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Comparison of the antennal sensilla and compound eye sensilla in four *Drosophila* (Diptera: Drosophilidae) species

Huanhuan Gao^{1,2,*}, Shouguo Lai^{2,*}, Yifan Zhai², Zhaoyun Lv², Li Zheng², Yi Yu^{2,*}, and Feng-Shan Ren^{1,*}

Abstract

Antennal sensilla and compound eyes of fruit flies, *Drosophila melanogaster* (Meigen), *Drosophila sukuzii* (Matsumura), *Drosophila immigrans* (Sturtevant), and *Drosophila hydei* (Sturtevant) (all Diptera: Drosophilidae), were observed with stereoscopic microscopy and scanning electron microscopy. The results showed that the antenna consists of 3 segments: a proximal scape, a pedicel, and a flagellum composed of a funiculus and a dendritic arista. Six morphologically distinct types of sensilla were observed on the antenna: chaetica, microtrichia, trichoid (Tr I, Tr II), basiconic, clavate, and coeloconic (Co I, Co II). Basiconic sensilla were significantly shorter than other sensilla in the funiculus of *D. melanogaster*. The number of clavate sensillae was less than other sensilla in the funiculus of *D. melanogaster* and *D. immigrans*, but was greater in *D. sukuzii* and *D. hydei*. Moreover, coeloconic sensilla were absent in *D. sukuzii* and *D. hydei*. The length and abundance of the chaetica sensilla on the compound eyes were different significantly among the 4 species. *Drosophila hydei* had chaotic sensilla with the greatest length and abundance; they were lowest for *D. sukuzii*. Based on the previous literature, the possible functions of these sensilla are discussed. We inferred that fruit flies may regulate their behaviors according to the information detected by these sensilla.

Key Words: fruit fly; sensory perception; SEM

Resumen

Se observaron las sensilas antenales y los ojos compuestos de moscas de la fruta, *Drosophila melanogaster* (Meigen), *Drosophila sukuzii* (Matsumura), *Drosophila immigrans* (Sturtevant) y *Drosophila hydei* (Sturtevant) (todos Diptera: Drosophilidae), con microscopía estereoscópica y microscopía electrónica de barrido (SEM). Los resultados mostraron que la antena consiste de 3 segmentos: un escapo proximal, un pedicelo, y un flagelo compuesto por un funículo y un arista dendrítica. Se observaron seis clases morfológicamente distintas de sensilas en la antena: chaetica, microtrichia, trichoid (Tr I, Tr II), basicónica, clavada, y coelocónica (Co I, Co II). Las sensilas basicónicas fueron significativamente más cortas que otras sensilas en el funículo de *D. melanogaster*. El número de sensilas clavadas fue menor que otras sensilas en el funículo de *D. melanogaster* y *D. immigrans*, pero fue mayor en *D. sukuzii* y *D. hydei*. Por otra parte, las sensilas coelocónicas estaban ausentes en *D. sukuzii* y *D. hydei*. La longitud y abundancia de las sensilas chaéticas en los ojos compuestos fueron significativamente diferentes entre las 4 especies. *Drosophila hydei* tenía sensilas caóticas con la mayor longitud y abundancia; fueron los más bajos para *D. sukuzii*. Con base en la literatura anterior, se discuten las posibles funciones de estas sensilas. Deducimos que las moscas de la fruta pueden regular su comportamiento de acuerdo con la información detectada por estas sensilas.

Palabras Clave: mosca de la fruta; percepción sensorial; SEM

There are about 3,700 described species of *Drosophila* fruit flies in the world, though most of them are not recognized as pests because their larvae mostly develop in damaged or rotting fruit (Bolda et al. 2010). However, *Drosophila sukuzii* (Matsumura) (Diptera: Drosophilidae) can feed on ripening cherries, berries, grapes, and > 60 other kinds of fruits (Mitsui et al. 2006), which has attracted the attention of fruit growers and researchers around the world (Cini et al. 2012). Therefore, among these *Drosophila* species, *D. sukuzii* were found to be the most harmful species because they oviposit in fresh fruits with their serrated ovipositor (Mitsui et al. 2006; Hauser et al. 2009). Subsequently, secondary infection by *Drosophila* or microor-

ganisms may contribute to further fruit deterioration, causing considerable damage (e.g., monilinia brown rots, botrytis rots, and sour rot) (Cini et al. 2012). Fruit flies are very difficult to control due to their short generation time, high reproductive capacity, and a wide range of fruit hosts (Bolda et al. 2010; Cini et al. 2012). Moreover, other *Drosophila* species also were reported to be fruit pests. Katoh et al. (2007) reported that *Drosophila immigrans* (Sturtevant) (Diptera: Drosophilidae) is one of the widespread fruit flies in the Japanese and East Asia regions. Ren et al. (2014) reported that *D. immigrans* and *Drosophilidae hydei* (Sturtevant) (Diptera: Drosophilidae) also can damage cherries in different regions of China. *Drosophila mela-*

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nogaster (Meigen) (Diptera: Drosophilidae) and *D. immigrans* were described as the principal *Drosophila* pests attacking cherry in Gansu Province, China (Guo 2007). These 4 *Drosophila* species are the dominant *Drosophila* pests in China, but have different ecological niches and biological characteristics.

