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Antennal Sensilla of Fig Wasps (Hymenoptera: Agaonidae): Function-Driven Elaboration in Females and Degeneration in Males

Jing Meng,[1] Dawei Huang,[2,3] Jinhua Xiao,[2] and Wenjun Bu[4]

[1]College of Plant Protection, Shandong Agricultural University, Tai'an 271018, China (mengjing@sibs.ac.cn), [2]Key Laboratory of Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China (huangdw@ioz.ac.cn; xiaojh@ioz.ac.cn), [3]Corresponding author, e-mail: huangdw@ioz.ac.cn, and [4]Insect Molecular Systematic Lab, Institute of Entomology, College of Life Sciences, Nankai University, Tianjin 300071, China (wenjunbu@nankai.edu.cn)

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Abstract

Within the closed fig cavity packed with hundreds to thousands of fig wasps from multiple species, sensory structures on the antennae permit males to locate conspecific females for reproduction. When fig wasp females are seeking suitable figs for oviposition, antennal sensory structures perceive volatile compounds released from the target figs. In the present study, we investigated the sexual dimorphism of these important antennal sensillae by scanning electron microscopy. The antennal sensilla of *Ceratosolen solmsi marchali* Mayr, *Philotrypesis pilosa* Mayr, *Philotrypesis* sp., and *Apocrypta bakeri* Joseph in *Ficus hispida* displayed extreme dimorphism, with elaborated structures in females compared with degenerated structures in males. Sensilla coeloconica were absent in *A. bakeri*, but present in females of the other three species. Sensilla styloconica were present in both males and females of *C. solmsi marchali*, but were seen only in female of the other three species. Sensilla campaniformica, leaf-like sensilla, stylet-like sensilla, and bomb's hairs were seen only in female *C. solmsi marchali*. Sensilla short chaetica were only seen in *Philotrypesis* sp. The degeneration of male antennal sensilla of all studied fig wasps was important, but variable between species. In conclusion, sexual dimorphism of antennal sensilla of four species in *Ficus hispida* was consistent with their divergent biological and behavioral functions.

Key words: sense, scanning electron microscope, biological function

Figs (*Ficus* spp., Moraceae) and their pollinators (Agaonidae, Chalcidoidea, Hymenoptera) constitute a classic example of obligate plant–pollinator mutualism, and have become an ideal system for addressing questions on coevolution, speciation, and maintenance of mutualism (Kjellberg et al. 2001, Ronsted et al. 2005). In addition to the pollinators, figs also host several types of nonpollinator parasitic wasps from a variety of chalcid subfamilies with varied natural histories and ecological strategies (e.g., inquilines, gallers, and parasitoids; Bouček 1993). All wasps sheltered in figs are called fig wasps (Kjellberg et al. 2001, Weiblen 2002).

After maturation within the fig, male fig wasps come out of the galls and search for females to mate. Once mated, females emerge from the galls with or without the help of the males (Kjellberg et al. 2005). There are usually hundreds, even more, fig wasps simultaneously staying inside one fig, often of different species. Most males and conspecific females display extreme dimorphism, and many nonpollinators even display evolved male dimorphism (Jousselin et al. 2004). Therefore, within a fig cavity crammed with multiple species, it is very difficult for males to find the conspecific females to mate or for the different species to distinguish one from another.

The closed environment of the fig syconium makes it very difficult to observe and survey the biology and behavior of fig wasps (Kjellberg et al. 2005). The diversity of species and behavior also impair the study of chemical mediation (Proffit et al. 2007). The antennal sensilla receive the sensory information and are the functional unit for environment perception and communication. They should have evolved many traits to adapt to the exceptional fig environment. Antennae sensilla of wasps are involved in various behaviors including host-searching, host-recognition, oviposition, and mating (Abdurahiman 1979, 1980, 1986; Da-Rong et al. 2002). Several studies characterized the antennal sensilla of wasps using electron microscopy techniques (Walther 1983, Wibel et al. 1984, Merivee et al. 2002, Bleeker et al. 2004, Van Baaren et al. 2007, Onagbola and Fadamiro 2008) and revealed the strong sexual dimorphism in structures and types of antennal sensilla (Wibel et al. 1984, Bleeker et al. 2004, Onagbola and Fadamiro 2008). However, it remains poorly known whether biological functions such as copulation, host searching, and oviposition have an impact on the evolution of the morphology of antennal sensilla. Only the evolution of the multiporous plate sensilla of fig wasps has been investigated (Ware and Compton 1992).

