MORPHOLOGY, HISTOLOGY, AND FINE STRUCTURE

Fine Structure and Distribution of Antennal Sensilla of Longicorn Beetles Leptura arcuata and Leptura aethiops (Coleoptera: Cerambycidae)

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ABSTRACT The longicorn beetles Leptura arcuata Panzer and Leptura aethiops Poda (Coleoptera: Cerambycidae) are predominant pollination beetles in Eurasia and North America. To further elucidate the mechanism of mate and host location, the type, number, and distribution of antennal sensilla of both species of the longicorn beetles were studied using scanning electron microscopy. The filiform antennae of both sexes of the both species consist of the scape, pedicel, and nine flagellomeres. Based on their morphology, three types of sensilla chaetica, one type of sensilla trichodea, four types of sensilla basiconica, and Böhm bristles were distinguished on the antennae in both sexes. No significant sexual differences in the types, numbers, and distribution of the antennal sensilla were found on the antennae, except for the number of sensilla basiconica type 2. The average number of sensilla basiconica type 2 on the antennae of the males was significant greater than that on the antennae of the females. Based on the ultrastructure we postulated that this type of sensillum on the male beetle’s antennae should be responsible for the reception of the sex pheromone produced by the female beetle. The putative functions of other sensillar types also are discussed with reference to their morphology, distribution, and ultrastructure.

KEY WORDS Leptura arcuata, Leptura aethiops, antennal sensilla, scanning electron microscopy

Pollinating insects play a critical role in reproduction of many plant species. Beetles of many species commonly visit flowers when they feed on nectar and pollen (Faegri and Van der Pijl 1979). Beetles are efficient and abundant pollinators (Kevan and Baker 1983, Sakai et al. 1999, Gibernau et al. 1999, Corlett 2004, Kato et al. 2008). Longicorn beetles are one of the most important pollinators in coleopteran species. Leptura arcuata Panzer and Leptura aethiops Poda (Coleoptera: Cerambycidae) are predominant pollinators in Eurasia and North America (Lawrence 1982). But information on mate and host finding mechanisms of the two species is lacking. Abundant information is available on the role of chemicals in mate and host location by longicorn beetles (Iwabuchi et al. 1987, Leal et al. 1995, Hanks 1999, Ginzel et al. 2003, Zhang et al. 2003, Lacey et al. 2004, Wang and Chen 2005, Yasui et al. 2008). Some information is also available on mate-finding behavior by visual cues in several longicorn beetles (Wang 2002; Fukaya et al. 2004, 2005). However, these studies mainly focused on behavioral, electrophysiological, and morphological investigations of cerambycid beetles. Mechanisms underlying mate location and recognition are still unknown for most longicorn beetles. Research on cerambycid mating behavior has indicated the importance of antennae in mate location and recognition. Numerous studies have characterized antennal sensilla of various insects (Zacharak 1980, Keil and Steinbrecht 1984, Stäbler 1984, Bland 1989, Pathipati and Kiyoshi 2001, Broeckling and Salom 2003, Castrejon Gómez and Carrasco 2008), whereas very few such studies have focused on Cerambycidae (Dyer and Seabrook 1975, Dai and Honda 1990, Lopes et al. 2002, Crook et al. 2003, Wang et al. 2005, Sun et al. 2010).

Insect antennae play important roles in various behaviors, including habitat searching, host location, discrimination, courtship, and mating behavior (Schneider 1964). Antennae of insects contain sensory sensilla that function in detection of various stimuli involved in host habitat and mate location (Chapman 1998). As part of our ongoing research on interspecies competition and mate and host location mechanisms between L. arcuata and L. aethiops, we characterized and determined the abundance and distribution of the antennal sensilla of these two species by using scanning electron microscopy (SEM) techniques. This work is a prerequisite for future electrophysiological studies of the antennal sensory system involved in chemical communication.

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Materials and Methods

**Insects.** Adults of *L. arcuata* and *L. aethiops* were collected from Changbai Mountain Nature Reserve, Jilin Province, northeastern China. Specimen vouchers were deposited in School of Life Sciences, Northeast Normal University, Changchun, China.

**SEM.** Antennae of specimens were carefully excised from the antennal sockets with fine forceps under a stereomicroscope (model SZX12, Olympus, Tokyo, 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% in each case 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 an E-102 high-resolution sputter coater (Hitachi, Tokyo, Japan). The specimens were examined in an S-570 (Hitachi) 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 *L. arcuata* and *L. aethiops* were observed. 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 also were compared with those described for other coleopteran insects (Inouchi et al. 1987, Kim and Yamasaki 1996, Hu et al. 2009). The data were analyzed using the *t*-test with the statistical program SPSS version 17.0 for Windows (SPSS Inc., Chicago, IL). Statistical results were expressed as mean ± SE (number of sensilla or the length of sensilla).

Results

**General Structure of Antennae.** Antennae of both sexes of *L. arcuata* and *L. aethiops* are morphologically similar. The filiform antennae were of the conventional type comprised of a basal scape, pedicel, and a long flagellum, which was composed of nine flagellomeres. Although the body size of the female adults is larger than the males, male adults bear much longer antennae than the females. Measurements of antennal segments are given in Table 1.

**Types of Sensilla.** Based on their morphology, three types of sensilla chaetica (SC1–3), four types of sensilla basiconica (SB1–4), one type of sensilla trichodea (ST), and Böhm bristles (BB) were distinguished on the antennae in both sexes. Characteristic morphological features of antennal sensilla of *L. arcuata* and *L. aethiops* are summarized in Table 2. The sensillar counts were made from both dorsal and ventral sides.

