Antennal Morphology and Sensilla Ultrastructure of Three *Tomicus* Species (Coleoptera: Curculionidae, Scolytinae)

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ABSTRACT The antennal morphology and sensilla ultrastructure of *Tomicus yunnanensis*, *T. minor*, and *T. brevipilosus* were studied by scanning electron microscopy and transmission electron microscopy. Eight common sensilla types were recorded: (1) *sensilla trichodea* (*S.tr.*) types 1 and 2 were located on the club and were innervated by five and eight dendrites, respectively; (2) *sensilla chaetica* (*S.ch.*) types 1 and 2 had no dendrites in the sensilla lymph lumen; (3) *sensilla basiconica* (*S.b.*), top-protuberated *S.b.* and fluted cones (*Fl.c.*) occurred on the club; and Böhm bristles *(B.b.)* occurred on the funicle. *S.b.* were the most abundant and were innervated by 10–14 dendritic branches. Top-protuberated *S.b.*, a new sensilla type, were innervated by one dendrite. *Fl.c.* were innervated by five dendrites. Only three *sensilla furcatea* were visible on the antennae of female *T. yunnanensis*. The possible functions of these sensilla are discussed in relation to their morphology and ultrastructure. No statistical differences between sexes were found in the size and numbers of each sensilla type. Although the three species had similar antennal morphology and sensilla type, sensilla on sub-segments 3 and 4 of the antennal club of *T. minor* were much sparser than those of *T. yunnanensis* or *T. brevipilosus*. Concerning the antennae of *T. yunnanensis*, there were more *S.tr.* type 2, *S.ch.* type 2 and *S.b.* and the size of *S.tr.* type 1 and *S.b.* were significantly greater than those of *T. minor. Microsc. Res. Tech. 75:1672–1681, 2012.*

INTRODUCTION

Tomicus yunnanensis Kirkendall and Faccoli, *T. minor* Hartig, and *T. brevipilosus* Eggers (Coleoptera: Curculionidae, Scolytinae) are important insect pests of pines, *Pinus* spp. (Kirkendall et al., 2008). *T. yunnanensis* primarily attacks Yunnan pine, *P. yunnanensis*, in Yunnan province, China (Liu et al., 2010). *T. minor* colonizes *P. sylvestris*, *P. nigra*, *P. brutia*, *P. halepensis* in Western Europe (Kohlmayr et al., 2002), and *P. massoniana*, *P. tabulaeformis*, and *P. yunnanensis* in Asia (Yin et al., 1984). *T. brevipilosus* infests *P. koraiensis*, *P. insularis* and *P. yunnanensis* in China and India (Kirkendall et al., 2008). In Yunnan, the three species feed on shoots and trunks of *P. yunnanensis*, seriously damaging several hundred thousand hectares of pine forests since the 1980s (Ye et al., 2004).

As the field of chemical ecology has developed, insect behavior has been correlated to their physiological, biochemical, and microanatomical features. A number of studies have examined antennal sensilla (Altner and Loftus, 1985; Li et al., 2009; Ross, 1992; Zacharuk, 1985). The antennae are the primary olfactory organs in bark beetles and are essential for activities such as host seeking, inter-specific and intra-specific communication, mating, and oviposition (Byers, 1995; Wigglesworth, 1972). The antennal sensilla house specialized sensory neurons that allow the beetles to detect stimuli that function in host selection, including location, recognition, discrimination, and acceptance of the habitat (Byers, 1995; Schneider, 1964).

Important features can be inferred from descriptive studies of antennal sensilla, which can be classified as *sensilla trichodea* (*S.tr.*), *sensilla basiconica* (*S.b.*), *sensilla chaetica* (*S.ch.*), and fluted cones (*Fl.c.*) (Borden and Wood, 1966; Dickens and Payne, 1978; Payne et al., 1973; Whitehead, 1981). These structures exhibit different sensory modalities, including touch (mechanosensilla) and smell and taste (chemosensilla) (Schneider, 1964; Zacharuk, 1985). For the sub-family Scolytinae alone, many papers have been published on the morphology, ultrastructure, and function of various sensilla (Borden and Wood, 1966; Borg and Norris, 1971; Chen et al., 2010; Dickens and Payne, 1978; Faucheux, 1989, 1994; Hallberg, 1982; Whitehead, 1981).

Antennal morphology and surface structure of *T. piniperda* L. from Yunnan province were observed, and the types, amounts and distributions of five antennal chemoreceptors were defined (Wu et al., 2000). Only *T. piniperda* and *T. minor* were reported in Yunnan at that time (Långström et al., 2002; Ye and Ding, 1999). Duan et al. (2004) found firstly *T. brevipilosus* in Yunnan province. Several years later, *T. piniperda* in Yunnan was reclassified as *T. yunnanensis* by

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Kirkendall et al. (2008). According to our observations that *T. yunnanensis* and *T. brevipilosus* have similar morphology and maternal gallery, we speculate that the beetles used by Wu et al. (2000) may include *T. yunnanensis* and *T. brevipilosus*. So, the antennal sensilla of the two species should be identified separately at present. We are not aware of any published information on the antennal sensilla of *T. minor*. These beetles are sympatric and can colonize the same individuals of Yunnan pine, so their antennal morphology and sensilla structure may share features or have unique characteristics.

In this article, we first investigated the antennal morphology of female and male *T. yunnanensis*, *T. minor*, and *T. brevipilosus* using scanning electron microscopy (SEM) and transmission electron microscopy (TEM). Second, we described the external morphology, abundance, distribution, and internal structure of the antennal sensilla. Finally, we compared inter- and intraspecies differences in the size and number of antennal-sensilla type. Our objectives were to provide the foundation for elctrophysiological studies of the three species and explore the relationships between structure and behavior.

MATERIALS AND METHODS

Animals

Adults of *T. yunnanensis*, *T. minor*, and *T. brevipilosus* were captured from trunks of *P. yunnanensis* in December, 2010. The first two species were collected on a mountain at Yuezhou town (N25°14′, E103°50′), Yunnan Province, and the third was collected at Beishan Forest Farm (N24°21′, E102°35′) of Yuxi, Yunnan Province, China.

Scanning Electron Microscopy

For SEM observation, antennae were cut at the base of the scape and then rapidly fixed in 2.5% glutaraldehyde mixed with phosphate buffer solution (PBS; 0.1*M*, pH 7.4) for 1 day at 4°C. The antennae were then cleaned for 20 min in 20% ethanol solution using an ultrasonic bath. This was followed by dehydration through a graded ethanol series (40%, 60%, 80%, 90%, and 100%; 20 min each). After natural drying for 12 h, the specimens were mounted on holders with electric adhesive tape in different orientations to obtain clear views of the ventral, dorsal, and both lateral sides. Then, the samples were sputter-coated with gold (model IB-5 ion sputterer, Hitachi, Tokyo, Japan) and observed using a Hitachi S-4800 SEM.