In the present study, scanning electron microscopy (SEM) was used to compare the detailed characteristics of antennal sensilla in morphology, types, abundance, and distribution patterns of the four species of fig wasps in *Ficus hispida*. The differences in antennal sensillum types and their distribution pattern between conspecific genders were studied. We also tried to understand whether the biological functions affected the evolution of the antennal sensilla of fig wasps.

Materials and Methods

Insects

Mature figs (*Ficus hispida*) were harvested from DanZhou, Hainan Province, China. The fig wasps were harvested in 75% alcohol and then identified to species and separated by genders. Wasps belonging to *Ceratosolen solmsi marchali* Mayr, *Philotrypesis pilosa* Mayr, *Philotrypesis* sp., and *Apocrypta bakeri* Joseph were selected. No specific permits were required for the field studies, which did not involve endangered or protected species, and the sampling location was not privately owned or state-protected in any way.

Electron Microscopy

SEM was performed in June 2008 at the Nankai University, Tianjin, China. The antennae of the wasps were successively dehydrated in 80, 90, 95, and 100% ethanol for one hour each and dried (critical point drying; van Baaren et al. 1996). The specimens were then sputter-coated with 10-nm platinum. The specimens were examined in a FEIQUANTA200 SEM (FEI, US). The types of sensilla were identified from SEM micrographs and their location and number were recorded. Characteristics of the antennal sensilla were compared between males and females.

Taxonomy and Sensillar Function

The types and possible function of sensilla were classified according to Zacharuk and Keil (Zacharuk 1985, Keil 1999). The sensillar types were compared to *Nasonia vitripennis* (Wibel et al. 1984), *Rhopalicus tutela* (Walker, 1836) (Pettersson et al. 2001), and *Pteromalus cerealellae* (Hymenoptera, Pteromalidae) (Onagbola and Fadamiro 2008).

Results

Elaborated Female Antennal Sensilla

The female antenna consisted of 11 segments in *C. solmsi marchali*, 12 segments in *A. bakeri*, and 13 segments in *P. pilosa* and *Philotrypesis* sp. The antennal sensilla of the females were very complex in morphology, types, distribution, and abundance (Table 1). We also observed that some kinds of antennal sensilla have not been mentioned in other studies such as leaf-like sensilla, stylet-like sensilla, and sensilla short chaetica, which are specific to pollinators.

Sensilla Trichodea

Sensilla trichodea (ST) were richly distributed on each segment of the antenna. In *C. solmsi marchali*, ST were mostly distributed on the outer side of scape, sides of pedicel, and throughout all other segments (Fig. 1A). In *A. bakeri*, ST were distributed on the scape, pedicel, funicles (Fig. 1B), and clava. The distribution of ST for *P. pilosa* and *Philotrypesis* sp. was similar to that of *A. bakeri*.

For nonpollinators, at the apex of the antenna, ST and other types of sensilla were abundant and formed micropilose areas, as shown in Fig. 3. However, such micropilose areas were not found in the pollinators. There were interspecies differences in morphology of ST. The tip of ST on the fifth to the eleventh segments of *C. solmsi marchali* was globular, which increases surface area, but the tip of ST on the funicle of *A. bakeri*, *P. pilosa*, and *Philotrypesis* sp. was pointed.

Sensilla Basiconica

Sensilla basiconica (SB) were distributed on the fifth segment of *C. solmsi marchali* (Fig. 1D) and the anelli of nonpollinators. The quantity was much less than for ST. The tip of SB of *C. solmsi marchali* was globular, whereas the tip of the nonpollinator species was pointed.

