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A closer look at the antennae of the invasive *Halyomorpha halys*: fine structure of the sensilla

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Abstract

The brown marmorated stink bug, *Halyomorpha halys*, is an invasive agricultural and urban pest capable of feeding on over 100 species of host plants. The antennae of this bug play an important role not only in detecting food and mates but also in short-range location of conspecifics when aggregating for diapause. The morphology and distribution of antennal sensilla of *H. halys* were investigated at an ultrastructural level using scanning and transmission electron microscopy approaches. Adults have 5-segmented antennae, made up of a scape, a 2-segmented pedicel and two flagellomeres, while 5th instar nymphs have shorter, 4-segmented antennae, with only one pedicel segment. Five types of sensilla are distinguished, based on their shape, length and basal width and the presence of basal socket and pores: sensilla basiconica (types A, B, C, D and E), sensilla coeloconica, sensilla trichoidea and sensilla chaetica (types A and B). Sexual dimorphism was not observed in this species, with respect to the morphological features and abundance of sensilla. The most abundant sensory structures are sensilla trichoidea showing characteristics typical of olfactory sensilla, whereas the least abundant are sensilla coeloconica which may be involved in thermo- and hygro-reception. Basiconic sensilla type A are solely identified on the antennae of 5th instar nymphs, where they presumably have a dual mechanosensory-gustatory role. The putative function of the remaining sensilla are herein discussed.

Key words: Pentatomidae, phytophagous, ultrastructure, sensory receptor, sexual dimorphism.

Introduction

Antennae of insects are indispensable sensory organs that bear a wide range of sensilla, serving an array of sensory modalities, such as olfaction, gustation, mechanoreception and thermo- and hygro-reception (Altner and Prillinger, 1980; Zacharuk, 1985). The role of sensilla can be presumed based on their morphology, number and distribution. For instance, multiporous sensilla are usually associated with olfactory function, whereas mechano- thermo- and hygro-receptors are often attributed to aporous sensilla (Keil, 1999).

Numerous investigations handled the structure and function of sensilla in pentatomid bugs (Brézot *et al*., 1997; Sinitsina and Krutov, 1996; Rani and Madhavendra, 1995; 2005; Silva *et al*., 2010; Zhang *et al*., 2014a; Ahmad *et al*., 2016; Barsagade and Gathalkar, 2016). Among the studied species, similar sets of sensilla have been recorded, including sensilla basiconica, trichoidea, coeloconica and chaetica. Pentatomids heavily rely on olfaction in their intra- and interspecific communication, through pheromones (aggregation, sexual and alarm) and kairomones (plant volatiles) respectively. Porous basiconic sensilla described in these studies were the major receptors involved in volatile perception.

The brown marmorated stink bug, *Halyomorpha halys* (Stal) (Hemiptera Pentatomidae), is an invasive agricultural and domestic pest, native to eastern Asia, that was accidently and repeatedly introduced into North America and Europe (Hoebeke and Carter, 2003; Haye *et al*., 2015; Cesari *et al*., 2018). Currently, *H. halys* has been detected in almost all the states of USA and Canada, as well as 15 European countries (EPPO, 2018; Fogain and Graff, 2011). This highly polyphagous pest, capable of feeding on over 100 species of host plants, thrives on many economically important crops, some of which are apples and pears. Over $21 billion worth of crops in USA have been estimated to be threatened by *H. halys* feeding damage (ODA, 2013). In Italy, *H. halys* was first recorded in the province of Modena in 2012 and has ever since expanded its range to most of the Italian regions (Maistrello *et al*., 2018; Malek *et al*., 2018). Due to its overwintering behaviour, *H. halys* is also considered an urban nuisance pest as it often aggregates in anthropogenic structures during late fall (Lee, 2015).

A previous study focused on the role of *H. halys* antennae in short-range location of conspecifics and aggregation (Toyama *et al*., 2006), and later electrophysiological studies demonstrated the presence of olfactory receptors on its antennae capable of detecting various essential oils (Zhang *et al*., 2014b). Paula *et al*. (2016) recently identified 30 odorant binding proteins involved in the chemosensory perception in the antennae of *H. halys*. Therefore, given their significance in host and mate location mechanisms, it became essential to closely investigate the antennae of this invasive pest, to provide insight into possible behavioural manipulation techniques. The latter can be applied by amending already existing pheromone traps with host plant volatiles aimed at mass trapping, and/or vibrational signals for mating disruption of *H. halys* to mitigate its spread and damage (Mazzoni *et al*., 2017).