Transmission Eelectron Microscopy

For TEM observation, excised fresh antennae were prefixed in 2% glutaraldehyde in PBS (0.1*M*, pH 7.4) with 5% sucrose for 1 day at 4°C, fully washed with PBS, postfixed in 1% osmium tetroxide in PBS at 4°C for 1 h, and finally cleaned with distilled water. Dehydration was carried out in a graded series of ethanol as described above and in three 10-min washes of 100% acetone. Then, the antennae were embedded in Epon 812 (Houston, TX) and cured at 60°C for two days. Ultrathin (60–100 nm) sections were cut using a Leica UC6 ultramicrotome (Wetzlar, Germany), mounted on formvar-coated 100 mesh copper grids, double-stained with uranyl acetate and 1% lead citrate, and observed with a Hitachi H-7500 TEM.

Statistical Analyses

Classification of sensilla types was based mainly on morphological characters described by Keil (1997, 1999), Schneider (1964), Whitehead (1981), and Yang et al. (2009). Ultrastructural nomenclature used here follows that of Isidoro et al. (1998, 2001), Ochieng et al. (2000), Pettersson et al. (2001), and Zacharuk (1980).

Eight females and eight males of each species were investigated in our study. Images were processed with Adobe Photoshop CS5 Extended (v. 12.0.3×32; Adobe Systems, Mountain View, CA). Antennae and sensilla were measured using ZWCAD software (v. 2012; ZWCAD sorftware, Guangzhou, China). Width was measured at the middle of the sensilla. The number of each sensilla type was counted.

We compared the lengths, widths, and numbers of antennal sensilla within species and among species. All data analyses were performed using SPSS software (v. 17; SPSS, Chicago, IL). A univariate ANOVA followed by least significant differences for multiple comparisons were used to assess significant differences in the size and number of sensilla. Sexual differences were analyzed using the Mann–Whitney *U* test (Gao et al., 2007).

RESULTS

General Antennal Morphology

Because the antennae (Fig. 1A) of *T. yunnanensis*, *T. minor*, and *T. brevipilosus* have similar morphology with an expanded scape, a narrow, six subsegmented funicle, and a long oval club (Fig. 1B), we expect the morphology described in Figure 1 could represent the antennal morphology of the three species. The greatest number and variety of sensilla occurred on the distal three-fourths of the club and were organized into three roughly-parallel sensory bands that completely encircled the club (Figs. 1B and 1C). By comparison, few sensilla were observed on the scape and funicle. The three sensory bands divided the club into four subsegments. Many hypodermal glandular pores were located on the surface of the club.

The antenna of *T. yunnanensis* (783.6 μm) was significantly longer than that of *T. brevipilosus* (741.3 μm) and *T. minor* (699.0 μm) (Table 1). *T. yunnanensis* had the longest club (250.8 μm) of the three species, followed by *T. brevipilosus* (226.7 μm) and *T. minor* (211.1 μm). The funicle was similar in length to the club. *T. yunnanensis* had a notably longer scape than the other two species. There were no evident differences in the lengths of the scapes, funicles, and clubs between male and female beetles. The antennal length of female *T. yunnanensis* (817.8 μm) was significantly longer than that of males (749.3 μm), although none of the antennal subunits differed significantly in length.

In addition, subsegments 2, 3, and 4 of the club were investigated. Sensilla quantity on each subsegment differed significantly among the three species (Fig. 2; Table 2). *T. brevipilosus* showed the most sensilla on the subsegment 2 (average of 11.5 per antenna) and 3 (69.3) of the three species. *T. brevipilosus* and *T. yunnanensis* had similarly high numbers of sensilla on the subsegment 4, averaging 91.2 and 96.3 per antenna, respec-

tively. In contrast, *T. minor* showed the fewest sensilla on each subsegment, especially the subsegment 3 and 4. More sensilla were located on the club of *T. yunnanensis* (703.3) than those of *T. minor* (615.4) (Table 2).

Antennal Sensilla Types

Analysis of sensilla patterns showed that females and males of *T. yunnanensis*, *T. minor*, and *T. brevipilosus* had essentially the same morphological sensilla types and ultrastructures. Because the antennae studied here represented three species, we expect that the types of sensilla described in Figures 1, 3, and 4 probably encompass all the sensilla types. We categorized the sensilla types based on the types described above as follows: two types of *S.tr.*, two types of *S.ch.*, one type each of *S.b.*, *Fl.c.*, top-protuberated *sensilla basiconica* (*T.p.s.b.*) and Böhm bristles (*B.b.*) (Figs. 3 and 4). Only three *sensilla furcatea* (*S.f.*) were found on the antennae of female *T. yunnanensis* (Fig. 4E).

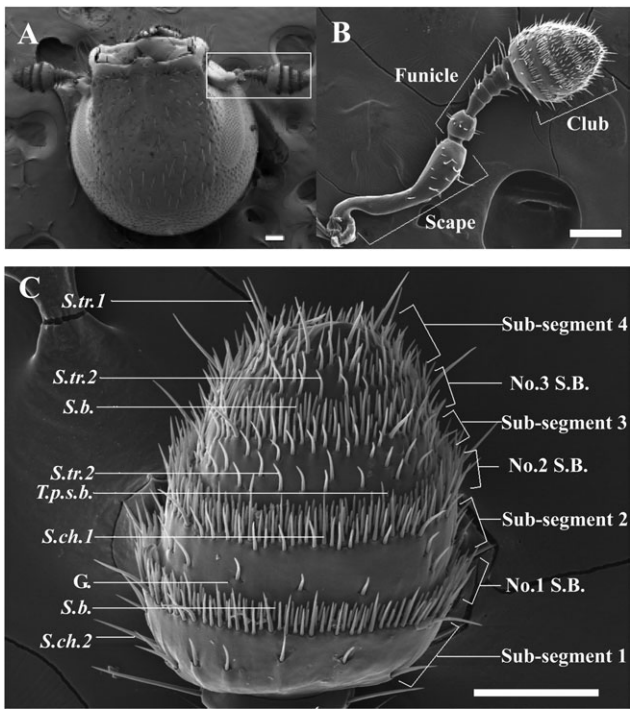

Fig. 1. SEM images of the antennae of *Tomicus yunnanensis*, *T. brevipilosus*, and *T. minor*. **A**: Location of the antenna on the head. **B**: Shapes of the scape, funicle, and club. **C**: Distribution of sensilla and glands on the club. Note the three sensory bands and four subsegments. Sensilla are located mainly in three sensory bands, subsegment 4 of the club. *S.tr.1* and *S.tr.2*, *sensilla trichodea* types 1 and 2, respectively; *S.ch.1* and *S.ch.2*, *sensilla chaetica* types 1 and 2, respectively; *S.b.*, *sensilla basiconica*; *T.p.s.b.*, top-protuberated *sensilla basiconica*; *Fl.c.*, fluted cones; *B.b.*, Böhm bristles; G, glands; S.B., sensory band. Scale bar = 100 μm.

The funicle and scape bore only a few *S.ch.2* and *B.b.* The highest sensilla concentration occurred on the club, where all types but *B.b.* were present. Sensilla on the club and the third, fourth, fifth, and sixth sub-segments of the funicle were evenly distributed between the dorsal and ventral sides. Therefore, the number of sensilla could be estimated using SEM images of only one side. Some *S.ch.2* were more dense on the dorsum of the scape. The sizes and numbers of eight antennal sensilla types in both sexes are summarized in Table 3.

