

RESEARCH ARTICLE

# Ultrastructure of antennal sensilla of three fruit borers (Lepidoptera: Crambidae or Tortricidae)

Yiping Li<sup>1,2</sup>, Fangfang Liu<sup>1,2</sup>, Xiao Du<sup>1,2</sup>, Zhumei Li<sup>1,2</sup>, Junxiang Wu<sup>1,2\*</sup>

**1** Key Laboratory of Plant Protection Resources and Pest Management, Northwest A&F University, Ministry of Education, Yangling, Shaanxi, China, **2** Key Laboratory of Integrated Pest Management on Crops in Northwestern Loess, Shaanxi, China

\* [junxw@nwsuaf.edu.cn](mailto:junxw@nwsuaf.edu.cn)



## Abstract

Three fruit borers *Conogethes punctiferalis* (Guenée) (Crambidae), *Grapholita molesta* Busck (Tortricidae), and *Spilonota albicana* Motschulsky (Tortricidae) are serious pests of fruit trees. In this study, their antennal morphology, types of sensilla, and distributions were observed by using SEM (Scanning Electron Microscope). Nine types of sensilla were found on the antennae of *C. punctiferalis*, while eight types of sensilla were presented on each of *G. molesta* and *S. albicana*. The sensilla trichodea with two subtypes were the most abundant sensilla among three fruit borers. Two subtypes of sensillum coeloconica (type I with spines and type II without spines) were observed on the antennae of *C. punctiferalis* and *G. molesta*. However, sensilla coeloconica (type I) were only found in *S. albicana*. Although the sensilla campaniformia were only found on the antennae of *C. punctiferalis*, our observations confirm sensilla campaniformia presence in the moths. In addition, the functions of these sensilla were discussed based on previously reported lepidopteran insects. As a result, our study may provide useful information for advanced electrophysiological and behavioral experiments to better understand the mechanisms related to pests control.

## OPEN ACCESS

**Citation:** Li Y, Liu F, Du X, Li Z, Wu J (2018) Ultrastructure of antennal sensilla of three fruit borers (Lepidoptera: Crambidae or Tortricidae). PLoS ONE 13(10): e0205604. <https://doi.org/10.1371/journal.pone.0205604>

**Editor:** Feng ZHANG, Nanjing Agricultural University, CHINA

**Received:** June 29, 2018

**Accepted:** September 27, 2018

**Published:** October 11, 2018

**Copyright:** © 2018 Li et al. This is an open access article distributed under the terms of the [Creative Commons Attribution License](https://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

**Data Availability Statement:** All relevant data are within the paper.

**Funding:** This research was supported by National Natural Science Foundation of China (Grant Nos. 31071693, 31871971, 31772503, and 31272043 to Dr. Yiping Li and Prof. Junxiang Wu) and the Agro-Industry R and D Special Fund of China (Grant No. 2017YFD0200900 to Dr. Yiping Li).

**Competing interests:** The authors have declared that no competing interests exist.

## Introduction

*Conogethes punctiferalis* (Guenée)(Crambidae), *Grapholita molesta* Busck (Tortricidae), and *Spilonota albicana* Motschulsky (Tortricidae) are common and serious pests in China [1]. More specifically, the yellow peach moth, *C. punctiferalis* is a polyphagous pest, which is widely distributed throughout in China, damaging in buds and fruits of various forests and fruit trees [2]. The oriental fruit moth, *G. molesta*, is a worldwide pest that severely damage stone fruit trees, such as pear, peach, plum, apricot, apple, cherry, and other Rosaceae plants [3]. The pear bud moth, *S. albicana* is mainly distributed in the east and north of China, attacking hawthorn, apple, pear, peach, and other fruit trees[1]. With the increasing growing cultivated area, the three fruit borers has becoming serious pests of many fruit orchards and crops and cause serious economic loss. At present, the control of them mainly relies on the utility of chemical insecticides. Nevertheless, chemical control also brings with it a series of problems such as

insecticide resistance, environmental pollutions and the decrease of biodiversity [4,5]. Consequently, the application of biological controls, including the use of sex pheromones, may become potentially effective measures to suppress the pest [6]. The antennal sensilla of insect is an important organ which can recognize the sex pheromones, so it is the most important step that obtain the ultrastructure of antennal sensilla of this three fruit borers [7].

In insect, the sensillum is a specialized structure of the epidermis, especially occur in the form of hairs, pegs, etc [8,9]. According to the morphology, the sensilla were termed as trichoid, chaetica, coeloconica, basiconica, Böhm bristles, etc. [10]. They play an important role in the feeling of various stimuli (odor, sound, heat, cold, humidity and tactile information) involved in finding suitable habitat and locating mates [11,12,13], on the other hand, play important roles in many behaviors, including detect sex pheromone and host plant volatiles [14,15]. As we know, a lot of studies have characterized the antennal sensilla of various insects, especially the structure and function of antennal sensilla in Lepidoptera, have been documented by ultrastructure in many families in the past few decades [16–20]. However, as far as we know, no compared work has been published on the antennal sensilla of three fruit borers mentioned above.

