

Morphology and Distribution of Antennal Sensilla of the Predatory Clerid Beetle, *Thanasimus substriatus* (Coleoptera: Cleridae)¹

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J. Entomol. Sci. 56(3): 441–455 (July 2021)

Abstract *Thanasimus substriatus* (Gebler) (Coleoptera: Cleridae) is an important predator of bark beetles (Scolytidae) and has been used in China for the biological control of the larch bark beetle, *Ips subelongatus* Motschulsky, and the spruce bark beetle, *Ips typographus* L. In this study, the number, external morphology, and distribution of antennal sensilla of *T. substriatus* were determined using scanning electron microscopy. The capitate antennae of both sexes consist of the scape, pedicel, and 9 flagellomeres. Two types of sensilla chaetica (SC1 and SC2), 2 types of sensilla trichodea (ST1 and ST2), 3 types of sensilla basiconica (SB1, SB2, SB3), and Böhm's bristles (BB) were identified according to the morphology and fine structure of each type of sensilla in both sexes. No differences in shape, structure, sensilla distribution, and typology were observed between the sexes. The density of sensilla was greater on the last 3 than on the first 8 segments. SC1 and SC2 occurred on all antennal segments in both sexes. SB1 were located only on the last 5 segments of the antennae. SB2 and SB3 were found only on the last 3 segments of the antennae and were absent on the first 8 segments in both sexes. ST1 and ST2 were absent from the scape and pedicel. BB only occurred on the scape and pedicel. The distal antennal sensilla of *T. substriatus* had notably more sensilla than proximal ones in type and number, indicating this is the main area to detect environmental stimuli for feeding or oviposition.

Key Words *Thanasimus substriatus*, antennal sensilla, scanning electron microscopy

Species of the genus *Thanasimus* Latreille (i.e., clerid beetles) are important predators of the bark and ambrosia beetles (scolytine weevils), usually hunting their prey on the surface of conifer trunks. The clerid beetles are commonly captured in pheromone traps targeting bark beetles and are attracted to aggregation sites of their prey (Erbilgin and Raffa 2001, Kim III and Jung 2006, Tommeras 1988).

In most predatory species, the precise mechanisms involved in the host searching and acceptance processes are still unknown. However, through descriptive study of antennal sensilla, it is possible to infer on important aspects of the roles of antennae in those processes. The antennae are important organs of insect predation, mating, habitat searching, and environmental sensing (Hansson and Stensmyr 2011). Antennal sensilla play an important role in intraspecific and

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interspecific information exchange and host recognition. Although sensilla are found on every part of the insect body, they are most concentrated on the antennae, and they represent the main channel through which insects sense external stimuli (Schneider 1964). Exploratory study of sense organs can help to understand the behavior of predators. Additionally, exploratory studies may also lead to more efficient mass rearing of predators for use in biological control.

So far, there has been much research conducted on sensilla on the antenna and mouthparts of Coleoptera. Well-studied examples include the following: Scolytidae (Hallberg 1982, Peng et al. 2012, Ranger et al. 2017), Elateridae (Faucheux and Kundrata 2017, Merivee et al. 1998, Ren et al. 2014), Chrysomelidae (Bartlett et al. 1999, Zhang et al. 2013), Carabidae (Di Giulio et al. 2012, Merivee et al. 2000, Merivee et al. 2002), Curculionidae (Kang et al. 2012, Smith et al. 1976, Yan et al. 2011), and Cerambycidae (Crook et al. 2003, Dai and Honda 1990, Liu et al. 2012). However, there are few studies of sensilla on the antenna of Cleridae.

In this study, we compared the sensilla type, number, and distribution in male and female adult *T. substriatus* using scanning electron microscopy, and present a preliminary discussion on the functions of sensilla, in order to provide a basic reference for future ultrastructure, electrophysiological, and comparative behavioral studies of *Thanasimus* species.

Materials and Methods

Insects. Adults of *T. substriatus* were collected in pheromone traps targeting bark beetles, *Ips typographus* L., located in Wangqing City, Jilin Province, northeastern China. The heads of the test insects were excised from the live insects and prepared for examination under the scanning electron microscope. Voucher specimens were deposited in School of Life Sciences, Changchun Normal University, Changchun, China.

Scanning electron microscopy (SEM). Antennae of specimens were carefully excised from the antennal sockets with fine forceps under a stereomicroscope (Olympus SZX12, Japan). The antennae were first kept in 70% ethanol for 24 h and then dehydrated in a graded alcohol series of 75%, 80%, 85%, 90%, and 100% for 10 min each. Antennae were individually mounted with dorsal or ventral sides on aluminum stubs with double-sided sticky tapes. Before examination, antennae were sputter coated with gold (20 nm) in a Hitachi E-102 high resolution sputter coater. The specimens were examined in a Hitachi S-570 (Hitachi, Tokyo, Japan) set at 20 kv. Ten antennae of each sex were examined under SEM.

Statistical analysis. The morphology and distribution of sensilla on the antennae of *T. substriatus* were observed and recorded. Sensilla on the dorsal and ventral surfaces of the antennae of both sexes were identified, counted, and measured. To characterize the sensilla, we used the nomenclature proposed by Schneider (1964) and Zacharuk (1980, 1985). The types were also compared with those described for other coleopteran insects (e.g., Chen et al. 2014, Hu et al. 2009, MacKay et al. 2014, Merivee et al. 1999, Yi et al. 2016). The data were analyzed using the *t* test with the statistical program SPSS version 17.0 (SPSS, Inc., Chicago, IL) for Windows. Statistical results were expressed as mean $\pm$ standard deviation (the number of sensilla or the length of sensilla).

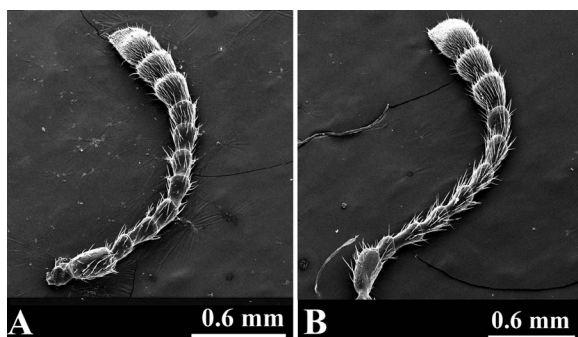


Fig. 1. Overview of female (A) and male (B) antennae of *T. substriatus*.