Female *D. melanogaster* preferentially oviposit on food substrates containing a high concentration of ethanol (Azanchia et al. 2013). Gao et al. (2018) found that *D. melanogaster* and *D. suzukii* occupy different ecological niches due to their differences in sensitivity and tolerance to ethanol from the host plant. Studies on the interaction between insects and host plant volatiles have shown that the olfactory system of insects plays a critical role in finding host plants, mating, and reproduction (Krieger et al. 1999). Antennae are the main olfactory organs in the olfactory system of insects, and play an important role in the survival of insects and a wide range of behaviors, such as habitat selection, host location, and sexual communication (Chapman 1998; Isidoro et al. 2001). The functions of antennae are facilitated by specialized parts of the antennal epidermis, called sensilla, which are the important neuronal receptors (chemoreceptors) for receiving the signal of volatiles (Bin et al. 1989), but also can serve as mechanoreceptors, thermoreceptors, hygroreceptors, and CO₂ receptors (Keil 1999; Stange & Stowe 1999). Moreover, compound eyes of insects are important visual organs. Different from antennae, the photoreceptor in compound eyes can help insects to find plants by receiving light signals from the environment (Chapman 1998). However, whether other receptors exist in the compound eyes needs to be studied. Therefore, analyzing the morphological structure and distribution of sensilla from different *Drosophila* species is important to understand the differences in olfactory behavior and host identification mechanisms of insects.

Much research has been reported on the distribution, external morphology, and ultrastructure of various sensilla located on the antennae of different fruit flies. Sensilla are borne directly on the antennae of insects in the form of hairs, pegs, pits, or cones. The antennae of *D. melanogaster* can have about 200 basiconic, 150 trichoid, and 60 coeloconic sensilla, about 75% of all sensilla, covering the surface of the funiculus (Stocker 1994; Shanbhag et al. 1999; Gao et al. 2007). However, the distribution or ultrastructure of various sensilla has not been studied in *D. suzukii*, *D. immigrans*, or *D. hydei*.

To improve our understanding of the peripheral sensory structures involved in the perception of pheromones, the external structure of the antennae, and the type and distribution of the antennal sensilla and compound eyes sensilla in the adults of *D. melanogaster*, *D. suzukii*, *D. immigrans*, and *D. hydei* species were observed using stereoscopic microscopy and scanning electron microscopy. This study can provide guidance for trapping insects using attractants such as plant-derived volatiles and synthetic sex pheromones (Howse et al. 1988), which will contribute to the management of fruit flies.

Materials and Methods

COLLECTION AND REARING OF FLIES

Drosophila melanogaster, *D. suzukii*, *D. immigrans*, and *D. hydei* were obtained from fields in Yantai (37.2316°N, 121.6000°E), People's Republic of China, in Jun 2016 and reared in the laboratory with an artificial diet. This diet was composed of mashed banana and apple, corn flour, sucrose, yeast extract, sorbitol and agar (Zhai et al. 2014). The colony was maintained in a climate-controlled growth chamber at

25 ± 0.5 °C, 70 ± 0.5% RH, and a photoperiod of 16:8 h (L:D). Flies were used in this study 6 d post-emergence.

LIGHT MICROSCOPY

For general morphology, the heads together with antennae were removed from 30 individuals of each species and were cleaned 3 times in a phosphate-buffered saline (pH 7.0). Then the antennae were removed from antennal fossa with a dissecting needle and placed on a glass slide in a drop of water. After being covered by a cover slip, the samples were observed using an Olympus BX53 stereoscopic microscope (Olympus Corp., Hamburg, Germany).

SCANNING ELECTRON MICROSCOPY (SEM)

Specimen Preparation

For each species, 30 individuals were transferred individually into 1.5 mL centrifuge tubes and rinsed 3 times in phosphate-buffered saline pH 7.0 for 15 min each, and placed in 2.5% glutaraldehyde at 4 °C for 24 h. After fixation, the specimens were washed 3 times in 0.1 M pH 7.0 phosphate buffer for 15 min each. Ethanol was used as the dehydration agent. Specimens were dehydrated in a series of ascending alcohols (30%, 50%, 70%, 90% [2 washes], 100% [3 or 4 washes], each for 2 h). Finally, excess alcohol was removed, and the specimen was submerged in amylacetate for 1 to 2 d. Specimens were air dried for 1 to 3 h at 35 °C. Then the specimen was fixed on an SEM specimen stub with sticky tapes. The specimen then was coated with gold film with 150 Å thickness using a JEOL sputtering device (JEOL Ltd., Tokyo, Japan) for 2 to 3 min.

SEM and Analysis

The specimen then was examined using a SUPRA55 SEM (Carl Zeiss AG, Oberkochen, Germany). The types of different sensilla were identified and classified according to the descriptions of Zacharuk (1985). The images of the sensilla on the surfaces of the antennae from different species were taken at magnifications of 1,500× to 3,500×.