In order to better understand their olfactory system related to the biological control of these three fruit borers, we observed and compared the morphology of antennae and type of antennal sensilla of the male and female between *C. punctiferalis*, *G. molesta*, *S. albicana* adults by using SEM (Scanning Electron Microscope).

## Materials and methods

### Sources of insects

All insects studied were obtained from the orchard of the College of Horticulture of Northwest A&F University, Yangling, Shaanxi Province in China. The fruits (i.e., apple, pear, plum, peach, apricot) which were infested by fruit bores larvae were collected in the orchard, then reared in the insect cages until adults emergence.

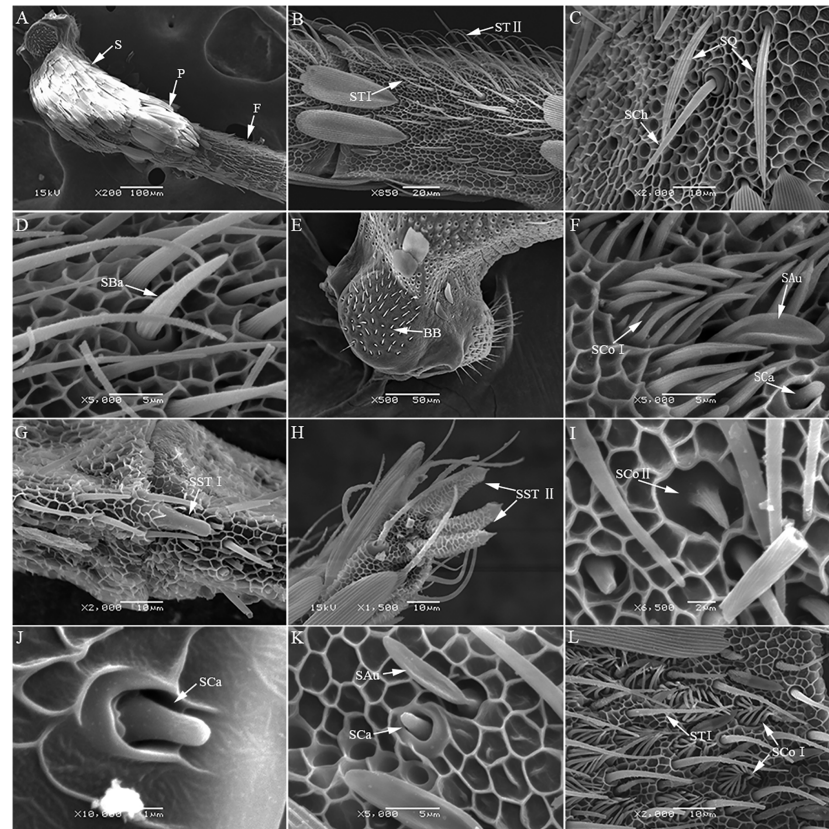
### Preparation of specimens

The adults antennae of 10 female and male of each of the three fruit borers were cut under a stereomicroscope by tweezers and sharp blades and washed in 70% ethanol solution (four times, each for 5 s) in an ultrasonic cleaner (KH-250DB; 15°C, 50HZ). After carbon dioxide critical point drying, the antennae were attached to a holder using electric adhesive tape, sputter-coated with gold, examined and photographed with a S-4800 SEM (at 10 kV~15 kV). The antennal sensilla were identified based on their morphology described by Schneider [8] and Na [21].

## Results

### Antennal morphology of *C. punctiferalis*

The filamentous antennae of *C. punctiferalis* consist of a basal scape, pedicel and elongated flagellum (about 61~75 sub-segments) (Fig 1A). The first two regions are covered with scales, as is on its dorsal surface of the flagellum. In contrast, the ventral surface of the flagellum is equipped with the sensilla. No significant differences are found between sexes, except the number of sub-segment of flagellum (Table 1). Nine types of sensilla are totally found on the antennae of *C. punctiferalis*: sensilla trichodea (Type I, II), sensilla chaetica, sensilla basiconica, Böhm bristles, sensilla auricillica, sensilla squamiformia, sensilla styloconica (Type I, II),



**Fig 1. Antennal sensilla of *Conogethes punctiferalis*.** A. Morphology of antennae of *Conogethes punctiferalis* S: Scape, P: Pedicel, F: Flagella; B. STI(sensilla trichodea I), STII(sensilla trichodea II); C. Sch(sensilla chaetica), SQ(sensilla squamiformia); D. SBa(sensilla basiconica); E. BB(Böhm bristles); F. SAu(sensilla auricullica), SCoI(sensilla coeloconica I), SCa(sensilla campaniformia); G. SST I(sensilla styloconica I); H. SSTII(sensilla styloconicaII); I. SCoII (sensilla coeloconicaII); J. SCa(sensilla campaniformia); K. SAu(sensilla auricullica), SCa(sensilla campaniformia); L. ST I(sensilla trichodea I), SCoI(sensilla coeloconica I).