Results

General structure of the antennae. Antennae of both sexes of *T. substriatus* were morphologically similar. The capitulate antennae were of the conventional type comprising a basal scape, pedicel, and a long flagellum, which was composed of 9 flagellomeres (Fig. 1A, B). Although the body size of the female adults is larger than the males, male adults have much longer antennae than the females (Table 1).

Sensilla chaetica 1 (SC1). SC1 were deeply and longitudinally grooved in cuticular shaft with a tight socket (Fig. 2A, B). This type of sensillum had a mean length and basal diameter ($\pm$ SD) of $39.00 \pm 14.93 \mu\text{m}$ and $2.16 \pm 0.80 \mu\text{m}$ (female) and $39.44 \pm 16.07 \mu\text{m}$ and $2.43 \pm 1.46 \mu\text{m}$ (male), respectively.

Sensilla chaetica 2 (SC2). SC2 were located dorsally and laterally on the distal edges of the flagellomere, and overlapped the proximal part of succeeding flagellomere. These sickle-shaped sensilla had deep longitudinal grooves and tapered toward the tip to a point (Fig. 2C, D). The sensilla were very stout hairs with blunt tips, $113.00 \pm 8.00 \mu\text{m}$ (female) and $108.84 \pm 8.25 \mu\text{m}$ (male) in length and $4.46 \pm 0.15 \mu\text{m}$ (female) and $4.59 \pm 0.06 \mu\text{m}$ (male) diameter at the base.

Sensilla trichodea 1 (ST1). ST1 were hair-like sensilla that were pointed apically and lay relatively parallel to the body of the antenna (Fig. 3A, B). On average ($\pm$ SD), ST1 measured $55.21 \pm 19.83 \mu\text{m}$ (female) and $50.60 \pm 20.93 \mu\text{m}$ (male) in length and $2.48 \pm 0.46 \mu\text{m}$ (female) and $2.41 \pm 0.49 \mu\text{m}$ (male) in basal diameter.

Sensilla trichodea 2 (ST2). ST2 inserted into tight sockets that were slightly elevated above the cuticle and possessed long and blunt tips that narrowed and curved at the distal region. The sensilla were longitudinally grooved (Fig. 3C, D). They measured $97.67 \pm 14.29 \mu\text{m}$ (female) and $98.96 \pm 16.51 \mu\text{m}$ (male) in length and $3.20 \pm 0.52 \mu\text{m}$ (female) and $3.37 \pm 0.40 \mu\text{m}$ (male) in basal diameter.

Sensilla basiconica 1 (SB1). SB1 were characterized by a short and sharp tip (Fig. 4A). They measured $11.13 \pm 1.01 \mu\text{m}$ (female) and $11.88 \pm 1.34 \mu\text{m}$ (male) in length.

Sensilla basiconica 2 (SB2). SB2 were straight, blunt-tipped smooth-walled pegs without longitudinal grooves, emerging from a slightly raised base without articulating socket and were oriented perpendicularly to the antennal surface (Fig.

Table 1. Means ($\pm$ SD) of lengths (mm) of *T. substriatus* (n = 5 per sex) antennal segments.

Sex	Scape	Pedicel	Flagellomeres			
			1	2	3	4
Female	0.281 $\pm$ 0.043	0.106 $\pm$ 0.023	0.158 $\pm$ 0.053	0.153 $\pm$ 0.013	0.146 $\pm$ 0.021	0.147 $\pm$ 0.024
Male	0.296 $\pm$ 0.019	0.148 $\pm$ 0.014	0.189 $\pm$ 0.035	0.154 $\pm$ 0.013	0.171 $\pm$ 0.011	0.171 $\pm$ 0.009

4B). They were $10.8 \pm 0.20 \mu\text{m}$ (female) and $11.01 \pm 0.29 \mu\text{m}$ (male) in length and $2.27 \pm 0.12 \mu\text{m}$ (female) and $2.35 \pm 0.07 \mu\text{m}$ (male) in width at the base. They were situated as a dense group close to the distal part of the ventral border from the fifth to eighth flagellomeres, on the distal part of the ventral surface of the ninth flagellomere, and individually elsewhere (Fig. 4D).

Sensilla basiconica 3 (SB3). SB3 were thinner and in most cases longer than SB1 and SB2. Similarly, these almost straight or slightly curved smooth-walled blunt-tipped slender pegs were represented on all flagellomeres (Fig. 4C). They

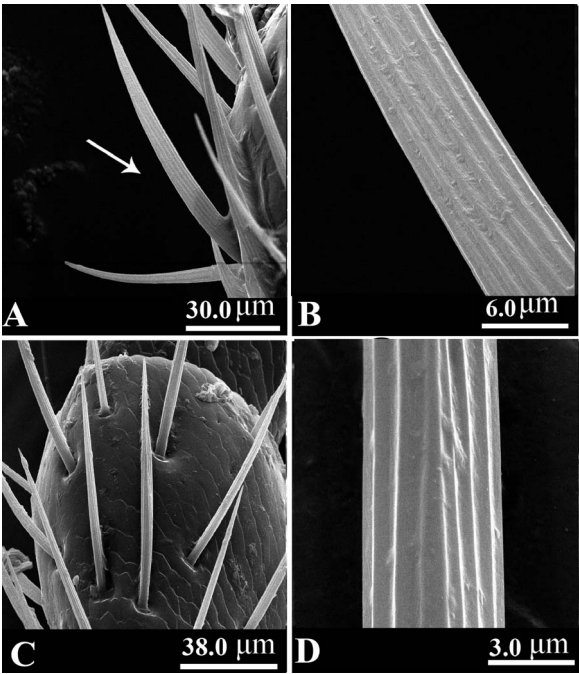


Fig. 2. Sensilla chaetica 1 (SC1) and sensilla chaetica 2 (SC2) on male *T. substriatus* antennae with SC1 on the lateral side of the fifth flagellomere (A) longitudinal grooves on the wall of SC1 (B), SC2 on the dorsal side of the third flagellomere (C), and longitudinal grooves on the wall of SC2 (D).