**SCI.** The SCI are long sickle-shaped strong bristles with longitudinal grooves accumulating toward the tip; they are located in an open articulating socket (Figs. 1A and B and 5A and B). These sensilla lie parallel to the surface and point toward the tip of the antenna. They cover the scape, pedicel, and the first

### Table 1. Measurements of (mean ± SE) of antennal segments (millimeters) of *L. arcuata* and *L. aethiops*

| Species | Sex | Scapae | Pedicel | Flagellomere | Total |
|---------|-----|--------|---------|--------------|-------|
| *L. arcuata* | Female | 1.116 | 0.217 | 1.233 | 1.566 |
|          | Male | 1.037 | 0.221 | 1.250 | 1.508 |
| *L. aethiops* | Female | 1.151 | 0.214 | 1.264 | 1.629 |
|          | Male | 1.044 | 0.220 | 1.250 | 1.614 |

N = 5 antennae in each sex.

### Table 2. Measurements of (mean ± SE) of antennal segments (millimeters) of *L. arcuata* and *L. aethiops*

| Species | Sex | Scape | Pedicel | Flagellomere | Total |
|---------|-----|-------|---------|--------------|-------|
| *L. arcuata* | Female | 1.156 | 0.213 | 1.264 | 1.583 |
|          | Male | 1.053 | 0.219 | 1.235 | 1.507 |
| *L. aethiops* | Female | 1.186 | 0.215 | 1.271 | 1.672 |
|          | Male | 1.080 | 0.221 | 1.238 | 1.539 |
four flagellomeres. SC1s measure $133.3 \pm 11.0 \mu m$ in length and $7.2 \pm 0.5 \mu m$ in basal diameter.

SC2. SC2 are located dorsally and laterally on the distal edges of the flagellomere, and overlapped the proximal part of succeeding flagellomere. They are absent from the scape and pedicel. These sickle-shaped sensilla have deep longitudinal grooves and taper toward the tip to a point (Figs. 1C and D and 5C and D). The sensilla are very stout hairs with blunt tips, $163.5 \pm 5.7 \mu m$ in length and $12.7 \pm 1.2 \mu m$ in basal diameter.

SC3. SC3 are similar to the SC1 and SC2; however, they are much smaller in dimensions and also bear longitudinal grooves ($57.8 \pm 4.4 \mu m$ in length, $4.3 \pm 0.2 \mu m$ in basal diameter; Figs. 2A and B and 6A and B). They are located along the entire length of the scape, pedicel, and flagellomere.

SB1. SB1 are straight, blunt-tipped smooth-walled pegs without longitudinal grooves, emerging from a slightly raised base without articulating socket and are oriented perpendicularly to the antennal surface (Figs. 3A and 7A). They are $8.2 \pm 0.4 \mu m$ in length and $2.3 \pm 0.1 \mu m$ in width at the base. They are situated as a dense group close to the distal part of the ventral border on the first to eighth flagellomeres, on the distal part of the ventral surface of the ninth flagellomere,

| Types of sensilla | Morphological characteristics of sensilla |
|-------------------|------------------------------------------|
|                  | Length ($\mu m$) | Diameter ($\mu m$) | Tip | Wall | Shape | Socket |
| SC1              | $133.3 \pm 11.0$ | $7.2 \pm 0.5$     | Sharp | Grooved | Curved | Wide |
| SC2              | $163.5 \pm 5.7$ | $12.7 \pm 1.2$    | Blunt | Grooved | Straight | Wide |
| SC3              | $57.8 \pm 4.4$  | $4.3 \pm 0.2$     | Sharp | Grooved | Straight or curved | Wide |
| ST               | $73.8 \pm 9.4$  | $4.4 \pm 0.2$     | Blunt | Grooved | Straight or curved | Wide |
| SB1              | $8.2 \pm 0.4$   | $2.3 \pm 0.1$     | Blunt | Smooth | Straight | Tight |
| SB2              | $12.5 \pm 0.7$  | $2.0 \pm 0.2$     | Blunt | Smooth | Straight | Tight |
| SB3              | $6.1 \pm 0.3$   | $1.6 \pm 0.2$     | Sharp | Grooved | Straight | Tight |
| SB4              | $3.7 \pm 0.5$   | $2.5 \pm 0.2$     | Blunt | Smooth | Straight | Wide |
| BB               | $17.7 \pm 1.9$  | $2.1 \pm 0.6$     | Sharp or blunt | Smooth | Straight | Tight |

Measurements (mean ± SEM) obtained from a total of 20 sensilla per type from antennae of males and females (10 per sex). SC1, sensilla chaetica 1; SC2, sensilla chaetica 2; SC3, sensilla chaetica 3; ST, sensilla trichodea; SB1, sensilla basiconica 1; SB2, sensilla basiconica 2; SB3, sensilla basiconica 3; SB4, sensilla basiconica 4; BB, Böhm bristles.

Fig. 1. SC1 and SC2 in male L. arcuata. (A) Dorsal side of the first flagellomere. Arrows show some SC1. Bar = 50 $\mu m$. (B) Longitudinal grooves on the wall of SC1. Bar = 10 $\mu m$. (C) Distal area of the ventral side of the third flagellomere. Arrows show some SC2. Bar = 75 $\mu m$. (D) Longitudinal grooves on the wall of SC2. Bar = 20 $\mu m$.