<https://doi.org/10.1371/journal.pone.0205604.g001>

sensilla coeloconica (Type I, II), and sensilla campaniformia. Notably, sensilla coeloconica can be found on the antennae of female only.

Sensilla trichodea (Fig 1B) are the most widely distributed sensilla on the antennae of *C. punctiferalis*; they are slender and hair-like, and occur in clusters along the ventral surface of flagellomere. Sensilla trichodea can be divided into two subtypes (Type I and II). Sensilla trichodea Type I (Fig 1L) is straight at the base and taper toward the end. Sensilla trichodea Type II (Fig 1B), is curved at the base, and parallel to the surface of antenna at the terminal end. Sensilla chaetica (Fig 1C), are upright and protrude similar to a thorn with a grooved surface, and they are mainly found on each flagellomere. Sensilla basiconica (Fig 1D) are short and robust with blunt setae. These sensilla present on the distal surface of each sub-segment of flagellum. Böhm bristles (Fig 1E), are thin and sharp with smooth cuticles. They are as in clusters at the base of the scape and pedicel only. Sensilla auricullica (Fig 1F and 1K) are ear-shaped, covered with many small pores on its surface of the cuticular. These sensilla are mainly scattered on the distal of the flagellum. Sensilla squamiformia (Fig 1C) are scale-like and more elongated than scape with a distal end tapering, found along the scape and pedicel among the scales. Sensilla styloconica are thumb-like with a small cone-shape tip. These sensilla are distributed at the

**Table 1. The differences in antennal sensilla of three fruit borers.**

Sensilla types	<i>Conogethes punctiferalis</i>		<i>Grapholitha molesta</i>		<i>Spilonota albicana</i>	
	♀	♂	♀	♂	♀	♂
sensilla trichodeal	+	+	+	+	+	+
sensilla trichodeaII	+	+	+	+	+	+
sensilla auricillica)	+	+	+	+	+	+
sensilla chaetica	+	+	+	+	+	+
sensilla basiconica	+	+	+	+	+	+
Böhm bristles	+	+	+	+	+	+
sensilla squamiformia	+	+	+	+	+	+
sensilla styloconicaI	+	+	+	+	+	+
sensilla styloconica II	+	+	+	+	+	+
sensilla coeloconicaI	+	+	+	+	+	+
sensilla coeloconicaII	+	-	+	+	-	-
sensilla coeloconica	+	+	-	-	-	-

Note: “+” indicates “with”; “-” indicates “without”.

<https://doi.org/10.1371/journal.pone.0205604.t001>

distal margin of each sub-segment of flagellum. Sensilla styloconica can also be divided into two subtypes (Type I and II). Sensilla styloconica Type I (Fig 1G) are feeding-bottle shaped with a smooth surface; In contrast, sensilla styloconica Type II (Fig 1H) have a grooved surface with a spine-like tip apically. Sensilla coeloconica (SCo I and SCo II) are only found on the distal of the flagellum. Sensilla coeloconica (SCo I) consist of a submerged central peg surrounded by a ring of cuticular spines, while sensilla coeloconica (SCo II) (Fig 1I) have a central peg only, without a ring of cuticular spines (Fig 1F and 1L). Sensilla campaniformia (Fig 1F, 1J and 1K) are hemispherical-like with a smooth surface, only a few these sensilla are found at the distal margin of sub-segment of flagellum.