Table 1. Extended.

Flagellomeres					
5	6	7	8	9	Total
0.139 ± 0.021	0.142 ± 0.006	0.170 ± 0.025	0.179 ± 0.012	0.322 ± 0.021	1.943 ± 0.262
0.154 ± 0.003	0.163 ± 0.009	0.176 ± 0.025	0.182 ± 0.010	0.339 ± 0.020	2.143 ± 0.168

measured a mean (± SD) of 13.67 ± 1.15 μm (female) and 11.43 ± 1.45 μm (male) in length and 2.17 ± 0.02 μm (female) and 2.19 ± 0.01 μm (male) in basal diameter.

Böhm bristles (BB). BB were located in a very wide cuticular sockets, and were surrounded by a shallow depression with smooth cuticles (Fig. 5B). BB were 7.33 ± 1.53 μm long (female) and 7.71 ± 2.24 μm long (male) straight pegs with a sharp tip occurring in a dense group on the intersegmental joints between the scape and the head and between the scape and the pedicel of female and male of *T. substriatus* (Fig. 5C).

The types and lengths of each antennal sensillum type are recorded in Table 2. The total numbers and distribution patterns of sensilla on the antennomeres of *T.*

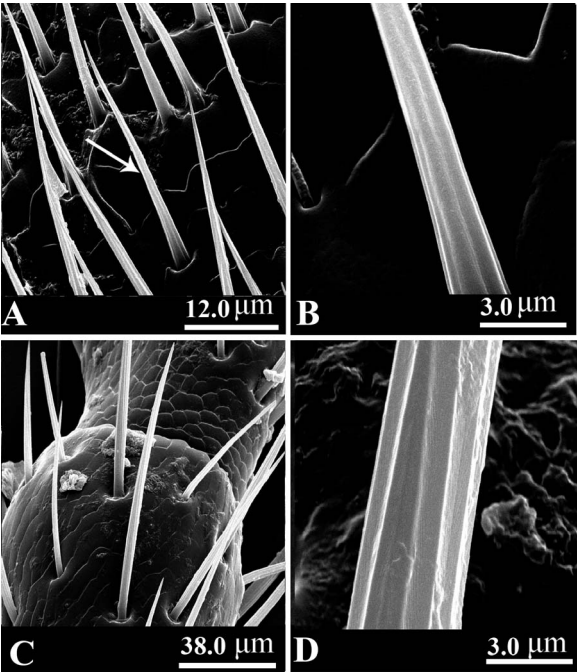


Fig. 3. Sensilla trichodea 1 (ST1) and sensilla trichodea 2 (ST2) on male *T. substriatus* antennae with ST1 (A), longitudinal grooves on the wall of ST1 (B), ST2 (C), and longitudinal grooves on the wall of ST2 (D).

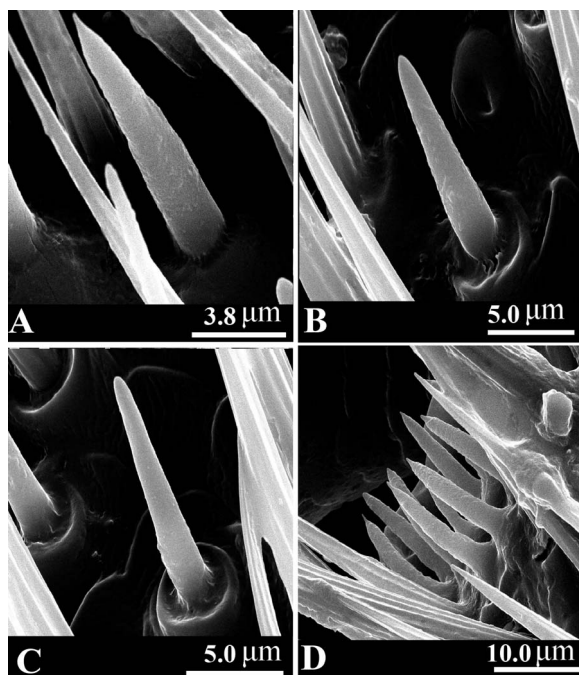


Fig. 4. Sensilla basiconica 1 (SB1), sensilla basiconica 2 (SB2), and sensilla basiconica 3 (SB3) on *T. substriatus* antennae with SB1 (A), SB2 (B), SB3 (C), and a dense group of SB1 and SB3 on the distal section of the fifth flagellomere (D).

substriatus are recorded in Tables 3 and 4. The distribution patterns of sensilla on the antennae of both sexes were similar. However, the density of sensilla was greater on the last 3 segments than on the front segments (Fig. 5D, 6A, D). SC1 were more abundant than the other types of sensilla on the antennae. In the current study, SC1 and SC2 occurred on all antennal segments in both sexes of *T. substriatus*, and no sexual differences were detected. Six to ten SC2 were arranged radially around the distal edge of each antennomere. SB1 were located only on the last 5 segments of the antennae. SB2 and SB3 were found only on the last 3 segments of the antennae and were absent on the first 8 segments in both sexes. ST1 and ST2 were absent from the scape and pedicel. BB only occurred on the scape and pedicel. The distal antennal sensilla of *T. substriatus* had notably more sensilla than proximal ones in type and number, indicating this is the main area to detect environmental stimuli for feeding or oviposition.

