Ultrastructure of antennal sensilla of female Ceratosolen solmsi marchali (Hymenoptera: Chalcidoidea: Agaonidae: Agaoninae)

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Abstract—Fig-pollinating wasps are phytophagous wasps that mainly use olfaction to locate their fig (Ficus L., Moraceae) hosts. To provide a morphological framework for studying agaonid olfaction, we examined the antennal sensilla of female Ceratosolen solmsi marchali Mayr by scanning and transmission electron microscopy. We identified and characterized (ultrastructure, distribution, abundance, and position) 13 types of sensilla: multiporous placoid sensilla (types 1 and 2), basiconic sensilla (types 1 and 2), basiconic capitate peg sensilla, sensilla chaetica (types 1–3), sensilla trichodea, sensilla coeloconica (types 1–3), and one specialized sensillum regarded as a sensillum obscurum. We suggest that five types are chemoreceptors because they are porous and innervated by multiple sensory neurons. Sensilla coeloconica type 1 may also function as chemoreceptors, based on external morphology. Other sensilla may be involved in mechanoreception, thermo- and (or) hygro-reception, or pressure detection. We discuss our results in relation to the lifestyle of C. solmsi marchali.

Introduction

Interactions between fig (Ficus L., Moraceae) trees and their wasp (Hymenoptera: Chalcidoidea: Agaonidae: Agaoninae) pollinators are a prominent example of obligate pollination mutualism (Wiebes 1979; Weiblen 2002). Most fig species depend on a single agaonine species for pollination (Wiebes 1979). The wasps in turn depend on one fig species for development; their larvae feed only on the endosperm tissue of the fig host. In
such a close mutualism, survival of both partners is dependent upon encounters between them. An efficient mechanism for detecting hosts is particularly important because the tiny (1–2 mm in length) and short-lived (<2 days; Kjellberg et al. 1988) pollinating wasps often have to disperse over long distances (Compton et al. 2000; Harrison 2003) to find figs that are ready to be pollinated. Moreover, most fig species live in complex rain-forest environments and each species of fig wasp must be able to detect and locate its particular host among the rich diversity of fig species found in these environments (Harrison and Rasplus 2006). Female wasps rely mainly on olfactory signals to locate a host (van Noort et al. 1989; Ware et al. 1993; Hossuert-McKey et al. 1994; Ware and Compton 1994; Song et al. 2001; Grison-Pigé et al. 2002; Chen and Song 2008).

In insects, the sensilla that serve as olfactory receptors are mainly distributed on the antennae. Other types of sensilla, including mechanoreceptors, thermoreceptors, and hygroreceptors (Keil 1999), are also found on the antennae and can play a complementary role in host location and host discrimination. The antennal sensilla of various insect species have been characterized (Schneider 1964; Zacharuk 1989; Isidoro et al. 1996; Amornsak et al. 1998; Chapman 1998; Keil 1999; Chiappini et al. 2001; Bleeker et al. 2004; Onagbola and Fadamiro 2008), but we are not aware of any published information on the antennal sensilla of female Agaonidae.

*Ceratasolen solmsi marchali* Mayr is the agaonine pollinator of *Ficus hispida* L. This pioneer functionally dioecious shrub or small tree is distributed along streams or on plains at altitudes of 700–1500 m in southern China, Southeast Asia, and Australia (Wu et al. 2003). Male trees produce pollen and host wasps; female trees produce seeds. Ripe figs are present year-round on different trees at our study site in Xishuangbanna, China (Yang et al. 2002), but development of the figs on any one tree is synchronized, and female wasps must disperse among trees.

As part of our ongoing research on the host-location mechanisms of female *C. solmsi marchali*, we complemented current work involving electroantennogram recordings and the behavioral ecology of this fig pollinator by identifying and characterizing the types of its antennal sensilla and their ultrastructure, with emphasis on sensilla involved in chemoreception. First, we investigated the external morphology, abundance, and distribution of the antennal sensilla using scanning electron microscopy (SEM). We then determined the internal structure of each type of sensillum using transmission electron microscopy (TEM). We discuss the results in relation to the lifestyle of fig wasps, using *C. solmsi marchali* as an example.