STATISTICAL ANALYSIS

The mean length of body, antennae, and each type of sensilla from different *Drosophila* species was calculated and analyzed using a 1-way ANOVA ($\alpha = 0.05$) and Student-Newman-Keuls multiple comparisons using the SPSS 19.0 statistical analysis package (IBM Corp., New York, USA; www.ibm.com). All micrographs were processed in Adobe Photoshop CS5 (Adobe Systems, Inc., San Jose, California, USA).

Results

MORPHOLOGY OF FLY ANTENNAE

The antennae of fruit flies were situated in the antennal fossa between 2 compound eyes. Each antenna was characterized by 3 segments, a proximal scape, a pedicel, and a flagellum composed of a funiculus and a dendritic arista (Fig. 1). The movable scape was attached to the pedicel, allowing the movement of antenna. Both the scape and the pedicel were heavily covered with microtrichia and possess bristles. The arista was found on the dorso-proximal end of the funiculus, which is an unsegmented flagellum.

For the 4 *Drosophila* species, the funiculus was about twice as long as the pedicel and 4 times longer than the scape (Table 1). The lengths

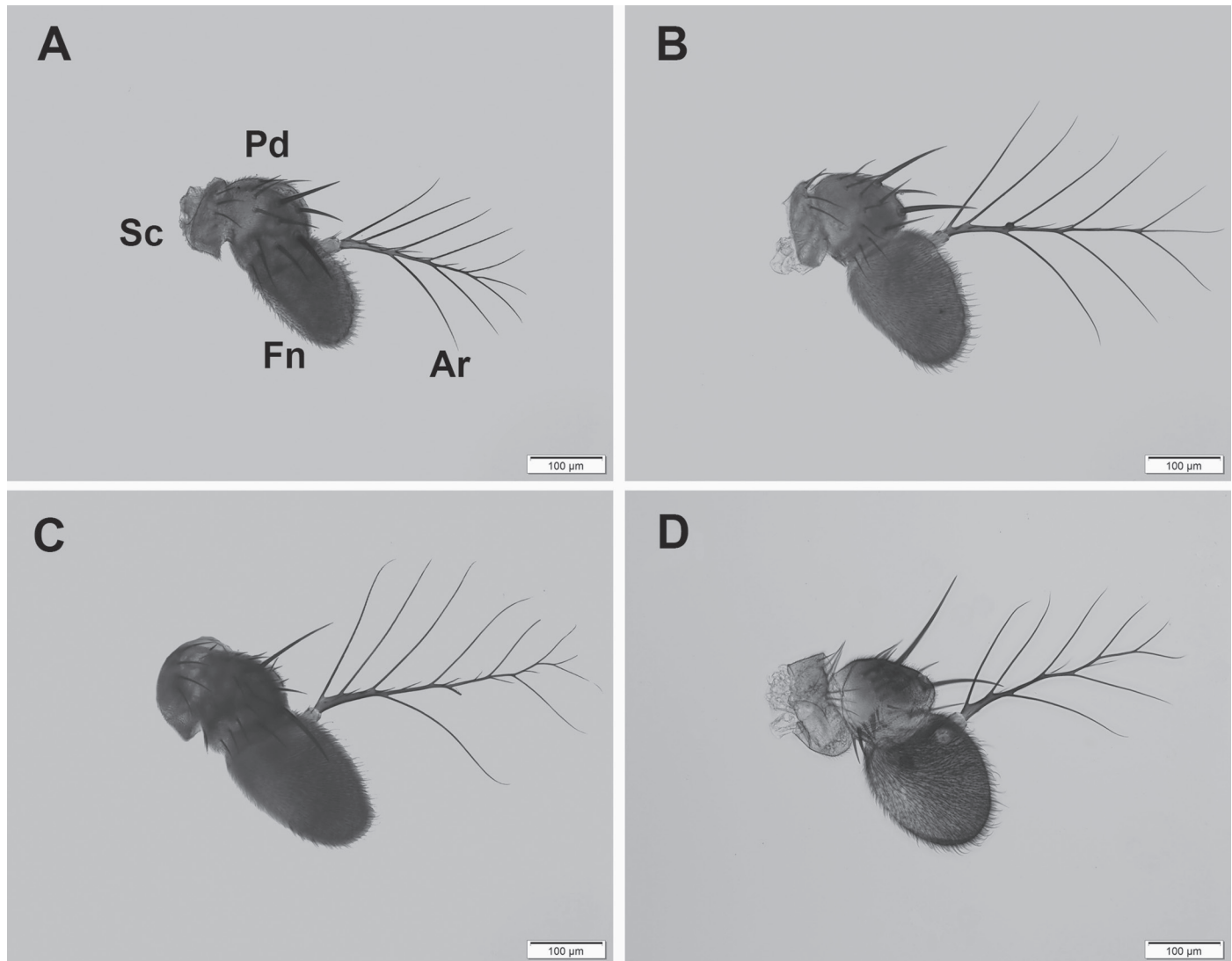


Fig. 1. The antenna of female fruit flies. (A) *Drosophila melanogaster*; (B) *D. suzukii*; (C) *D. immigrans*; (D) *D. hydei*. Scale bar 100 μ m. Abbreviations: Sc, scape; Pd, pedicel; Fn, funiculus; Ar, arista.

of each part of the antennae in different species were significantly different. The length of the scape in *D. hydei* was greater than that of *D. immigrans* and *D. melanogaster*, and that in *D. suzukii* was shortest among the 4 species ($F = 14.83$; $df = 3$; $P = 0.001$). *Drosophila immigrans* had the longest funiculus and arista, which were shortest in *D. melanogaster* (funiculus: $F = 21.80$; $df = 3$; $P < 0.01$; arista: $F = 101.93$; $df = 3$; $P < 0.01$) (Table 1).