Discussion

We identified 8 types of sensilla on the antenna of *T. substriatus*. These are sensilla chaetica (2 types), sensilla trichodea (2 types), sensilla basiconica (3

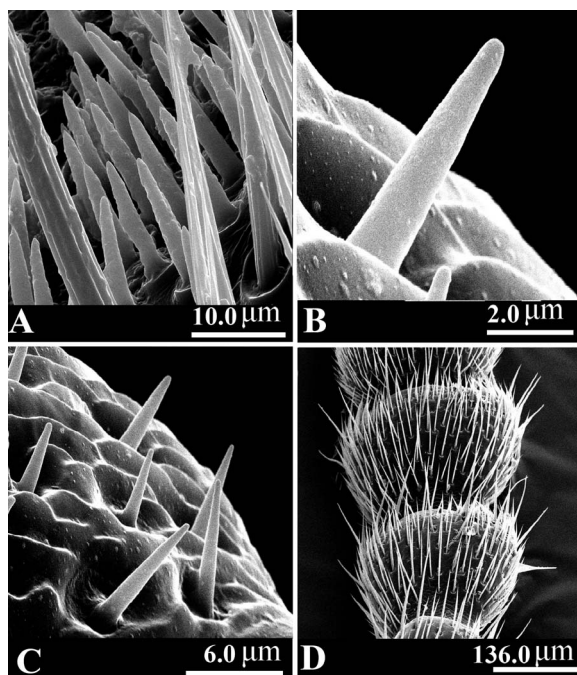


Fig. 5. Dense group of SB2 and SB3 on the distal end of the seventh flagellomere (A), Böhm sensilla (BB) on the base of the scape (B), and a dense group of BB located between the scape and pedicel (C), ventral surface of the seventh and the eighth flagellomere of female (D).

types), and Böhm bristles. We discuss each with comparisons in the following paragraphs.

Sensilla similar to SC1 of this study are also found in other beetles, such as the “hair plate sensilla” of *Psylliodes chrysocephala* L. (Bartlett et al. 1999), the “sensilla chaetica” of *Melanotus villosus* (Geoffroy) (Merivee et al. 1999), and the “sensilla chaetica subtype 2” of *Tetropium fuscum* (F.) (MacKay et al. 2014). Merivee et al. (1999) revealed that sensilla chaetica are sensitive to mechanical stimuli. Aporous SC1 function as tactile mechanoreceptors enabling the beetle to determine the position of the antennae with respect to its surroundings (Altner 1977, Faucheux and Kundrata 2017, Zacharuk 1985).

SC2 in our study could be similar to the “sensilla chaetica type II” in *Psacotheta hilaris* (Pascoe) (Cerambycidae) (Dai and Honda 1990), the “sensilla chaetica 2” in *Agrilus mali* Matsumura (Buprestidae) (Yi et al. 2016), and “sensilla chaetica III” in *Trogoderma granarium* Everts and *Trogoderma variabile* Ballion (Dermestidae) (Wei et al. 2015). The aporous long bristles identified in this study can be the first to contact the substrate, so they could have a mechano-sensitive function (e.g., providing the position information for antennae) (Crook et al. 2008, Saïd et al. 2003, Shields 2004). These sensilla could also play a role in mate recognition and

Table 2. Means ($\pm$ SD) of lengths and diameters (μm) as well as morphological characteristics of different types of antennal sensilla of *T. substriatus* (n = 10 per sex).

Types of Sensilla*	Sex	Length	Diameter	Morphological Characteristics of Sensilla			
				Tip	Wall	Shape	Socket
SC1	Female	39.00 $\pm$ 14.93	2.16 $\pm$ 0.80	Sharp	Grooved	Straight or curved	Wide
	Male	39.44 $\pm$ 16.07	2.43 $\pm$ 1.46				
SC2	Female	113.00 $\pm$ 8.00	4.46 $\pm$ 0.15	Sharp	Grooved	Straight or curved	Wide
	Male	108.84 $\pm$ 8.25	4.59 $\pm$ 0.06				
SB1	Female	11.13 $\pm$ 1.01	2.10 $\pm$ 0.10	Blunt	Smooth	Straight	Tight
	Male	11.88 $\pm$ 1.34	2.14 $\pm$ 0.12				
SB2	Female	10.8 $\pm$ 0.20	2.27 $\pm$ 0.12	Blunt	Smooth	Straight	Tight
	Male	11.01 $\pm$ 0.29	2.35 $\pm$ 0.07				
SB3	Female	13.67 $\pm$ 1.15	2.17 $\pm$ 0.02	Blunt	Smooth	Straight	Tight
	Male	11.43 $\pm$ 1.45	2.19 $\pm$ 0.01				
ST1	Female	55.21 $\pm$ 19.83	2.48 $\pm$ 0.46	Sharp	Grooved	Straight	Tight
	Male	50.60 $\pm$ 20.93	2.41 $\pm$ 0.49				
ST2	Female	97.67 $\pm$ 14.29	3.20 $\pm$ 0.52	Blunt	Grooved	Straight	Wide
	M						
BB	Male	98.96 $\pm$ 16.51	3.37 $\pm$ 0.40	Sharp or blunt	Smooth	Straight	Wide
	Female	7.33 $\pm$ 1.53	1.23 $\pm$ 0.15				
	Male	7.71 $\pm$ 2.24	1.26 $\pm$ 0.16				

* SC1, Sensilla chaetica 1; SC2, Sensilla chaetica 2; SB1, Sensilla basiconica 1; SB2, Sensilla basiconica 2; SB3, Sensilla basiconica 3; ST1, Sensilla trichoidea 1; ST2, Sensilla trichoidea 2; BB, Böhm bristles.

Table 3. Mean numbers per segment ($\pm$ SD) and distribution of different types of antennal sensilla female and male *T. substriatus* (n = 5 antennae per sex)*.