**Methods**

**Wasp collection**

Female *C. solmsi marchali* emerging from figs of male *F. hispida* plants were collected at the Xishuangbanna Tropical Botanical Garden (21°41′S, 101°25′E) in Yunnan Province, China. Newly emerged individuals were anesthetized by ethyl acetate. Some wasps were placed directly in 2% glutaraldehyde for SEM; others were decapitated with a fine scalpel and immersed in 3.5% glutaraldehyde containing 0.1 mol/L phosphate buffer solution (PBS) and 4% paraformaldehyde for TEM. All samples were stored at 4 °C for 3 days.

**Scanning electron microscopy**

Sample wasps were warmed to room temperature prior to heads being separated from bodies and then sonicated for 30 s to remove debris using an ultrasonic cleaner. Samples were then cleaned in 0.2 mol/L PBS for 10 min and dehydrated in a graded ethanol series (50%, 75%, 80%, 95%, and 99.9%) and isoamyl acetate (100%) (10 min each step), and finally dried using a critical-point dryer. Specimens were mounted on aluminum stubs with double-sided conductive adhesive tape, sputter-coated using a precision etching and coating system (PECS-682, Gatan, Inc., Warrrendale, Pennsylvania, United States of America) for 45 s to improve electrical conductivity, and finally examined under a Philips XL-30 Environmental scanning electronic microscope at 20–30 kV. In total, 10 antennae were examined from different aspects.
Transmission electron microscopy
Sample wasps were fully rinsed in PBS, postfixed in 1% osmium tetroxide mixed with PBS (pH 7.4) at 4 °C for 2 h, and dehydrated in an ethanol series as described above. The samples were then transferred into 100% epichlorohydrin and infiltrated with Epon 618 and acetone mixtures at a 1:1 (v:v) ratio at room temperature for 2 days. After the head was excised, the antennae were divided into three segments (scape, pedicel, and flagellum), then individually embedded in pure Epon resin, and finally polymerized at 60 °C for 2 days. Ultrathin sections were cut with a diamond knife on a Leica-U ultramicrotome and stained with 4% uranyl acetate and 1% lead citrate before examination in a JEM-1010 transmission electronic microscope.

Statistical analysis
Classification of sensillum types was based on the terminology of Schneider (1964), Zacharuk (1989), Keil (1999), and Bleeker et al. (2004). Ultrastructural nomenclature follows that of Barlin and Vinson (1981), Isidoro et al. (1996), Ochieng et al. (2000), and Pettersson et al. (2001).

Antennae and sensilla were measured using WonderWebware Screen Ruler (http://wonderwebware.com/) software. The number of sensilla recorded on each segment was estimated from views of two-thirds of the surface area. To obtain accurate images, background color was removed from photographs and marked using Adobe Photoshop 7 (http://www.adobe.com/). A Kruskal–Wallis test was used to determine the significance of variation in abundance and length of multiporous placoid sensilla among flagellar segments using SAS software (SAS Institute Inc. 1999).

Results
Antennal map for female C. solmsi marchali
The antennae of C. solmsi marchali are geniculate and located frontally on the head between the compound eyes. Each antenna consists of a scape, pedicel, and flagellum (Fig. 1A). The scape is the broadest segment and is irregular in shape with two relatively deep grooves on the ventral surface (Figs. 1A, 1B, 7A), which may serve a protective function by holding part of the flagellum when it is appressed to the scape. The radicle (scape base) articulates with the torulus, the basal ring joint that is surrounded by membrane and upon which the enlarged base of the radicle (a half-ball joint) articulates with the head, allowing movement in all directions (Fig. 1B). The pedicel is pear-shaped (Figs. 1A, 1C, 1D). The scape–pedicel joint is a ginglymus (hinge joint) (Fig. 1B), which indicates that the primary movement of the pedicel is in a single plane. The rest of the flagellum (eight segments, F1–F8) is more elongate and broadens distally, with the last three segments forming a clava (club) (Fig. 1A). The basal section of F1 expands into a large hook-shaped apical projection (Figs. 1A, 2C, 6D), clearly visible on the antenna (Fig. 1A). The sensilla on the ventral and dorsal surfaces of each flagellar segment are similar, whereas those on the pedicel are of different types (Figs. 1C, 1D).