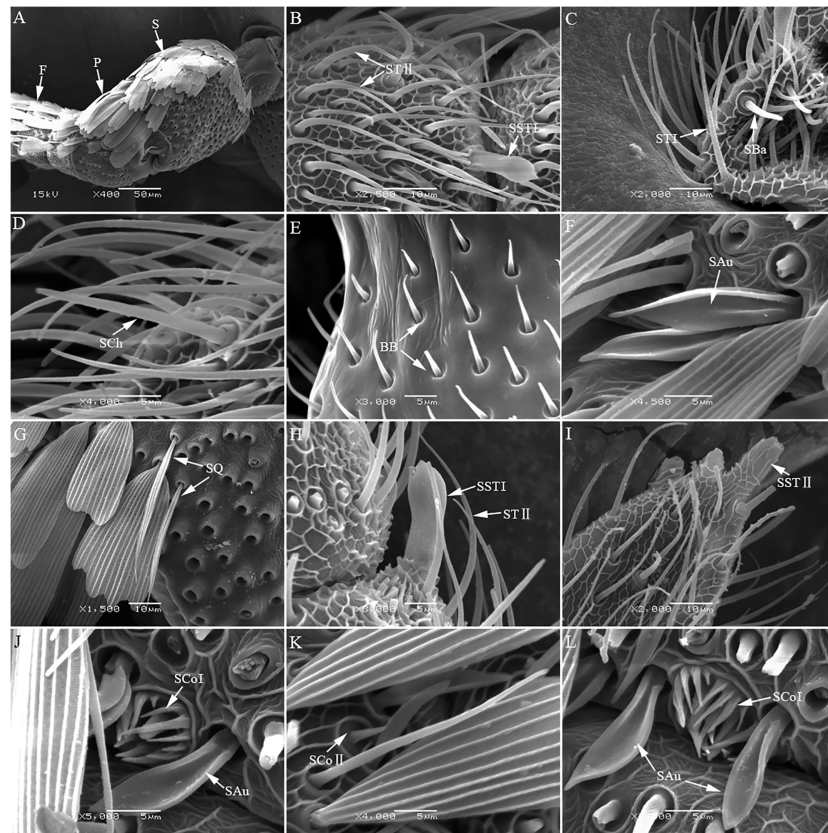
### Antennal morphology of *G. molesta*

The antenna of *G. molesta* is filose, and nearly the entire scape and pedicel on the dorsal surface are covered with scales, the flagellum consists of about 41~49 sub-segments (Fig 2A). The number of flagellomere is also different between the sexes. In total, eight types of sensilla were found on the antennae of *G. molesta*: sensilla trichodea (ST, Type I and II) (Fig 2C, 2B and 2H), sensilla chaetica (SCh) (Fig 2D), sensilla basiconica (SBa) (Fig 2C), Böhm bristles (BB) (Fig 2E), sensilla auricillica (SAu) (Fig 2F, 2J and 2L), sensilla squamiformia (SQ) (Fig 2G), sensilla styloconica (SST, type I and II) (Fig 2B, 2H and 2I), and sensilla coeloconica (SCo, type I and II) (Fig 2J, 2L and 2K).

### Antennal morphology of *S. albicana*

The antennae of *S. albicana* is similar to above two species, except the number of flagellum (about 52~56 sub-segments). Similarly, eight types of sensilla are observed totally: sensilla trichodea (Type I, II) (Fig 3B and 3C), sensilla chaetica (Fig 3C and 3I), sensilla basiconica (Fig 3D), Böhm bristles (Fig 3E), sensilla auricillica (Fig 3F), sensilla squamiformia (Fig 3G), sensilla styloconica (Type I, II) (Fig 3C and 3H), and sensilla coeloconica (Fig 3F).





**Fig 2. Antennal sensilla of *Grapholitha molesta*.** A. Morphology of antennae of *Grapholitha molesta* S: Scape, P: Pedicel, F: Flagella; B. STII (sensilla trichodea II), SST I (sensilla styloconica I); C. ST I (sensilla trichodea I), SBa (sensilla basiconica); D. SCh (sensilla chaetica); E. BB (Böhm bristles); F. SAu (sensilla auricillica); G. SQ (sensilla squamiformia); H. STII (sensilla trichodea II), SST I (sensilla styloconica I); I. SSTII (sensilla styloconica II); J. SCoI (sensilla coeloconica I), SAu (sensilla auricillica); K. SCoII (sensilla coeloconica II); L. SCoI (sensilla coeloconica I), SAu (sensilla auricillica).

<https://doi.org/10.1371/journal.pone.0205604.g002>

## Discussion

### Sensilla trichodea

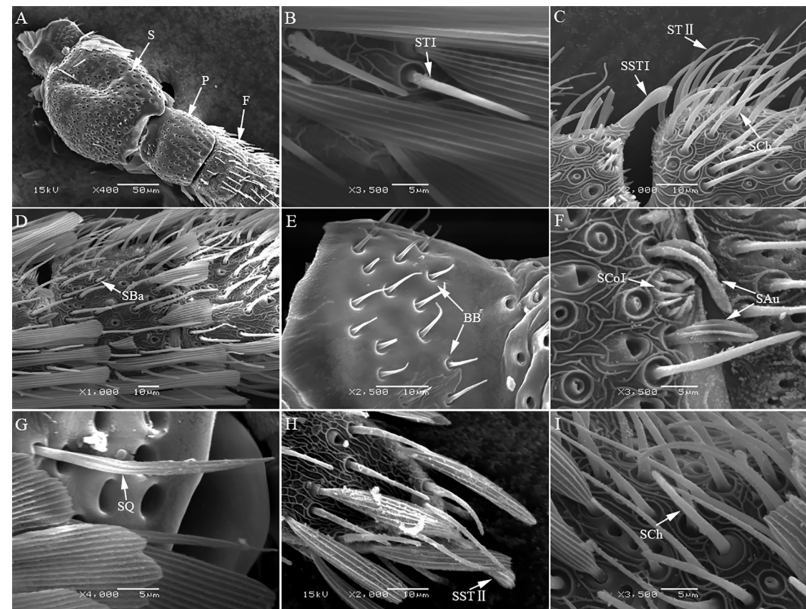
Sensilla trichodea, as the most abundant sensilla in this study, were similar in shape between these three fruit borer moths and other lepidopteran insects [22]. According to their size and density, sensilla trichodea could be divided into more subtypes, for example, three subtypes were found on *Ostrinia nubilalis* [23]. But, only two subtypes of sensilla trichodea were identified among the three fruit borer moths in our study. These types of sensilla are olfactory reception of host plant volatiles and sex pheromones [22].