Sensilla Placodea (Multiporous Plate Sensilla)

The distribution patterns of multiporous plate sensilla (MPS) differed among the four species studied here. In *C. solmsi marchali*, MPS were distributed in two to three arrays after the fourth segment. In *A. bakeri*, there was only one array on the funicle and the clava. In *P. pilosa* and *Philotrypesis* sp., there were one array on the funicles and one array on the clava. The morphology of MPS also showed differences between species. MPS of *C. solmsi marchali* (Fig. 1A) had a columnar shape with a rounded tip, while MPS of nonpollinators had a flat surface and a triangular tip (Fig. 1B, C, and E). MPS were much more developed in the females of the four species. This might be a selective evolution result because the females need to find suitable figs quickly for laying eggs during their short life span.

Sensilla Chaetica

Sensilla chaetica (SC) were mostly distributed at the tip of the antenna of females (Fig. 1C), and there were no distinct differences in abundance between the species. Abundance of SC and ST at the tip of antennae suggests that this micropilose area is extraordinarily important in sensory function. Especially, SC were located at the utmost tip, implying an important role in detecting substances on the fig surface.

Sensilla Coeloconica

Sensilla coeloconica (SCo) were scattered on the scape and two were present on the third segment in *C. solmsi marchali* (Fig. 1F). Both *P. pilosa* and *Philotrypesis* sp. had one on the first claval (the eleventh segment; Fig. 2A). We did not observe SCo in *A. bakeri*. SCo of *C. solmsi marchali* were cone-like, obviously morphologically different from the peg-like shape in *P. pilosa* and *Philotrypesis* sp.

Sensilla Styloconica

For *C. solmsi marchali*, three to six sensilla styloconica (SS) were distributed on the ventral side of each segment after the fourth, locating on the segment-joint region and between tips of MPS (Fig. 2B). In nonpollinators, there was only one SS on the dorsal side of each flagellum segment (Fig. 2C).

Sensilla Campaniformica

Sensilla campaniformica (SCa) were only seen on the scape of *C. solmsi marchali* (Fig. 2D).

Table 1. Antennal segments, types, distribution, and relative abundance of antennal sensilla of four fig wasp species in *Ficus hispida*

		Ceratosolen solmsi marchali		*Apocrypta bakeri*		*Philotrypesis pilosa*		*Philotrypesis sp.*	
		Female	Male	Female	Male	Female	Male	Female	Male
No. of antennal segments		11	4	12	3	13	9	13	9
ST	Abundance	+++	+	+++	+	+++	+	+++	+
	Distribution	S/P/A/F/C	Fourth segment	S/P/A/F/C	All segments	S/P/A/F/C	All segments	S/P/A/F/C	All segments
SB	Abundance	+	–	+	–	+	–	+	–
	Distribution	F	/	A	/	A	/	A	/
MPS	Abundance	+++	–	++	–	++	–	++	–
	Distribution	F/C	/	F/C	/	F/C	/	F/C	/
SC	Abundance	+	+	+	+	+	+	+	+
	Distribution	C	C	C	C	C	C	C	C
SCo	Abundance	++	–	–	–	+	–	+	–
	Distribution	S	/	/	/	C	/	C	/
SS	Abundance	++	+	+	–	+	–	+	–
	Distribution	F	C	F	/	F	/	F	/
SCa	Abundance	+	–	–	–	–	–	–	–
	Distribution	S	/	/	/	/	/	/	/
SLl	Abundance	++	–	–	–	–	–	–	–
	Distribution	P	/	/	/	/	/	/	/
SSl	Abundance	+	–	–	–	–	–	–	–
	Distribution	A	/	/	/	/	/	/	/
BH	Abundance	+	–	–	–	–	–	–	–
	Distribution	S	/	/	/	/	/	/	/
SSC	Abundance	–	–	–	–	–	–	+	–
	Distribution	/	/	/	/	/	/	F	/
No. of sensilla types		10	3	5	2	6	2	7	2

+: presence of the specific type of antennal sensilla; +: low; ++: moderate; +++: very abundant.

