Ultrastructural Observations of Antennal Sensilla in *Phauda flammans* Walker (Lepidoptera: Zygaenidae)[1]

J.Y. Liu, Y.J. Zhang, Z.Y. Huang, Z.S. Dong, Y.B. Duan, W. Lu[2], and X.L. Zheng[2]

Guangxi Key Laboratory of Agric-Environment and Agric-Products Safety, College of Agriculture, Guangxi University, Nanning, China

J. Entomol. Sci. 53(3): 281–294 (July 2018)

Abstract *Ficus microcarpa* L. and *F. racemosa* L. are often extensively damaged by the defoliating pest *Phauda flammans* Walker (Lepidoptera: Zygaenidae). The structure, morphology, abundance, and distribution of the antennal sensilla of *P. flammans* were studied using scanning electron microscopy. Six types and eight subtypes of sensilla were observed on the filiform antennae of both sexes, including trichodea (subtypes I and II), basiconica (subtypes I and II), coeloconica, styloconica, chaetica, and Böhm bristles. The most numerous sensilla were the trichodea on the antennae of both sexes. Sexual dimorphism was observed, with the male antennae having more sensilla trichodea than the female antennae. This information is essential for understanding the electrophysiological and behavioral aspects of chemical communication in *P. flammans*.

Key Words *Phauda flammans*, antennal sensilla, scanning electron microscopy

Ficus (Urticales: Moraceae) trees are the primary decorative trees used to line avenues in urban landscapes of the southern cities in China and countries in Southeast Asia, and are vital to maintaining ecological balance by actively cycling nutrients and gases (e.g., carbon dioxide and oxygen) and providing a cumulative leaf area for the impingement, absorption, and accumulation of air pollutants (e.g., construction, industrial, and vehicle emissions) that decreases the pollution ratio in the urban atmosphere (Escobedo et al. 2008). However, *Ficus microcarpa* L. and *F. racemosa* L. are often extensively damaged by the defoliating pest *Phauda flammans* (Walker) (Lepidoptera: Zygaenidae) in China (Liu et al. 2014, 2015a, 2015b, 2016) and India (Nageshchandra et al. 1972, Verma and Dogra 1982).

Phauda flammans exhibits two to three generations per year in Nanning City, Guangxi, southern China. Adults primarily are attracted to the host plants during the daytime when they oviposit eggs on leaves. Peaks in the number larvae in the first generation occur from mid-May to late June and in the second generation from early August to mid-October. Larvae can even be found on *F. microcarpa* leaves during winter months. Pupation most frequently occurs near roots and exposed tussocks on the ground, with only a few individuals pupating in the topsoil. Previous work includes reports of biological characteristics (Liu et al. 2014, 2015a, 2015b; Zheng et al. 2017), occurrence (Nageshchandra et al. 1972, Verma and Dogra 1982), and

---

[1] Received 19 April 2017; accepted for publication 18 June 2017.

[2] Corresponding authors: W. Lu (email: luwenlwen@163.com) and X.L. Zheng (email: zheng-xia-lin@163.com).

control (Liu et al. 1985, Zheng et al. 2015). Chemical insecticides remain as the most effective management tactic, but widespread use is no longer feasible due to development of insecticide resistance and negative impacts on biodiversity and environmental health.

Sex pheromone–based monitoring, mass trapping, and mating disruption have been identified as effective alternative control methods (Witzgall et al. 2010). Reproductive behavior in many insects is governed by sex pheromones, which are detected via chemical receptors and expressed in olfactory receptor neurons (Kurtovic et al. 2007). Pheromone identification is frequently part of the study of the electrophysiological response of antennal receptors (Bill et al. 1989), especially the antennal sensilla (Lopes et al. 2002).

In the study presented herein, scanning electron microscopy (SEM) was used to characterize the ultrastructure of the antennal sensilla of adult male and female *P. flammans*, and to identify the types, distribution, and numbers of antennal sensilla in both sexes of the adults. Our ultimate goal is to provide a basis for subsequent electrophysiological and behavioral studies that will lead to the identification of the *P. flammans* sex pheromone so that the mechanisms of sexual communication in this species can be determined.

Materials and Methods

Insects. *Phauda flammans* pupae were collected from *F. microcarpa* and/or *F. racemosa* branch angles and root cracks in the field in Nanning City, Guangxi, China, in early May 2016. Individual pupae were placed in a plastic container (15 × 10 × 10 cm) and held at 26 ± 2°C and 70 ± 10% relative humidity with a 16L:8D natural light photoperiod. After emergence, male and female moths were supplied with a 5% (v/v) honey solution *ad libitum*. Heads were removed from newly emerged moths (1 or 2 d old) and placed in 70% ethyl alcohol until processed for SEM studies.

SEM. Antennae from each *P. flammans* specimen were removed from the head and cleaned twice in a JP-010T ultrasonic bath (Skymen Cleaning Equipment Co., Ltd., Shenzhen, China) at 250 W for 180 s each time. They were then immersed individually in 2.5% glutaraldehyde at 4°C for 12 h and then fixed in phosphate buffer solution (0.01 mol/L, pH = 7.0) for 30 min until impurities were removed and the antennae cleared. The antennae were dehydrated through an ascending ethanol series (70, 80, 85, 90, 95%; 10 min per solution) and then completely dehydrated twice in 100% ethanol (15 min each time). The prepared antennae were dried with a desiccant for 24 h in a glass container, after which the specimens were mounted on a holder using double-sided tape, and were sputter coated with gold-palladium. The antennae samples were then observed and photographed with an SU-8020 SEM (Hitachi Ltd., Tokyo, Japan) at 15 kV.

Terminology and statistical analysis. The morphological terms used herein are those of Zacharuk (1985). The features of the sensory structures of *P. flammans* were compared to those described in the scientific literature for other Lepidoptera, including *Plodia interpunctella* Hübner (Ndomo-Moualeu et al. 2014), *Cydia pomonella* L. and *C. succedana* Denis & Schiffermüller (Roh et al. 2016), and *Tuta absoluta* Meyrick (Bawin et al. 2017).