	SC1		SC2		SB1		SB2	
	Female	Male	Female	Male	Female	Male	Female	Male
Scape	25.7 $\pm$ 1.5	22.3 $\pm$ 3.5	25.3 $\pm$ 3.1	24.3 $\pm$ 2.1				
Pedicel	6.3 $\pm$ 0.6	15.7 $\pm$ 3.1	2.0 $\pm$ 0.0	8.3 $\pm$ 1.5				
1	5.3 $\pm$ 0.6	8.3 $\pm$ 2.5	2.3 $\pm$ 1.2	19.7 $\pm$ 1.5				
2	8.3 $\pm$ 1.5	8.7 $\pm$ 1.5	3.3 $\pm$ 0.6	8.7 $\pm$ 2.1				
3	8.3 $\pm$ 2.5	5.7 $\pm$ 0.6	9.0 $\pm$ 2.0	8.7 $\pm$ 2.1				
4	11.3 $\pm$ 3.1	6.7 $\pm$ 0.6	9.0 $\pm$ 1.7	20.7 $\pm$ 10.0				
5	16.0 $\pm$ 3.0	16.0 $\pm$ 3.0	8.3 $\pm$ 1.5	17.0 $\pm$ 2.7	5.3 $\pm$ 0.6	16.7 $\pm$ 3.1		
6	21.0 $\pm$ 6.1	36.3 $\pm$ 4.0	14.7 $\pm$ 2.5	12.7 $\pm$ 2.5	8.0 $\pm$ 1.3	12.3 $\pm$ 1.5		
7	12.0 $\pm$ 2.6	44.7 $\pm$ 5.0	16.0 $\pm$ 3.0	21.3 $\pm$ 1.5	13.0 $\pm$ 2.0	24.7 $\pm$ 2.1	3.7 $\pm$ 0.6	5.3 $\pm$ 1.5
8	43.0 $\pm$ 11.1	81.0 $\pm$ 4.0	24.7 $\pm$ 2.1	23.7 $\pm$ 2.1	19.7 $\pm$ 1.5	42.0 $\pm$ 11.1	16.7 $\pm$ 3.5	9.7 $\pm$ 1.2
9	58.3 $\pm$ 8.1	80.7 $\pm$ 5.0	29.7 $\pm$ 1.5	35.0 $\pm$ 5.0	30.7 $\pm$ 1.5	37.7 $\pm$ 3.1	19.7 $\pm$ 1.5	31.3 $\pm$ 3.5
Total	215.5 $\pm$ 38.7	326.1 $\pm$ 32.8	144.3 $\pm$ 19.2	200.1 $\pm$ 33.1	76.7 $\pm$ 6.9	133.4 $\pm$ 20.9	40.1 $\pm$ 5.6	46.3 $\pm$ 6.2

* No significant difference in total number of antennal sensilla between the sexes (Student's *t* test, *P* > 0.05). SC1, Sensilla chaetica 1; SC2, Sensilla chaetica 2; SB1, Sensilla basiconica 1; SB2, Sensilla basiconica 2.

Table 4. Mean numbers per segment ($\pm$ SD) and distribution of different types of antennal sensilla female and male *T. substriatus* (n = 5 antennae per sex)*

	SB3		ST1		ST2		BB	
	Female	Male	Female	Male	Female	Male	Female	Male
Scape							17.7 $\pm$ 4.9	21.7 $\pm$ 10.0
Pedicel							5.3 $\pm$ 0.6	6.3 $\pm$ 0.6
1			3.0 $\pm$ 0.0	2.3 $\pm$ 0.6	6.7 $\pm$ 0.6	2.0 $\pm$ 0.0		
2			3.3 $\pm$ 0.6	6.7 $\pm$ 0.6	8.3 $\pm$ 2.5	3.3 $\pm$ 0.6		
3			4.7 $\pm$ 0.6	5.3 $\pm$ 0.6	16.3 $\pm$ 3.2	16.7 $\pm$ 5.1		
4			15.0 $\pm$ 4.0	15.0 $\pm$ 3.0	17.3 $\pm$ 5.0	8.3 $\pm$ 0.6		
5			17.3 $\pm$ 3.2	10.3 $\pm$ 0.6	16.7 $\pm$ 3.8	23.7 $\pm$ 2.1		
6			32.0 $\pm$ 4.0	33.7 $\pm$ 4.0	17.3 $\pm$ 3.5	19.7 $\pm$ 1.5		
7	2.3 $\pm$ 0.6	7.7 $\pm$ 1.5	60.3 $\pm$ 13.2	59.3 $\pm$ 8.1	40.0 $\pm$ 7.2	44.0 $\pm$ 11.1		
8	8.3 $\pm$ 1.5	9.0 $\pm$ 1.7	48.3 $\pm$ 8.1	73.7 $\pm$ 13.0	41.3 $\pm$ 8.1	48.7 $\pm$ 6.4		
9	16.7 $\pm$ 3.1	16.7 $\pm$ 2.5	143.0 $\pm$ 6.1	108.7 $\pm$ 11.1	80.0 $\pm$ 4.0	80.0 $\pm$ 4.0		
Total	27.3 $\pm$ 5.2	33.4 $\pm$ 5.7	200.6 $\pm$ 39.8	223.0 $\pm$ 41.6	180.6 $\pm$ 37.9	183.1 $\pm$ 31.4		

* No significant difference in total number of antennal sensilla between the sexes (Student's *t* test, *P* > 0.05). SB3, Sensilla basiconica 3; ST1, Sensilla trichoidea 1; ST2, Sensilla trichoidea 2; BB, Böhm bristles.

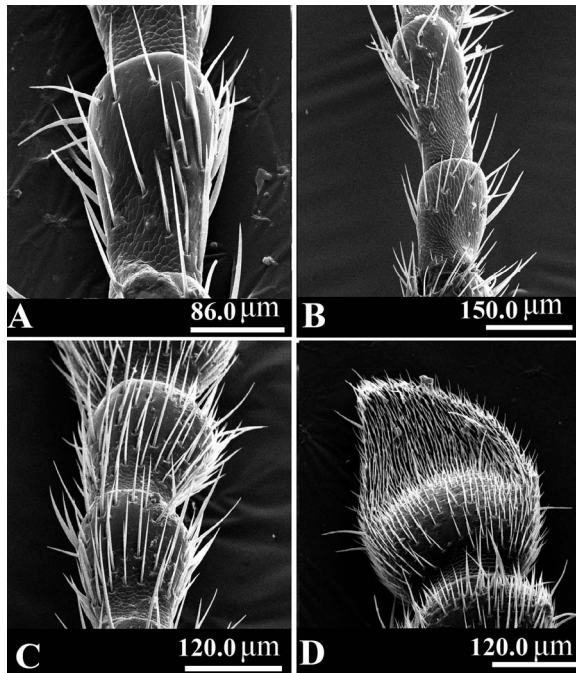


Fig. 6. Dorsal side of scape of male (A), dorsal surface of the scape and pedicel of female (B), ventral surface of the fifth and the sixth flagellomere of female (C), and posterior surface of the terminal flagellomere of male (D).

perception of specific hydrocarbons on the cuticle of female *T. substriatus* that elicit courtship behaviors in this insect, as per studies of Silk et al. (2011) and MacKay et al. (2014).