### Sensilla chaetica

Sensilla chaetica have been commonly presented in many lepidopteran insects [24–26]. In this study sensilla chaetica were similar in structure among the three moths. Sensilla chaetica could perceive the movement of antennae as proprio receptors as shown previously [27,28] and considered to be chemoreceptors [29].

### Sensilla basiconica

Sensilla basiconica are larger sensilla with papula surface, sensory cones, and extensively pitted surface [30–33]. Our results showed that sensilla basiconica were morphologically similar in



**Fig 3. Antennal sensilla of *Spilonota albicana*.** A. Morphology of antennae of *Spilonota albicana* S: Scape, P: Pedicel, F: Flagella; B. ST I (sensilla trichodea I); C. ST II (sensilla trichodea II), SST I (sensilla styloconica I), Sch (sensilla chaetica); D. SBA (sensilla basiconica); E. BB (Böhm bristles); F. SAu (sensilla auriculica), SCoI (sensilla coeloconica I); G. SQ (sensilla squamiformia); H. SST II (sensilla styloconica II); I. Sch (sensilla chaetica).

<https://doi.org/10.1371/journal.pone.0205604.g003>

the three moths. This types of sensilla observed in this study also closely resembled to that observed in many other families of Lepidoptera [22]. Sensilla basiconica on the antennae are deduced to possess olfactory function [22,34].

### Böhm bristles

Böhm bristles found in our study morphologically resemble to those observed in many other families of Lepidoptera [35]. In several studies, this type sensilla were considered to be the mechanoreceptors with a proprioceptive function [29,36].

### Sensilla auriculica

Our observation showed that Sensilla auriculica in the three fruit borer moths were consistent with that in butterfly and moth species, even though their distribution and external morphology were variously. Previous studies reported that sensilla auriculica were behaviorally sensitive to plant volatiles in *Cydia pomonella* [35,37].

### Sensilla squamiformia

Sensilla squamiformia were widely distributed among Lepidoptera, though the shape and distribution of these sensilla were different in several reported moth species [22]. However, the function of sensilla squamiformia were seldom reported so far, and these sensilla were inferred to have a mechanoreceptive function [38]. Consequently, further electrophysiological and behavioral studies are necessary to elucidate its function.

### Sensilla styloconica

Two subtype of sensilla styloconica were found on the antennae of the three fruit borer moths in this study, which were identical to those in *Sitotroga cerealella* (Gelechiidae) [39]. The

structure and function of these sensilla have already been well studied so far, and they were considered as temperature and humidity receptors [29].

### Sensilla coeloconica

In term of sensilla coeloconica, two subtypes (type I with spines and type II without spines) were observed on the antennae of *C. punctiferalis* and *G. molesta*, which were similar to those in *Sitotroga cerealella*, and *Manduca sexta* and *Mythimna separate* etc., [39]. However, sensilla coeloconica (type I) were only found in *S. albicana*, which were identical to those observed in skipper butterflies *Parnara* sp. and *Pelopidas* sp. [35]. These sensilla may respond to plant volatiles and also have a temperature and humidity-sensitive function [29].

### Sensilla campaniformia

Generally, a few studies reported that sensilla campaniformia were present in Lepidoptera insects, instead, this type of sensilla were more easily found in Hymenoptera, Hemiptera, Coleoptera and Diptera [30,40–42]. In this study, our observations confirm their presence in the moths, though sensilla campaniformia were only found on the antennae of *C. punctiferalis*. Several studies considered sensilla campaniformia as mechanoreceptors while other suggest they were sensitive to temperature and the perception of CO<sub>2</sub> [22,29].

Previously, Li et al. [43] had already described seven types of antennal sensilla of *C. punctiferalis*. However, we confirmed the presence of Böhm bristles and sensilla squamiformia on the antennae of *C. punctiferalis*. Meanwhile, Zhang et al. [44] examined the antennae of *G. molesta* and found seven types of sensilla. Our results confirmed sensilla squamiformia on the antennae of *G. molesta*. For *S. albicana*, it is the first time to describe their antennal sensilla in this study, which were similar to those found in *G. molesta* and other species from Tortricidae [45,46].

In general, it can be inferred that the antennal sensilla in Lepidoptera are very rich. Correspondingly, sensilla trichodea, sensilla chaetica, sensilla basiconica, sensilla auricillica, sensilla squamiformia, sensilla coeloconica, and sensilla styloconica are commonly present in lepidopteran insects [24–26]. Sensilla chaetica belongs to tactile sensor and mechanical sensor which suggest that this sensor maybe has Location feature [47]. Sensilla basiconica is a kind of chemical sensor and may detect the shock of air [48]. There are many narrow aperture on sensilla auricillica and appears to be accept sound waves [49]. Sensilla coeloconica can be used as feeling the vapour, CO<sub>2</sub> and plant smell [50,51].