The sensilla on the ventral and dorsal surfaces of the antenna of both sexes of *P. flammans* were identified, counted, and measured with ImageJ Launcher software version 1.48u (Broken Symmetry Software, National Institutes of Health, Bethesda, MD) (Ndomo-Moualeu et al. 2014). Data were recorded for 10 antennae from individual male and female adults, and measurements were obtained from 40 individual structures per type of sensillum for both sexes. A *t* test was used to check for possible sexual dimorphism in the antennal sensilla of males and females using SPSS version 16.0 (SPSS Inc., Chicago, IL) at a significance level of $P \leq 0.05$.

Results

Antennae of the female and male moths were filiform, each consisting of a scape, pedicel, and a flagellum of more than 40 flagellomeres (Fig. 1A). The scape was the largest antennal segment for both sexes. In comparing the length of the antennal segments between males and females, the male scape ($t = -4.304$; df = 8; $P = 0.006$) and pedicel ($t = -3.392$; df = 8; $P = 0.009$) were significantly longer than those of the females, but the flagellum length was not ($t = -1.238$; df = 58; $P = 0.221$). In contrast, the width of the scape ($t = -1.098$; df = 8; $P = 0.304$) and pedicel ($t = -1.000$; df = 8; $P = 0.347$) did not differ between the sexes, but the female flagellum was wider than that of the male ($t = -2.167$; df = 58; $P = 0.034$) (Table 1). Each flagellomere could be divided into two main areas (Fig. 1B, C). Scales and sparse sensilla were distributed on the dorsal surface (Fig. 1C, D), while the ventral surface had no scales but was covered with various types of sensilla (Fig. 1B, E).

Six types and eight subtypes of sensilla were observed on the flagellar subsegments of the antennae of both sexes, including sensilla trichodea (s. trichodea) (subtypes I and II), sensilla basiconica (s. basiconica) (subtypes I and II), sensilla coeloconica (s. coeloconica), sensilla styloconica (s. styloconica), sensilla chaetica (s. chaetica), and Böhm bristles (B. bristles). Sexual dimorphic characters are presented in Tables 2 and 3, and each of the different sensilla are described in the following paragraphs.

Sensilla trichodea. The s. trichodea was the most abundant type of sensillum on the antennae of both sexes. It was observed on the ventral surface of the entire flagellum and was also found arranged randomly on the dorsal surface. The surfaces of these sensilla were multiporous and showed an annular ridge pattern (Fig. 2B, D) that was divided into two subtypes (Fig. 2A, C). The length ($t = 0.209$; df = 78; $P = 0.514$) and diameter ($t = 1.159$; df = 78; $P = 0.250$) of subtype I and the length ($t = 0.146$; df = 78; $P = 0.884$) and diameter ($t = -1.679$; df = 78; $P = 0.097$) of subtype II did not differ between males and females (Table 2). The numbers of subtype I on the ventral surface ($t = 1.509$; df = 16; $P = 0.151$) and dorsal surface ($t = 0.803$; df = 16; $P = 0.433$) also were similar in both sexes (Table 3). In contrast, the number of subtype II on the ventral surface ($t = 2.763$; df = 16; $P = 0.014$) was greater in males than in females, but the number on the dorsal surface ($t = -1.307$; df = 16; $P = 0.210$) did not differ (Table 3).

Sensilla basiconica. The s. basiconica was also divided into two subtypes (I and II) and appeared in large numbers on all flagellomeres in both sexes (Table