SB of *T. substriatus* are similar in morphology to those described on the antennal flagellum of several coleopteran species. SB1 of *T. substriatus* resemble the “stout sensilla basiconica” in the longicorn beetles *Monochamus notatus* (Drury) and *Monochamus scutellatus* (Say) (Dyer and Seabrook 1975), the “sensilla basiconica type I” in the click beetle *Limonius aeruginosus* (Olivier) (Merivee et al. 1998), the “sensilla basiconica type II” in *Phoracantha semipunctata* F. (Lopes et al. 2002), and the “sensilla basiconica type II” in *Callosobruchus chinensis* L. and *Callosobruchus maculatus* F. (Hu et al. 2009). SB2 resemble the “large trichoidea sensillum” in the click beetle *L. aeruginosus* (Merivee et al. 1998) and the “sensilla basiconica III” in the lady beetle, *Hippodamia variegata* (Geoeze) (Hao et al. 2020). The SB3 of *T. substriatus* are similar to the “sensilla basiconica type I” in *P. dorsalis* (Dai and Honda 1990), the “sensilla basiconica type II” in *L. aeruginosus* (Merivee et al. 1998), the “sensilla basiconica type I” in *P. semipunctata* (Lopes et al. 2002), and the “sensilla basiconica type I” in *C. chinensis* and *C. maculatus* (Hu et al. 2009).

In male and female adults of *T. substriatus*, SB were distributed in clusters that formed a line along the posterior border from the fifth to the eighth flagellomere (Figs. 4D, 5A). This clustering may improve the ability to sense olfactory molecules. SB clusters also have been found in *Hypera meles* (F.) (Smith et al. 1976), *P. dorsalis* (Dai and Honda 1990), *P. semipunctata* (Lopes et al. 2002), *Phoracantha recurva* Newman (Faucheux 2011), *Xylotrechus grayii* (White) (Chen et al. 2014), and *T. fuscum* (MacKay et al. 2014). These olfactory sensilla clusters have been deduced to have sensory functions and may constitute an expanded odor-sensing area to facilitate long-distance olfactory detection (Inouchi et al. 1987). The sexual dimorphism in SB distribution was observed in *Apriona germari* (Hope), which had clustered SB only found on the male antennae (Zhuge et al. 2009). Moreover, in some Coleoptera, males have more SB than females, suggesting that they are involved in perceiving female sex pheromones (Hu et al. 2009, Merivee et al. 1998, Zhang et al. 2011).

ST1 have been described as the “sensillum trichodeum” in the desert locust *Schistocerca gregaria* (Forskål) (Ochieng and Hallberg 1998), the “sensilla trichodea” in the cabbage stem beetle *P. chrysocephala* (Bartlet et al. 1999), the “sensilla trichoid 2” in the bruchid beetles *C. chinensis* and *C. maculatus* (Hu et al. 2009), and the “sensilla trichodea” in the phytophagous beetle *Chrysolina aeruginosa* Falder (Zhang et al. 2013). In many moths and the click beetles, sensilla trichodea have been shown to respond to the female sex pheromone (Keil and Steinbrecht 1984, Merivee et al. 1999, Zacharuk 1980). Striking differences in the number of these trichodea sensilla on the antennae of *M. villosus* (Geoffroy) (Merivee et al. 1999) and *C. maculatus* (Hu et al. 2009) suggest that they probably function as sex pheromone receptors in males of some beetles. In contrast, no striking sexual differences in the number of the blunt-tipped trichodea sensilla were found in the predatory clerid beetle *T. substriatus*, indicating that these sensilla probably respond to aggregation pheromone produced by the individuals of the same species.

ST2 of *T. substriatus* are similar to the “sensilla trichodea” of the click beetle *L. aeruginosus* (Merivee et al. 1998) and the “sensilla trichodea 1” of the ground beetle *Bembidion lampros* (Herbst) (Ploomi et al. 2003). Sensilla trichodea have been found to play a major role in sensing mechanical stimuli and in recognizing chemical stimuli in insects (Amornsak et al. 1998, Onagbola and Fadamiro 2008, Roth and Willis 1951, Roux et al. 2005). ST2 of *T. substriatus* are more likely to have a tactile function.

Sensilla similar to Böhm bristles of this study are found on the antennae of other beetle species, such as *Semiadalia undecimnotata* Schneider (Jourdan et al. 1995), *C. chinensis* (L.) (Hu et al. 2009), and *Tetrigus lewisi* Candèze (Ren et al. 2014). Böhm sensilla, described for the first time in Lepidoptera (Böhm 1911), are typical bristles found at the base of the scape and at the base of the pedicel and most probably are homologous in all insects (Schneider 1964). Merivee et al. (1999) described Böhm bristles as classical mechanoreceptors. The placement of Böhm bristles in dense groups in the articulation between the head and scape, and scape and pedicel, suggests a role in proprioception of antennal position and movement.

In this study, we describe a fundamental morphological study of the mechanical and olfactory sensilla in *T. substriatus*. These findings also provide important information for further research on the host location and habitat searching behavior

of this predatory beetle. We hope that our findings will provide a useful foundation for future studies of the olfactory system and, therefore, assist in biological control using *T. substriatus*.

Acknowledgments

This work was supported by the PhD's Start-Up Research Grant Program from Changchun Normal University, the Natural Science Foundation of Changchun Normal University (grant 2019-12) and Shenyang City Science and Technology Development Plan Item of China (grant 18-400-3-03). The authors thank colleagues for their assistance in specimen collection of the insects.