Only their antennal morphology and types of sensilla of these three fruit borers were observed and compared in this study, the size and more information of sensilla were focused in our further studies.

### Conclusions

In summary, the numbers of sub-segments of flagellum were varied among these three species, *C. punctiferalis* has the highest sub-segments of flagellum. Furthermore, we identified nine types of antennal sensilla on *C. punctiferalis* and eight types of antennal sensilla on *G. molesta*, and *S. albicana*. Insects, through evolution and divergence, may evolve different behavioral characteristics [52]. Accordingly, we found the differences on the antennal sensilla of *C. punctiferalis*, *G. molesta*, and *S. albicana*, which may relate to their different hosts and life habits. The comparison between male and female showed that sensilla coeloconicaII existed in *C. punctiferalis* and *G. molesta* for female, while it existed only in *G. molesta* for male. Regard to the sensilla coeloconica, it was found only on the *C. punctiferalis* in this study (Table 1). Consequently, our study may provide useful information for taxonomy of Lepidoptera, further

advanced electrophysiological and behavioral studies to better understand the mechanisms related to pests control.

## Acknowledgments

We would like to thank the anonymous reviewers for valuable comments on the manuscript. We thank Prof. John Richard Schrock from Emporia State University, Kansas, USA for advice and editing of the manuscript.

## Author Contributions

**Conceptualization:** Yiping Li, Junxiang Wu.

**Formal analysis:** Zhumei Li.

**Funding acquisition:** Yiping Li, Junxiang Wu.

**Investigation:** Xiao Du.

**Methodology:** Zhumei Li.

**Project administration:** Yiping Li, Xiao Du, Junxiang Wu.

**Writing – original draft:** Fangfang Liu.

**Writing – review & editing:** Yiping Li, Xiao Du.

## References

1. Wang JL, Li CL, Yuan KF. The development and control of fruit trees budworm. *Mod Agric Sci Tech*. 2010; 219–219.
2. Lu JQ, Wang Z.Y., He K.L., and Liu Y. Research history, progresses and prospects in the yellow peach moth, *Conogethes punctiferalis*. *Acta Phytophy Sin*. 2010; 36: 31–38.
3. Song YQ, Xie XC, Dong JF, Wu JX. cDNA cloning, expression profiling and binding properties of odorant-binding protein GmolOBP3 in the oriental fruit moth, *Grapholita molesta* (Lepidoptera: Tortricidae). *Acta Entomologica Sinica*. 2014; 57: 274–285.
4. Gao XW. Current status and development strategy for chemical control in China. *Acta Phytophy Sin*. 2010; 36: 19–22.
5. Lu PF, Huang LQ, Wang CZ. Semiochemicals used in chemical communication in the oriental fruit moth, *Grapholitha molesta* Busck (Lepidoptera: Tortricidae). *Acta Entomologica Sinica*. 2010; 53: 1390–1403.
6. Wang AZ, Li DH, Liang TT, Cai SL. The survey of sex pheromone trapping effects and the occurrence for *Grapholitha molesta* (Busck). *Acta Entomologica Sinica*. 2012; 21: 203–206.
7. Wang KQ, Li XM, Liu CL, Liu XL, Wang S, Sun YM. Control of soybean pod borer (*Leguminivoraglycinivorella* (Mats)) with synthetic sex pheromone. *Chin Agric Sci Bull*. 2009; 25: 190–193.
8. Schneider D. *Insect Antennae*. *Annu Rev Entomol*. 1964; 9: 103–122.
9. Altner H, Prillinger L. Ultrastructure of Invertebrate Chemo-, Thermo-, and Hygroreceptors and Its Functional Significance. *International Review of Cytology*. 1980; 67: 69–139.
10. Keil TA. *Morphology and Development of the Peripheral Olfactory Organs*. 1999; 5–47 p.
11. Altner H, Prillinger L. Ultrastructure of Invertebrate Chemo-, Thermo-, and Hygroreceptors and Its Functional Significance. *International Review of Cytology*. 1980; 67: 69–139.
12. Chapman RF (1998) *The insects: structure and function*: Academic Press. 132–141 p.
13. Godfray HCJ. Parasitoids: behavioral and evolutionary ecology. *Environmental Entomology*. 1994; volume 24: 483–484(482).
14. Wang GR, Guo YY, Wu KM. Observation on the Ultrastructures of Antennal Sensilla in *Helicoverpa armigera*. *Sci Agric Sin*. 2002; 35: 1479–1482.
15. Wang H, Wang B, Tian X. Ultrastructural Studies on the Sensilla of Antennae in *Ricania sublimbata* Jacobi Adult. *Acta Entomologica Sinica*. 2011; 20: 174–177.