SENSILLA OBSERVED ON THE SCAPE AND PEDICEL

Figure 2 shows the sensilla on the scape and pedicel segments of 4 *Drosophila* species. There were no differences in sensilla types among the 4 species. Two distinct morphological types of sensilla, chaetia, and microtrichia sensilla were observed in these segments. These 2 types of sensilla were mainly distributed on the forward side of the scape and pedicel. A small number of microtrichia sensilla were distributed at the base of the funiculus. Chaetia sensilla, spread over the surface of the pedicel, were bristle-like structures with some in a single row, running along the periphery of the scape. The length of chaetia sensilla varied from 27 μ m to 64 μ m (Table 2). Numerous microtrichia sensilla distributed on the surface of the scape and pedicel were hair-

like, with the length from 5.6 μ m to 9.1 μ m. The number and lengths of chaetia and microtrichia sensilla were not significantly different among the 4 species ($F = 1.325$; $df = 3$; $P = 0.277$ for number; $F = 1.643$; $df = 3$; $P = 0.197$ for length).

SENSILLA OBSERVED ON THE FUNICULUS

Four types of sensilla were observed on the funiculus surface: trichoid, basiconic, clavate, and coeloconic sensilla. All sensilla were distributed mostly on the windward side of the funiculus surface, oriented toward the tip of the antenna (Fig. 3).

Trichoid sensilla were most abundant and had the widest distribution on the funiculus of these species. Trichoid sensilla tapered from the base, terminating in a pointed, needle-like structure. Two types of trichoid sensilla were observed, both with a length of about 12 to 14 μ m. Trichoid sensilla I (Tr I) is straight and has ridges, whereas Trichoid sensilla II (Tr II) is a crooked structure. The abundance, distribution, and morphology of the sensilla on the funiculus of these *Drosophila* species were not significantly different (Table 3)

Basiconic sensilla were distributed at the surface of the funiculus, arising from a raised cuticular collar at the surface of the cuticle and

Table 1. The antennal length of the 4 *Drosophila* species.

Parameters	<i>D. melanogaster</i> (cm)	<i>D. suzukii</i> (μm)	<i>D. immigrans</i> (μm)	<i>D. hydei</i> (μm)
Body	2.37 ± 0.66 d*	2.87 ± 0.73 c	3.83 ± 0.44 a	3.37 ± 0.52 b
Scape	47.58 ± 4.18 c	39.22 ± 1.83 d	52.96 ± 7.63 bc	66.67 ± 3.58 a
Pedicle	97.74 ± 16.42 a	104.05 ± 5.45 a	102.49 ± 3.64 a	109.63 ± 10.97 a
Funiculus	153.04 ± 14.51 d	190.86 ± 2.87 b	214.45 ± 6.32 a	210.37 ± 15.49 a
Arista	297.03 ± 7.63 e	416.76 ± 18.09 a	430.77 ± 4.48 a	355.58 ± 11.23 c

*The same letters followed by mean lengths indicate no significant difference at *P* > 0.05.

slightly curved or not. They were characterized as digitiform (finger-like) structures with a rounded point and a smooth surface. The number of basiconic sensilla was less than that of trichoid sensilla. These basiconic sensilla on *D. melanogaster* (9.4–11 μm) were significantly shorter than the others (18–24 μm) (*F* = 187.106; *df* = 3; *P* = 0.000).

Clavate sensilla were shorter than trichoid sensilla, and less widespread on the surface of the funiculus. The clavate sensilla had abruptly blunt tips. They were similar to, but shorter and thicker than, the basiconic sensilla. The length of clavate sensilla was about 9.5 to 12.6 μm. There were few clavate sensilla observed on *D. melanogaster* and *D. immigrans*, but they were more abundant on *D. suzukii* and *D. hydei*.

Coeloconica sensilla were scattered irregularly on the surface of the funiculus, and were the shortest (3.1–4.1 μm) and least abundant sensilla. They arose from a sunken cavity that had a single opening with an irregular rounded margin at the cuticle surface. Two types of coelo-

conica sensilla can be observed on the funiculus surface. Coeloconica sensilla I (Co I) was characterized by a short peg with grooves over the sensilla, whereas Coeloconica sensilla II (Co II) was usually smooth, curved and approximately triangular in shape. Coeloconica sensilla were observed in *D. melanogaster* and *D. immigrans*, but absent in *D. suzukii* and *D. hydei*.