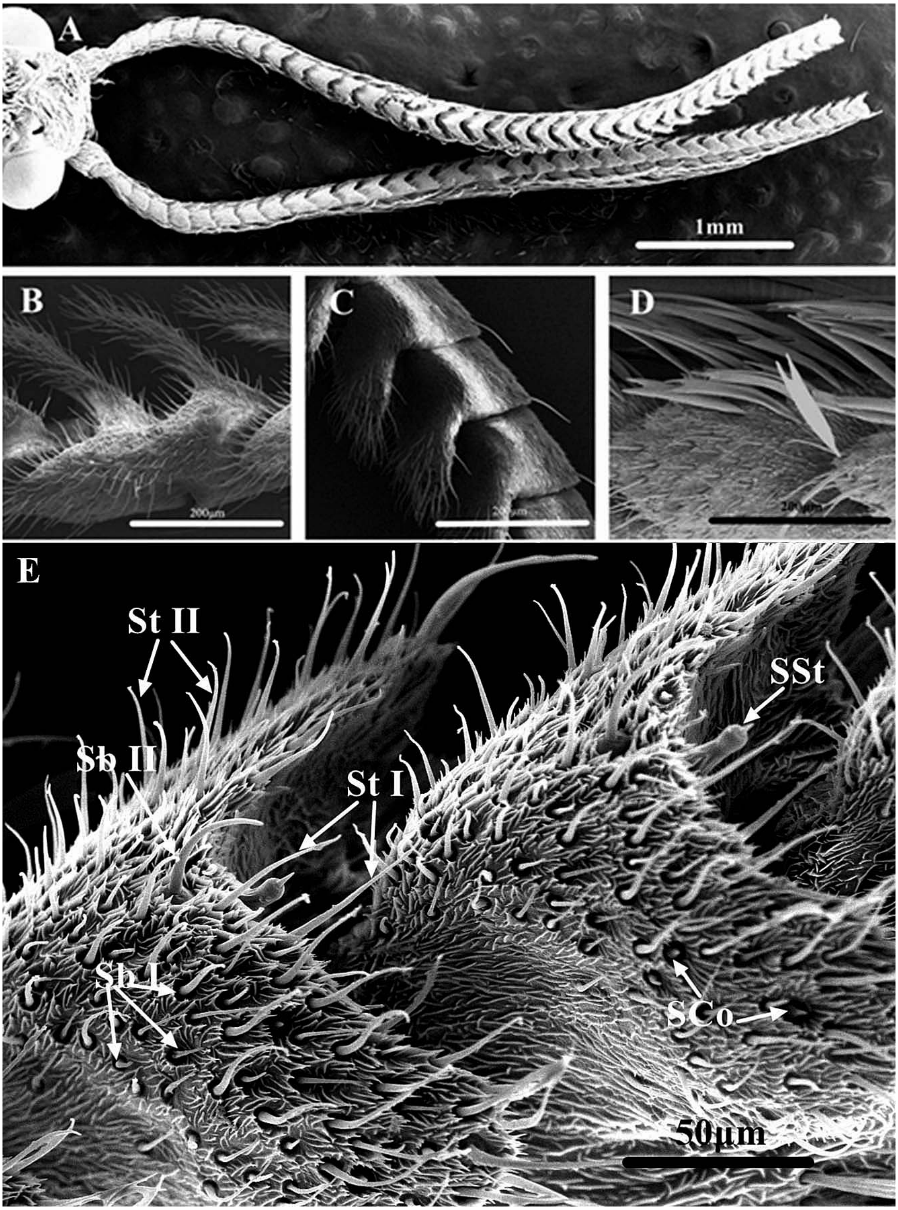

Fig. 1. Ultrastructure of antennal flagella of male *P. flammans* (A); ventral surface of the female *P. flammans* antenna (B); dorsal surface of the female *P. flammans* antenna, noting the sensilla trichodea, sensilla basiconica, and sensilla chaetica (C); squama assembled on the flagellum of the male antenna (D); and numerous sensilla on the ventral surface (E).

Table 1. Mean ± SE length and width of the scape, pedicel, and antennal flagellum of *P. flammans.**

Antennal structure	Length (mm)		Width (mm)	
	♀	♂	♀	♂
Scape	0.36 ± 0.07 (5)	0.32 ± 0.03 (5)	0.16 ± 0.04 (5)	0.15 ± 0.03 (5)
Pedicel	0.11 ± 0.01 (5)	0.11 ± 0.01 (5)	0.19 ± 0.03 (5)	0.18 ± 0.02 (5)
Flagellomere	0.13 ± 0.04 (30)	0.13 ± 0.04 (30)	0.11 ± 0.03 (30)	0.12 ± 0.03 (30)

* Numbers in parentheses indicate the sample size.

3). Subtype I were distributed on the ventral surface of the flagellomeres (Fig. 3A), and only subtype II was observed on the dorsal surface of the antennae (Fig. 4A). Subtype I was ribbed with transverse grooves with some pores (Fig. 3B), and it was significantly longer ($t = 2.480$; df = 78; $P = 0.016$) and wider ($t = 2.357$; df = 78; $P = 0.021$) in male than in female antennae (Table 2). The number of this subtype on the ventral surface did not differ between the sexes ($t = 0.114$; df = 16; $P = 0.910$) (Table 3). Subtype II was longer than subtype I and was also multiporous with transverse grooves (Fig. 4C); the base formed an approximately 70° angle to the antenna and was regularly spaced on the dorsal surface (Fig. 4A, B). The length ($t = 0.661$; df = 78; $P = 0.510$) and diameter ($t = -0.441$; df = 78; $P = 0.661$) of these sensilla were not significantly different between the sexes (Table 2), and the number of subtype II on the ventral ($t = 0.093$; df = 16; $P = 0.927$) and dorsal (t

Table 2. Mean ± SE dimensions of the sensilla on the antennae of *P. flammans.*

Type of Sensillum*	Length (μm)		Diameter (μm)	
	♀	♂	♀	♂
S. trichodea I	46.91 ± 1.15	47.29 ± 1.37	2.67 ± 0.09	2.81 ± 0.08
S. trichodea II	48.14 ± 1.28	48.40 ± 1.21	3.16 ± 0.07	2.98 ± 0.08
S. basiconica I	8.05 ± 0.16	8.74 ± 0.23	1.67 ± 0.02	1.75 ± 0.02
S. basiconica II	44.86 ± 0.79	45.63 ± 0.86	2.87 ± 0.05	2.84 ± 0.04
S. coeloconica	2.99 ± 0.03	2.97 ± 0.04	2.00 ± 0.04	2.13 ± 0.05
S. styloconica	17.64 ± 0.39	17.29 ± 0.35	6.09 ± 0.13	5.92 ± 0.12
S. chaetica	84.57 ± 8.18	91.45 ± 10.05	3.01 ± 0.02	2.99 ± 0.02
B. bristles	6.87 ± 0.16	6.89 ± 0.14	1.63 ± 0.05	1.61 ± 0.04

* S., Sensilla; B., Böhm.

Table 3. Mean ± SE number of sensilla* on the dorsal (D) side and ventral (V) side of *P. flammans*.

Antennal views	S. trichodea I	S. trichodea II	S. basiconica I	S. basiconica II
D				
♀	46.44 ± 3.01	169.44 ± 5.05	0.00	50.11 ± 2.01
♂	50.67 ± 4.30	160.89 ± 4.17	0.00	48.00 ± 2.07
V				
♀	1,085.33 ± 18.28	1,181.78 ± 13.69	688.22 ± 26.49	546.44 ± 29.18
♂	1,127.33 ± 20.99	1,247.89 ± 19.62	692.22 ± 22.89	550.00 ± 24.49

* S., Sensilla; B., Böhm.

= −0.731; df = 16; $P = 0.475$) surfaces did not differ significantly between males and females (Table 3).