Sensilla Trichodea 1. The *S.tr.1* type was distinctly concentrated at the apex of the club and at the edges of the three sensory bands (Figs. 1C, 3A, and 3A1). There were 26.8–29 hairs per antenna in the three species (Table 3). They were characterized by their pronounced length, a longitudinal grooved surface, and an apical pore (Figs. 1C, 3A2, and 3A3). The apical pore ~50 nm in diameter was observed at the rounded tip (Fig. 3A2). The sensillum was inserted in the antennal wall through a large socket with 2–4 glandular pores at the base (Fig. 3A). The length varied from 37.2 to 54.2 μm and the width varied from 1.5 to 2.0 μm (Table 3). Viewed in cross-section, the nonporous cuticular wall was about 0.5–0.8 μm thick near the middle of the sensilla, and a sensillum lymph lumen contained five dendrites within a sheath (Fig. 3A4).

Sensilla Trichodea 2. The *S.tr.2* type was abundant on the three sensory bands and on subsegments 2, 3, and 4 of the club, with 99.3–156.3 hairs per antenna (Figs. 1C and 3B; Table 3). These structures had fine tips that inclined away from the club, especially those on the club sub-segment 3, which bent distinctly near their middles. The cuticular wall was perforated by multiple pores (26–30 pore/μm^2) distributed primarily on the upper half of the hair (Fig. 3B1). A tight socket and 1–2 glandular pores were located at the sensilla

TABLE 1. Lengths of antennae and antennal regions of three species of Tomicus

Antennal region	Species	Length (μm)[a] ♀	Length (μm)[a] ♂	Length (μm)[b]
Club	*T. yunnanensis*	260.1 ± 13.2a	241.5 ± 15.0a	250.8 ± 14.7a
	T. minor	209.3 ± 4.1a	212.8 ± 5.2a	211.1 ± 4.8c
	T. brevipilosus	233.0 ± 21.8a	220.4 ± 12.5a	226.7 ± 15.2b
Funicle	*T. yunnanensis*	251.2 ± 15.1a	236.7 ± 13.7a	244.0 ± 11.4a
	T. minor	193.3 ± 4.6a	196.3 ± 5.6a	194.8 ± 5.1c
	T. brevipilosus	231.3 ± 18.9a	216.8 ± 5.4a	224.1 ± 16.5b
Scape	*T. yunnanensis*	342.4 ± 28.2a	309.9 ± 11.6a	326.2 ± 12.9a
	T. minor	295.2 ± 11.8a	291.5 ± 10.5a	293.4 ± 10.2b
	T. brevipilosus	287.5 ± 22.9a	288.7 ± 19.6a	288.1 ± 15.2b
Antenna	*T. yunnanensis*	817.8 ± 55.5a	749.3 ± 37.2b	783.6 ± 37.2a
	T. minor	697.7 ± 12.9a	700.3 ± 14.8a	699.0 ± 10.8c
	T. brevipilosus	756.9 ± 31.2a	725.7 ± 34.8a	741.3 ± 35.9b

[a]Data are mean ± S.E. In each row, data in the female and male columns followed by the same letter were not significantly different between the sexes (Mann–Whitney *U* test; $P = 0.05$). $N = 8$ per sex.
[b]Data are mean ± S.E. In the column, data followed by the same letter were not significantly different among the three species by the least significant difference test ($P = 0.05$). $N = 16$ per species.

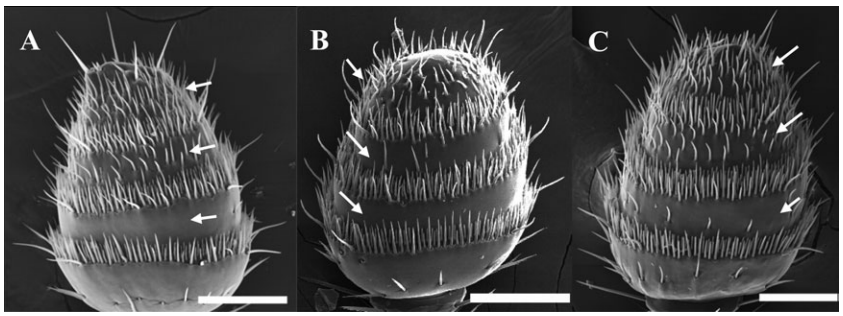

Fig. 2. SEM images of sub-segments 2, 3, and 4 of the club in each species. **A**: *Tomicus yunnanensis*: note the three subsegments (arrows) with the second most sensilla. **B**: *T. minor*: note the three sub-segments (arrows) with the fewest sensilla. The sub-segment 3 (middle arrow) has only sparse sensilla. **C**: *T. brevipilosus*: note the three sub-segments (arrow) with the most sensilla. Bar = 100 μm.

TABLE 2. Comparison of sensilla number on the club in three species of Tomicus[a]

Species	Number of sensilla per club			
	Club	Sub-segment 2	Sub-segment 3	Sub-segment 4
T. yunnanensis	703.2 ± 23.5a	4.8 ± 2.8b	53.4 ± 6.2b	93.6 ± 8.1a
T. minor	615.4 ± 24.8b	3.3 ± 1.7c	17.8 ± 3.4c	57.3 ± 4.3b
T. brevipilosus	671.3 ± 35.9ab	11.5 ± 2.8a	69.3 ± 5.6a	91.2 ± 2.9a

[a]Data are mean ± S.E. In each column, data followed by the same letter were not significantly different by the least significant differences test ($P = 0.05$). $N = 16$ per species.

base (Fig. 3B). The sizes of these sensilla varied from 18.2 to 24 μm in length and 1 to 1.2 μm in width (Table 3). Cross-sections of the sensilla indicated that eight dendrites with tubes surrounded by sheaths hung in a sensillum lymph lumen (Fig. 3B2).

Sensilla Chaetica 1. Straight *S.ch.1* with longitudinal grooves were set in distinct sockets and tapered gradually toward their apices, ending in sharp tips (Figs. 1C, 3C–3C2). An average of 87.3–97.5 *S.ch.1* per antenna were dispersed in the same positions as *S.tr.2*, with the lengths ranging from 25.6 to 32.9 μm and widths ranging from 1.3 to 1.6 μm (Table 3). In transverse sections, the thick nonporous wall surrounded a lumen diameter of 0.1–0.2 μm at the middle of the sensilla (Fig. 3C3). Longitudinal sections through *S.ch.1* indicated the cuticular wall at the base of sensillum was about 2 μm deep (Fig. 3C4). TEM images indicated an absence of dendrites in the lumen.

Sensilla Chaetica 2. Socketed and grooved peg *S. ch.2* with sharp tips were distributed predominately on the proximal end of the club, on the first, third, fourth, fifth, and sixth subsegments of the funicle, and on the dorsal scape (Figs. 1C, 3D, and 3D1). The *S.ch.2* were more or less evenly distributed on the fourth, fifth, and sixth subsegments of the funicle, and sloped towards the base of the club at an angle of 50°–70°. A distinctive character distinguishing these sensilla from the others was 2–7 saw-tooth gibbosities (Figs. 3D, 3D2, and 3D3). Two saw teeth were side-by-side on some sensilla (Fig. 3D3). The antennae averaged 44.3–58.8 bristles that were 42.2–57.2 μm long and 2–2.4 μm wide (Table 3). Considering the oblate cross-section, the widths at mid-length here were the maximum value (Fig. 3D4). These sensilla showed a thick cuticle wall and a lumen diameter of 0.15 μm.