References Cited

- Altner, H. 1977.** Insect sensillum specificity and structure: an approach to a new typology, Pp. 295–303. In Le Magnen, J. and P. MacLeod (eds.), *Olfaction and Taste*. Vol. VI. Paris. Information Retrieval, London.
- Amornsak, W., B. Cribb and G. Gordh. 1998.** External morphology of antennal sensilla of *Trichogramma australicum* Girault (Hymenoptera: Trichogrammatidae). *Int. J. Insect Morphol.* 27: 67–82.
- Bartlett, E., R. Romani and I.H. Williams. 1999.** Functional anatomy of sensory structures on the antennae of *Psylliodes chrysocephala* L. (Coleoptera: Chrysomelidae). *Int. J. Insect Morphol.* 28: 291–300.
- Böhm, L.K. 1911.** Die antennalen Sinnesorgane der Lepidopteren. *Arb. Zool. Inst. Wien.* 19: 219–246.
- Chen, J.M., H.L. Qiao, J. Chen, C.Q. Xu, S. Liu, Z.M. Lian and K. Guo. 2014.** Observation of antennal sensilla in *Xylotrechus grayii* (Coleoptera: Cerambycidae) with scanning electron microscopy. *Microsc. Res. Techniq.* 77: 264–273.
- Crook, D.J., L.M. Kerr and V.C. Mastro. 2008.** Distribution and fine structure of antennal sensilla in emerald ash borer (Coleoptera: Buprestidae). *Ann. Entomol. Soc. Am.* 101: 1103–1111.
- Crook, D.J., R.A. Higgins and S.B. Ramaswamy. 2003.** Antennal morphology of the soybean stem borer *Dectes texanus texanus* LeConte (Coleoptera: Cerambycidae). *J. Kansas Entomol. Soc.* 76: 397–405.
- Dai, H. and H. Honda. 1990.** Sensilla on the antennal flagellum of the yellow spotted longicorn beetle, *Psacotha hilaris* (Pascoe) (Coleoptera: Cerambycidae). *Appl. Entomol. Zool.* 25: 273–282.
- Di Giulio, A., E. Maurizia and M.V.R. Stacconi. 2012.** Functional structure of antennal sensilla in the myrmecophilous beetle *Paussus faveri* (Coleoptera, Carabidae, Paussini). *Micron* 43: 705–719.
- Dyer, L.J. and W.D. Seabrook. 1975.** Sensilla on the antennal flagellum of the sawyer beetles *Monochamus notatus* (Drury) and *Monochamus scutellatus* (Say) (Coleoptera: Cerambycidae). *J. Morphol.* 146: 513–532.
- Erbilgin, N. and K.F. Raffa. 2001.** Kairomonal range of generalist predators in specialized habitats: responses to multiple phloeophagous species emitting pheromones vs. host odors. *Entomol. Exp. Appl.* 99: 205–210.
- Faucheux, M.J. 2011.** Antennal sensilla of the yellow longicorn beetle *Phoracantha recurva* Newman, 1840: distribution and comparison with *Phoracantha semipunctata* (Fabricius, 1775) (Coleoptera: Cerambycidae). *Bull. Inst. Sci. (Rabat)* 33: 19–29.
- 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.

- Hallberg, E. 1982.** Sensory organs in *Ips typographus* (Insecta: Coleoptera) fine structure of antennal sensilla. *Protoplasma* 111: 206–214.
- Hansson, B.S. and M.C. Stensmyr. 2011.** Evolution of insect olfaction. *Neuron* 72: 698–711.
- Hao, Y.N., Y.X. Sun, and C.Z. Liu. 2020.** Functional morphology of antennae and sensilla of *Hippodamia variegata* (Coleoptera: Coccinellidae). *PLoS One* 15(8): e0237452.
- Hu, F., G.N. Zhang and J.J. Wang. 2009.** Scanning electron microscopy studies of antennal sensilla of bruchid beetles, *Callosobruchus chinensis* (L.) and *Callosobruchus maculatus* (F.) (Coleoptera: Bruchidae). *Micron* 40: 320–326.
- Inouchi, J., T. Shibuya, O. Matsuzaki and T. Hatanaka. 1987.** Distribution and fine structure of antennal olfactory sensilla in Japanese dung beetles, *Geotrupes auratus* Mtos. (Coleoptera: Geotrupidae) and *Copris pecuarius* Lew. (Coleoptera: Scarabaeidae). *Int. J. Insect Morphol.* 16: 177–187.
- Jourdan, H., R. Barbier, J. Bernard and A. Ferran. 1995.** Antennal sensilla and sexual dimorphism of the adult ladybird beetle *Semiadalia undecimnotata* Schn. (Coleoptera: Coccinellidae). *Int. J. Insect Morphol.* 24: 307–322.
- Kang, G.J., Z.R. Zhu, J.A. Cheng and M.O. Way. 2012.** Antennal sensilla of parthenogenetic and bisexual *Lissorhoptrus oryzophilus* (Coleoptera: Curculionidae). *Florida Entomol.* 95: 8–15.
- Keil, T.A. and R.A. Steinbrecht. 1984.** Mechanoreceptive and olfactory sensilla in insects, Pp. 477–516. In King, R.C. and H. Akai (eds.). *Insect Ultrastructure*. Plenum, New York.
- Kim III, J.I. and B.H. Jung. 2006.** Taxonomic review of the Cleridae (Coleoptera) in Korea (Part 1): Clerinae Latreille, 1802. *Entomol. Res.* 36: 6–15.
- Liu, X.H., Y.Q. Luo, C.J. Cao and S.X. Zong. 2012.** Scanning electron microscopy of antennal sensible of *Anoplistes halodendri halodendri* and *Anoplistes halodendri ephippium* (Coleoptera: Cerambycidae). *Microsc. Res. Techniq.* 75: 367–373.
- Lopes, O., E.N. Barata, H. Mustaparta and J. Araujo. 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.
- MacKay, C.A., J.D. Sweeney and N.K. Hillier. 2014.** Morphology of antennal sensilla of the brown spruce longhorn beetle, *Tetropium fuscum* (Fabr.) (Coleoptera: Cerambycidae). *Arthrop. Struct. Dev.* 43: 469–475.
- Merivee, E., A. Ploomi, M. Rahi, A. Luik and V. Sammelselg. 2000.** Antennal sensilla of the ground beetle *Bembidion lampros* Hbst (Coleoptera: Carabidae). *Acta Zool.* 81: 339–350.
- Merivee, E., A. Ploomi, M. Rahi, J. Bresciani, H.P. Ravn, A. Luik and V. Sammelselg. 2002.** Antennal sensilla of the ground beetle *Bembidion properans* Steph. (Coleoptera: Carabidae). *Micron* 33: 429–440.
- Merivee, E., M. Rahi, J. Bresciani, H.P. Ravn and A. Luik. 1998.** Antennal sensilla of the click beetle, *Limoniis aeruginosus* (Olivier) (Coleoptera: Elateridae). *Int. J. Insect Morphol. Embryol.* 27: 311–318.
- Merivee, E., M. Rahi and A. Luik. 1999.** Antennal sensilla of the click beetle, *Melanotus villosus* (Geoffroy) (Coleoptera: Elateridae). *Int. J. Insect Morphol. Embryol.* 28: 41–51.
- Ochieng, S. and E. Hallberg. 1998.** Fine structure and distribution of antennal sensilla of the desert locust, *Schistocerca gregaria* (Orthoptera: Acrididae). *Cell Tissue Res.* 291: 525–536.
- Onagbola, E.O. and H.Y. Fadamiro. 2008.** Scanning electron microscopy studies of antennal sensilla of *Pteromalus cerealellae* (Hymenoptera: Pteromalidae). *Micron* 39: 526–535.
- Peng, G.D., J.P. Shu, A.L. Zhang, J.T. Wang, T.S. Xu and H.J. Wang. 2012.** Antennal sensilla of the click beetle, *Melanotus cribricollis* (Coleoptera: Elateridae). *Sci. Silvae Sin.* 48: 106–114.
- Ploomi, A., E. Merivee, M. Rahi, J. Bresciani and H. Ravn. 2003.** Antennal sensilla in ground beetles (Coleoptera: Carabidae). *Agro. Res.* 1: 221–228.