Sensilla coeloconica. In both sexes, some s. coeloconica were distributed on the ventral surfaces of the antennae on each flagellar subsegment; these short, peg-shaped sensilla emerge from hollow pits with analogous strip-shaped sensory shafts (Fig. 3A, C). The length of the s. coeloconica did not differ between the sexes ($t = -0.616$; df = 78; $P = 0.540$), but the diameter was greater in males than in females ($t = 2.073$; df = 78; $P = 0.042$) (Table 2). Furthermore, the number of s. coeloconica did not differ between the sexes ($t = 1.060$; df = 16; $P = 0.305$) (Table 3).

Sensilla styloconica. In the upper middle area of each flagellar subsegment, single s. styloconica were often found rising from a cylindrical protrusion to form a peak (Fig. 5C). There were no differences in the length ($t = -0.680$; df = 78; $P = 0.499$) and diameter ($t = -0.971$; df = 78; $P = 0.335$) of this type of sensillum between males and females (Table 2), but the mean number was much greater in females than in males ($t = -3.362$; df = 16; $P = 0.004$) (Table 3).

Sensilla chaetica. The s. chaetica, whose surfaces were covered with vertical slots, were distributed over each flagellomere subsegment (Fig. 5B) and were set in central sockets and were straight, wide at the base, smooth at the apex, and without pores (Fig. 5A). The length ($t = 0.293$; df = 78; $P = 0.597$) and diameter ($t = -0.657$; df = 78; $P = 0.513$) of these sensilla did not differ between the sexes (Table 2), and the numbers on the ventral ($t = 0.697$; df = 16; $P = 0.496$) versus the dorsal ($t = 1.817$; df = 16; $P = 0.088$) surfaces were not different with respect to sex (Table 3).

Böhm bristles. The spinelike B. bristles taper toward the apex without a papilliform tip and are distributed only on the dorsal surface of the scape and the pedicel (Fig. 5D). The length ($t = 0.076$; df = 78; $P = 0.940$) and diameter ($t = -0.567$; df = 78; $P = 0.572$) (Table 2) as well as the number of B. bristles ($t = -0.417$; df = 16; $P = 0.684$) (Table 3) were similar in males and females.

Table 3. Extended.

S. coeloconica	**S. styloconica**	**S. chaetica**	**B. bristles**
0.00	0.00	61.89 ± 3.03	43.33 ± 3.42
0.00	0.00	69.11 ± 2.57	41.78 ± 1.49
553.89 ± 12.45	49.00 ± 1.34	89.00 ± 3.57	0.00
575.00 ± 15.54	43.11 ± 1.12	92.89 ± 4.28	0.00

Discussion

Although there have been no reports on the antennal sensilla of members of the family Zygaenidae, studies of many other lepidopteran species have shown that the general shape, structure, and types of sensilla of the antenna of adult *P. flammans* are similar to those described in other species, such as *Plodia interpunctella* (Ndomo-Moualeu et al. 2014), *Catocala remissa* Staudinger (Zheng et al. 2014), *Holcocerus hippophaecolus* Hua (Wang et al. 2015), *Monema flavescens* Walker (Yang et al. 2016), *C. pomonella*, *C. succedana* (Roh et al. 2016), and *T. absoluta* (Bawin et al. 2017). The functions of all these sensilla have been reported to be primarily sensory, and all of these species are endowed with the sensilla responsible for olfactory detection and the perception of tactile signals (Lena et al. 2005).

Specifically, many studies have shown that s. trichodea are responsible for mechanical and chemical reactions, and these sensilla could be further divided into subtypes by the number of sensory cells or pores on the sensillum wall (Onagbola and Fadamiro 2008), size (Zheng et al. 2014), or other indicators. Two subtypes, which were named “long s. trichodea” by Roh et al. (2016), were identified in our study. Furthermore, s. basiconica are believed to be integrated olfactory stimuli receptors that are sensitive to host volatiles, mates, oviposition attractants, etc. (Rebijith et al. 2016). Our results corroborate the view of Ndomo-Moualeu et al. (2014) that they are composed of two subtypes. Additionally, the multiporous structure suggests that they are key olfactory receptors (Monteforti et al. 2002). Generally, the two s. coeloconica subtypes differ in the presence or absence of a circular fence (Roux et al. 2005), but only subtype II, without the circular fence, was found in our study. These sensilla are apparently sensitive to humidity, temperature, CO_2, olfactory stimuli, etc. (Galvani et al. 2008, Kristoffersen et al. 2006, Kuřavová et al. 2017, Ren et al. 2014). In s. styloconica, the two subtypes are divided based on the presence or absence of apical structures and only the subtype with apical structures, which are associated with the thermo-hygroreceptor function (Steinbrecht and Müller 1991), was found in our