Fig. 2. SC3, ST, and BB in male L. arcuata. (A) SC3 on the dorsal side of the third flagellomere. Bar = 17.6 $\mu m$. (B) Longitudinal grooves on the wall of SC3. Bar = 1.2 $\mu m$. (C) ST on the ventral side of the fourth flagellomere. Bar = 20 $\mu m$. (D) BB located on the base of pedicel. Bar = 30 $\mu m$. (E) Smooth cuticle of BB at higher magnification. Bar = 1.5 $\mu m$. 

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and individually elsewhere (Fig. 4A). The cuticular wall of SB1 is perforated by pores irregularly distributed along its length (Figs. 3B and 7B).

SB2. SB2 are thinner and in most cases longer than SB1. Similarly, these almost straight smooth-walled blunt-tipped slender pegs are distributed on the flagellum surface with uniform density (Figs. 3C and 7C). They are arranged perpendicularly to the antennal surface and have a mean length 12.5 ± 0.7 μm and basal diameter 2.0 ± 0.2 μm. The cuticular wall of SB2 also has numerous pores (Figs. 3D and 7D).

SB3. SB three are rare measuring 6.1 ± 0.3 μm in length. They’re sharp-tipped pegs with basal diameters of 1.6 ± 0.3 μm and possess longitudinal grooves distally without pores (Figs. 4B and C and 8A and B). They are typically inserted into a small dome, bear no articulating socket, and are oriented perpendicularly to the antennal surface. They are situated on the ventral surface of the third to ninth flagellomeres.

SB4. The SB4 are very tiny and stout cones (3.7 ± 0.5 μm in length; 2.5 ± 0.2 μm basal diameter) and when viewed at high magnification their wall is smooth with no pores or grooves on the surface (Figs. 4D and E and 8C and D). As the tip of some cones only barely reaches above the level of the socket, these sensilla resemble sensilla campaniformia. They can only be found on the first flagellomere.

ST. The ST are stout, straight or slightly curved, blunt-tapered hairs with longitudinal grooves that gradually become faint toward their tip (Figs. 2C and 6C). They are inserted into a well-developed, flexible socket. They project perpendicularly to the antennal surface. They are distributed throughout the flagellum measuring 73.8 ± 9.4 μm and 4.4 ± 0.2 μm in length and basal diameter.

BB. The BB are 17.7 ± 1.9-μm-long 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 male of L. arcuata and L. aethiops (Figs. 2D and 6D). BB are located in a very wide cuticular socket and are surrounded by a shallow depression with smooth cuticles (Figs. 2E and 6E).

Abundance and Distribution of Antennal Sensilla. The types and lengths of each antennal sensillum type are recorded in Tables 1 and 2. The total numbers and distribution patterns of sensilla on the antennomeres of L. arcuata and L. aethiops are recorded in Tables 3-6. The distribution patterns of sensilla on the antennae of both sexes of the longicorn beetles are similar. SC3 and SB2 are more abundant than the other types of sensilla on the antennae. The number of SB2 is significantly higher on the antennae of males compared with the females. SC1 are located on the scape, pedicel, and first four flagellomeres. SC2, SB2, and SB3 are absent from the scape and pedicel. SC3 and ST are distributed throughout the antennae. Three subtypes of sensilla basiconica are located on the antennal flagellum. SB4 only occur on the first flagellomere.
Discussion

The various types of sensilla and their distribution on the antennae of male and female *L. arcuata* and *L. aethiops* as revealed in this study were similar with those reported for other coleopteran insect species (Jourdan et al. 1995, Merivee et al. 1998, Hu et al. 2009). The antennae of insects have been typically described as consisting of three segments: the scape, pedicel, and flagellum (Chapman 1998). Our study revealed nine morphologically different types of sensilla on the antennae of male and female of *L. arcuata* and *L. aethiops*, similar to those described for other longicorn beetles (Dai and Honda 1990, Crook et al. 2003).

Shorter or longer blunt-tipped hairs that do not articulate at their base, such as ST in *L. arcuata* and *L. aethiops*, occur abundantly on the antennae of many wasps and beetles (Merivee et al. 1999, Bleeker et al. 2004, Lopes et al. 2005, Onagbola and Fadamiro 2008). In wasps, it has been shown that these sensilla bear functions such as mechanoreceptors, olfactory receptors, proprioceptors, and sex pheromone receptors (Hansson et al. 1991, Amornsak et al. 1998, Bleeker et al. 2000). Sensilla trichodea have traditionally been thought of as the contact chemoreceptors (Schneider 1964). They have been reported to perform either or both mechanano- and chemosensory functions, based on their internal structure (Daly and Ryan 1979, Hallberg 1982, Jourdan et al. 1995). Bioassay experiments of the mating behavior on *Phoracantha semipunctata* (F.) demonstrated that sensilla trichodea served as a contact chemoreceptor (Lopes et al. 2005). The function of ST is also thought to be chemoreceptors in *L. arcuata* and *L. aethiops* (Zacharuk 1985).