Types of antennal sensilla
Thirteen types of sensilla occur on the antennae of female C. solmsi marchali: 3 types each of sensilla chaetica and sensilla coeloconica, 2 types each of multiporous placoid and basiconic sensilla, and 1 type each of sensilla trichodea, basiconic capitate peg sensilla, and a sensillum obscurum. Sensilla trichodea are long, slender, and hairlike with longitudinal grooves on the shaft, and were distinguished according to size and shape. They are distinguished from sensilla chaetica by their cuticular attachment and the presence of a smooth-surfaced shaft tapering to a sharp tip. Basiconic sensilla are peg-shaped with a perpendicular stalk tapering to a blunt tip. Basiconic capitate peg sensilla have longitudinal grooves and are recessed in shallow pits, differentiating them from sensilla coeloconica, which are recessed in deep cuticular pits. Multiporous placoid sensilla are the largest and most conspicuous sensilla on hymenopteran antennae (e.g., Isidoro et al. 1996; Bleeker et al. 2004; Onagbola and Fadamiro 2008). Sensilla obscura are specialized sensilla occurring only on the pedicel.
similar structures have not been reported from other insects. The abundance and distribution of these different types of sensilla on each antennal segment are summarized in Table 1.

Multiporous placoid sensilla

Multiporous placoid sensilla (MPS) are elongated plate-like sensory organs with corrugated shafts containing numerous pores (Figs. 2A, 2B). Each sensillum is generally aligned parallel with the longitudinal axis of the flagellar segment (Figs. 2A, 2C, 3B, 6D). Based on differences in structure, shape, and distribution, we separated them into type 1 (MPS-1) (Figs. 2A, 3B) and type 2 (MPS-2) (Figs. 2C, 6D).

Each MPS-1 is a nonsocketed plate elevated above the antennal surface and is located between rows of sensilla trichodea (Figs. 2A, 2C, 3B). The distal end is free from the antennal surface (Figs. 2A, 3C). MPS-1 occur on F3–F8 (Table 1) and have a ringlike distribution. They are $31.67 \pm 4.75$ μm (mean ± SD) in length and $4.21 \pm 0.63$ μm in width. Numerous pores are present on the shaft of MPS-1 (Fig. 2B) at a density of $31.6 \pm 7.4$
pores/μm², and each pore is 0.08 ± 0.02 μm in diameter. In transverse section (Fig. 2D), 28–35 neurons innervate each MPS-1. The neurons are situated peripherally in the hemo-lymph space in the center of the antenna. The dendrite expands in the ciliary region and enters the sensillar lymph lumen through one median channel between the septa. The dendrite then branches and turns toward the distal end of the sensillum, traversing its longitudinal axis. Each dendrite appears to terminate at a pore. Pores connect with the interior through a channel (Fig. 2D). MPS-1 on flagellar segments 3–8 vary significantly in number ($\chi^2 = 21.53$, $P = 0.014$, $n = 10$) but not in length ($\chi^2 = 10.81$, $P = 0.403$, $n = 10$) (Table 1).

MPS-2 resemble MPS-1 in shape, but unlike the latter they are surrounded by a shallow groove and a cuticular ridge (Figs. 2C, 6D). These sensilla are present only on F2 (Table 1). MPS-2 measure 30.43 ± 4.52 μm in length and 4.13 ± 1.13 μm in width. Multiple pores can be seen on the surface of MPS-2 at a density of 28.9 ± 8.1 pores/μm², each with a diameter of 0.05 ± 0.02 μm. Their TEM sections are similar in appearance to those of MPS-1 (Fig. 2E), though there are fewer neurons. Between 17 and 25 neurons were counted under the septa. Pore channels were also clearly discernible (Fig. 2E). Surprisingly, one thick, more electron-dense structure (a trichogen cell; Fig. 2E) was not retracted from the sensillum lumen after performing its morphogenetic role.

### Basiconic sensilla

The two types of basiconic sensilla (BS-1 and BS-2) are distinguished by their structure, shape, and distribution. BS are peglike structures, each set in a tight, inflexible socket (Figs. 3A, 3C).