–: absence of the specific type of antennal sensilla.

SB, sensilla basiconica; SC, sensilla chaetica; SCa, sensilla campaniform; SCo, sensilla coeloconica; ST, sensilla trichodea; MPS, multiporous plate sensilla; SCo, sensilla coeloconica; SLl, leaf-like sensilla; SS, sensilla styloconica; SSl, stylet-like sensilla; BH, bomb's hair; SSC, sensilla short chaetica.

S, scape; P, pedicel; A, anelli in nonpollinators or third segment in pollinators; F, funicles; C, clava.

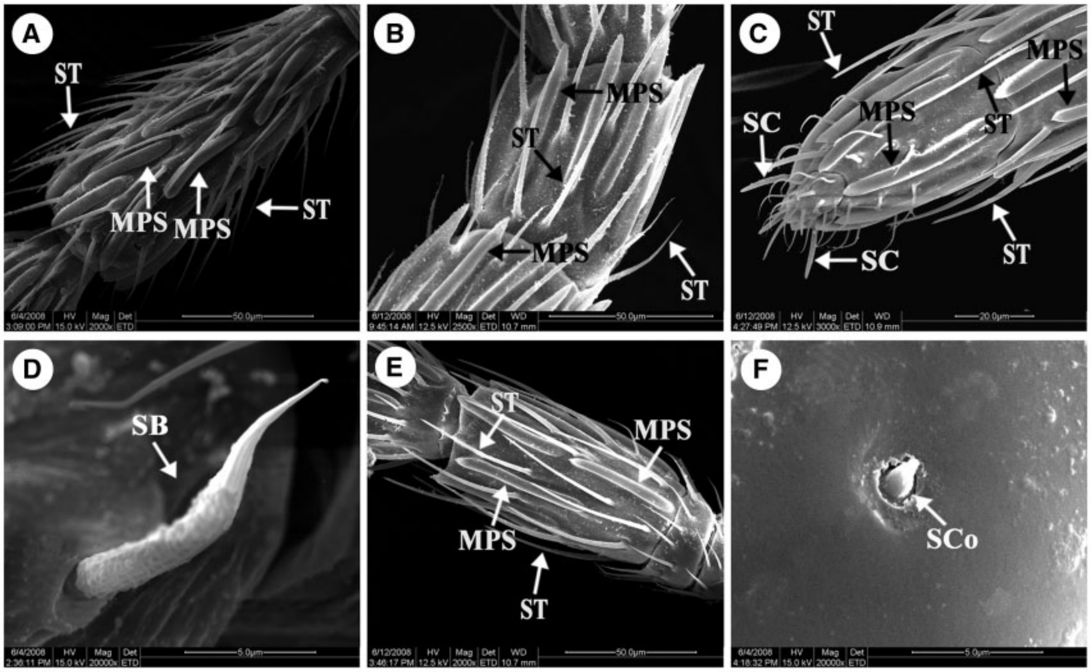

Fig. 1. Antennal sensillar types of females. (A) Fifth segment of female *C. solmsi marchali.* (B) Funicle of female *A. bakeri.* (C) Claval micropilose area of female *P. pilosa.* (D) Sensilla basiconica on the fifth segment of female *C. solmsi marchali.* (E) Funicle of female *Philotrypesis* sp. (F) Sensilla coeloconica on the scape of female *C. solmsi marchali.* Abbreviations: SB, sensilla basiconica; SC, sensilla chaetica; SCo, sensilla coeloconica; ST, sensilla trichodea; MPS, multiporous plate sensilla.