Sensilla Basiconica. Multiporous and nonsocketed *S.b.* were cylindrical for most of their lengths and tapered sharply to points (Figs. 1C and 4A). An average of 339.5–394.5 bristles per antenna were the most dense at the three sensory bands and at the club apex (Table 3). There was no glandular pore at the sensilla base. The cuticular walls were about 0.12 μm thick and penetrated by 110–130 pores/μm^2 (Fig. 4A1). The pore funnels, about 30 nm in length and 10 nm in width, were arranged in parallel rows along the longitudinal axis of the sensilla. The *S.b.* were 10.6–15.5 μm long and 1.2–1.5 μm wide (Table 3). In transverse section, these sensilla were usually innervated by 10–14 dendrites (Fig. 4A2). The distinct pore kettles were arranged radially in the cuticular wall. Longitudinal sections also indicated that the cuticular wall was densely perforated, but only four dendrites appeared in the lumen (Fig. 4A3).

Top-Protuberated Sensilla basiconica. Short *T.p.s.b.*, as a new sensilla type, were distinguished by 7–10 protuberances about 0.1 μm high and by 2–6 pitted pores 15–20 nm in diameter on their uneven tops (Figs. 1C and 4B–4B2). The sensilla, without glandular pores, had a well-defined basal socket 2–2.5 μm in diameter. The smooth-surfaced *T.p.s.b.* tapered gradually from the base to the blunt end. There were 13.8–16.5 bristles per antenna, with few on the three sensory bands and on the club sub-segments 2, 3, and 4 (Table 3). The length was 4.8–5.8 μm and the width was 1.0–1.2 μm (Table 3). In cross-section, the sensillum lymph lumen was encircled by a thin cuticular wall and contained only one dendrite (Fig. 4B3).

Fluted Cones. The *Fl.c* were nonsocketed and double-walled pegs scattered in the three sensory bands and on the club subsegment 4 with lengths similar to *T.p.s.b.* (Figs. 4C and 4C2). The upper part of the sensillum, surrounded by nine finger-like projections, was slightly swollen but tapered gradually to a blunt tip (Fig. 4C1). There were some longitudinal pores

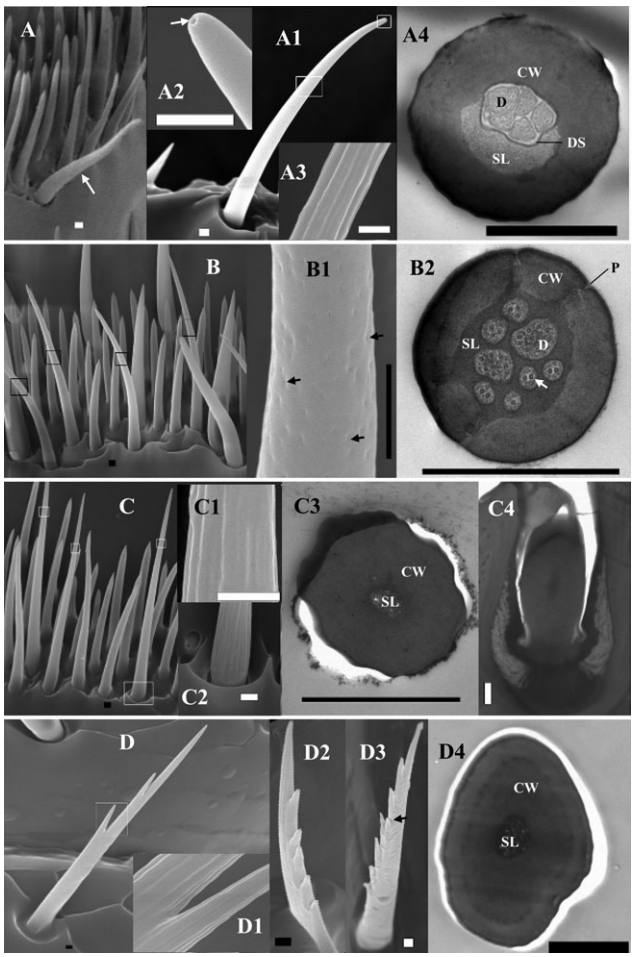

Fig. 3. Morphology and ultrastructure of antennal sensilla in *Tomicus yunnanensis*, *T. brevipilosus*, and *T. minor* (Part 1). **A**: *Sensilla trichodea 1* morphology showing two glandular pores (square, A1) and the socket (arrow) at the base; (A2) an apical pore (arrow); (A3) grooved surface; (A4) transverse section showing the cuticular wall and five dendritic branches enclosed in the sensilla sheath. **B**: *Sensilla trichodea 2* morphology showing the socket(square); (B1) multiporous surface (arrow); (B2) transverse section showing sparse pores on the wall and eight dendritic branches with tubes (arrow). **C**: *Sensilla chaetica 1* morphology (square); (C1) grooved surface; (C2) obvious socket and exocrine gland; (C3) transverse and (C4) longitudinal sections showing thick wall and no dendrites in the lumen. **D:** *Sensilla chaetica 2* morphology showing one saw tooth (square); (D1) grooved surface; (D2) unilateral branch; (D3) two saw-teeth side by side (arrow); (D4) oblate cross-section showing thick wall and no dendrites in the lumen. CW, cuticular wall; D, dendrite; DS, dendrite sheath; P, pore; and SL, sensillum lymph lumen. Scale bar = 1 μm.