The dendritic arista, with many bifurcations, was located proximally near the base of the funiculus. The hair of the arista in females was significantly longer than that of males in the 4 species (*F* = 101.983; *df* = 7; *P* < 0.001) (Table 1).

SENSILLA OBSERVED ON THE COMPOUND EYES

Only chaetica sensilla were observed on the surface of the compound eyes (Fig. 4). The length and abundance of the chaetica sensilla

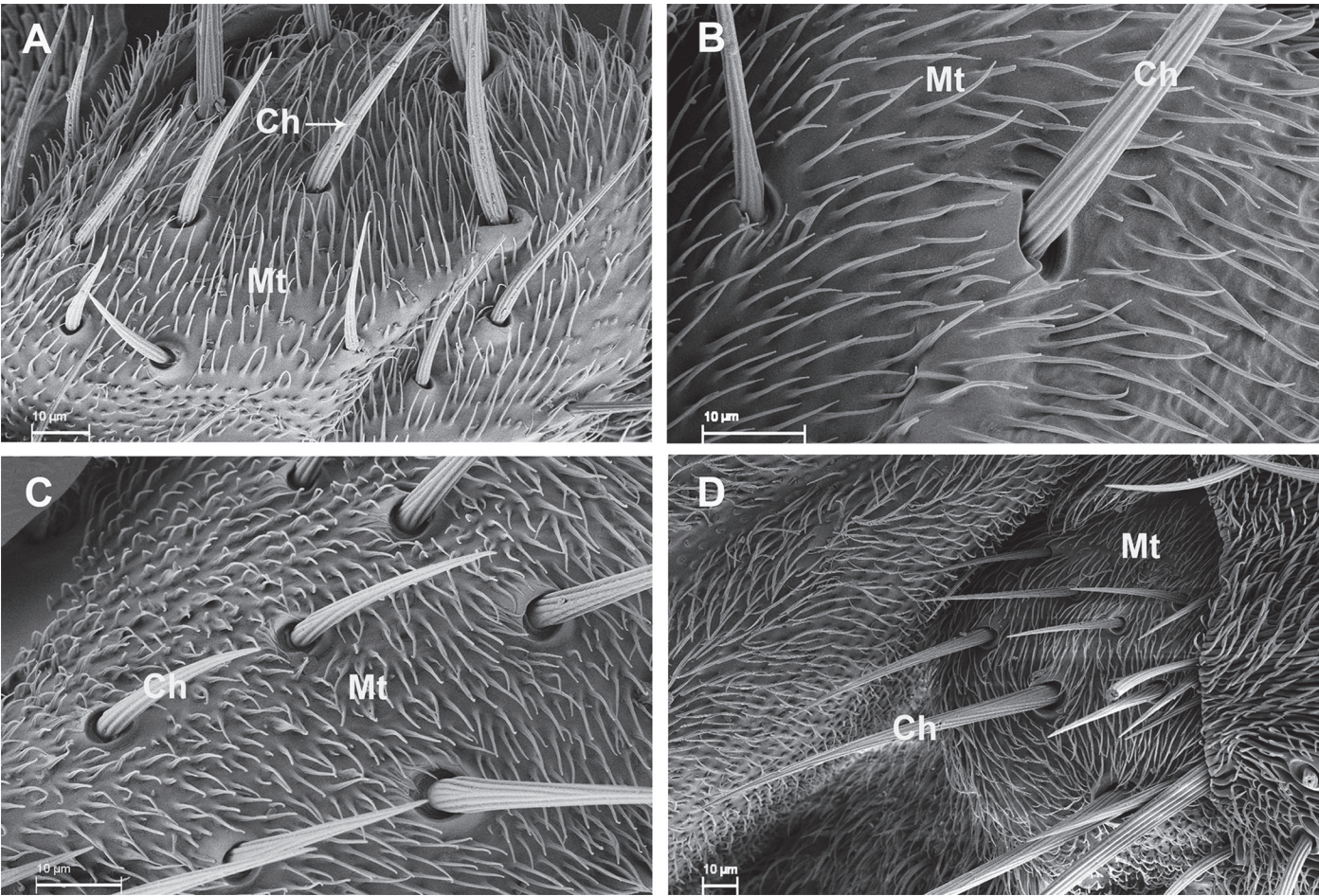


Fig. 2. Chaetica and microtrichia sensilla on pedicel. (A) *Drosophila melanogaster*; (B) *D. suzukii*; (C) *D. immigrans*; (D) *D. hydei*. Scale bar 10 μm. Abbreviations: Ch, chaetica; Mt, microtrichia.

Table 2. Length and amount of sensilla observed on the scape, pedicel and compound eyes.