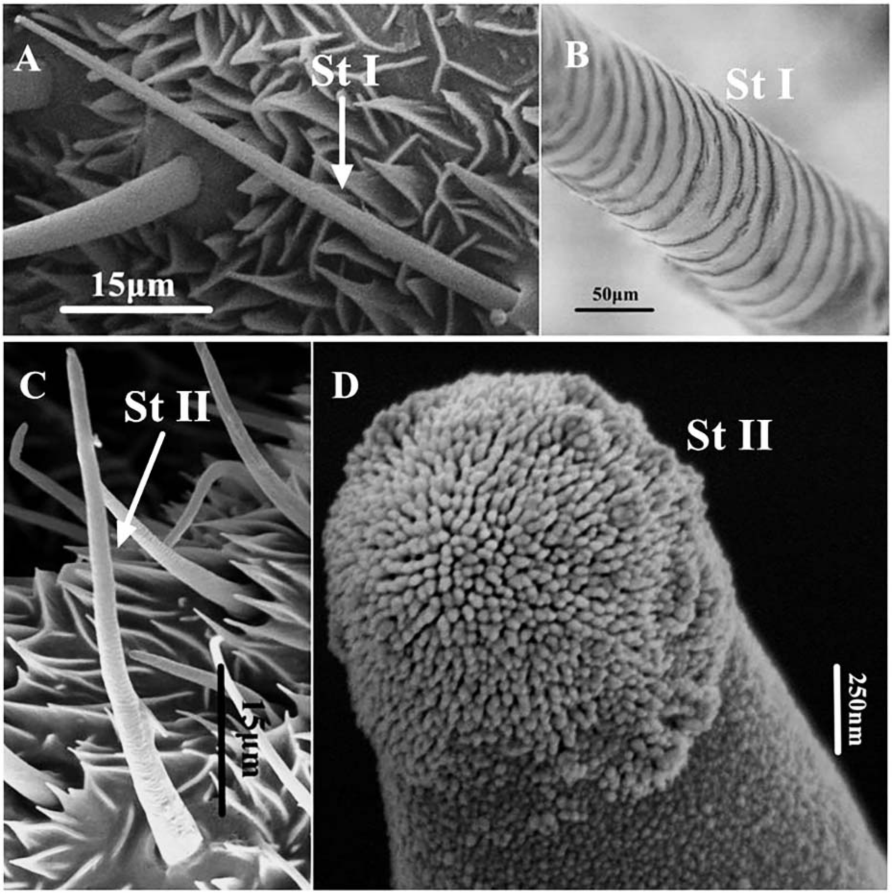

Fig. 2. Ultrastructure of two subtypes of sensilla trichodea (s. trichodea) (St I and St II) on antennal flagellomeres of *P. flammans*—long and straight s. trichodea I (A), the annular ridge pattern of the s. trichodea surface (B), s. trichodea II slightly curved toward the apex (C), and the multiporous pattern of the s. trichodea apex (D).

study. Several previous studies classified s. chaetica as terminal pore sensilla, suggesting that they function as contact chemoreceptors and mechanoreceptors (Seada 2015), but this pore was not observed in *P. flammans*. Therefore, s. chaetica may have no receptor function or only a mechanoreceptive function (Wang et al. 2010), such as identifying sounds or air currents (Keil 1999) or protecting other sensilla (Chang et al. 2015). It has been suggested that another specialized sensillum, the B. bristles that only occur on the scape and pedicel in the antennae of *P. flammans*, might be membrane acceptors on the segment membranes between the scape and pedicel or a mechanosensory unit that monitors the position of the antennae in flight (Krishnan et al. 2012).

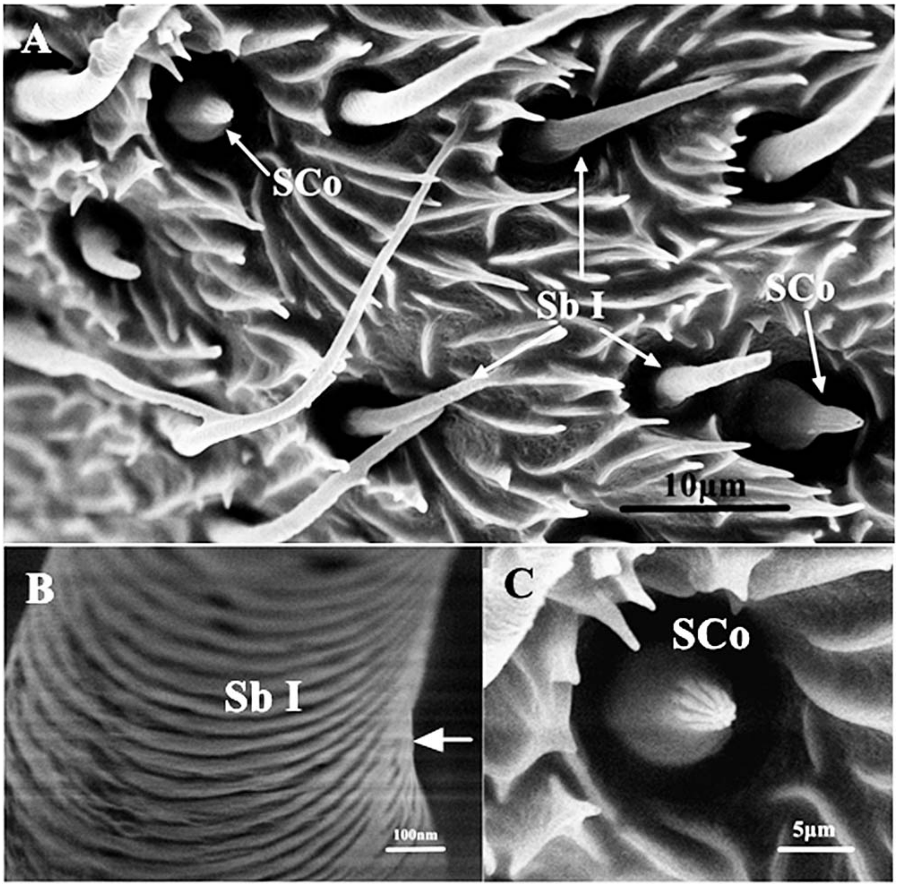

Fig. 3. Ultrastructure of sensilla basiconica (s. basiconica) subtype I (Sb I) and sensilla coeloconica (s. coeloconica) (SCo) on antennal flagellomeres of *P. flammans* (A). Basal part of s. basiconica I showing transverse grooves with some pores (arrow) present on the sensillum surface (B); short, peg-shaped s. coeloconica (C).