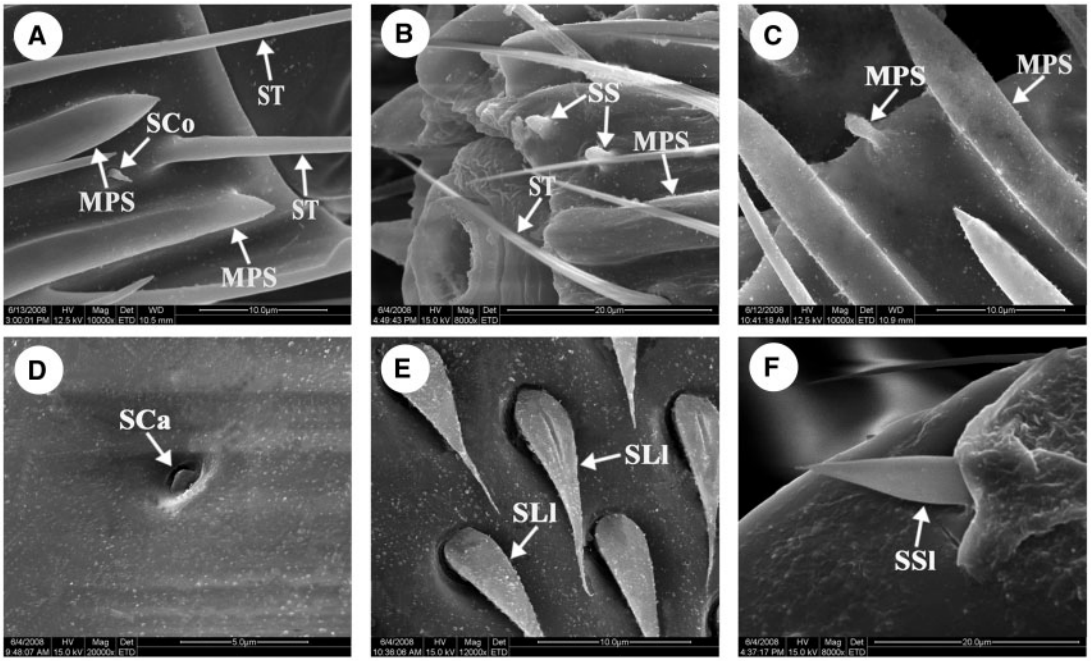

Fig. 2. Antennal sensillar types of females. (A) Sensilla coeloconica on the clava of female *P. pilosa.* (B) Sensilla styloconica of female *C. solmsi marchali.* (C) Sensilla styloconica of female *A. bakeri.* (D) Sensilla campaniformica on scape of female *C. solmsi marchali.* (E) Leaf-like sensilla on pedicel of female *C. solmsi marchali.* (F) Stylet-like sensilla on the thorn of the third segment of female *C. solmsi marchali.* Abbreviations: SCo, sensilla coeloconica; SLl, leaf-like sensilla; SS, sensilla styloconica; SSl, stylet-like sensilla; ST, sensilla trichodea; MPS, multiporous plate sensilla.

Leaf-like Sensilla

Leaf-like sensilla (SLl) were seen scattered on the antennae of *C. solmsi marchali*, covering all dorsal surface of the pedicel (Fig. 2E). Between zero and three grooves were present on the exterior surface of each SLl.

Stylet-style Sensilla

Only one stylet-like sensillum (SSl) was located on the base of the curved spine derived from the third segment of *C. solmsi marchali* (Fig. 2F).

Bomb's Hairs

Bomb's hairs (BH) were observed on the scape of *C. solmsi marchali* (Fig. 3A).

Sensilla Short Chaetica

Sensilla short chaetica (SSC) are much shorter and smaller than SC and with a truncated end, and were only present in *Philotrypesis* sp. (Fig. 3B). Absence of SSC was the sole difference between *P. pilosa* and *Philotrypesis* sp. in term of types, morphology, distribution, and abundance of antennal sensilla.

Degenerated Male Antennal Sensilla

Compared with females, males had degenerated antennae, and the antennal sensilla were obviously fewer in types and abundance, showing extreme sexual dimorphism (Table 1). Only ST, SC, and SS were observed in males.