BS-1 occur on the distal end of F2–F8 (Table 1), primarily on the ventral surface. BS-1 have a smooth cuticle covered with small pores (Figs. 3A, 3B) and are slightly enlarged basally, with a length and basal diameter of 12.39 ± 2.93 and 1.51 ± 0.25 μm, respectively. Numerous dendritic branches within the sensillar lymph innervate the lumen (Fig. 3B).

BS-2 are present on F7 and F8 (Table 1) and are especially prominent at the apex of segment 8 (Fig. 3B). Each is characterized by a longitudinal groove (Fig. 3C) and projects slightly more from the axis of the antenna than either sensilla trichodea or BS-1. Because of the length and orientation of BS-2, their

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**Table 1.** Abundance and distribution of different types of sensilla on the antennae of female *Ceratosolen solmsi marchali.*

<table>
<thead>
<tr>
<th>Sensilla</th>
<th>Scape</th>
<th>Pedicel</th>
<th>F1</th>
<th>F2</th>
<th>F3</th>
<th>F4</th>
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<th>F6</th>
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*Note: Values are the approximate numbers of different types of sensilla on each antennal segment. F1–F8, flagellar segments 1–8; MPS-1, -2, multiporous placoid sensilla types 1 and 2; BS-1, -2, basiconic sensilla types 1 and 2; BCPS, basiconic capitate peg sensilla; ST, sensilla trichodea; ChS-1, -2, -3, sensilla chaetica types 1, 2, and 3; CoS-1, -2, and -3, sensilla coeloconica types 1, 2, and 3; SO, sensillum obscurum.*
Tips are well above the level of other sensilla (Fig. 3B). BS-2 are 17.22 ± 2.57 μm in length and 1.56 ± 0.33 μm in basal diameter. Each has a thick nonporous cuticular wall surrounding the sensillar lymph lumen, with multiple dendrites of sensory neurons. Around four individual neurons terminate at the tip (Figs. 3E, 3F).

**Basiconic capitate peg sensilla**

Basiconic capitate peg sensilla (BCPS) are distinguished by their external structure, shape, and distribution (Figs. 3B, 4A). They are mastoid-like structures (Fig. 4A), each set in a shallow cuticular depression 3.30 ± 1.72 μm in diameter and sometimes hidden under MPS-1 (Fig. 3B). Each BCPS is 3.61 ± 1.08 μm in length and 1.68 ± 0.17 μm in basal width, with 10 or 11 longitudinal grooves and many pores on the surface of the head-shaped protrusion (Fig. 4A). The lumen is surrounded by a thick porous wall and innervated by multiple dendrites (Fig. 4B). There are 10 BCPS (Table 1),...
2 each on the distoventral surface of F3–F7.

Sensilla trichodea
Sensilla trichodea (ST) constitute about 56% of all sensilla, with approximately 3%, 3%, and 50% on the scape, pedicel, and flagellar segments, respectively (Table 1). Each ST is a hairlike structure with a longitudinally grooved stalk tapering to a sharply pointed apex, which is inclined and slightly curved toward the antennal axis (Figs. 2A, 3B, 5A, 7A, 7B). ST are 26.99 ± 5.52 μm in length and 1.32 ± 0.28 μm in width. Each inserts into a flexible socket 1.85 ± 0.34 μm in diameter. The ST cuticle has a thick nonporous wall that is not innervated by dendrites (Fig. 5B).

Chaetica sensilla
We classified three types of sensilla chaetica (ChS-1, -2, and -3) on the basis of external structure, size, and cuticular attachment (Figs. 6A–6D).
ChS-1 are distributed on the scape and pedicel (Figs. 6A, 6D) and vary greatly in length (1.5–14.8 µm), with the longest sensillum on the ventral portion of the pedicel. Although they vary in length according to location, their cuticular attachment and shaft morphology are consistent (Figs. 6A, 6B). ChS-1 are bristle-like, pointed, or slightly curved, and have smooth walls. Each is situated in a flexible cuticular socket (Fig. 6B) 0.81 ± 0.05 µm in diameter. Thick nonporous cuticular walls surround the sensillar lymph lumen, which is not innervated by dendrites (Fig. 6E).

