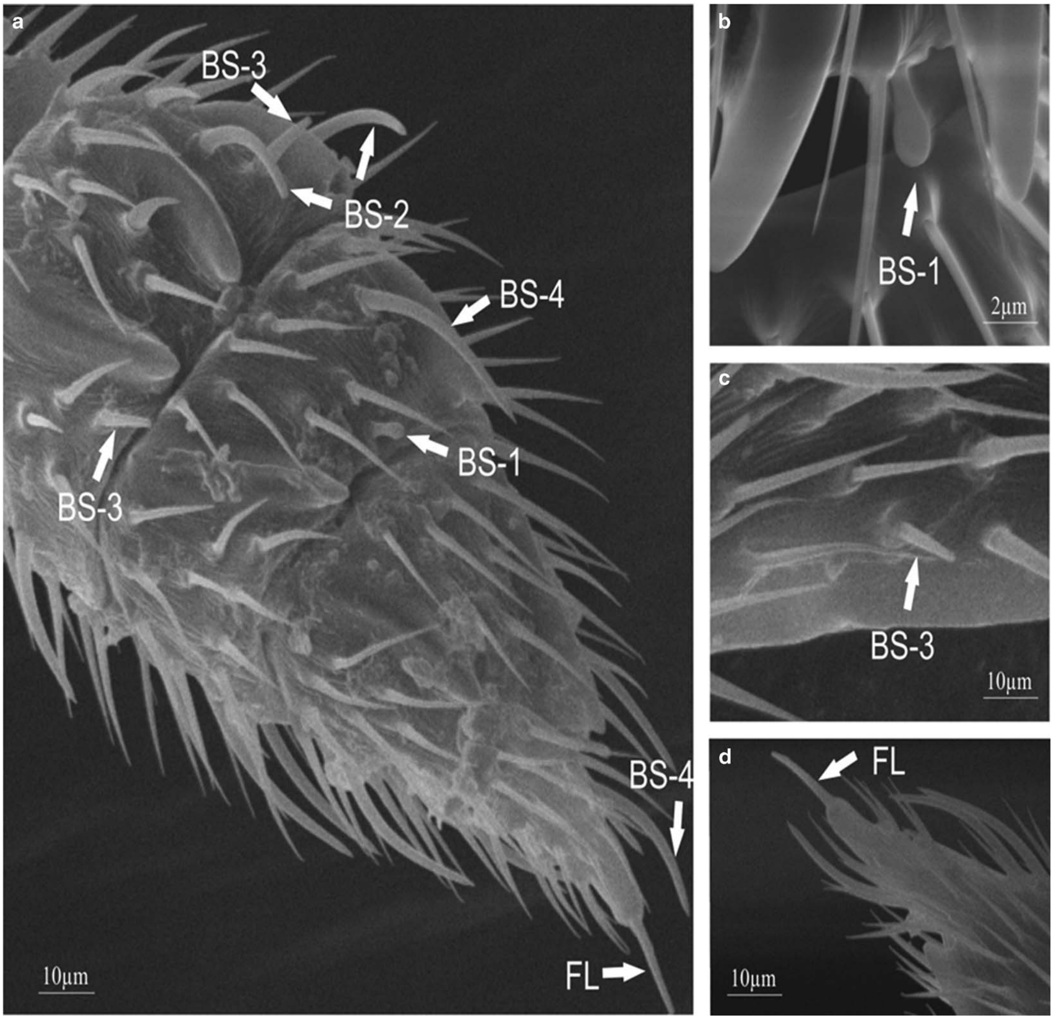

Figure 4. Scanning electron micrographs of the antenna of *Trichospilus pupivorus* (Hymenoptera: Eulophidae) male. **a:** Clava with basiconic sensilla-1 (BS-1), basiconic sensilla-2 (BS-2), basiconic sensilla-3 (BS-3), basiconic sensilla-4 (BS-4) and finger-like sensilla (FL). **b:** BS-1 in the second funicle. **c:** BS-3 in the second antennomer of the clava. **d:** Finger-like sensilla FL on the distal region of the last antennomer of the clava.

1993; Zhou et al., 2013*a*) with gustatory functions (Isidoro et al., 1996; Barbarossa et al., 1998).

BS-3 occur in small numbers in the antennae of males and females *T. pupivorus*, as reported for other parasitoids (Olson & Andow, 1993; Amornsak et al., 1998; Zhou et al., 2013*a*), but its main function is still unrevealed in Hymenoptera. Nevertheless, it has been suggested that the BS-3 may act as a contact chemoreceptor (Olson & Andow, 1993) associated with the recognition and acceptance of the host (Weseloh, 1972; Borden et al., 1973). The low concentration of BS-3 may be associated with the presence of other sensilla that perform the same function as BS-2, and placoid sensilla, largely found in *T. pupivorus* females.

Among the BS, BS-4 occurs in higher numbers in both sexes of *T. pupivorus*. These sensilla have been described as “Sensilla trichoid WP” (Bleeker et al., 2004), “s. basiconic type 2” (Ochieng et al., 2000), “curved non-fluted basiconic sensilla” (Norton & Vinson, 1974) and “s. basiconica B” (Navasaro & Elzen, 1991). Although, its function remains unknown, they are likely to be olfactory sensilla (Steinbrecht, 1997).