SC1 resemble the “trichoid type 3 sensilla” *Nebria brevicollis* (F.) (Daly and Ryan 1979), “sensilla chaetica type I” in the *Psacothea hilaris* (Pascoe) (Dai and Honda 1990), “sensilla trichodea type 2” in *Carabus fiduciaris saishutoicus* Csiki (Kim and Yamasaki 1996), “sensilla chaetica type 3” in *Bembidion lampros* (Herbst) (Merivee et al. 2000), and “sensilla chaetica type 4” in *Platynus dorsalis* (Pontoppidan) (Merivee et al. 2001). In *Monochamus notatus* (Drury) and *Monochamus scutellatus* (Say), they can be considered as the receptors responding to sound, wind, or touch (Dyer and Seabrook 1975). SC1 lack pores and protrude above all other sensilla, so they also are presumed to function as mechanoreceptor in *L. arcuata* and *L. aethiops* (Altner and Prillinger 1980).

Large articulated bristles with blunt tip, SC2 in *L. arcuata* and *L. aethiops* seem to be identical with the “trichoid type 2 sensilla” in *N. brevicollis* (Daly and Ryan 1979), “sensilla chaetica type II” in *P. hilaris* (Dai and Honda 1990), “bristle type 1” in the cigarette beetle, *Lasioderma serricorne* (F.) (Okada et al. 1992), “sensilla trichodea type 3” in the ground beetle *C. f. saishutoicus* (Kim and Yamasaki 1996), “sensilla chaetica type 2” in *B. lampros* (Merivee et al. 2000), and “sensilla chaetica type 2” in *P. dorsalis*.
(Merivee et al. 2001). Although the longicorn beetles are able to rotate the antennae 180°, the general downward facing curvature of the antennae is always retained. SC2 found on the distal edges of each segment seem to help retain the curved shape of the antennae. Their location at the segment junctions suggested a role for these sensilla in mechanoreception. Sensilla chaetica have five neurons, one of which terminates in the tubular body, and the others are unbranched in the hair in N. brevicollis. Therefore, these sensilla were inferred to function as mechanoreceptor and contact chemoreceptor (Daly and Ryan 1979).

Large sickle-shaped bristles with pointed tips, similar to SC3 of L. arcuata and L. aethiops, are common on the antennae of many beetles. These sensilla resemble the “trichoid type 1 sensilla,” “sensilla chaetica type III,” “sensilla trichodea type 1,” “sensilla chaetica type 1,” and “sensilla chaetica type I” in the N. brevicollis, P. hilaris, C. f. saishutoicus, B. lampros, and P. dorsalis, respectively (Daly and Ryan 1979; Dai and Honda 1990; Kim and Yamasaki 1996; Merivee et al. 2000, 2001). They are one of the most abundant types of sensilla on the antennae of these and many other beetles. SC3 are distributed on the segments and cover the whole surface of the antenna in many beetles. Ultrastructural evidence in the ground beetle N. brevicollis suggested that the most probable function of these sensilla is mechanoreception (Daly and Ryan 1979). The predomiance of SC3 in L. arcuata and L. aethiops indicates that antenna play a key role in mechanoreception.

Sensilla basiconica of L. arcuata and L. aethiops are similar in morphology to those described on the antennal flagellum of several coleopteran species. SB1 of L. arcuata and L. aethiops resemble the “stout sensilla basiconica” in the longicorn beetles M. notatus and M. scutellatus (Dyer and Seabrook 1975), “sensilla basiconica type II” in P. dorsalis (Dai and Honda 1990), “Sensilla basiconica type I” in the click beetle Limonius aeruginosus (Olivier) (Merivee et al. 1998), “Sensilla basiconica type II” in Phoracantha semipunctata F. (Lopes et al. 2002), and “Sensilla basiconica type II” in Callosobruchus chinensis (L.) and Callosobruchus maculatus (F.) (Hu et al. 2009). Although SB2 of L. arcuata and L. aethiops look like the “thin sensilla basiconica” in the longicorn beetles M. notatus and M. scutellatus (Dyer and Seabrook 1975), “Sensilla basiconica type I” in P. dorsalis (Dai and Honda 1990), “Sensilla basiconica type II” in L. aeruginosus (Merivee et al. 1998), “Sensilla basiconica type I” in P. semipunctata (Lopes et al. 2002), and “Sensilla basiconica type I” in C. chinensis and C. maculatus (Hu et al. 2009). The cuticular wall of SB1 and SB2 bear numerous pores (Figs. 3B and D and 7B and D). SB1 and SB2 should correspond to the “thin-walled” (Slifer 1970); “single-walled, wall pore sensilla” (Altner and Prillinger 1980); and “multiporous chemosensilla” (Zacharuk 1980). SB bear structural features such as a nonflexible base; a thin, multiporous cuticular wall; a pore-tubule system; and branched dendritic segments (Zacharuk 1980). The numerous pores and branched dendrites are traditionally considered to be
Table 3. Numbers (mean ± SEM) and distribution of sensilla on the antenna of female and male L. arcuata