ChS-2 occur on the radicle (basal section of the scape) (Figs. 1B, 6C). Typically, each tapers from a bulbous base and projects perpendicular to the antennal axis from a socket 1.69 ± 0.10 µm in diameter. The sensillar cuticle is thick and nonporous (Fig. 6F). ChS-2 are 4.72 ± 1.03 µm in length and 1.22 ± 0.06 µm in basal diameter.

ChS-3 are strong and wedge-like basally (Fig. 6D). Each projects from the cuticular wall from a flat, oval socket. ChS-3 are 18.97 ± 2.74 µm long and 3.43 ± 0.24 µm in basal diameter and have a smooth cuticle. A transverse section taken beneath the cuticle shows a thick nonporous wall with no dendrites (Fig. 6G). ChS-3 are relatively rare; we found only one, on the dorsolateral portion of the hook-shaped apical projection (Fig. 6D).

Sensilla coeloconica

Three types of sensilla coeloconica (CoS-1, -2, and -3) can be distinguished by their external structure, size, and distribution.
CoS-1 are present only on the dorsal surface of the hook-shaped apical projection (Fig. 6D). Each is composed of a mushroom-shaped protrusion 0.76 ± 0.33 μm in length and 0.88 ± 0.06 μm in basal width within a deep circular socket (1.30 ± 0.03 μm diameter) with a central opening 0.6 ± 0.03 μm wide. The protruding head is smoother than the base and extends slightly above the antennal surface. The pit is deeper on its distal side (toward the flagellar segments) and shallower proximally (toward the scape), where it usually merges with the antennal surface (Fig. 7C). Whether or not the CoS-1 sensillar lymph space was innervated could not be determined because of the rarity of CoS-1 and the orientation of our ultrathin sections.

CoS-2 are found on the hook-shaped apical projection and the scape (Figs. 7A, 7B). Each consists of a smooth, aporate peg (Fig. 5D) 1.24 ± 0.17 μm in length and 0.96 ± 0.11 μm in basal diameter protruding from a small socket 1.25 ± 0.30 μm in diameter. The apex
Fig. 7. Sensilla coeloconica types 1, 2, and 3 (CoS-1, -2, -3) on the antenna of a female *Ceratosolen solmsi marchali*: A, distribution of types 2 and 3 on the scape (SEM); B, distribution of types 2 and 3 on the hook-shaped apical projection (SEM); C, D, E, external morphology of types 1, 2, and 3, respectively (SEM); F, G, transverse sections of types 2 and 3, respectively (TEM). DD, dendritic branches in the sensillar lymph; Gr, deeper grooves; Ho, hook-shaped apical projection; Sc, scape; SL, sensillar lymph; ST, sensilla trichodea; SW, sensillum wall.
of the peg is obviously higher than the antennal surface and usually curves toward the scape (Fig. 7D). CoS-2 have a thick nonporous wall that surrounds the sensillar lymph lumen and has many dendrites (Fig. 7F).

CoS-3 are small pegs $0.86 \pm 0.37 \mu m$ in length and $0.78 \pm 0.17 \mu m$ in basal diameter, in a wide socket $1.88 \pm 0.39 \mu m$ in diameter. Each has a thick, solid wall lacking pores and the sensillar lymph lumen is not innervated (Fig. 7G). CoS-3 occur on the hook-shaped apical projection of F1 and on the scape, and are commonly interspersed with CoS-2 (Figs. 7A, 7B).

**Sensilla obscura**

Sensilla obscura (SO) are distinctly leaf-shaped and flattened (Fig. 1C), with a length of $11.75 \pm 2.19 \mu m$ and width of $2.60 \pm 0.23 \mu m$. Each SO is inserted into a wide oval socket, with its slender protruding apex level with the antennal surface (Fig. 8A), and it has a thick nonporous wall without dendrites in the sensillar lymph lumen (Fig. 8B). There are approximately 55 SO grouped dorsally on the pedicel with their apices aligned with the longitudinal antennal axis toward the scape (Fig. 1C).