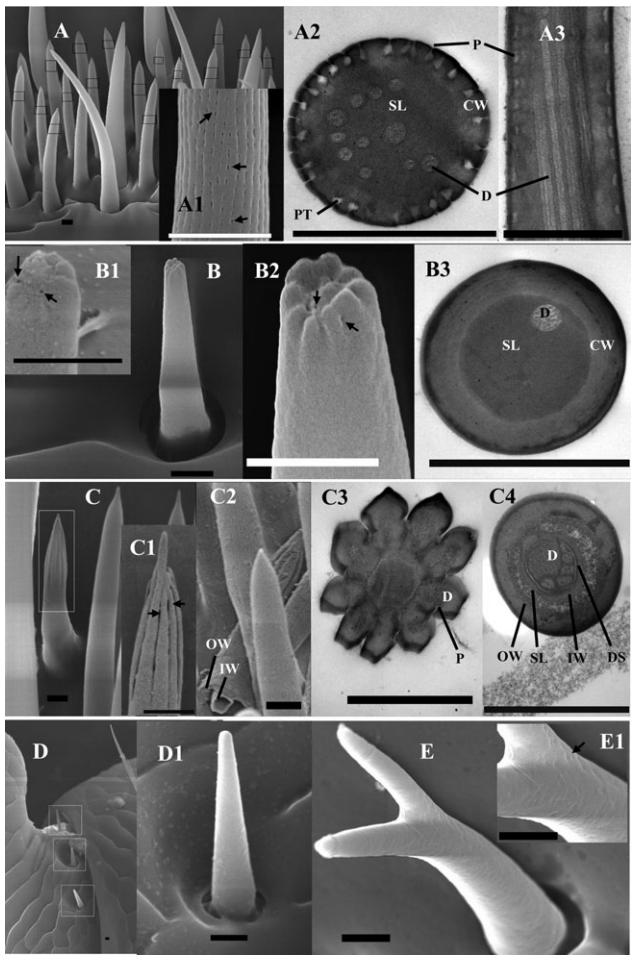

Fig. 4. Morphology and ultrastructure of antennal sensilla in *Tomicus yunnanensis*, *T. brevipilosus*, and *T. minor* (Part 2). **A**: *Sensilla basiconica* morphology (square); (A1) multiporous surface (arrow); (A2) transverse section showing multiporous wall and 10 dendritic branches in the lumen; (A3) longitudinal section showing four dendritic branches. **B**: Top-protuberated *sensilla basiconica* morphology with obvious socket; (B1, B2) multiporous surface (arrow); (B3) transverse section showing a single dendrite in the lumen. **C**: Fluted cones morphology (square); (C1) multiporous finger-like projections (arrow); (C2) outer and inner walls; (C3) transverse section showing finger-like projections with embolic pores; (C4) transverse section showing outer and inner walls, sensilla lumen, and five dendrites surrounded by a sheath. **D**: Böhm bristles morphology; (D1) socket. **E**: *Sensilla furcatea* morphology; (E1) multiporous surface (arrow). CW, cuticular wall; D, dendrite; DS, dendrite sheath; IW, inner wall; OW, outer wall; P, pore; PT, pore kettle; and SL, sensillum lymph lumen. Scale bar = 1 μm.

between the finger-like projections. The lower sensillum surface was smooth. There were 14.5–16.8 bristles of 4.9–6.1 μm length and 1.0–1.1 μm width per antenna (Table 3). No basal glandular pore was seen. In cross-section, sensilla were innervated by five dendrites within a sheath (Fig. 4C4). A sensillum lumen was found between the outer wall and inner wall. The inner lumen of each finger projection was surrounded by a porous wall and contained one dendrite (Fig. 4C3).

Böhm Bristles. A very few *B.b.* were scattered on the proximal end of the first subsegment of the funicle with 3.5–3.8 bristles per antenna (Fig. 4D and 4D1; Table 3). The spine-like and smooth bristles were ranged in length from 5.2 to 6.1 μm and in width from 0.7 to 0.9 μm (Table 3). The sensilla protruded from a visible socket and lacked glandular pores at the base. These structures were not imaged by TEM.

Sensilla Furcatea. Socketed and multiporous *S.f.* possessed two branches from their middle regions. Only three *S.f.* were sparsely distributed on subsegments 2 and 3 of the club of female *T. yunnanensis* (Figs 4E and 4E1). They resembled *S.tr.2* in length, width, and surface structure. No TEM images were taken. This sensilla type was not included in the following comparisons of the antennal size and number.

TABLE 3. Comparison of the size and numbers of eight antennal sensilla types between sexes and within species

Sensilla	Species	Length (μm)			Width (μm)			Number		
		♀[a]	♂[a]	Mean[b]	♀[a]	♂[a]	Mean[b]	♀[a]	♂[a]	Mean[b]
S.tr.1	*T. yunnanensis*	54.2 ± 3.4a	52.5 ± 2.4a	53.8 ± 4.8a	2.0 ± 0.2a	2.0 ± 0.1a	2.0 ± 0.2a	28.0 ± 2.1a	28.5 ± 1.9a	28.3 ± 2.8a
	T. minor	37.2 ± 2.0a	40.7 ± 1.9a	39.0 ± 2.6b	1.7 ± 0.1a	1.7 ± 0.1a	1.7 ± 0.1b	29.0 ± 1.2a	28.5 ± 3.0a	28.8 ± 2.1a
	T. brevipilosus	51.7 ± 6.8a	45.1 ± 2.9a	48.4 ± 5.9a	1.5 ± 0.1a	1.7 ± 0.1a	1.6 ± 0.1b	28.5 ± 1.3a	26.8 ± 1.5a	27.6 ± 1.6a
S.tr.2	*T. yunnanensis*	23.4 ± 0.8a	24.0 ± 2.2a	23.7 ± 2.1a	1.0 ± 0.1a	1.2 ± 0.1a	1.1 ± 0.1ab	152.5 ± 7.3a	138.0 ± 9.6a	145.3 ± 16.6a
	T. minor	22.0 ± 1.5a	20.9 ± 1.4a	21.5 ± 2.8ab	1.2 ± 0.1a	1.2 ± 0.1a	1.2 ± 0.1a	99.3 ± 4.7a	108.5 ± 12.2a	103.9 ± 12.1b
	T. brevipilosus	20.7 ± 2.8a	18.2 ± 2.1a	19.5 ± 2.8b	1.0 ± 0.1a	1.0 ± 0.2a	1.0 ± 0.2b	156.3 ± 7.8a	147.0 ± 6.6a	151.6 ± 15.9a
S.ch.1	*T. yunnanensis*	31.4 ± 3.1a	32.9 ± 1.4a	32.1 ± 3.5a	1.6 ± 0.1a	1.5 ± 0.2a	1.6 ± 0.1a	89.8 ± 9.9a	97.5 ± 3.4a	93.6 ± 8.3a
	T. minor	27.9 ± 1.2a	25.8 ± 1.3a	26.9 ± 1.5b	1.4 ± 0.2a	1.5 ± 0.1a	1.5 ± 0.2ab	92.3 ± 8.5a	96.5 ± 4.4a	93.4 ± 6.9a
	T. brevipilosus	25.6 ± 2.3a	26.7 ± 2.4a	26.1 ± 1.7b	1.3 ± 0.1a	1.3 ± 0.1a	1.3 ± 0.1b	87.3 ± 8.6a	89.5 ± 6.5a	88.4 ± 7.2a
S.ch.2	*T. yunnanensis*	57.2 ± 11.8a	52.4 ± 10.4a	54.8 ± 17.5a	2.2 ± 0.1a	2.0 ± 0.2a	2.1 ± 0.4a	54.5 ± 6.3a	58.8 ± 3.8a	56.7 ± 5.3a
	T. minor	42.2 ± 10.6a	45.2 ± 16.6a	43.7 ± 12.8a	2.3 ± 0.1a	2.2 ± 0.2a	2.3 ± 0.2a	44.3 ± 6.6a	45.3 ± 3.0a	44.8 ± 4.8c
	T. brevipilosus	46.8 ± 10.7a	44.3 ± 11.2a	45.6 ± 12.7a	2.4 ± 0.2a	2.4 ± 0.1a	2.4 ± 0.3a	52.8 ± 6.1a	47.8 ± 2.5a	50.3 ± 4.9b
S.b.	*T. yunnanensis*	14.9 ± 0.6a	15.5 ± 1.4a	15.2 ± 1.0a	1.5 ± 0.2a	1.4 ± 0.1a	1.5 ± 0.1a	394.5 ± 14.9a	385.3 ± 12.3a	389.9 ± 13.6a
	T. minor	11.9 ± 0.6a	10.6 ± 0.5a	11.3 ± 0.8c	1.2 ± 0.1a	1.3 ± 0.1a	1.3 ± 0.1b	363.0 ± 18.1a	339.5 ± 9.4a	351.3 ± 18.3b
	T. brevipilosus	12.1 ± 1.5a	14.1 ± 1.5a	13.0 ± 1.5b	1.3 ± 0.1a	1.3 ± 0.1a	1.3 ± 0.1b	363.8 ± 10.2a	357.5 ± 15.8a	360.6 ± 18.7b
T.p.s.b.	*T. yunnanensis*	4.8 ± 1.1a	5.7 ± 0.9a	5.3 ± 1.0a	1.2 ± 0.1a	1.2 ± 0.1a	1.2 ± 0.1a	16.5 ± 2.5a	15.0 ± 1.2a	15.8 ± 1.9a
	T. minor	5.5 ± 1.0a	5.7 ± 0.8a	5.6 ± 0.7a	1.0 ± 0.1a	1.1 ± 0.2a	1.0 ± 0.2a	15.0 ± 1.2a	13.8 ± 2.1a	14.4 ± 1.7a
	T. brevipilosus	5.0 ± 0.8a	5.8 ± 0.9a	5.4 ± 0.9a	1.1 ± 0.1a	1.1 ± 0.1a	1.1 ± 0.1a	14.5 ± 3.0a	16.3 ± 1.0a	15.4 ± 2.3a
Fl.c.	*T. yunnanensis*	4.9 ± 0.8a	5.1 ± 0.2a	5.0 ± 0.5a	1.0 ± 0.1a	1.0 ± 0.1a	1.0 ± 0.1a	16.3 ± 1.3a	14.8 ± 1.5a	15.5 ± 1.5a
	T. minor	5.5 ± 0.7a	6.1 ± 1.4a	5.8 ± 1.0a	1.0 ± 0.1a	1.1 ± 0.1a	1.1 ± 0.1a	16.8 ± 1.0a	16.5 ± 1.3a	16.6 ± 1.1a
	T. brevipilosus	5.2 ± 0.6a	4.9 ± 0.2a	5.1 ± 0.4a	1.1 ± 0.1a	1.0 ± 0.2a	1.0 ± 0.2a	14.5 ± 1.3a	15.5 ± 1.3a	15.0 ± 1.3a
B.b.	*T. yunnanensis*	6.1 ± 0.5a	5.2 ± 0.6a	5.7 ± 0.7a	0.9 ± 0.1a	0.9 ± 0.1a	0.9 ± 0.1a	3.8 ± 0.5a	3.5 ± 0.6a	3.6 ± 0.5a
	T. minor	6.0 ± 0.8a	5.3 ± 1.0a	5.7 ± 0.8a	0.8 ± 0.1a	0.7 ± 0.1a	0.7 ± 0.1a	3.8 ± 0.5a	3.8 ± 0.5a	3.8 ± 0.5a
	T. brevipilosus	5.2 ± 0.5a	5.9 ± 0.8a	5.6 ± 0.7a	0.8 ± 0.1a	0.7 ± 0.1a	0.8 ± 0.1a	3.5 ± 0.6a	3.3 ± 0.5a	3.4 ± 0.5a