Antennal sensilla sexual dimorphism, which is intimately connected to the important tasks of feeding, mate location, dispersal, oviposition, and other functions that are central to the life-history evolution of the species, is an especially ubiquitous form of intraspecific variation in moths (Allen et al. 2011). Faucheux and Kundrata (2017) speculated that sexual differences in the numbers of antennae sensilla may be linked with sex-specific differences in behavior. In *P. flammans*, sensilla of the male antennae, particularly the s. trichodea, were generally more numerous than on the female antennae (Table 3). Similar results have been reported in *Talponia batesi* Heinrich (Gómez and Carrasco 2008) and *T. absoluta* (Bawin et al. 2017). Faucheux et al. (2006) demonstrated that the s. trichodea of the male antennae are

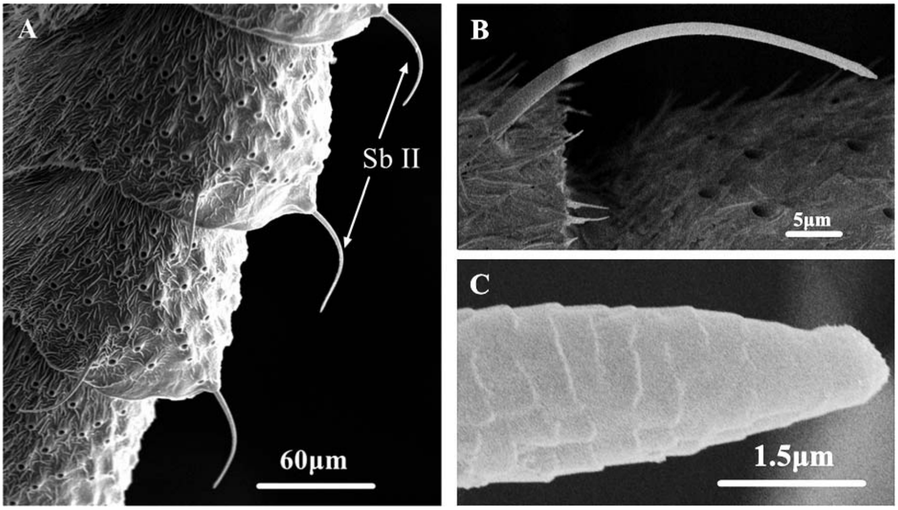

Fig. 4. Ultrastructure of sensilla basiconica (s. basiconica) subtype II (Sb II) distributed regularly on the dorsal surface (A); the base of s. basiconica II forming an approximately 70° angle to the antenna (B); transverse grooves with some pores present at the s. basiconica II apex (C).

the receptors of female sex pheromones, but further study is needed to determine whether there is an inherent relationship between the number or distribution of s. trichodea and sensitivity to chemicals.

Some nocturnal moths have the same filiform antennae as the diurnal *P. flammans*. Previous studies also reported the s. trichodea, s. basiconica, s. coeloconica, s. styloconica, and s. chaetica sensilla on the antennae of both nocturnal and diurnal moths, that is, *T. batesi* (Gómez and Carrasco 2008), *Synanthedon scitula* Harris (Frank et al. 2010), *Algedomia coclesalis* Walker (Liu et al. 2013), *C. remissa* (Zheng et al. 2014), and now *P. flammans* as reported in this study. However, numerous s. auricillica sensilla, which are considered to be olfactory receptors for sex pheromones (Alnter et al. 1977), occur on the antennae of nocturnal moths, but not *P. flammans*. This difference could be attributed to the environmental adaptability of *P. flammans* because compound eyes could be used for courtship in some diurnal Zygaenidae, such as *Zygaena filipendulae* L. and *Z. trifolii* Esper (Naumann et al. 1999). Therefore, compound eyes may compensate for the lack of olfactory function of the s. auricillica in diurnal Zygaenidae.

In conclusion, this study identifies and characterizes the ultrastructural morphology, abundance, and distribution of the different types of sensilla occurring on the antennae of *P. flammans*. This information helps in our understanding of the electrophysiological and behavioral elements of chemical communication in *P. flammans*. In future research, transmission electron microscopy will be used to confirm the functions of the different sensilla identified in this study.

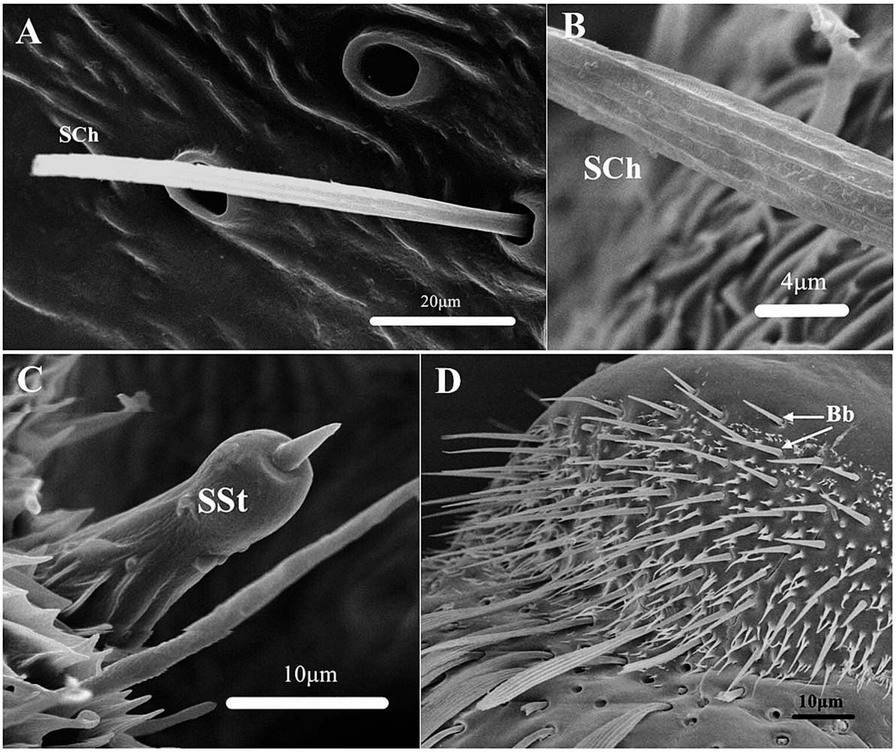

Fig. 5. Distribution of several subtypes of sensilla on the antennal flagellomeres of *P. flammans*—sensilla chaetica are straight but wide at the base and smooth at the apex (A) with vertical slots covering the surface (B), sensilla styloconica emerging from a cylindrical protrusion forming a peak (C), and spine-like Böhm bristles (D).