**Discussion**

Our study revealed 13 types of sensilla on the antennae of female *C. solmsi marchali*. In their external morphology, types, distribution, and ultrastructure, these sensilla are somewhat similar to those reported for other Hymenoptera (Barlin and Vinson 1981; Isidoro et al. 1996; Amornsak et al. 1998; Bleeker et al. 2004; Gao et al. 2007; T. Cockerill, personal communication), with some exceptions. SO may be unique to female agaonine wasps. F1 is present in the antennae of nearly in all female agaonines and has a large, hook-shaped branch (Fig. 1A), an adaptation for entering the fig ostiole (Weiblen 2002; Kjellberg et al. 2005), which is a characteristic feature of agaonines.

We assume that MPS (i.e., MPS-1 and -2) are the main chemoreceptors; they are the most common sensilla on the flagellar segments of *C. solmsi marchali*, as is the case in other Hymenoptera (Barlin and Vinson 1981; Basibuyuk and Quicke 1999; Ochieng et al. 2000; Chiappini et al. 2001; Roux et al. 2005). We found numerous pore systems and sensory neurons in MPS-1 and MPS-2 (Figs. 2D, 2E), as reported for other Chalcidoidea (Barlin and Vinson 1981), indicating an olfactory function (Keil 1999). Odorant substances can diffuse through the pores and combine with odorant-binding proteins in the sensillar lymph (Calvello et al. 2005). Ochieng et al. (2000), suggesting that MPS respond in a dose-dependent manner to plant volatiles.

External MPS morphology has been used for phylogenetic evaluation in Hymenoptera (Basibuyuk and Quicke 1999). We observed two morphologically distinct types of MPS in *C. solmsi marchali*. MPS-1 (Figs. 2A, 3B) are similar to MPS in other Chalcidoidea (Barlin and Vinson 1981; Ware and Compton 1992; Chiappini et al. 2001), whereas MPS-2 (Figs. 2C, 6D) resemble the MPS of Ichneumonidae and Braconidae (Aphidiinae) (Bas-
BS-1 and -2 also occur in other parasitic wasps (Ochieng et al. 2000; Bleeker et al. 2004; Gao et al. 2007). BS-1 were previously described as sensilla basiconica B (Navasero and Elzen 1991), multiporous pitted sensilla trichodea C (Olson and Andow 1993), and sensilla trichodea WP (Pettersson et al. 2001; Bleeker et al. 2004). BS-2 are similar to some sensilla formerly described as fluted basiconic sensilla (Norton and Vinson 1974), tapering fluted setae (Dahms 1984), apical sensilla (Chiappini et al. 2001), sensilla trichodea TP (Bleeker et al. 2004), and uniporous chaetica sensilla (Onagbola and Fadamiro 2008). We found differences between BS-1 and -2 in external shape and also in dendritic innervation (Figs. 3D, 3E). The multiporous wall and multiple dendrites in BS-1 indicate an olfactory function. In BS-2 the neuronal dendrites are subdivided within the lymph into about four neurons that terminate at the tip (Fig. 3F), suggesting a combined gustatory/mechanosensory function (T. Keil, personal communication). While walking on the outside of a host fig, female C. solmsi marchali usually drum the tips of their antennae on the fig surface. We found most BS-2 on the apex of F8 (terminal), which supports the hypothesis that they are involved in perception of host-plant-related substances, which Chiappini et al. (2001) assumed to be important for microhabitat recognition.

BCPS are remarkably different from other sensilla we observed, being characterized by a rounded capitate peg with longitudinal grooves (Figs. 3B, 4A). In their morphology and location they resemble multiporous peg sensilla on Tetrastichus hagenowii (Ratzburg) (Hymenoptera: Eulophidae) (Barlin et al. 1981), sensillum coeloconicum types I and II on Cotesia Cameron (Hymenoptera: Braconidae) (Bleeker et al. 2004; Roux et al. 2005) and other braconids (Ochieng et al. 2000), and basiconic capitate peg sensilla on Pteromalus cereadellae (Ashmead) (Hymenoptera: Pteromalidae) (Onagbola and Fadamiro 2008). We observed pores on BCPS walls (Fig. 4B), suggesting an olfactory function as previously reported (Steinbrecht 1997; Keil 1999; Ochieng et al. 2000; Roux et al. 2005). In other Hymenoptera these sensilla may also be mechanoreceptors (Amornsak et al. 1998) or thermohygroreceptors (Altner et al. 1983).