- Ranger, C.M., L. Horst, J. Barnett, M.E. Reding, B. Anderson and C.R. Krause. 2017. Comparative morphology and distribution of antennal sensilla on *Xylosandrus germanus* and *Xylosandrus crassiusculus* (Coleoptera: Curculionidae: Scolytinae). *Ann. Entomol. Soc. Am.* 110: 172–188.
- Ren, L.L., Y. Wu, J. Shi, L. Zhang and Y.Q. Luo. 2014. Antennal morphology and sensilla ultrastructure of *Tetrigus lewisi* Candèze (Coleoptera: Elateridae). *Micron* 60: 29–38.
- Roth, L.M. and E.R. Willis. 1951. The effects of desiccation and starvation on the humidity behavior and water balance of *Tribolium confusum* and *Tribolium cataneum*. *J. Exp. Zool.* 118: 337–361.
- Roux, O., J. van Baaren, C. Gers, L. Arvanitakis and L. Legal. 2005. Antennal structure and oviposition behavior of the *Plutella xylostella* specialist parasitoid: *Cotesia plutellae*. *Microsc. Res. Techniq.* 68: 36–44.
- Saïd, I., D. Tauban, M. Renou, K. Mori and D. Rochat. 2003. Structure and function of the antennal sensilla of the palm weevil *Rhynchophorus palmarum* (Coleoptera, Curculionidae). *J. Insect Physiol.* 49: 857–872.
- Schneider, D. 1964. Insect antennae. *Annu. Rev. Entomol.* 9: 103–122.
- Silk, P.J., J. Sweeney, J. Wu, S. Sopow, P.D. Mayo and D. Magee. 2011. Contact sex pheromones identified for two species of longhorned beetles (Coleoptera: Cerambycidae) *Tetropium fuscum* and *T. cinnamopterum* in the subfamily Spondylidinae. *Environ. Entomol.* 40: 714–726.
- Shields, V.D.C. 2004. Ultrastructure of insect sensilla, Pp. 4009–4023. *In* Encyclopedia of Entomology. Springer, Netherlands.
- Smith, C.M., J.L. Frazier, L.B. Coons and W.E. Knight. 1976. Antennal sensilla of the clover head weevil *Hypera meles* (F.) (Coleoptera: Curculionidae). *Int. J. Insect Morphol.* 5: 349–355.
- Tommeras, B.A. 1988. The clerid beetle, *Thanasimus formicarius*, is attracted to the pheromones of the ambrosia beetle, *Trypodendron lineatum*. *Experientia* 44: 536–537.
- Wei, C.Y., B.Z. Ren, X. Chen, X. Zhou, W.L. Wang and Z.G. Wang. 2015. Scanning electron microscope observations on the antennal sensilla of two stored grain pests *Trogoderma granarium* and *Trogoderma variabile* (Coleoptera: Dermestidae). *Florida Entomol.* 98: 140–148.
- Yan, S.C., Z.J. Meng, L. Peng and D. Liu. 2011. Antennal sensilla of the pine weevil *Pissodes nitidus* Roel. (Coleoptera: Curculionidae). *Microsc. Res. Techniq.* 74: 389–396.
- Yi, Z.H., D.G. Liu, X.N. Cui and Z.M. Shang. 2016. Morphology and ultrastructure of antennal sensilla in male and female *Agrilus mali* (Coleoptera: Buprestidae). *J. Insect Sci.* 16: 1–10.
- Zacharuk, R.Y. 1980. Ultrastructure and function of insect chemosensilla. *Annu. Rev. Entomol.* 25: 27–47.
- Zacharuk, R.Y. 1985. Antennae and sensilla, Pp. 1–69. *In* Kerkut, G.A. and L.I. Gilbert (eds.). *Comparative Insect Physiology, Biochemistry and Pharmacology*. Vol. 6. Pergamon Press, London.
- Zhang, J., L. Guan and B.Z. Ren. 2011. Fine structure and distribution of antennal sensilla of longicorn beetles *Leptura arcuata* and *Leptura aethiops* (Coleoptera: Cerambycidae). *Ann. Entomol. Soc. Am.* 104: 778–787.
- Zhang, L., L.L. Ren, Y.Q. Luo and S.X. Zong. 2013. Scanning electron microscopy analysis of the cephalic sensilla of *Chrysolina aeruginosa* Fald. (Coleoptera, Chrysomelidae). *Microsc. Res. Techniq.* 76: 423–431.
- Zhuge, P.P., H.M. Ge, M.Q. Wang, S.B. Wu, S.L. Luo and G.A. Zhang. 2009. Observation of sensilla on the cephalic appendage of *Apriona germari* with scanning electron microscopy (in Chinese with English summary). *Chinese Bull. Entomol.* 46: 238–243.