The aim of the present study was to describe the morphology, location, abundance and distribution of the sensilla present on the antennae of *H. halys* adults (females and males) and fifth instars nymphs by means of Scanning Electron Microscopy (SEM). Transmission Electron Microscope (TEM) techniques were employed to confirm the classification of the sensilla types based on SEM, while highlighting their possible functions. This work is a prerequisite for our ongoing research on host location mechanisms and other electro-physiological studies of the antennal sensory system involved in the chemical communication of *H. halys*.

Materials and methods

Insect rearing

Wild *H. halys* were collected periodically from July through September 2016 from the field in the cities of Modena and Reggio Emilia (Italy). The bugs were kept on a diet of organic peanuts, fresh organic green beans, carrots, and tomatoes under controlled conditions (24 ± 2 °C; 70 ± 5% RH; 16:8 L:D). Fifth instar nymphs and adults were used in this study.

Length of antennal segments

To measure the length of each antennal segment, five replicates of male, female and fifth instar's antennae were used. Each antenna was mounted on a slide with Faure's mounting medium, and the length of each segment was measured using a stereo microscope (MZ 12.5, Leica) equipped with an ocular micrometer (Leitz).

Scanning Electron Microscopy (SEM)

Six *H. halys* adults (three males and three females) and five 5th instar nymph individuals were used. The insects were anesthetized by freezing and their antennae were excised from the head capsule using fine forceps and placed in a lens cleaner liquid for 24 h. Dehydration in a graded series of ethanol (from 70% up to 99%) followed, prior to overnight drying at 30 °C. After drying, the specimens were mounted on aluminum stubs with double-sided sticky tape, positioned on dorsal or ventral side to obtain a total sensillar count for each replicate. The specimens were then sputter-coated with gold (Emitech k550, Quorum Technologies Ltd., UK) prior to their examination with Scanning Electron Microscope (Nova NanoSEM™ 450, FEI, USA).

Sensilla mapping

To determine the number of sensilla and their spatial distribution, antennae were oriented on the stubs in a way to display either their dorsal or ventral sides. The observation and classification of sensilla present on the antennae was carried out by analysing the details of high-resolution images taken by SEM. SEM pictures of three portions (proximal, medial and distal) of each antennal segment were taken with a resolution of 6144 × 4096 dpi and at a magnification of 730X. Because SEMs offer a view of only one side of the antenna, we only examined sensilla on the dorsal surface (abundant in sensilla) of each antennomere. In order to avoid counting any sensillum more than once, different types of sensilla were marked with color-coded dots using the Microsoft Paint Software (Redmond, Washington). Afterwards, the sensilla were counted manually.

Transmission Electron Microscopy (TEM)

For TEM observations, four males and four females were paralyzed by exposure to cold temperatures (−18 °C) for 60 seconds, then immediately immersed into a solution of glutaraldehyde and paraformaldehyde 2.5% in 0.1 M cacodylate buffer +5% sucrose, pH 7.2-7.3. Each antenna was detached from its base, single antennomeres were isolated and reduced in size by cutting them into two parts to facilitate fixative penetration and left at 4 °C for 2 hours. The specimens were kept at 4 °C overnight in the same buffer, then they were post-fixed in 1% OsO_4 (osmium tetroxide) for 1 hours at 4 °C and rinsed in the same buffer. Dehydration, in a graded ethanol series from 60% to 99%, was followed by embedding in Epon-Araldite with propylene oxide as bridging solvent. Thin sections were taken with a diamond knife on a LKB "Nova" ultramicrotome and mounted on formvar coated 50 mesh grids. Then, sections on grids were stained with uranyl acetate (20 minutes, room temperature) and lead citrate (5 minutes, room temperature). Finally, the sections were investigated with a Philips® EM 208. Digital pictures (1376 × 1032 pixels, 8b, uncompressed greyscale TIFF files) were obtained using a high-resolution digital camera MegaViewIII (SIS®) connected to the TEM.

Statistical analysis

To explore the differences between the length of each antennal segment and to compare the numbers of sensilla among them and among males, females and 5th instar nymphs, the statistical analyses were performed using parametric ANOVA test with Tukey HSD post-hoc test. This test was used since data showed a normal distribution evaluated with the Levene test. All statistical analyses were carried out using the IBM SPSS Statistics Software (25 version).