ST were the most abundant sensilla on C. solmsi marchali (Table 1) and are usually considered to be mechanoreceptors (Isidoro et al. 1996; Keil 1999; Chapman 1998; Ochieng et al. 2000; Bleeker et al. 2004). Based on insertion of the basal shafts into flexible sockets, spatial distribution, and non-porous walls, we consider ST to be mechanoreceptors. However, other authors have proposed that sensilla of this type may play a role in perception of chemical stimuli and act as olfactory/gustatory receptors (Amornsak et al. 1998; Chiappini et al. 2001).

We found three types of aporous ChS on the scape and pedicel. The presence of aporous ChS has also been reported on the antennae of other parasitic wasps (Amornsak et al. 1998; Ochieng et al. 2000; Gao et al. 2007). ChS morphology and location are consistent with those reported in braconids (Ochieng et al. 2000; Gao et al. 2007), mymarids (Hymenoptera: Mymaridae) (van Baaren et al. 1999), and the agaonid Liporrhopalum tentacularis (Grandi) (T. Cockerill, personal communication). Based on their location and structure, ChS are usually thought to be mechanosensors (Amornsak et al. 1998; Ochieng et al. 2000) or to have mixed functions (van Baaren et al. 1999). Aporous ChS appear to be mechanoreceptors, as demonstrated for ST. However, their functions are likely different in C. solmsi marchali. Based on structure, size, and location, ChS-1 and -3 likely play a role in monitoring wasp passage through fig ostioles, whereas ChS-2 (which occur only on the radicle) are probably associated with the monitoring of antennal position.

Generally, two types of CoS are common in parasitic wasps (Ochieng et al. 2000; Bleeker et al. 2004; Roux et al. 2005); however, we found three types in C. solmsi marchali. CoS-1 was the rarest type (Table 1). The ridge outside the stumplike peg may indicate a characteristic type of sensilla or protect the peg from physical damage (Yang et al. 2009). In external morphology, CoS-1 are similar to
sensilla coelocapitula in *Apis mellifera* L. (Hymenoptera: Apidae) (Yokohari *et al.* 1982). We were unable to observe CoS-1 because of their rarity and the orientation of the ultrathin sections that we cut. Hunger and Steinbrecht (1998) found that sensilla of this type have multiporous walls and contain numerous neurons. Ameismeier (1985) suggested that some of the longitudinal grooves allow odour molecules reach the receptors. However, Yokohari *et al.* (1982) proposed that sensilla of this type may be receptive to heat and humidity.

CoS-2 and CoS-3 of *C. solmsi marchali* resemble the single-walled poreless CoS of Lepidoptera both externally (Faucheux *et al.* 2006; Yang *et al.* 2009), though they differ in shape (Figs. 7D, 7E), and in their internal structure (Figs. 7F, 7G). CoS-2 lumina are innervated by neuronal dendrites, whereas CoS-3 lumina are empty. Because female fig wasps use the hook-shaped apical projection to gain initial entry through the fig bracts, sensilla on its surface are likely to serve a function during ostiole entry. CoS-2 may function as thermohygroreceptors (Altner *et al.* 1983), whereas CoS-3 likely play a role in perception of external pressure (Pophof 1997).

In morphology, SO slightly resemble sensilla auricillica or sensilla squamiformia in Lepidoptera (Schneider 1964; Denotter *et al.* 1978; Zacharuk 1989). Our observations of *C. solmsi marchali* SO (Fig. 8B) revealed them to be non-olfactory. Because SO shafts are connected to elliptical basal sockets by cuticular membranes, Chapman (1998) suggested that SO have a mechanosensory function. SO occur in a dorsal group on the pedicel and point toward the wasp’s head (Fig. 1C), suggesting that they monitor pressure when, for example, the female wasp pushes its way through the bracts of the host fig.

In our study, at least five types of chemosensory sensilla were characterized. Presumably they are used to detect chemicals emanating from their host fig trees and figs (Hossaert-McKey *et al.* 1994; Song *et al.* 2001; Chen and Song 2008) and enable female *C. solmsi marchali* to locate hosts efficiently. We also identified and characterized some mechanoreceptors, such as SO, whose exact function we hope to elucidate with electrophysiological experiments.

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**References**


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