Sensilla Trichodea

The morphology of ST in males was distinct from that of females, being much shorter and thinner. ST were present on the fourth segment of *C. solmsi marchali*, while sparsely covered all antennal segments of *A. bakeri*. In *P. pilosa* (Fig. 3C) or *Philotrypesis* sp., they were located on the lateral sides of each segment, being longer and present in a higher number than that of *C. solmsi marchali* or *A. bakeri*.

Sensilla Chaetica

SC were present at the tip of antenna of the males (Fig. 3D). The abundance and distribution of SC differed between species. In *C. solmsi marchali*, SC were only present on the ventral and dorsal of antennal apex, while in *A. bakeri*, they encircled the whole antennal apex. In *P. pilosa* or *Philotrypesis* sp., SC were localized in a ventral micropilose area of the antennal apex (Fig. 3E) and were in a higher number than in *C. solmsi marchali* and *A. bakeri*.

Sensilla Styloconica

SS were only present on the apex of antenna of male *C. solmsi marchali* (Fig. 3F). The morphology of SS in males was much different from that of females: they were shorter with a smoother surface.

Differences Between Pollinators and Nonpollinators

Table 1 presents the differences between pollinators and nonpollinators according to male and female. ST and SC were present in all four species, both in males and females. SB and MPS were seen in all the females of the four species. SCo were absent in *A. bakeri*, but present in the females of the other three species. SS were present in both males and females of *C. solmsi marchali*, but were only present in the females of the other three species. SCa, SLl, SSl, and BH were seen only in the females of *C. solmsi marchali*, while SSC were seen only in female *Philotrypesis* sp.

Discussion

Females had 10 types of sensilla for pollinators and 5–7 types for nonpollinators, according to species. Furthermore, females had