[a]Data are mean ± S.E. In each row, data in the female and male column followed by the same letter were not significantly different between the sexes by the Mann–Whitney *U* test ($P = 0.05$). $N = 8$ per sex.
[b]Data are mean ± S.E. In the column, data followed by the same letter were not significantly different among the three species by the least significant difference test ($P = 0.05$). $N = 16$ per species. *S.tr.1* and *S.tr.2, sensillae trichodea* types 1 and 2, respectively; *S.ch.1* and *S.ch.2, sensillae chaetica* types 1 and 2, respectively; *S.b., sensillae basiconica; T.p.s.b.*, top-protuberated *sensillae basiconica*; Fl.c., *fluted cones*; B.b., *Böhm bristles*.

Percentage of Antennal Sensilla Types

The total numbers of antennal sensilla per antenna of *T. yunnanensis*, *T. minor*, and *T. brevipilosus* were 748.5, 654.5, and 710.9, respectively. In the three species, the greatest percentage of sensilla was *S.b.* (−50.9% per species), followed by *S.tr.2*, *S.ch.1*, *S.ch.2*, *S.tr.1*, *T.p.s.b.*, and *Fl.c.* The percentage of *B.b.* was the smallest (−0.55%).

Comparison of Antennal Sensilla Size and Number Between Sexes

There were no significant differences in the length, width, and number of antennal sensilla types between male and female beetles in any of the three species (Table 3).

Comparison of Antennal Sensilla Size and Number Among the Three Species

Table 3 also compares the mean lengths, widths, and numbers of the eight sensilla types among the three species. The size of *S.tr.1* and *S.b.* in *T. yunnanensis* were significant larger than those in *T. minor*. These beetles varied remarkably in abundance of *S.tr.2*, *S.ch.2*, and *S.b*, which were the most numerous (145.3, 56.7, and 389.9 per antenna, respectively) in *T. yunnanensis* and the least (103.9, 44.8, and 351.3, respectively) in *T. minor*. No statistical differences were detected in the size or number of *T.p.s.b.*, *Fl.c.*, and *B.b.* among the species.

DISCUSSION

Antenna Morphology

In general, the antennae of *T. yunnanensis*, *T. minor*, and *T. brevipilosus* have similar morphology of the scape, funicle, and club. The second subsegment of the funicle shows no sensilla in any of these bark beetles. The sensilla can be distributed on all the three parts of the antenna but their density tends to be significantly higher on the distal segments (Hallberg, 1982; Zacharuk, 1985). In every antenna of these bark beetles, the scape and funicle appear to have less than 45 sensilla, while the club bears more than 615 sensilla belonging to seven different types.

Antennal Sensilla Type

Current reports on the antennal sensilla of bark beetles have focused mostly on the genera *Ips* and *Dendroctonus* (Borden and Wood, 1966; Borden, 1968; Chen et al., 2010; Faucheux, 1989, 1994; Payne et al., 1973; Whitehead, 1981), while less attention has been given to the genus *Tomicus*. Using SEM and TEM of both ventral and dorsal antennal surfaces, we identified eight common antennal sensilla types on females and males of the three *Tomicus* species and described their morphology, distribution, abundance, and internal ultrastructure. All three *Tomicus* species share similar and special antennal sensilla types compared with other genera of the subfamily Scolytinae, but *B.b.* and the new sensilla type *T.p.s.b.* were not recorded in other bark beetles at present. Description of these types could broaden knowledge of the antennal sensory structures of these beetles. Different sensilla types generally have different functions.

The *S.tr.1* described here resembled the *S.ch.* of *Ips paraconfusus* Lanier (Coleoptera: Curculionidae) (Borden, 1968; Borden and Wood, 1966) and the *S.tr.1* of *Dendroctonus valens* LeConte (Coleoptera: Curculionidae) (Chen et al., 2010). The *S.tr.1* functions as contact chemo- and mechanoreceptors (Zacharuk, 1985). The *S.tr.2* have also been identified in *Dendroctonus frontalis* Zimmerman, *D. brevicomis* LeConte (Payne et al., 1973), *D. ponderosae* Hopkins (Payne et al., 1973; Whitehead, 1981), *Ips sexdentatus* Boerner, *I. typographus* L. (Faucheux, 1989), and *I. pini* Say (Faucheux, 1994). The *S.tr.2* show fewer cuticular pores than *S.b.* (Figs. 3B1 and 4A2). Many studies have demonstrated that *S.tr.* respond well to pheromones and poorly to other odorants (Hallberg et al., 1994; Hondo et al., 2006). The nomenclature of antennal sensilla is not entirely consistent because of their structural complexity and the application of different standards. Sensilla without cuticular wall pores but with an apical pore were termed *S.tr.1* by Chen et al. (2010) and *S.tr.3* by Faucheux (1989) and Whitehead (1981). In this article, these sensilla were called *S.tr.1* because they were most similar to those of *D. valens*.