Part	Type of sensillia	Parameter	<i>D. melanogaster</i>	<i>D. sukukii</i>	<i>D. immigrans</i>	<i>D. hydei</i>
Scape and Pedicel	chaetica	Length (μm)	39.71 ± 18.67 a	49.11 ± 17.80 a	40.22 ± 13.66 a	49.72 ± 17.25 a
		Number	A	A	A	A
	microtrichia	Length (μm)	7.73 ± 1.93 a	7.38 ± 1.19 a	6.31 ± 1.00 a	7.52 ± 1.90 a
		Number	D	D	D	D
Compound eyes	chaetica	Length (μm)	13.24 ± 1.63 c	7.62 ± 0.68 d	17.65 ± 1.23 b	22.17 ± 1.64 a
		Number	C	A	B	D

Letters "A" to "D" indicate relative numbers of sensilla; different letters followed by mean lengths indicate significant difference at $P > 0.05$.

were significantly different among the 4 species ($F = 126.287$; $df = 3$; $P < 0.001$) (Table 2). The length and abundance of the chaetica sensilla were greatest for *D. hydei*, followed by *D. melanogaster* or *D. immigrans*, and were the least for *D. sukukii*.

Discussion

The antennal morphology of *Drosophila* in this study is similar to that in other cyclorrhapha species such as *Bactrocera dorsalis* Hendel, *Bactrocera tau* Walker, *Bactrocera zonata* Saunders (all Diptera: Tephritidae), *Eristalis* (Diptera: Syrphidae), and *Liriomyza huidobrensis* Blanchard (Diptera: Agromyzidae) (Cai et al. 2014; Awad et al. 2015), which consists of 3 segments and a long arista. Eight morphologically distinct types of

sensillae were observed on the antenna of 4 *Drosophila* species, such as chaetica, microtrichia, trichoid (Tr I, Tr II), basiconic, clavate, and coeloconica sensillae (Co I, Co II). In profile, all of the *Drosophila* species had similar antennal sensilla, except that coeloconica sensilla were absent in *D. sukukii* and *D. hydei*. Unlike the *Drosophila* species, 7 types of sensilla, including placodea sensilla, were found in *Lysiphlebus fabarum* (Marshall) (Hymenoptera: Braconidae) but clavate sensillae were not observed (Xi et al. 2010). In 6 species of Noctuidae, there were 9 antennal sensilla on the antennal segments, such as trichoid, chaetica (I, II), coeloconica, basiconic, and 4 other sensilla types (Wei 2015). Therefore, trichoid, chaetica, coeloconica, and basiconic sensilla were widely distributed on the different types of insect antenna.

The sensillae in insects occur in different numbers, morphologies, and have different functions (Romani et al. 2009). The chaetica and mi-