|       | SCI          | SC2          | SC3          | ST           | BB           |
|-------|--------------|--------------|--------------|--------------|--------------|
| Female| Male         | Female       | Male         | Female       | Male         |
| Scape | 354.0 ± 24.8 | 517.0 ± 29.0 | 0            | 0            | 0            |
| Pedicel| 100.7 ± 16.6 | 69.7 ± 12.1  | 0            | 0            | 0            |
| 1     | 678.3 ± 23.7 | 844.3 ± 38.7 | 46.0 ± 4.0   | 64.3 ± 4.7   | 153.0 ± 8.7  |
| 2     | 968.0 ± 17.9 | 658.0 ± 24.5 | 41.3 ± 2.6   | 47.1 ± 1.5   | 149.7 ± 7.5  |
| 3     | 954.0 ± 24.5 | 517.2 ± 35.9 | 37.3 ± 3.0   | 38.7 ± 1.2   | 545.7 ± 17.3 |
| 4     | 0            | 60.0 ± 0.0   | 26.3 ± 2.6   | 24.7 ± 1.5   | 1,905.0 ± 95.3 |
| 5     | 0            | 0            | 17.3 ± 0.9   | 14.3 ± 0.9   | 1,986.0 ± 95.0 |
| 6     | 0            | 0            | 19.3 ± 0.9   | 15.7 ± 1.8   | 1,729.7 ± 51.4 |
| 7     | 0            | 0            | 18.3 ± 1.9   | 13.1 ± 1.2   | 2,012.3 ± 125.7 |
| 8     | 0            | 0            | 16.3 ± 1.2   | 13.1 ± 1.2   | 1,928.7 ± 56.6 |
| 9     | 0            | 0            | 16.0 ± 1.5   | 7.0 ± 0.0    | 1,866.0 ± 117.0 |
| Total | 2,692.7 ± 95.5 | 2,019.0 ± 140.2 | 238.1 ± 18.6 | 236.0 ± 14.0 | 12,203.4 ± 492.1 |

Values are mean number of different types of sensilla on each antennal segment (n = 5 antennae per sex). SCI, sensilla chaetica 1; SC2, sensilla chaetica 2; SC3, sensilla chaetica 3; ST, sensilla trichoid; BB, Bohm bristles. Total numbers for each sensilla type having different letters are significantly different between male and female (P < 0.05; t-test).

evidence that these SB function as olfactory receptors (Altner and Prillinger 1980, Zacharak 1985). Based on the ultrastructure observed by SEM, SB1 and SB2 are inferred as the olfactory receptors in L. arcuata and L. aethiops. The clusters of SB1 are located on the distal part of the flagellomeres (Fig. 4A). Clusters of olfactory sensilla basiconica also have been identified in other coleopteran species, including M. notatus and M. scutellatus (Dyer and Seabrook 1975; Hypera meles (F.) (Smith et al. 1976); P. dorsalis (Dai and Honda 1990); Phyllotera cruciferaceae (Goze), Psylloides punctulata Melsh, Epitrix cucumeris (Harris), Psylloides affinis (Payk) (Ritcey and McIver 1990); and Geotrupes auratus lovides affinis (Okada et al. 1992), "Agriotes obscurus" (Fourcroy) (Merivee et al. 1999), and "C. cheniensis" and C. maculatus (Hu et al. 2009). We postulate that this type of sensillum on the male antennae is responsible for the reception of the sex pheromone produced by the females. In P. semipunctata, no sexual dimorphism was found. Ultrastructural and electrophysiological evidence in P. semipunctata indicated that the flagellar sensilla basiconica of type I and II play a functional role in olfactory recognition of plant odors (Lopes et al. 2002).

The appearance and small number of sensilla basiconica (SB3) of L. arcuata and L. aethiops are similar with "sensillum basiconica type VII" in the click beetle Agriotes obscurus L. (Merivee 1992), "sensillum styloconicum" in the cigarette beetle (Okada et al. 1992), "double-walled sensilla" in Ips typographus (L.) (Hallberg 1982), and "sensillum basiconica II" in the ladybird beetle Semiolela undecimnotata Schneider (Jourdan et al. 1995). SB3 are smooth at the base and bear grooves from the middle to the top (Figs. 4C and SB). Sensilla without

Table 4. Numbers (mean ± SEM) and distribution of sensilla on the antenna of female and male L. arcuata

|       | SB1          | SB2          | SB3          | SB4          |
|-------|--------------|--------------|--------------|--------------|
| Female| Male         | Female       | Male         | Female       |
| Scape | 42.3 ± 2.0   | 11.3 ± 0.9   | 0            | 11.3 ± 0.9   |
| Pedicel| 25.3 ± 0.9   | 6.0 ± 0.0    | 0            | 7.0 ± 0.0    |
| 1     | 139.3 ± 6.2  | 58.3 ± 10.0  | 188.0 ± 15.6 | 136.3 ± 9.6  |
| 2     | 150.0 ± 7.5  | 73.7 ± 8.4   | 418.9 ± 23.1 | 1,452.7 ± 54.0 |
| 3     | 145.7 ± 7.5  | 263.5 ± 18.2 | 442.7 ± 25.8 | 1,839.0 ± 86.9 |
| 4     | 200.2 ± 13.0 | 265.7 ± 17.3 | 758.0 ± 52.2 | 1,762.3 ± 70.4 |
| 5     | 206.7 ± 14.8 | 166.0 ± 8.4  | 994.7 ± 56.5 | 1,148.7 ± 60.7 |
| 6     | 157.0 ± 7.5  | 155.0 ± 14.2 | 805.3 ± 31.8 | 1,749.7 ± 73.6 |
| 7     | 242.3 ± 22.6 | 216.3 ± 19.7 | 947.0 ± 28.9 | 1,761.7 ± 76.3 |
| Total | 1,317.0 ± 82.0 | 1,198.3 ± 96.2 | 4,609.1 ± 294.8 | 9,870.4 ± 433.2a |

Values are mean number of different types of sensilla on each antennal segment (n = 5 antennae per sex). SB1, sensilla basiconica 1; SB2, sensilla basiconica 2; SB3, sensilla basiconica 3; SB4, sensilla basiconica 4. Total numbers for each sensilla type having different letters are significantly different between male and female (P < 0.05; t-test).