Results

General description of *H. halys* antennae

The filiform antennae of *H. halys* are located frontally on the head capsule, anterior to the eyes. In adults (both males and females), the antenna is composed of five distinct segments: a short basal scape, a two-segmented pedicel and two segments of the flagellum (flagellomeres Fl1 and Fl2) (figure 1A, C). It has a dark brownish colour with characteristic light-coloured bands on the base and apex of the Fl1 segment and the base of the Fl2 segment (figure 1C). The antennae are not sexually dimorphic in length (table 1), even though the body size of females is generally bigger than that of males (Nielsen *et al*., 2008).

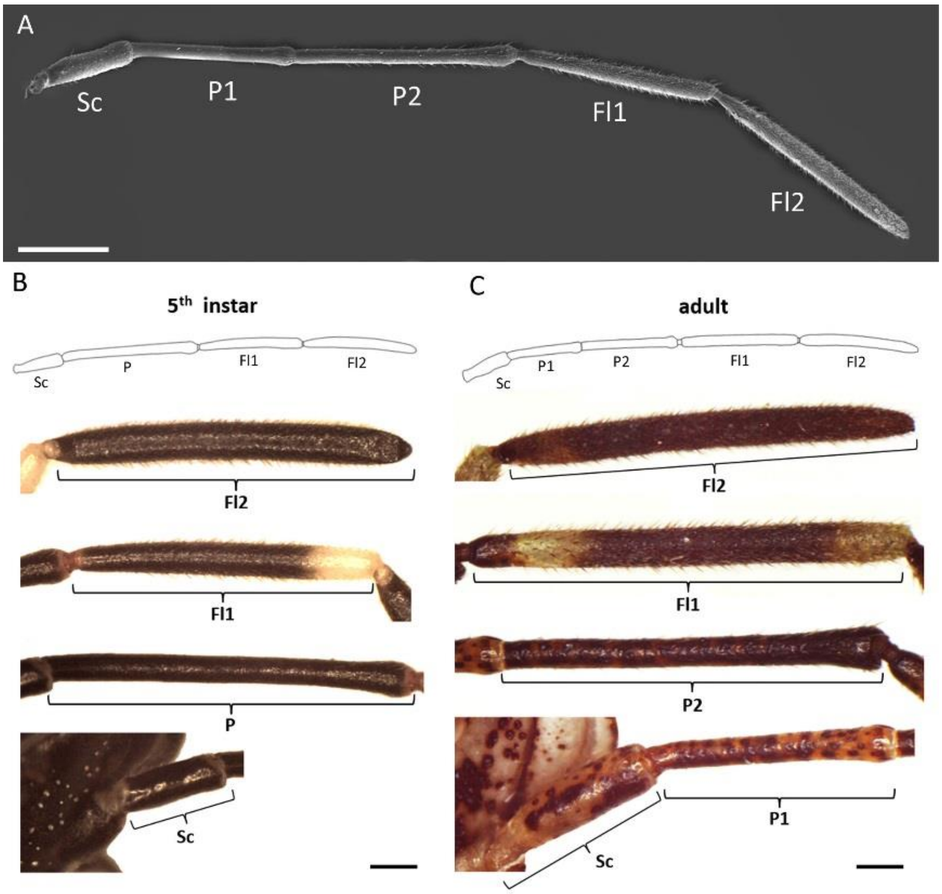

Figure 1. *H. halys* antennae. (**A**) adult female (SEM). (**B**) 5th instar nymph. (**C**) adult female. Sc, scape. P, pedicel of nymph. P1 and P2, pedicels of adult. Fl1 and Fl2, flagella. Scale bars = 1 mm.

Table 1. Mean length ± SE (in mm) of antennal segments of *H. halys* females, males and 5th instar nymphs (n = 5) (Sc: scape; P1: first pedicel segment; P2: second pedicel segment; Fl1: first flagellomere, Fl2: second flagellomere). Means with different letters in the same column are significantly different.

Developmental stage	Sc	P1	P2	Fl1	Fl2	Whole antenna
Adult female	0.92 ± 0.03	1.58 ± 0.07	2.10 ± 0.08	2.52 ± 0.10	2.35 ± 0.16	9.47 ± 0.31a
Adult male	0.95 ± 0.07	1.60 ± 0.11	2.15 ± 0.16	2.53 ± 0.12	2.47 ± 0.15	9.69 ± 0.42a
5th instar	0.90 ± 0.04	3.00 ± 0.15	-	2.25 ± 0.11	2.30 ± 0.06	8.44 ± 0.25b

The antenna of the 5th instar nymph consists of four segments, with only one pedicel segment, and thus is evidently shorter than the antennae of adults (figure 1B, table 1). The scape and flagellomere 1 of 5th instar nymphs are shorter with respect to those of the adult females ($p < 0.001$ and $p = 0.006$, respectively) and males ($p = 0.001$ and $p = 0.005$, respectively). In both males and females, the length of each segment of the antennae increases gradually from the scape to the first flagellomere (table 1).