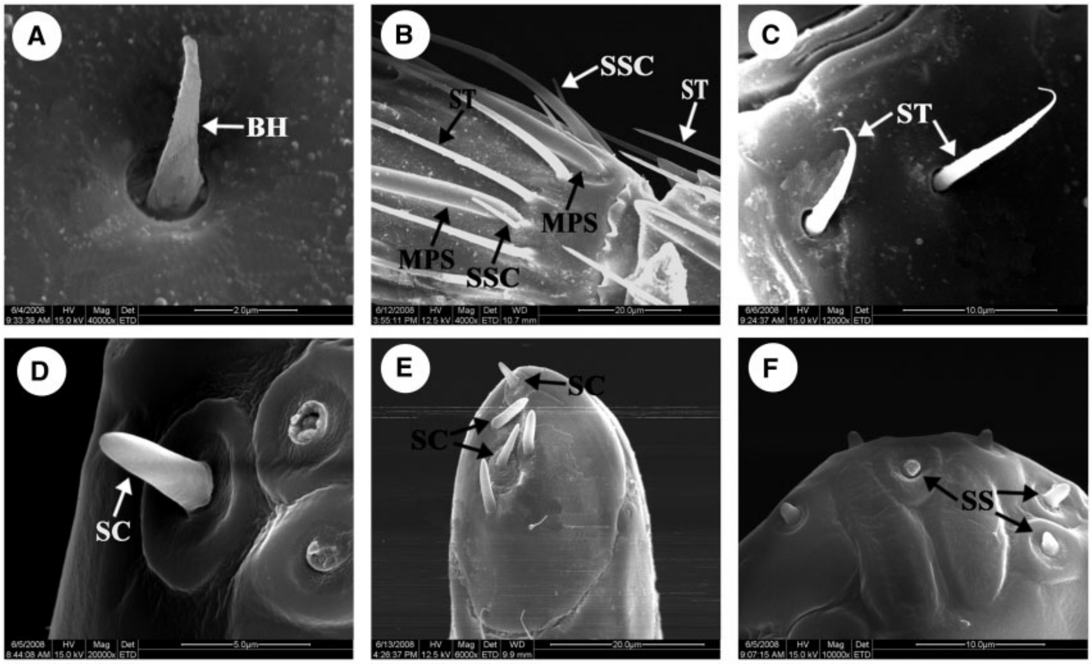

Fig. 3. Antennal sensillar types. (A) Bomb's hair on the scape of female *C. solmsi marchali*. (B) Special sensilla short chaetica on the funicle of female *Philotrypesis* sp. (C) Sensilla trichodea of male *P. pilosa*. (D) Sensilla chaetica at the tip of the antenna of male *C. solmsi marchali*. (E) Claval micropilose area showing the presence of sensilla chaetica in male *P. pilosa*. (F) Sensilla styloconica at the tip of antenna in male *C. solmsi marchali*. Abbreviations: BH, bomb's hair; SC, sensilla chaetica; SS, sensilla styloconica; SSC, sensilla short chaetica; ST, sensilla trichodea; MPS, multiporous plate sensilla.

more complex morphology and more types of sensilla than males. In contrast, males had much fewer types of antennal sensilla with scarce abundance and simpler morphology. This phenomenon strongly suggests an extreme sexual dimorphic pattern of antennal sensilla among fig wasps.

Several types of sensilla are encountered in fig wasps, all playing a number of different roles. ST widely exist in insects and are one of the most important sensory organs, functioning as mechano-, chemo-, or thermoreceptors. SB are normally regarded as mechano- or chemoreceptors or even as thermo- or hygroreceptors. Sensilla placodea are now generally considered as MPS, and are chemoreceptors that are widely present in Hymenoptera. They are one of the key characteristics used in morphology and evolution studies. SC are mechano- or chemoreceptors, morphologically standing still, thick, flat at the end, porous or not porous. SCo have been regarded as thermo-, hygro-, or chemoreceptors. SS are mechano- or chemoreceptors, and often present deep troughs on the surface. SCa function as mechanoreceptors; this kind of sensilla may greatly help the pollinator in finding sites for oviposition or pollination within the syconium. SLl were not previously described in the insects studied here; they are used as a taxonomic characteristic but have never been mentioned as sensilla. SSl could be putative mechano-, thermo-, or hygroreceptors. While entering the fig, at a cost of losing the flagellum and the wings, most pollinating wasps press the remnant antenna forward and push through the compact ostiolar scales of the figs. SLl locating on the pedicel, a protruding segment on the remnant antenna, could be the major mechanoreceptor helping the female sensing the mechanical pressure. The existence of specialized SLl is an evidence of the pollinators' adaptation to the figs. To enter the fig, most pollinating wasps use the curved spine to lift the ostiolar scales. SSl could putatively assist the pollinator female to detect the environmental factors within the syconium such as temperature, pressure, and humidity, which is another robust evidence to prove the pollinators' adaptation to the figs. BH function as mechanoreceptors. Like other special sensilla of *C. solmsi marchali*, i.e., SCa, SLl, and SSl, BH may be related to the behavior of the females when entering the fig. Together, these sensilla provide the insects with the perception they need to interact with their environment and other wasps (Jourdan et al. 1995, Basibuyuk and Quicke 1999, Merivee et al. 2002, Van Baaren et al. 2007).

The extreme sexual dimorphism observed in the present study may be correlated with the different biological functions of both genders, which has been observed in parasitoid wasps (Walther 1983, Van Baaren et al. 2007, Onagbola et al. 2009, Das et al. 2011). After mating, mature females of *F. hispida* climb out of the figs, fly a distance, and then find a suitable fig. These successive processes are called host-searching and host-recognition, which have to be completed quickly and accurately (Abdurahiman 1979, 1980; Da-Rong et al. 2002). However, males live their whole life within the fig. They die soon after they come out of the galls (Murray 1990, Da-Rong et al. 2002). The aim and the proximate function of their lives are to mate and provide sperms. They seem to have no need for numerous and different types of sensilla. Therefore, the present study indicates that the antennae of fig wasps display extreme sexual dimorphism in morphology, as well as in types, abundance, and distribution, which should be elucidated as the results of function-driven evolution.