Acknowledgments

We are grateful to Jingxian Wen of Guangxi University for technical help with SEM in this study. The experiment was funded by the China National Natural Science Foundation (31660206) and the Guangxi Natural Science Foundation (2015GXNSFAA139056).

References Cited

Allen, C.E., B.J. Zwaan and P.M. Brakefield. 2011. Evolution of sexual dimorphism in the Lepidoptera. Annu. Rev. Entomol. 56: 445–464.

Alnter, H., H. Sas and I. Alnter. 1977. Relationship between structure and function of antennal chemo-, hygro-, and thermo-receptive sensilla in *Periplaneta americana*. Cell Tissue Res. 176: 389–405.

Bawin, T., F. Collardb, L.D. Backer, B.B. Yaroua, P. Compère, F. Francis and F.J. Verheggen. 2017. Structure and distribution of the sensilla on the antennae of *Tuta absoluta* (Lepidoptera: Gelechiidae). Micron 96: 16–28.

Bill, S.H., N.C. Jan, D.P. Van and L. Jan. 1989. Comparison of male and female olfactory cell response to pheromone compounds and plant volatiles in the turnip moth, *Agrotis segetum*. Physiol. Entomol. 14: 147–155.

Chang, X.Q., S. Zhang, L. Lv and M.Q. Wang. 2015. Insight into the ultrastructure of antennal sensilla of *Mythimna separata* (Lepidoptera: Noctuidae). J. Insect Sci. 115: 124. doi: 10.1093/jisesa/iev103.

Escobedo, F.J., J.E. Wagner and D.J. Nowak. 2008. Analyzing the cost effectiveness of Santiago Chile's policy of using urban forest to improve air quality. J. Environ. Manage. 86: 148–291.

Faucheux, M.J., N.P. Kristensen and S.H. Yen. 2006. The antennae of neopseustid moths: Morphology and phylogenetic implications, with special reference to the sensilla (Insecta: Lepidoptera: Neopseustidae). Zool. Anz. 245: 131–142.

Faucheux, M.J. and R. Kundrata. 2017. Comparative antennal morphology of male Drilini with special reference to the sensilla (Coleoptera: Elateridae: Agrypninae). Zool. Anz. 266: 105–119.

Frank, D.L., T.C. Leskey and J.C. Bergh. 2010. Morphological characterization of antennal sensilla of the dogwood borer (Lepidoptera: Sesiidae). Ann. Entomol. Soc. Am. 103: 993–1002.

Galvani, G.L., B.P. Settembrini and A. Roig-Alsina. 2008. Morphology of antennal sensilla in *Doeringiella nobilis* (Hymenoptera: Apidae). J. Kans. Entomol. Soc. 81: 142–152.

Gómez, V.R.C. and J.V. Carrasco. 2008. Morphological characteristics of antennal sensilla in *Talponia batesi* (Lepidoptera: Tortricidae). Ann. Entomol. Soc. Am. 101: 181–188.

Keil, T.A. 1999. Morphology and development of the peripheral olfactory organs, Pp. 5–47. In Hansson B.S. (ed.), Insect olfaction. Springer, Berlin.

Krishnan, A., S. Prabhakar, S. Sudarsan and S.P. Sane. 2012. The neural mechanisms of antennal positioning in flying moths. J. Exp. Biol. 215: 3096–3105.

Kristoffersen, L., E. Hallberg, R. Wallén and O. Anderbrant. 2006. Sparse sensilla array on *Trioza apicalis* (Homoptera: Triozidae) antennae—An adaptation to high stimulus level. Arthropod Struct. Dev. 35: 85–92.

Kuřavová, K., R.A. Wahab and P. Kočárek. 2017. External morphology of the antennae and sense organs of the groundhopper *Discotettix belzebuth* (Orthoptera: Tetrigidae). Zool. Anz. 226: 120–128.

Kurtovic, A., A. Widmer and B.J. Dickson. 2007. A single class of olfactory neurons mediates behavioural responses to a *Drosophila* sex pheromone. Nature 446: 542–546.

Lena, A., I. Rickard, L. Jan and S.H. Bill. 2005. Responses to sex pheromone and plant odours by olfactory receptor neurons housed in sensilla auricillica of the codling moth, *Cydia pomonella* (Lepidoptera: Tortricidae). J. Insect Physiol. 51: 1066–1074.

Liu, J.Y., Q.L. He, S. Su, H. Wei, J. Yang, W. Lu and X.L. Zheng. 2014. Investigated method of *Phauda flammans* pupae. China Plant Prot. 34: 51–53. (in Chinese with English summary).

Liu, J.Y., Q.L. He, H. Wei, J. Yang, J. Li, W. Lu and X.L. Zheng. 2015a. Developmental duration, threshold temperature and effective accumulated temperature of *Phauda flammans* under natural temperature indoor. Plant Prot. 41: 137–140. (in Chinese with English summary).

Liu, J.Y., Q.L. He, H. Wei, J. Yang, J. Li, W. Lu and X.L. Zheng. 2015b. Studies on the biological characteristics of *Phauda flammans* (Lepidoptera: Zygaenidae). Plant Prot. 41: 188–192. (in Chinese with English summary).

Liu, J.Y., Z.H. Ma, S.Y. Wu, M.Y. Lin, J. Zhang, W. Lu and X.L. Zheng. 2016. Studies on the feeding preferences of *Phauda flammans* Walker (Lepidoptera: Zygaenidae). J. Environ. Entomol. 38: 924–930. (in Chinese with English summary).

Liu, M., C.G. Ren, M.F. Yang, S.L. Yao and S.Y. Xu. 2013. Ultrastructures of the antennal sensilla in *Algedomia coclesalis*. Sci. Silvae Sin. 9: 107–111. (in Chinese with English summary).