16. Merivee E, Ploomi A, Rahi M, Bresciani J, Ravn HP, Luik A, et al. Antennal sensilla of the ground beetle *Bembidion properans* Steph. (Coleoptera, Carabidae). *Micron*. 2002; 33: 429–440. PMID: [11976030](#)
17. Onagbola EO, Meyer WL, Boina DR, Stelinski LL. Morphological characterization of the antennal sensilla of the Asian citrus psyllid, *Diaphorina citri* Kuwayama (Hemiptera: Psyllidae), with reference to their probable functions. *Micron*. 2008; 39: 1184–1191. <https://doi.org/10.1016/j.micron.2008.05.002> PMID: [18573664](#)
18. Sukontason K, Methanitikorn R, Chaiwong T, Kurahashi H, Vogtsberger RC, Sukontason KL. Sensilla of the antenna and palp of *Hydrotaea chalcogaster* (Diptera: Muscidae). *Micron*. 2007; 38: 218–223. <https://doi.org/10.1016/j.micron.2006.07.018> PMID: [16978868](#)
19. Ahmed T, Zhang TT, Wang ZY, He KL, Bai SX. Morphology and ultrastructure of antennal sensilla of *Macrocentrus cingulum* Brischke (Hymenoptera: Braconidae) and their probable functions. *Micron*. 2013; 50: 35–43. <https://doi.org/10.1016/j.micron.2013.04.003> PMID: [23669211](#)
20. Chang XQ, Shu Z, Liang L, Wang MQ. Insight Into the Ultrastructure of Antennal Sensilla of *Mythimna separata* (Lepidoptera: Noctuidae). *Journal of Insect Science*. 2015; 15.
21. Na J, Yu WX, Li YP, Dong X, Jiao J. Types and physiological ecology significance of insect antenna sensilla. *J Shenyang Normal Univ (Nat Sci)*. 2008; 26: 213–216.
22. C FL, K EW, P JR. Sensilla on the antenna and ovipositor of the parasitic wasps *trichogramma galloi* Zucchi and *T. pretiosum* Riley (Hym., Trichogrammatidae). *Microsc Res Tech*. 1999; 45: 313–324. [https://doi.org/10.1002/\(SICI\)1097-0029\(19990515/01\)45:4/5<313::AID-JEMT15>3.0.CO;2-4](https://doi.org/10.1002/(SICI)1097-0029(19990515/01)45:4/5<313::AID-JEMT15>3.0.CO;2-4) PMID: [10383124](#)
23. Hallberg E, Hansson BS, Steinbrecht RA. Morphological characteristics of antennal sensilla in the European cornborer *Ostrinia nubilalis* (Lepidoptera: Pyralidae). *Tissue and Cell*. 1994; 26: 489–502. PMID: [18621276](#)
24. Berg BG, Galizia CG, Brandt R, Mustaparta H. Digital Atlases of the Antennal Lobe in Two Species of Tobacco Budworm Moths, the Oriental Helicoverpa *assulta* (Male) and the American *Heliothis virescens* (Male and Female). *J Comp Neurol*. 2002; 446: 123–134. PMID: [11932931](#)
25. Burguiere L, Marion-Poll F, Cork A. Electrophysiological responses of female *Helicoverpa armigera* (Hübner) (Lepidoptera; Noctuidae) to synthetic host odours. *J Insect Physiol*. 2001; 47: 509–514. PMID: [11166315](#)
26. Wang X, Jing XU, Liu FY, Chen HB, Jiang-Xing WU, Yong-Jun DU. Ultrastructure of antennal sensilla of *Maruca testulalis* (Lepidoptera:Pyralidae) adult and its sensory responses to sex pheromone and plant volatiles. *Acta Entomologica Sinica*. 2008; 51: 1225–1234.
27. Zhou H, Wu WJ, Niu LM, Fu YG. Antennal sensilla of female *Encarsia guadeloupeae* Viggiani (Hymenoptera: Aphelinidae), a nymphal parasitoid of the spiraling whitefly *Aleurodicus dispersus* (Hemiptera: Aleyrodidae). *Micron*. 2013; 44: 365–372. <https://doi.org/10.1016/j.micron.2012.09.001> PMID: [23036370](#)
28. Romani R, Stacconi MV, Riolo P, Isidoro N. The sensory structures of the antennal flagellum in *Hyalesthes obsoletus* (Hemiptera: Fulgoromorpha: Cixiidae): a functional reduction? *Arthropod Structure & Development*. 2009; 38: 473–483.
29. Ma RY, Du JW. Insect antennal sensilla. *Entomol Knowl*. 2000; 37: 179–183.
30. Merivee E, Ploomi A, Rahi M, Luik A, Sammelselg V. Antennal sensilla of the ground beetle *Bembidion lampros* Hbst (Coleoptera, Carabidae). *Acta Zoologica*. 2001; 81: 339–350.
31. Domenichini G. Strutture di *Trialeurodes vaporariorum* (Westw.) e loro funzioni (Homoptera, Aleyrodidae). *Memorie—Societa entomologica italiana*. 1982.
32. Binkmoenen RM. Revision of the African whiteflies (Aleyrodidae), mainly based on a collection from Tchad. 1983; 10: 1–211.
33. Gerling D. Whiteflies: their bionomics, pest status and management; 1990.
34. Chinta S, Dickens JC, Baker GT. Morphology and distribution of antennal sensilla of the tarnished plant bug, *Lygus lineolaris* (Palisot de beauvois) (Hemiptera: Miridae). *Int J Insect Morphol Embryol*. 1997; 26: 21–26.
35. Yuan XQ, Gao K, Yuan F, Zhang Y. Ultrastructure of antennal sensilla of four skipper butterflies in *Parnara* sp. and *Pelopidas* sp. (Lepidoptera, Hesperidae). *ZooKeys*. 2014; 399: 17–27.
36. Li X, Bai S. Ultrastructural studies on the antennal sensilla of *Diadegma semiclausum* Hellen (Hym., Ichneumonidae). *J Henan Agric Univ*. 2004; 38: 45–48.
37. Ansebo L, Ignell R, Lofqvist J, Hansson BS. 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*. 2005; 51: 1066–1074. <https://doi.org/10.1016/j.jinsphys.2005.05.003> PMID: [15964591](#)