The total number of sensilla do not differ significantly between male and female antennae, while 5th instar nymphs have a lower number with respect to females ($p = 0.020$) and males ($p = 0.031$), in relation to the lower number of sensilla in Fl1 ($p = 0.004$ and $p = 0.005$, respectively). The scape and pedicel are sparsely populated while the flagellar segments showed a higher density of sensilla.

In both adults and 5th instar nymphs, the surface of the scape, pedicels and proximal part of the flagellomere Fl1 is characterized by a rhomboid pattern (figure 2A), while the surface of the distal part of the flagellomere Fl1 and the flagellomere Fl2 is smooth. Small rounded pores (≈ 0.5 µm in diameter) are scattered on the rhomboid surface of the antennomers (figure 2B-C). In addition, short filaments (1-2 µm in length, ≈ 0.5 µm in diameter) protrude from some scattered small pores (≈ 0.5 µm in diameter) present in the scapes, pedicels, and flagellomeres Fl1 of adults and 5th instar nymphs (figure 2E). In addition to these short filaments, longer and flexible filaments (10-25 µm) are also observed in nymphs; with highest numbers on the pedicel (200-400) (figure 2D, F), while they are less abundant on the scape (40-100) and flagellomere Fl1 (10-30). However, no filaments are recorded on flagellomere Fl2. The structure and function of the pores and filaments are still unknown.