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pores are either mechanosensitive or thermo-/hydro-sensitive (Altner and Prillinger 1980, Keil 1999). The putative function of these uniporous and sparse sensilla is hygro- or thermo-reception inferred from the ultrastructural evidence (Altner et al. 1981, Hallberg 1982).

Sensilla basiconica (SB4) located on the first flagellomere of L. arcuata and L. aethiops are very similar to the “sensilla basiconica type 4” of the ground beetle B. lampros (Merivee et al. 2000) and “sensilla basiconica type 3” of the ground beetle P. dorsalis (Merivee et al. 2001). In this study, we did not detect pores or grooves in the cuticle of SB4 (Figs. 4E and 5D). Electrophysiological and behavioral experiments are needed to confirm their function.

The BB located on the intersegmental joints between the scape and the head and between the scape and the pedicel in L. arcuata and L. aethiops are similar to those of “sensilla basiconica type 2” of N. brevicollis (Daly and Ryan 1979), “Bohm sensilla” of B. lampros (Merivee et al. 2000), “sensilla basiconica type 5” of P. dorsalis (Merivee et al. 2001), and “sensilla basiconica type 6” of B. properans (Merivee et al. 2002), and probably in all other coleopteran species as well. The location of BB on the scape and pedicel only suggests that these might be mechanoreceptors (Schneider 1964, Zacharuk 1985). Concentration of BB at the intersegmental joints between the scape and the head as well as between the scape and the pedicel, in many insects, indicates that these sensilla probably perceive the antennal position and movements. Electrophysiological experiments on the honey bee, Apis mellifera L., antenna showed that these sensilla are demonstrated to be phasic-ionic mechanoreceptors (Schneider 1964). The structure of their wide articula socket, and their location only on the joints of the antenna in the basal part of the scape and pedicel suggests that they function as proprioceptors perceiving the antennal position and movements.

The presence of sensilla coeloconica and sensilla campaniformia typically found on other coleopteran insects (Jourdan et al. 1995, Merivee et al. 1998) were not found in L. arcuata and L. aethiops.

Future functional antennal morphology and anatomy studies are needed to confirm the proposed functions of the sensillum identified in this study. These results provide necessary background information for our ongoing study on electrophysiology and chemical ecology of L. arcuata and L. aethiops.

Table 5. Numbers (mean ± SEM) and distribution of sensilla on the antenna of female and male L. aethiops

|                  | SC1 Male | SC2 Male | SC3 Male | ST Male | BB Male |
|------------------|---------|---------|---------|--------|--------|
| Scape            | 854.3 ± 63.5 | 605.0 ± 36.2 | 637.7 ± 6.9 | 2287 ± 17.4 | 340 ± 1.5 |
| Pedicel          | 90.7 ± 6.7 | 82.3 ± 8.4 | 23.7 ± 0.9 | 113 ± 0.9 | 10.3 ± 0.3 |
| 1                | 78.0 ± 7.5 | 710.0 ± 26.0 | 592 ± 6.7 | 81.3 ± 10.4 | 342 ± 5.2 |
| 2                | 634.0 ± 3.5 | 707.0 ± 18.6 | 603 ± 4.1 | 1530 ± 17.4 | 457 ± 5.5 |
| 3                | 852.3 ± 57.7 | 829 ± 18.5 | 510 ± 9.8 | 581 ± 34.9 | 452 ± 6.9 |
| 4                | 70 ± 10.0 | 7.0 ± 0.0 | 307 ± 1.5 | 187 ± 0.9 | 47 ± 6.4 |
| 5                | 0 ± 1.0 | 0 ± 0.0 | 262 ± 1.5 | 203 ± 1.2 | 457 ± 5.2 |
| 6                | 0 ± 1.0 | 0 ± 0.0 | 213 ± 0.7 | 177 ± 0.3 | 457 ± 5.2 |
| 7                | 0 ± 1.0 | 0 ± 0.0 | 147 ± 0.9 | 177 ± 1.2 | 457 ± 5.2 |
| 8                | 0 ± 1.0 | 0 ± 0.0 | 113 ± 0.3 | 177 ± 1.2 | 457 ± 5.2 |
| 9                | 0 ± 1.0 | 0 ± 0.0 | 177 ± 0.3 | 103 ± 0.3 | 457 ± 5.2 |
| Total            | 3,209 ± 221.3 | 2,935 ± 107 | 292.7 ± 30.8 | 273.3 ± 21.5 | 12,891 ± 709.9 |

Values are mean number of different types of sensilla on each antennal segment (n = 5 antennae per sex). SC1, sensilla chaetaica 1; SC2, sensilla chaetaica 2; SC3, sensilla chaetaica 3; ST, sensilla trichodea; BB, Bohm bristles. Total numbers for each sensilla type having different letters are significantly different between male and female (P < 0.05; t-test).