Liu, Q.L., R.G. Wu and C.X. Zeng. 1985. Nuclear polyhedrosis virus collected from *Phauda flammans*. Guangdong For. Sci. Technol. 14: 29–30. (in Chinese with English summary).

Lopes, O., E.N. Barata, H. Mustaparta and J. Araújo. 2002. Fine structure of antennal sensilla basiconica and their detection of plant volatiles in the eucalyptus woodborer, *Phoracantha semipunctata* Fabricius (Coleoptera: Cerambycidae). Arthropod Struct. Dev. 31: 1–13.

Monteforti, G., S. Angeli, R. Petacchi and A. Minnocci. 2002. Ultrastructural characterization of antennal sensilla and immunocytochemical localization of a sensory protein in *Carausius morosus* Brunner (Phasmida: Phasmatidae). Arthropod Struct. Dev. 30: 195–205.

Nageshchandra, B.K., B.K. Rajagopal and R. Balasubramanian. 1972. Occurrence of slug caterpillar *Phauda flammans* Wlk. (Lepidoptera: Zygaenidae) on *Ficus racemosa* L. in South India. Mysore J. Agr. Sci. 6: 186–189.

Naumann, C.M., G.M. Tarmann and W.G. Tremewan. 1999. The western Palaearctic Zygaenidae. Apollo Books, Stenstrup, Denmark. 304 pp.

Ndomo-Moualeu, A.F., C. Ulrichs, R. Radek and C. Adler. 2014. Structure and distribution of antennal sensilla in the Indianmeal moth, *Plodia interpunctella* (Hübner, 1813) (Lepidoptera: Pyralidae). J. Stored Prod. Res. 59: 66–75.

Onagbola, E.O. and H.Y. Fadamiro. 2008. Scanning electron microscopy studies of antennal sensilla of *Pteromalus cerealellae* (Hymenoptera: Pteromalidae). Micron 39: 526–535.

Rebijith, K.B., R. Asokan, H.R. Hande, N.K. Kumar, V. Krishna, J. Vinutha and N. Bakthavatsalam. 2016. RNA interference of odorant-binding protein 2 (OBP2) of the cotton aphid, *Aphis gossypii* (Glover), resulted in altered electrophysiological responses. Appl. Biochem. Biotechnol. 178: 251–266.

Ren, L.L., Y. Wu, J. Shi, L. Zhang and Y.Q. Luo. 2014. Antenna morphology and sensilla ultrastructure of *Tetrigus lewisi* Candèze (Coleoptera: Elateridae). Micron 60: 29–38.

Roh, H.S., K.C. Park, H.W. Oh and C.G. Park. 2016. Morphology and distribution of antennal sensilla of two tortricid moths, *Cydia pomonella* and *C. succedana* (Lepidoptera). Microsc. Res. Tech. 79: 1069–1081.

Roux, O., B.J. Van, C. Gers, L. Arvanitakis and L. Legal. 2005. Antennal structure and oviposition behavior of the *Plutella xylostella* specialist parasitoid: *Cotesia plutellae*. Microsc. Res. Tech. 68: 36–44.

Seada, M.A. 2015. Antennal morphology and sensillum distribution of female cotton leaf worm *Spodoptera littoralis* (Lepidoptera: Noctuidae). J. Basic Appl. Zool. 68: 10–18.

Steinbrecht, R.A. and B. Müller. 1991. The thermo-/hygrosensitive sensilla in the silkmoth *Bombyx mori*: Morphological changes after dry- and moist-adaptation. Cell Tissue Res. 266: 441–456.

Verma, T.D. and G.S. Dogra. 1982. Occurrence of *Phauda flammans* Wlk. (Lepidoptera: Zygaenidae) on *Ficus* species in Himachal Pradesh. J. Tree Sci. 1: 130–132.

Wang, R., L. Zhang, L.L. Xu, S.X. Zong and Y.Q. Luo. 2015. Sensilla on the antennae and ovipositor of the sea buckthorn carpenter moth, *Holcocerus hippophaecolus* Hua et al (Lepidoptera: Cossidae). Neotrop. Entomol. 44: 68–76.

Wang, X.Y., Z.Q. Yang and J.R. Gould. 2010. Sensilla on the antennae, legs and ovipositor of *Spathius agrili* Yang (Hymenoptera: Braconidae), a parasitoid of the emerald ash borer *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae). Microsc. Res. Tech. 73: 560–571.

Witzgall, P., P. Kirsch and A. Cork. 2010. Sex pheromones and their impact on pest management. J. Chem. Ecol. 36: 80–100.

Yang, S., H. Liu, J.T. Zhang, J. Liu, H. Zheng and Y. Ren. 2016. Scanning electron microscopy study of the antennal sensilla of *Monema flavescens* Walker (Lepidoptera: Limacodidae). Neotrop. Entomol. 44: 1–7.

Zacharuk, R.Y. 1985. Antennae and sensilla. Compar. Insect Physiol. Biochem. Pharmacol. 6: 1–69.

Zheng, H.X., H.X. Liu, S.Y. Guo, Y. Yan, S.X. Zong and J.T. Zhang. 2014. Scanning electron microscopy study of the antennal sensilla of *Catocala remissa*. Bull. Insectol. 67: 63–71.

Zheng, X.L., J. Li, L. Su, J.Y. Liu, L.Y. Meng, M.Y. Lin, J. Zhang and W. Lu. 2015. Ecological and morphological characteristics of parasitoids in *Phauda flammans* (Lepidoptera: Zygaenidae). Parasite 22: 36. doi: 10.1051/parasite/2015036.

Zheng, X.L., J.Y. Liu, Z.Y. Huang, L.Y. Meng, J. Li and W. Lu. 2017. Cold hardiness of *Phauda flammans* (Lepidoptera: Zygaenidae) larvae. Entomol. Fennica 28: 9–15.