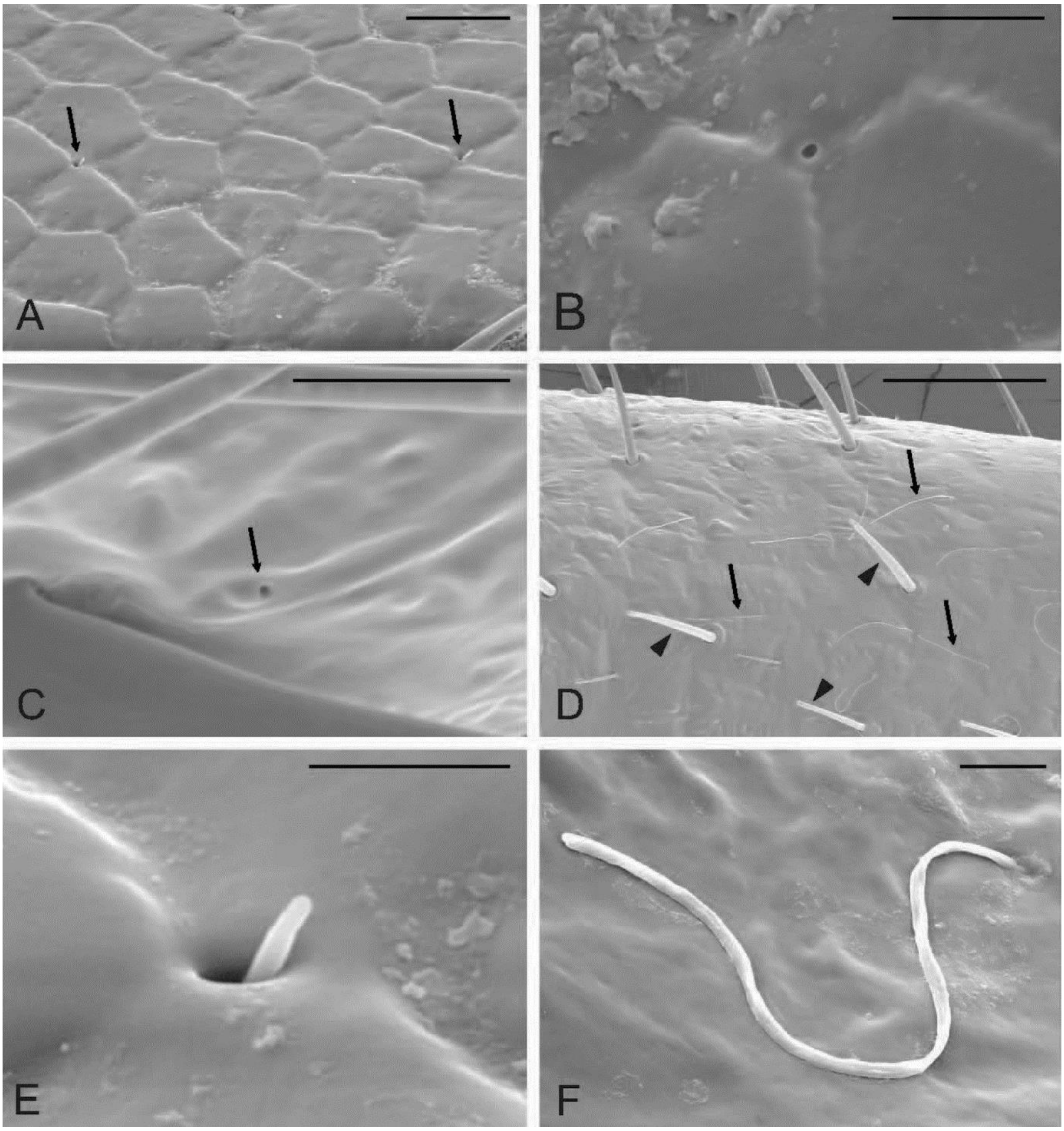

Figure 2. *H. halys* antennae. (**A**) rhomboid patterns on the surface of the scape of a female with short filament protruding from pores (arrows). (**B**) a pore on the surface of the scape of a female. (**C**) a pore (arrow) on the surface of the flagellum 1 (Fl1) of a female. (**D**) filaments (arrows) protruding from pores among sensilla SB-A (arrowheads) on the Fl1 of a 5th instar nymph. (**E**) short filament protruding from a pore of the scape of a female (enlargement of **A**). (**F**) long flexible filament present on the pedicel of 5th instar nymph. A-F (SEM). Scale bars: A = 10 μm; B, C = 5 μm; D = 50 μm; E, F = 2 μm.

Sensilla types

The identification of sensilla and the terminology used in the present study were based on the classifications made on different species of Hemiptera (Brézot *et al.*, 1997; Romani and Rossi Stacconi, 2009; Silva *et al.*, 2010; Gonzaga-Segura *et al.*, 2013; Missbach *et al.*, 2014; Olson *et al.*, 2014; Zhang *et al.*, 2014a; Kim *et al.*, 2016).

Based on their shape, size, presence or absence of pores, grooved or smooth surface, and presence or absence of socket at the base of the sensilla, four main types of sensilla (subdivided in morphologically different types) were recorded on the antennae of *H. halys* adults and 5th instar nymphs. These include sensilla basiconica (SB) with five types (A, B, C, D and E), sensilla chaetica (SCh) with two types (A and B) and one type of sensilla coeloconica (SCo) and of sensilla trichoidea (ST). The distribution of the different sensilla types on each antennal segment is shown in table 2 (and supplemental material table S1).

Table 2. Abundance and distribution of different sensilla on the antennae of *H. halys* males, females and 5th instar nymphs (n = 3).