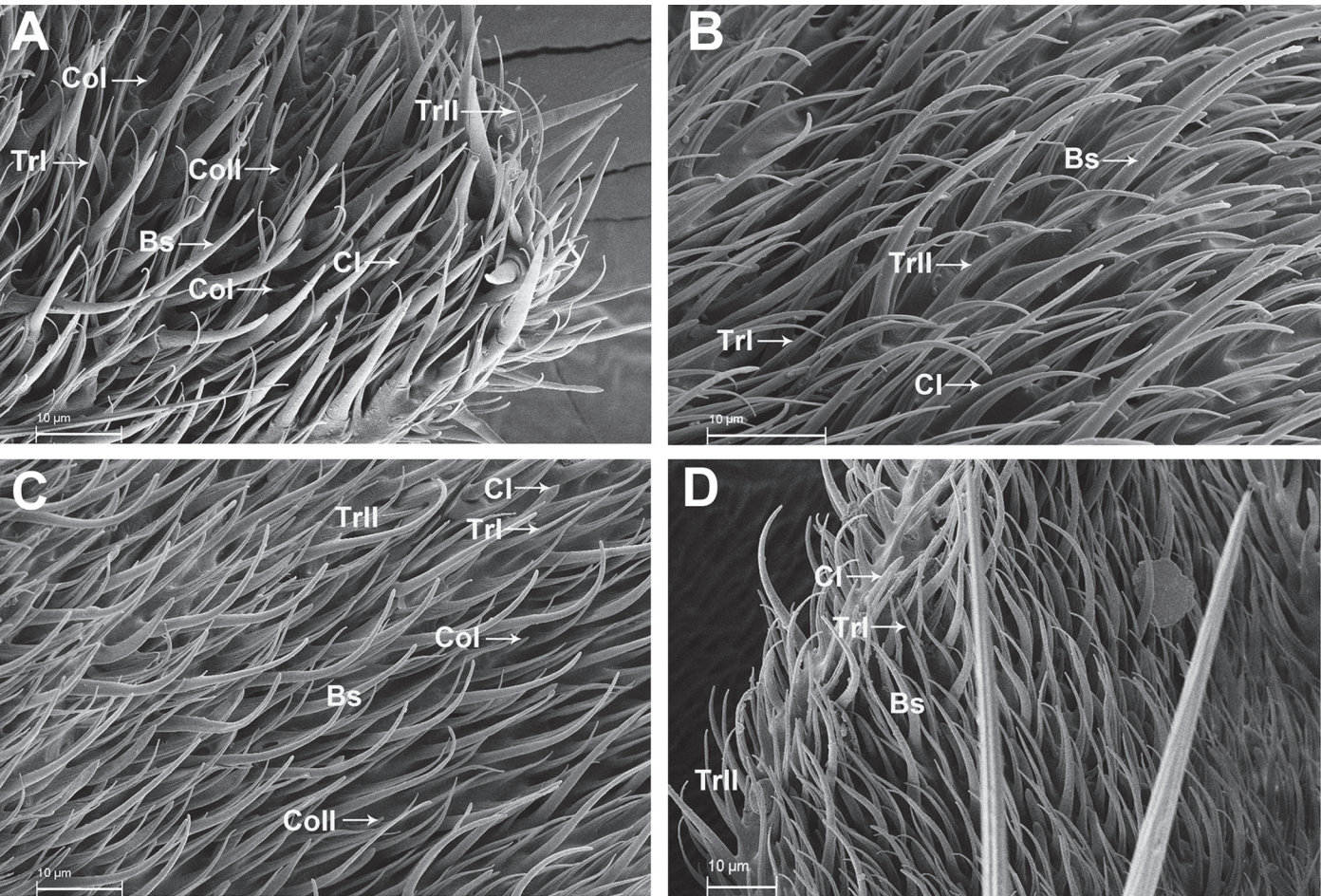


Fig. 3. Different types of sensilla observed on the funiculus segment. (A) *Drosophila melanogaster*; (B) *D. sukukii*; (C) *D. immigrans*; (D) *D. hydei*. Scale bar 10 μm. Abbreviations: Tr I, II: trichoid I, II; Bs: basiconic; Cl: clavate; Co I, II: coeloconic I, II.

Table 3. Types and amount of sensilla observed on the funiculus.

Type of sensillia	Parameter	<i>D. melanogaster</i>	<i>D. sukukii</i>	<i>D. immigrans</i>	<i>D. hydei</i>
trichoid I, II	Length (μm)	12.88 ± 1.58 a	13.18 ± 0.87 a	13.07 ± 1.32 a	13.20 ± 1.55 a
	Number	D	D	D	D
bascionic	Length (μm)	10.23 ± 1.83 b	23.36 ± 0.96 a	22.75 ± 1.26 a	22.46 ± 1.64 a
	Number	C	C	C	C
clavate	Length (μm)	11.35 ± 1.11 a	11.4 ± 0.52 a	11.81 ± 0.33 a	10.65 ± 1.02 a
	Number	A	B	A	B
coeloconic I, II	Length (μm)	3.54 ± 0.43 a	Absent	3.77 ± 0.71 a	Absent
	Number	A		A	

Letters “A” to “D” indicate relative numbers of sensilla; different letters followed by mean lengths indicate significant difference at *P* > 0.05.

crotrichia sensilla were observed on the scape and pedicel in the *Drosophila* species in this study. Compared to the other sensilla, chaetica sensilla were larger, thicker, and higher on the antenna, and initially could contact signals in the environment. Hu et al. (2010) and Awad et al. (2015) reported that the possible functions of the chaetica and microtrichia sensilla on the surface of scape and pedicel in *B. tau*, *Bactrocera minax* Enderlein (Diptera: Tephritidae), *B. zonata*, and 3 other *Bactrocera* species might have a function of mechanoreception. Moreover, chaetica and microtrichia sensilla have been shown to have olfactory functions (Seada 2015). The abundance and length of chaetica and microtrichia sensilla of antennae were not significantly different in *D. melanogaster*, *D. immigrans*, *D. sukukii*, and *D. hydei*. Interestingly,

chaetica sensilla observed on the surface of complex eyes were significantly different among the 4 species. As is well known, the function of complex eyes is attributed to the photoreceptor in compound eyes, which can receive light signals (Chapman 1998). There is no research about sensilla on the surface of the complex eye. In this study, the *D. hydei*, *D. melanogaster*, or *D. immigrans* had more numerous chaetica sensilla than *D. sukukii*. Possibly, mechanoreception is similar for the antenna of *Drosophila* species, but not the reason for differences in ecological niches among them. However, the function of compound eyes also may be involved in recognizing the softer rotted fruits in addition to mechanoreception by chaetica sensilla, though this needs to be assessed in future research.