Table 6. Numbers (mean ± SEM) and distribution of sensilla on the antenna of female and male L. aethiops

|                  | SB1 Male | SB2 Male | SB3 Male | SB4 Male |
|------------------|---------|---------|---------|---------|
| Scape            | 10.3 ± 0.9 | 14.7 ± 0.7 | 0 ± 0.0 | 18.7 ± 0.9 |
| Pedicel          | 0 ± 0.0 | 0 ± 0.0 | 0 ± 0.0 | 0 ± 0.0 |
| 1                | 67.0 ± 4.6 | 153 ± 4.4 | 195 ± 15.6 | 414 ± 26.2 |
| 2                | 157.3 ± 15.6 | 286 ± 17.6 | 449 ± 24.6 | 987 ± 52.3 |
| 3                | 246.7 ± 5.7 | 305 ± 29.7 | 528 ± 30.6 | 1,520 ± 77.2 |
| 4                | 263.3 ± 6.2 | 257 ± 12.7 | 91 ± 0.7 | 1,719 ± 103.2 |
| 5                | 298.0 ± 10.7 | 232 ± 12.7 | 1,093 ± 58.3 | 1,716 ± 109.7 |
| 6                | 272.7 ± 9.5 | 260 ± 17.6 | 966 ± 71.7 | 1,705 ± 57.8 |
| 7                | 644.0 ± 20.2 | 365 ± 36.7 | 1,290 ± 91.8 | 2,128 ± 74.0 |
| Total            | 1,993 ± 76.4 | 1,639 ± 131.6 | 5,742 ± 355.9b | 1,017 ± 505.6a |

Values are mean number of different types of sensilla on each antennal segment (n = 5 antennae per sex). SB1, sensilla basiconica 1; SB2, sensilla basiconica 2; SB3, sensilla basiconica 3; SB4, sensilla basiconica 4. Total numbers for each sensilla type having different letters are significantly different between male and female (P < 0.05; t-test).
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References Cited
Alten, H., and L. Prillinger. 1980. Ultrastructure of invertebrate chemo-, thermo-, and hygrococceptors and its functional significance. Int. Rev. Cytol. 67: 69–139.
Alten, H., C. H. Routil, and R. Lofthus. 1981. The structure of bimodal chemo-, thermo-, and hygro-receptive sensilla on the antenna of Locusta migratoria. Cell Tissue Res. 215: 289–309.
Amorowski, W., B. Cribb, and G. Gordh. 1998. External morphology of antennal sensilla of Tricho gramma australicum Girault (Hymenoptera: Trichogrammatidae). Int. J. Insect Morphol. Embryol. 27: 67–82.
Bland, R. G. 1989. Antennal sensilla of Acrididae (Orthoptera) in relation to subfamily and food preference. Ann. Entomol. Soc. Am. 82: 365–354.
Bleeker, M.A.K., H. M. Smid, A. C. Aelst, J.J.A. van Loon, and F. M. Fukaya, M., H. Yasui, T. Yasuda, T. Akino, and S. Wakamura. 1987. Distribution and fine structure of antennal olfactory sensilla in Japanese dung beetles, Geotrupes auratus Mots. (Coleoptera: Geotrupidae) and Copris pecuraria Lew. (Coleoptera: Scarabaeidae). Int. J. Insect Morphol. Embryol. 16: 177–187.
Iwabuchi, K., J. Takahashi, and T. Sakai. 1987. Ultrastructure of antennal olfactory organs, pp. 5–47. Insect olfaction. Springer, Berlin Heidelberg, New York.
Kim, J. L., and T. Yamasaki. 1996. Sensilla of Callconophora solinoense (Araneae) in French Guiana. Int. J. Plant Sci. 160: 1135–1143.
Gibert, M. D., G. J. Blomquist, J. G. Millar, and L. M. Hawks. 2003. Role of contact pheromones in mate recognition in Xylotrechus colonus. J. Chem. Ecol. 29: 533–545.
Hallberg, E. 1982. Sensory organs in Ips typographus (Insecta: Coleoptera) fine structure of antennal sensilla. Protoplasma 111: 206–214.
Hanks, L. M. 1999. Influence of the larval host plant on reproductive strategies of cerambycid beetles. Annu. Rev. Entomol. 44: 483–505.
Hansson, B. S., J.N.C. Van Der Pers, H. E. Högbé, E. Hedenstro¨m, O. Anderbrant, and J. L¨ofqvist. 1991. Sex pheromone perception in male pine sawflies, Neodiprion sertifer (Hymenoptera: Diprionidae). J. Comp. Physiol. 168: 533–538.
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. Matsuzakia, and T. Hatanaka. 1987. Distribution and fine structure of antennal olfactory sensilla in Japanese dung beetles, Geotrupes auratus Mots. (Coleoptera: Geotrupidae) and Copris pecuraria Lew. (Coleoptera: Scarabaeidae). Int. J. Insect Morphol. Embryol. 16: 177–187.
Iwabuchi, K., J. Takahashi, and T. Sakai. 1987. Occurrence of 2, 3-octanediol and 2-hydroxy-3-octanone, possible male sex pheromone in Xylotrechus chinensis Chevrolat (Coleoptera: Cerambicidae). Appl. Entomol. Zool. 22: 110–111.
Jourdan, H., R. Barbier, J. Bernard, and A. Ferran. 1995. Antennal sensilla and sexual dimorphism of the adult ladybird beetle Semiacladula undecimnotata Schn. (Coleoptera: Coccinellidae). Int. J. Insect Morphol. Embryol. 24: 307–322.
Kato, M., Y. Kosaka, A. Kawakita, Y. Okuyama, C. Kobayashi, T. Phimminith, and D. Thongphan. 2008. Fine structure of antennal sensilla basiconica and their role in feeding behaviour in male white-spotted longicorn beetle, Anoplophora malasiaca. J. Chem. Ecol. 30: 1493–1507.
Lawrence, J. F. 1982. Coleoptera, pp. 482–553. In S. P. Parker [ed.], Synopsis and classification of living organisms, vol. 2. McGraw-Hill, New York.
detection of plant volatiles in the eucalyptus woodborer, *Phoracantha semipunctata* Fabricius (Coleoptera: Cerambycidae). Arthropod Struct. Dev. 31: 1–13.