The *S.ch.1* in our study were the same type of sensilla commonly seen in other insects, such as *Microplitis pallidipes* Szepligeti (Gao et al., 2007) and *M. croceipes* Cresson (Hymenoptera: Braconidae) (Ochieng et al., 2000) and *Ips pini* (Faucheux, 1994). The sensilla of the three *Tomicus* species were located mainly along the edges of three sensory bands on the club, but those in *M. pallidipes* and *M. croceipes* occurred on the scape and pedicel. We hypothesize that *S.ch.1* protect *S.b.*, *T.p.s.b.*, *Fl.c.*, and *S.tr.2*, because *S.ch.1* were longer and stronger than those sensilla, and arranged along the edges of the sensory bands. Thus, *S.ch.1* is usually considered to have a thigmotactic function.

Compared with *S.ch.1* and *S.ch.2* have a distinctive shape and location. These branched types fit the description of sensilla suggested to have mechanoreceptor functions in *Typodendron lineatum* Olivier (Coleoptera: Scolytidae) (Moeck, 1968), *I. paraconfusus* (Borden and Wood, 1966), and *Scolytus multistriatus* Marsham (Coleoptera: Curculionidae) (Borg and Norris, 1971). The long *S.ch.2* on the basal regions of the antenna may help the insect to position their antenna with respect to the surroundings through contact mechanoreception with the substrate, or they may perform the role of wind velocity detection (Dyer and Seabrook, 1978).

The bulk of the three sensory bands comprised of *S.b.* (Figs. 1C, 2A–2C, and 4A) similar to those of *I. sexdentatus*, *I. typographus* (Faucheux, 1989), and *D. ponderosae* (Whitehead, 1981). Morphologically, *S.b.* is multiporous chemosensilla with pitted surfaces (MPP; Zacharuk, 1980). The pores were far denser (about 110–130 pores/μm^2) than described by Faucheux (1989) in *I. sexdentatus* and *I. typographus* (36–41 pores/μm^2), although Faucheux did not specify the sexes. The numerous pores and branched dendrites are considered to be evidence that these *S.b.* function as olfactory receptors (Altner and Prillinger, 1980; Zacharuk, 1985) that may be involved in odor recognition and discrimination, and host location. In *D. frontalis*, phasic-tonic responses form neurons associated with these sensilla were elicited by pheromones and by host terpenes (Dickens and Payne, 1978).

We are not aware of any published information on the *T.p.s.b*. type. They had 7–10 apical protuberances with 2–6 pitted pores and were innervated by a single dendrite. On the basis of morphology and ultrastructure, we infer the sensilla may be chemoreceptors.

The *Fl.c*. were previously described in the antennal sensory bands of *D. frontalis* (Dickens and Payne, 1978), *D. ponderosae* (Whitehead, 1981), *D. valens* (Chen et al., 2010), *I. pini* (Faucheux, 1994), *I. sexdentatus*, and *I. typographus* (Faucheux, 1989). These structures are short, double-walled sensilla belonging to the multiporous chemosensilla with deep longitudinal grooves (MPG) (Zacharuk, 1980). MPG has been associated with thermo-chemical receptors (Hallberg, 1982), thermo-hygro receptors (Altner and Prillinger, 1980), or more often with olfactory receptors; in particular, thick-walled MPGs seem to be more selective and are stimulated by pheromones (Zacharuk, 1985). MPG has been found also in *Oncopeltus fasciatus* Dallas (Heteroptera: Lygaeidae), where they are the second most abundant sensilla type on the apical flagellar segment (Harbach and Larsen, 1976). Females and males of these beetles possess small numbers of these sensilla, suggesting that *Fl.c*. have a similar function in both sexes (Faucheux, 1989). By chance, the outer and inner walls were found in the SEM of a broken *Fl.c*. (Fig. 4C2), and TEM (Fig. 4C4) indicated that they were separated by a sensillum lumen. Double walls were not visible in *D. ponderosae* (Whitehead, 1981), *D. valens* (Chen et al., 2010), *I. sexdentatus* or *I. typographus* (Faucheux, 1989).

The *B.b*. were also found in *Callosobruchus maculatus* Fabricius (Coleoptera: Bruchidae) (Hafez et al., 2009), *Cnaphalocrocis medinalis* Guenée (Lepidoptera: Pyralidae) (Sun et al., 2011), *Coleophora obducta* Meyrick (Lepidoptera: Coleophoridae) (Yang et al., 2009), *Leptura arcuata* Panzer and *L. aethiops* Poda (Coleoptera: Cerambycidae) (Zhang et al., 2011), but not in *D. frontalis*, *D. brevicomis* (Payne et al., 1973), *D. ponderosae* (Payne et al., 1973; Whitehead, 1981), *D. valens* (Chen et al., 2010), *I. sexdentatus*, *I. typographus* (Faucheux, 1989), or *I. pini* (Faucheux, 1994). Our TEM revealed these sensilla to be devoid of wall pores, suggesting a nonolfactory role. Cuperus (1983) interpreted *B.b*. as membrane acceptors on segment membranes between the scape and pedicel, and Schneider (1964) speculated that they were gravity receptors.

The *S.f*. have been only reported in *C. obducta* (Yang et al., 2009), which were furcated at the tip and ornamented with veins. However, the sensilla in female *T. yunnanensis* were furcated at the middle and had a multiporous surface. On the basis of morphology (although the TEM images were lacking), they may have the same roles as *S.tr.2*. We assume the sensillum is a morphological variant of *S.tr.2*.

Olfactory receptor cells were studied electrophysiologically in *I. typographus* (Tømmerås, 1985; Tømmerås and Mustaparta, 1987; Tømmerås et al., 1984). Our analyses provide a base to study the functions of antennal sensilla of *T. yunnanensis*, *T. minor*, and *T. brevipilosus*. Further single sensillum recording researches are needed for the more detailed functions of these sensilla.

Insects rely on multiple, distinct organs for olfaction. The organs differ in location and numerical complexity, in the receptors that they express, and in the targets of their neurons within the central nervous system (Su et al., 2009). Some reports have clearly indicated large numbers of chemosensilla on the mouthparts, tarsi, and ovipositors in other insects (Städler, 1984; Whitehead, 1981). Therefore, we should conduct an extensive investigation in the sensilla of the different organs.