Finger-like sensilla also described as “Nonporous finger-like sensilla” (Zhou et al., 2013*b*) are easily recognized by their morphology, and although they have been rarely described in Hymenoptera, they are found in similar antennal locations in other parasitoids (Viggiani, 1982; Zhou et al., 2013*a*, 2013*b*). Unlike other species, one single finger-like sensilla occurs at the claval tip in *T. pupivorus*. *Encarsia guadeloupae* Viggiani (Hymenoptera: Aphelinidae) and has four finger-like sensilla (Zhou et al., 2013*b*). Finger-like sensilla were similar in both *T. pupivorus* sexes. These sensilla may receive stimuli from a substrate such as a host, but their main function is unknown (Zhou et al., 2013*a*, 2013*b*).

Sensilla chaetica occur in the antennal radicula of *T. pupivorus* males and females and are similar to those found in the Braconidae *Macrocentrus cingulum*, *Microplitis*

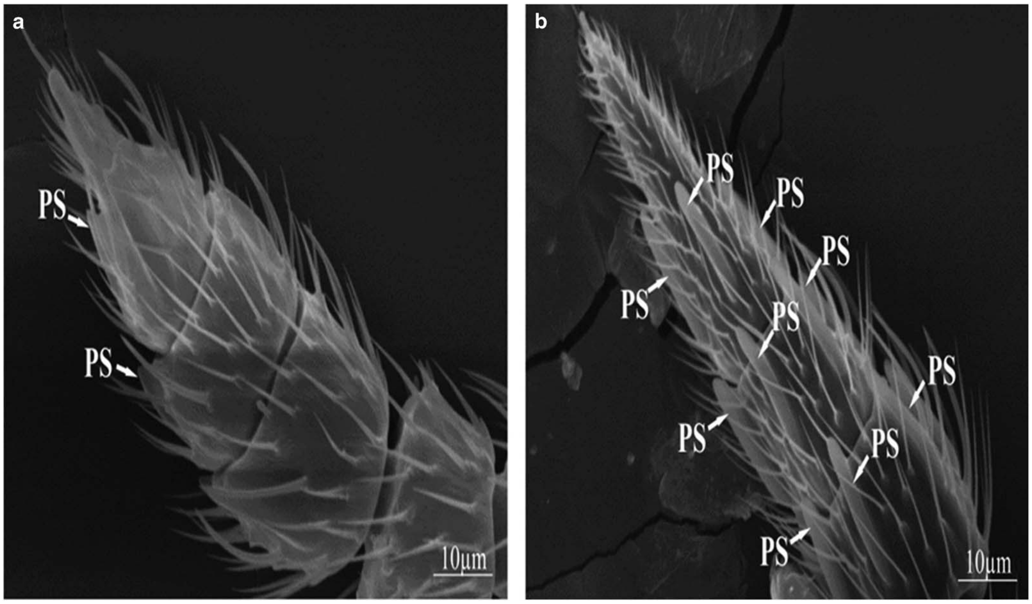

Figure 5. Scanning electron micrographs of the antennal clava of *Trichospilus pupivorus* (Hymenoptera: Eulophidae). **a:** Male showing some placoid sensilla (PS). **b:** Female showing many placoid sensilla (PS).

croceipes, and *Apanteles cypris* (Ochieng et al., 2000; Zhou et al., 2011; Ahmed et al., 2013). Due to their location, the sensilla chaetica probably have a mechanosensorial function with perception of the antennal movement (Ochieng et al., 2000; Dweck, 2009; Zhou et al., 2011). These sensilla are inserted into cuticular depressions with a possible role as proprioceptors (Zhou et al., 2011; Ahmed et al., 2013).

Placoid sensilla found in Eulophidae (Li et al., 2013), are located in the flagellum funicles of *T. pupivorus* and in higher numbers and greater size on females than males. Similarly, females of *M. parasaissetiae* had a higher density and size of placoid sensilla than males, and this discrepancy may be related to the location of the host or partner for mating (Zhou et al., 2013*a*). On the other hand, placoid sensilla have been found in greater numbers (Bleeker et al., 2004; Roux et al., 2005) and size (Roux et al., 2005) in males of *Cotesia*. In males, placoid sensilla also have tactile functions and chemoreceptors correlate to olfactory responses in the female at the same location (Schneider, 1964; Ochieng et al., 2000), however, they are required in small numbers on antennae of *T. pupivorus* males. The high number and large size of placoid sensilla on the female clava are probably related to their olfactory function for perception of important volatiles from the hosts, where the high concentration of these sensilla in the antennal apex could facilitate the perception of external stimuli (Barlin & Vinson, 1981; Gao et al., 2007; Onagbola & Fadamiro, 2008).

In conclusion, both sexes of *T. pupivorus* have the same types of sensilla. However, females have longer antennal segments than males. Our findings indicate that females obtain higher sensory sensitivity as the placoid sensilla were found in higher number. This dimorphism is important because they provide a morphological basis for understanding behavior mediated by antennal perception between sexes of *T. pupivorus* and insights on its function in closely related species. Overall, this study provides basic information for further applications involving functional morphology and comprehension of the mechanisms associated with behavioral responses to semiochemicals used in host recognition and mating.

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