Lopes, O., P. C. Marques, and J. Araujo. 2005. The role of antennae in mate recognition in *Phoracantha semipunctata* (Coleoptera: Cerambycidae). J. Insect Behav. 18: 243–257.

Merivee, E. 1992. Antennal sensilla of the female and male elaterid beetle *Agrionites obscurus* L. (Coleoptera: Elateridae). Proc. Estonian Acad. Sci. Biol. 41: 189–215.

Merivee, E., M. Rahi, and A. Luik. 1999. Antennal sensilla of the click beetle, *Melanotus villus* (Geoffroy) (Coleoptera: Elateridae). Int. J. Insect Morphol. Embryol. 29: 41–51.

Merivee, E., M. Rahi, J. Bresciani, H. P. Ravn, and A. Luik. 1998. Antennal sensilla of the click beetle, *Limonia aeruginosus* (Olivier) (Coleoptera: Elateridae). Int. J. Insect Morphol. Embryol. 27: 311–318.

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. (Stockholm) 81: 339–350.

Merivee, E., A. Ploomi, M. Rahi, A. Luik, and V. Sammelselg. 2001. Antennal sensilla of the ground beetle *Platynus dorsalis* (Pontoppidan, 1763) (Coleoptera: Carabidae). Microsc. Res. Technol. 55: 339–349.

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.

Okada, K., M. Mouri, K. Shimazaki, and T. Chuman. 1992. Morphological studies on the antennal sensilla of the cigarette beetle, *Lasioderma serricorne* (F.) (Coleoptera: Anobiidae). Appl. Entomol. Zool. 27: 269–276.

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

Pathipati, U. R., N. Kiyoshi. 2001. Morphology of antennal sensilla, distribution and sexual dimorphism in *Trogossita japonica* (Coleoptera: Trogossitidae). Ann. Entomol. Soc. Am. 94: 917–927.

Ritecy, G. M., and S. McIver. 1990. External morphology of antennal sensilla of four species of adult flea beetles (Coleoptera: Chrysomelidae: Alticinae). Int. J. Insect Morphol. Embryol. 19: 141–153.

Sakai, S., K. Momose, T. Yumotoa, M. Kato, and T. Inoue. 1999. Beetle pollination of *Shorea parvifolia* (section *Mu- tica*, Dipterocarpaceae) in a general flowering period in Sarawak, Malaysia. Am. J. Bot. 86: 62–69.

Schneider, D. 1964. Insect antennae. Annu. Rev. Entomol. 9: 103–122.

Slifer, E. H. 1970. The structure of arthropod chemoreceptors. Annu. Rev. Entomol. 15: 121–142.

Smith, C. M., J. L. Frazierb, L. B. Coonset, and W. E. Knight. 1976. Antennal sensilla of the clover head weevil *Hypera rufipes* (F.) (Coleoptera: Curculionidae). Int. J. Insect Morphol. Embryol. 5: 349–355.

Städdler, E. 1984. Contact chemoreception, pp. 33–35. In W. J. Bell and R. T. Cardé. Chemical ecology of insects. Chapman & Hall, London, United Kingdom.

Sun, F., X. R. Li, X. X. Liu, and Q. W. Zhang. 2010. Ultrastructure of six types of antennal sensilla in *Monochamus alternatus*. Chin. Bull. Entomol. 47: 347–354.

Wang, Q. 2002. Sexual selection of *Zorion guttigerum* Westwood (Coleoptera: Cerambycidae: Cerambycinae) in relation to body size and color. J. Insect Behav. 15: 675–687.

Wang, Q., and L. Y. Chen. 2005. Mating behavior of a flower- visiting longhorn beetle *Zorion guttigerum* (Westwood) (Coleoptera: Cerambycidae: Cerambycinae). Naturwissenschaften 92: 237–241.

Wang, S. B., H. C. Zhou, X. X. Miao, M. Z. Fan, Z. Z. Li, S. L. Si, and Y. P. Huang. 2005. Scanning electron microscopic observations of *Monochamus alternatus* antennal sensilla and their electroantennographic responses. Chin. J. Appl. Ecol. 16: 317–322.

Yasui, H., T. Akino, M. Fukaya, S. Wakamura, and H. Ono. 2008. Sesquiterpenes hydrocarbons: kairomones with a releaser effect in the sexual communication of the whitespotted longicorn beetle, *Anoplophora malasiaca* (Thom- son) (Coleoptera: Cerambycidae). Chemoecology 18: 233–242.

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 G. A. Kerkt and L. Y. Gilbert [eds.], Comprehensive insect physiology, biochemistry and pharmacology, vol. 6. Pergamon, Oxford, United Kingdom.

Zhang, A., J. E. Oliver, K. Chauhan, B. Zhao, L. Xia, and Z. Xu. 2003. Evidence for contact sex recognition pheromone of the Asian longhorned beetle, *Anoplophora glabripennis* (Coleoptera: Cerambycidae). Naturwissenschaf- ten 90: 410–413.

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