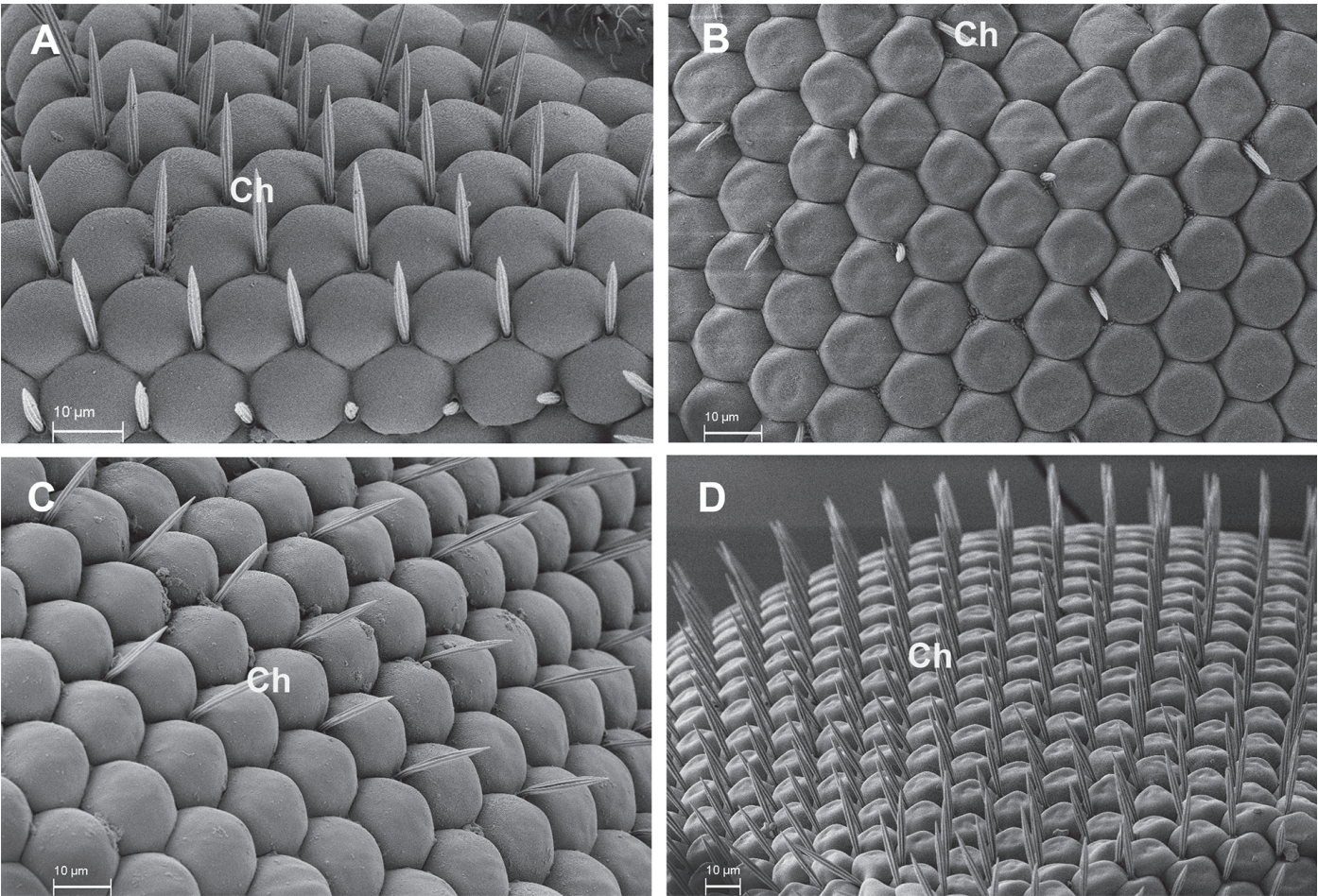


Fig. 4. Chaetica sensilla on compound eye. (A) *Drosophila melanogaster*; (B) *D. sukukii*; (C) *D. immigrans*; (D) *D. hydei*. Scale bar 10 μm.

The pyriform funiculus is the most conspicuous segment of the antenna, housing a variety of sensilla. Six types of antennal sensilla, including trichoid (Tr I, Tr II), basiconic, clavate, and coeloconica (Co I, Co II) sensilla were observed on the funiculus of *Drosophila* species. Generally, trichoid sensilla were the most abundant, and function of mechanoreceptors or proprioceptors (Ochieng et al. 2000; Fernandes et al. 2002). Sukontason et al. (2004) reported that the trichoid sensilla had both chemoreceptor and mechanoreceptor functions in Calliphoridae, Sarcophagidae, and Muscidae. Basiconic and clavate sensilla were considered to be olfactory receptors to a wide range of simple molecules such as carbon dioxide, ammonia, esters, amines, or volatile n-alcohols (Stocker 1994; Lopes et al. 2002; Onagbola & Fadamiro 2008). In this study, basiconic sensilla were significantly shorter in *D. melanogaster* than the other 3 *Drosophila* species studied. The number of clavate sensillae of *D. melanogaster* and *D. immigrans* was lower than that of *D. suzukii* and *D. hydei*. Possibly basiconic and clavate sensilla are involved in host location and selection for different *Drosophila* species. The coeloconica sensilla in *Drosophila* antennae had highly specialized neurons and performed chemosensory function (Yao et al. 2005). However, coeloconica sensilla were sensitive to temperature and humidity in *Manduca sexta* L. (Lepidoptera: Sphingidae) (Shields & Hildebrand 1999) and had olfactory functions in wasps (Van Baaren et al. 2007). Therefore, the function of coeloconica sensilla varies significantly in different insects. In this study, coeloconica sensillae were absent in *D. suzukii* and *D. hydei*. Therefore, in *Drosophila* species, coeloconica sensillae may not be the principal sensilla for location of hosts and identification of signals in the environment. The function of all the sensilla in *Drosophila* species, especially *D. immigrans*, *D. suzukii*, and *D. hydei*, need to be verified by single-cell recording and electroantennography studies.

The results presented here could be valuable for further investigation of insect olfactory behavior and host identification mechanisms, and provide the basis to study the relationships between morphology, and insect behavior and taxonomy, in *Drosophila* species.

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