38. Yu HZ. Research progress of insect Antennal Sensilla. *J Anhui Agric Sci.* 2007; 35: 4238–4240.
39. Ma M, Chang MM, Lu Y, Lei CL, Yang FL. Ultrastructure of sensilla of antennae and ovipositor of *Sitotroga cerealella* (Lepidoptera: Gelechiidae), and location of female sex pheromone gland. *Sci Rep.* 2017; 7: 40637. PMID: [28094781](#)
40. Dietz A, Humphreys WJ. Scanning Electron Microscopic Studies of Antennal Receptors of the Worker Honey Bee, including Sensilla Campaniformia. *Ann Entomol Soc Am.* 1971; 64: 919–925.
41. Meng Y, Qin D. Fine morphology of the antennae and mouthparts of *Dentatissus damnosa* (Chou & Lu) (Hemiptera: Issidae). *Zool Anz.* 2017; 268: 64–74.
42. Agrawal S, Grimaldi DA, Fox JL. Haltere morphology and campaniform sensilla arrangement across Diptera. *Arthropod Struct Dev.* 2017; 46: 215–229. <https://doi.org/10.1016/j.asd.2017.01.005> PMID: [28161605](#)
43. Li Q, Zhang T, Bai S, He K, Wang Q, Li Y, et al. Ultrastructure observation and electroantennogram response of *Conogethes punctiferalis* antennae to corn silk volatiles. *Acta Phytophy Sin.* 2014; 40: 70–76.
44. Zhang GH, Song YQ, Tian XL, Wu JX. Ultrastructure of antennal sensilla of oriental fruit moth, *Grapholitha molesta*. *J Northwest Sci-Tech Univ Agric For (Nat Sci Ed).* 2014; 42: 51–56.
45. Yang X, Zhao KJ, Wang KQ, Han LL, Yang S. Observation on antennal sensillia of *Leguminivora glycinivorella* with scanning electron microscope. *Chin J Appl Entomol.* 2012; 49: 1321–1326.
46. Zhao X, Zhang YL, Feng JN. Ultrastructural observation on antennal sensilla of the adult codling moth, *Cydia pomonella* (L.) (Lepidoptera: Tortricidae). *J Northwest Sci-Tech Univ Agric For (Nat Sci Ed).* 2012; 40: 119–124.
47. Cónsoli FL, Kitajima EW, Parra JR. Sensilla on the antenna and ovipositor of the parasitic wasps *trichogramma galloi* Zucchi and *T. pretiosum* Riley (Hym., Trichogrammatidae). *Microscopy Research & Technique.* 1999; 45: 313–324.
48. Olson DM, Andow DA. Antennal sensilla of female *Trichogramma nubilale* (Ertle and Davis) (Hymenoptera: Trichogrammatidae) and comparisons with other parasitic Hymenoptera. *International Journal of Insect Morphology & Embryology.* 1993; 22: 507–520.
49. VDGVN Wm, Den Otter CJ, Maes FW. Olfactory sensitivity in tsetse flies: a daily rhythm. *Chemical Senses.* 1998; 23: 351–357. PMID: [9669048](#)
50. Bruce TJ, Cork A. Electrophysiological and behavioral responses of female *Helicoverpa armigera* to compounds identified in flowers of African marigold, *Tagetes erecta*. *Journal of Chemical Ecology.* 2001; 27: 1119–1131. PMID: [11504018](#)
51. Park KC, Hardie J. Functional specialisation and polyphenism in aphid olfactory sensilla. *Journal of Insect Physiology.* 2002; 48: 527–535. PMID: [12770080](#)
52. Hora KH, Roessingh P. Oviposition in *Yponomeuta cagnagellus*: the importance of contact cues for host plant acceptance. *Physiol Entomol.* 1999; 24: 109–120.