Antennal Sensilla in the Sexes

We found no obvious differences between the sexes of *T. yunnanensis*, *T. minor*, and *T. brevipilosus* in the types, numbers, locations, or sizes of the antennal sensilla. In fact, many other insects, such as *Phyllotetra cruciferae* Goeze (Coleoptera: Chrysomelidae), *Psylloides punctulata* Melsh (Coleoptera: Chrysomelidae), *Epitrix cucumeris* Harris (Coleoptera: Chrysomelidae), *Psylloides affinis* Paykull (Ritcey and Mciver, 1990), and *D. valens* (Chen et al., 2010) also showed no apparent sexual dimorphism in the relative number of antennal sensilla. The lack of sexual differences indicates that the sensilla probably have similar functions in both sexes. Our investigations may be linked to two experiments: (1) *T. yunnanensis* beetles captured on *P. yunnanensis* bolts with only males did not differ significantly from those on bolts with only females (Liu et al., 2010); and (2) sex ratio of *T. yunnanensis*, *T. minor*, and *T. brevipilosus* beetles captured in traps with different lures were ~1:1 (Ping-Yan Wang et al., unpublished data). However, field tests of *T. minor* in Sweden indicated that males were caught significantly more frequently than females in traps containing both a log and some monoterpene alcohols (Lanne et al., 1987). Judging from these results, we speculate the responses of these beetles to the active irritants are probably different even though female and male possess the same types and quantities of antennal sensilla.

Both sexes of *T. piniperda* responded similarly to a concentration range of several monoterpenes (including (−)-α-pinene, (+)-α-pinene, terpinolene, and (+)-3-carene) from Scot pines in the olfactometer (Byers et al., 1985). In electroantennography (EAG) test, no response differences between sexes were found when the antennae of *T. piniperda* beetles were exposed to (R)- and (S)-α-pinene, (1S,6R)-3-carene, terpinolene, and myrcene (Lanne et al., 1987). In the open-arena olfactometer, the attraction of female and male *T. piniperda* to a blend of monoterpenes was evidently reduced by (−)-verbenone, which was released by the males (they contain verbenone), infested male–female logs or female-only logs (Byers et al., 1989). These results indicate that antennal sensilla types and the number of each type may be similar between sexes of *T. piniperda*. In *Ips*, males are generally the first to attack the host pine (Byers, 1989). Males of *I. typographus* were more responsive than females to S-(−)-α-pinene, an enantiomer of a pheromone precursor (Dickens, 1978). This could be explained by the greater number of *S.b*. in males (Faucheux, 1989).

At present, we still cannot determine completely the behavioral mechanisms in two sexes of the three *Tomicus* species, although a preliminary study on the morphology and ultrastructure of sensilla were conducted in this study. Further investigations are needed to identify any anatomical or molecular differences in sensilla between males and females.

Difference of Antennal Sensilla in the Species

Differences among these bark beetles were described by Kirkendall et al. (2008), who drew attention to the punctures on the sloping posterior portion of the elytra and to antenna color. In this study, we discover two new distinctions: (1) the lengths of the scape, funicle, and entire antenna differed significantly among the three species; antennae of *T. yunnanensis* were the longest, followed by *T. brevipilosus* and *T. minor*. (2) There are significant differences in the density of sensilla on subsegments 2, 3, and 4 of the club. *T. minor* showed distinctly fewer sensilla on each of the subsegment than the two other species, especially on the subsegments 3 (with 17.8 per antenna) and 4 (57.3) (Fig. 2; Table 2). We could distinguish *T. minor* from *T. yunnanensis* and *T. brevipilosus* by the second trait. We preliminarily deduce that *T. yunnanensis* and *T. brevipilosus* are more closely related and the conclusion was supported by a previous report that the genetic distance between *T. yunnanensis* and *T. brevipilosus* was the closest among the three species (Li et al., 2010). In fact the sensilla on the subsegments 2, 3, and 4 were mainly *S.tr.2*, with a few *S.b*. and *S.ch.1*.

Kohlmayr et al. (2002) suggested separating *T. piniperda*, *T. minor* and *T. destruens* Wollaston by the density of setae occurring on the surface of subsegment 3 of the antennal club, where *T. minor* has only sparse sensilla, *T. piniperda* only a few and *T. destruens* many more. *T. yunnanensis* were similar to *T. piniperda* in the distribution of sensilla on the subsegment 3 while *T. brevipilosus* were similar to *T. destruens*. A new morphological difference in *T. piniperda* and *T. destruens* was found by Faccoli (2006). In 83.5% of *T. piniperda* the No. 1 sensory band had two different types of sensilla, one short and one long, placed in a single row, whereas 86% of *T. destruens* had only short sensilla. Although the sensilla morphology of the two species were not studied currently, the long sensilla may be *S.ch.1* and the short may be *S.b*. on the basis of our observations.

Lanne et al. (1987) showed that trans-verbenol was attractive to *T. minor* but hardly or not at all to *T. piniperda* in EAG test, so, there may be some differences on the type, number or chemical sensory mechanism of antennal sensilla between both species. *T. yunnanensis*, *T. minor*, and *T. brevipilosus* with the same sensilla types may have similar responses to semiochemicals, but the differences of *S.tr.1*, *S.tr.2*, *S.ch*.2, and *S.b*. among species are likely to result in different behaviors. These analyses can be related to the following laboratory and field tests. EAG analyses of head-space volatiles from fresh *P. yunnanensis* bolts revealed that 1S-(−)-β-pinene, 1R-(+)-α-pinene and S-(−)-α-pinene consistently elicited antennal responses in *T. yunnanensis*, *T. minor* and *T. brevipilosus*. Whereas, the response of *T. minor* to S-(−)-α-pinene was distinctly stronger than those of the other two species (Ping-Yan Wang et al., unpublished data). The field trapping trial in June 2010 showed that the proportion of each species captured in traps baited with same lures was conspicuously different (Ping-Ding Han et al., unpublished data).

These bark beetles together colonize *P. yunnanensis* but have different ecological niches. *T. yunnanensis* and *T. brevipilosus* mainly attack the mid-upper trunk, while *T. minor* mainly attacks the lower trunk. We assume that *S.tr.1*, *S.tr.2*, *S.ch.2*, and *S.b*. have important effects on positional localization and mate selection. Additional research is needed to explore the semiochemical responses of olfactory receptors.

Exocrine Glands

There were distinct exocrine glands at the bases of *S.tr.1*, *S.tr.2*, *S.ch.1*, and *S.ch.2*. The morphology, location and size of these glands are directly related to their function. Data have been published on *Psylliodes chrysocephala* L. (Coleoptera: Chrysomelidae) (Bartlet et al., 1994), *Platynus dorsalis* Pontoppidan (Coleoptera, Carabidae) (Weis et al., 1999) and *D. valens* (Chen et al., 2010) antennal glands; the functional role is assumed to be involved the enzymatic degradation of pheromone molecules (Prestwich, 1987; Taylor et al., 1981; Vogt and Riddiford, 1981) or plant-host volatiles (Dickens et al., 1992) to prevent them from overloading antennal chemosensilla. Further research is needed to clarify the functions of the antennal cuticular glands in the three species.

In conclusion, this study described the differences in antennal morphology among three species of *Tomicus*, identified eight common sensilla types, and compared the lengths, widths and numbers of each type intersexually and interspecifically. The SEM and TEM images provide indirect and direct evidence on the functional morphology of the sensilla. Variation in sensilla in the three species may lead to a better understanding of the different behavior mechanisms of these forest pests.

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