The antennal sensilla of females had some differences between the four studied species. Results showed that the main differences between pollinators and nonpollinators were the micropilose areas at antennal tip. In nonpollinator females, these micropilose areas were clearly discernible, and the number of different sensilla types and the amount of each sensillum were high. However, these sensilla-rich micropilose areas were not found in pollinator females. Such difference can be correlated to the different oviposition behaviors of nonpollinators and pollinators, in which the three nonpollinator females oviposit from outside the figs, while the pollinators must enter into the figs to oviposit. The sensilla-rich micropilose area in nonpollinators could be much helpful in assisting females to detect suitable sites for oviposition by tapping on the surface of the figs using antennal tip (Abdurahiman 1979, 1980, 1986; Zhen et al. 2004; Li et al. 2009). Such a terminal claval segment has been described in Mymaridae, Encyrtidae, Trichogrammatidae, Ichneumonidae, Diapriidae, and Pteromalidae (Van Baaren et al. 2007). However, for pollinators, the antennal segments after the third one are usually broken off during their entry into the syconium through the ostiole, and there was no evolutional pressure to evolve a special sensilla-rich functional micropilose area at the antennal tip like the one observed in nonpollinators (Van Baaren et al. 2007).

Another difference of antennal sensilla between pollinators and nonpollinators related to oviposition behaviors is the performance of scape and pedicle of the pollinators, on which evolved many unique kinds of sensilla such as sensilla campaniformica, SLl, SSl, and BH, by which the pollinators can successfully receive sensory information while entering figs and inside the syconia after their antennal flagellum broke off. The nonpollinators do not have these particular antennal sensilla perhaps because they oviposit from outside the syconium and the sense function is mainly operated by the funicle and clava.

Compared with females, the segment numbers, antennal length, and antennal sensilla were degenerated in males. These degenerated antennal sensilla showed many differences between the studied species, suggesting that different mating strategies constrain the morphological evolution of the male antennal sensilla. A recent study has shown that differences in the antennae between male and female fig wasps are driven by the *Or2* genes (Lu et al. 2009). In males, SC were very short, thick, and obtuse, similar to pillars, which are perhaps degenerated from the pre-SC in order to adapt to the inner environment of the syconium (Van Baaren et al. 2007).

The antennae of *C. solmsi marchali* males were reduced to only four segments and antennal sensilla were mostly degenerated, mainly on the apex of antenna. Though the antenna sensilla were degenerated, males' high numbers, compared with males of nonpollinator species (unpublished observation from our group), could compensate and help the males finding the females. The antennae of *A. bakeri* males were reduced to three segments and antennal sensilla were less degenerated than in *C. solmsi marchali*. ST was seen to be scattered on the whole antenna and SC encircled the apex of the antenna, which may help *A. bakeri* males to find female mates in the deep layer of the galls. The antennae of *P. pilosa* and *Philotrypesis* sp. males were reduced to nine segments and the antennal sensilla were slightly degenerated compared with *C. solmsi marchali* and *A. bakeri*. ST were located at the lateral side of every segment, in a greater abundance and longer than that of *C. solmsi marchali* or *A. bakeri*, which could provide a sensory information involved in their behaviors of searching and protecting females, and also in running on smooth galls and fighting in the open space of the syconium. In addition, distinctly from *C. solmsi marchali* and *A. bakeri*, SC of *P. pilosa* and *Philotrypesis* sp. males formed a special micropilose area on the ventral side of the last segment, which may be useful for searching for females by tapping on galls in which the females hide (Li et al. 2009).

In conclusion, in this comparative study of antennal sensilla of four species in *Ficus hispida*, we observed extreme dimorphism between genders, with females having elaborated antennal sensilla, while they were degenerated in males. In females, there were many differences in sensilla types, abundance, and distribution patterns between pollinators and nonpollinators. In males, the degeneration of antennal sensilla was different in different species, and might be related to different mating strategies. The present study helps understanding the behavior and communication of fig wasps, and provides a basis for the morphological and ethological study in fig wasps.

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