Sensilla	Developmental stage	Antennal segments				
		Sc	P1	P2	Fl1	Fl2
SB-A	Adult female	0	0	0	0	0
	Adult male	0	0	0	0	0
	5th instar	3.7 (2.3)	36.3 (8.3)	-	17.3 (7.6)	0
SB-B	Adult female	29.7 (19.9)	45.3 (5.0)	33.0 (6.1)	10.0 (9.5)	0
	Adult male	16.7 (4.7)	41.3 (11.8)	34.3 (14.3)	5.3 (7.6)	0
	5th instar	22.7 (13.7)	63.7 (16.3)	-	3.3 (2.9)	0
SB-C	Adult female	0	0	0	71.0 (6.2)	113.3 (9.9)
	Adult male	0	0	0	60.3 (11.0)	112.7 (23.5)
	5th instar	0	0.3 (0.6)	-	41.0 (9.2)	85.0 (20.4)
SB-D	Adult female	0	0	1.0 (1.0)	13.3 (6.8)	46.7 (21.2)
	Adult male	0	0	0	10.7 (11.7)	48.0 (30.6)
	5th instar	0.3 (0.6)	1.0 (1.0)	-	14.0 (8.5)	45.3 (10.7)
SB-E	Adult female	0	0	5.0 (5.0)	212.0 (30.6)	295.3 (37.0)
	Adult male	0	0.3 (0.6)	2.3 (4.0)	218.3 (27.8)	275.7 (29.1)
	5th instar	0	0.3 (0.6)	-	92.3 (13.6)	200.7 (9.5)
SCo	Adult female	2.0 (1.7)	4.3 (3.5)	7.7 (4.9)	3.3 (3.1)	1.3 (1.5)
	Adult male	4.3 (3.2)	4.0 (4.4)	9.0 (5.2)	0.7 (1.2)	0
	5th instar	1.3 (1.5)	2.0 (2.0)	-	7.3 (6.7)	3.7 (2.1)
ST	Adult female	0	0	0	542.0 (29.5)	793.7 (85.9)
	Adult male	0	0	0	528.0 (81.0)	754.0 (136.6)
	5th instar	0	0.3 (0.6)	-	290.7 (44.3)	538.0 (87.0)
SCh-A	Adult female	12.3 (8.4)	5.0 (4.4)	42.9 (16.5)	140.3 (35.9)	112.7 (44.2)
	Adult male	13.0 (2.0)	6.0 (3.6)	38.7 (11.0)	151.0 (12.5)	146.0 (42.2)
	5th instar	2.0 (2.0)	3.3 (4.2)	-	107.3 (13.7)	144.7 (18.0)
SCh-B	Adult female	4.0 (3.5)	5.3 (1.5)	15.0 (2.6)	7.6 (6.4)	31.0 (19.7)
	Adult male	4.3 (2.1)	8.3 (0.6)	18.3 (4.9)	12.0 (14.9)	2.3 (4.0)
	5th instar	1.7 (1.5)	17.0 (7.2)	-	7.3 (7.5)	12.7 (14.2)

Values represent mean numbers and their respective standard deviations (in parentheses) of different types of sensilla on each antennomere. SB-A: sensilla basiconica type A; SB-B: sensilla basiconica type B; SB-C: sensilla basiconica type C; SB-D: sensilla basiconica type D; SB-E: sensilla basiconica type E; SCo: sensilla coeloconica; ST: sensilla trichoidea; SCh-A: sensilla chaetica type A; SCh-B: sensilla chaetica type B; Sc: scape; P1: first pedicel segment; P2: second pedicel segment; Fl1: first flagellomere, Fl2: second flagellomere.

Sensilla basiconica type A (SB-A)

SB-A arise from a flexible socket and are characterized by a long straight shaft, with a bulb-like structure at the tip (figure 3A-B). Their length ranges from 7 to 35 µm (1.2-3.4 µm in basal diameter). When observed under high magnification, longitudinal grooves run along its cuticular surface and converge toward an apical area where numerous pores are likely to be located (figure 3B). Cross-sections at the base of the sensillum show four dendrites (figure 3C) that extend in the hair lumen. These sensilla have a grooved, single non-perforated thick wall (0.5-0.8 µm) and are inserted in the antennal wall through a socket, where a fifth sensory neuron becomes evident, ending in a tubular body (figure 3D). SB-A are exclusive to 5th instar nymphs and are present abundantly on the pedicel and absent in the Fl2 (table 2, table S1).

Sensilla basiconica type B (SB-B)

SB-B are 13-30 µm long (1.4-3.5 µm in basal diameter) with a straight shaft and a rounded tip and are inserted in a flexible socket (figure 3E-F). They are characterized by a smooth surface with only few longitudinal grooves on the apical part (figure 3E-F). Apart from the second flagellomere, these sensilla are present on all the segments of the antennae in both adults and 5th instar nymphs, and their highest concentration is on the pedicel and lowest on Fl1 (table 2, table S1).

Sensilla basiconica type C (SB-C)

SB-C are short (9-12 µm in length; 1.7-2.1 µm in basal diameter) and straight sensilla ending with a blunt tip terminating with a moulting pore (figure 4A-B). Such pores were reported by Berg and Schmidt (1997) in their comparative studies on the basiconic sensilla of *Lepisma saccharina* L. and *Machilis* sp., whereby scars are left on the cuticular apparatus of the sensillum during the moulting process. These sensilla are the second most numerous sensilla basiconica after SB-E (table 2, table S1), and they are shorter and thicker than SB-B. Evident longitudinal grooves are present on the central and distal parts of the sensilla, while the proximal part is smooth (figure 4A, C). Many fine pores penetrate the bottom of the grooves. The pores expand to form tubules, and the latter open inwards to the lumen of the sensillum. Cross-sections of SB-C show a double cuticular wall (outer

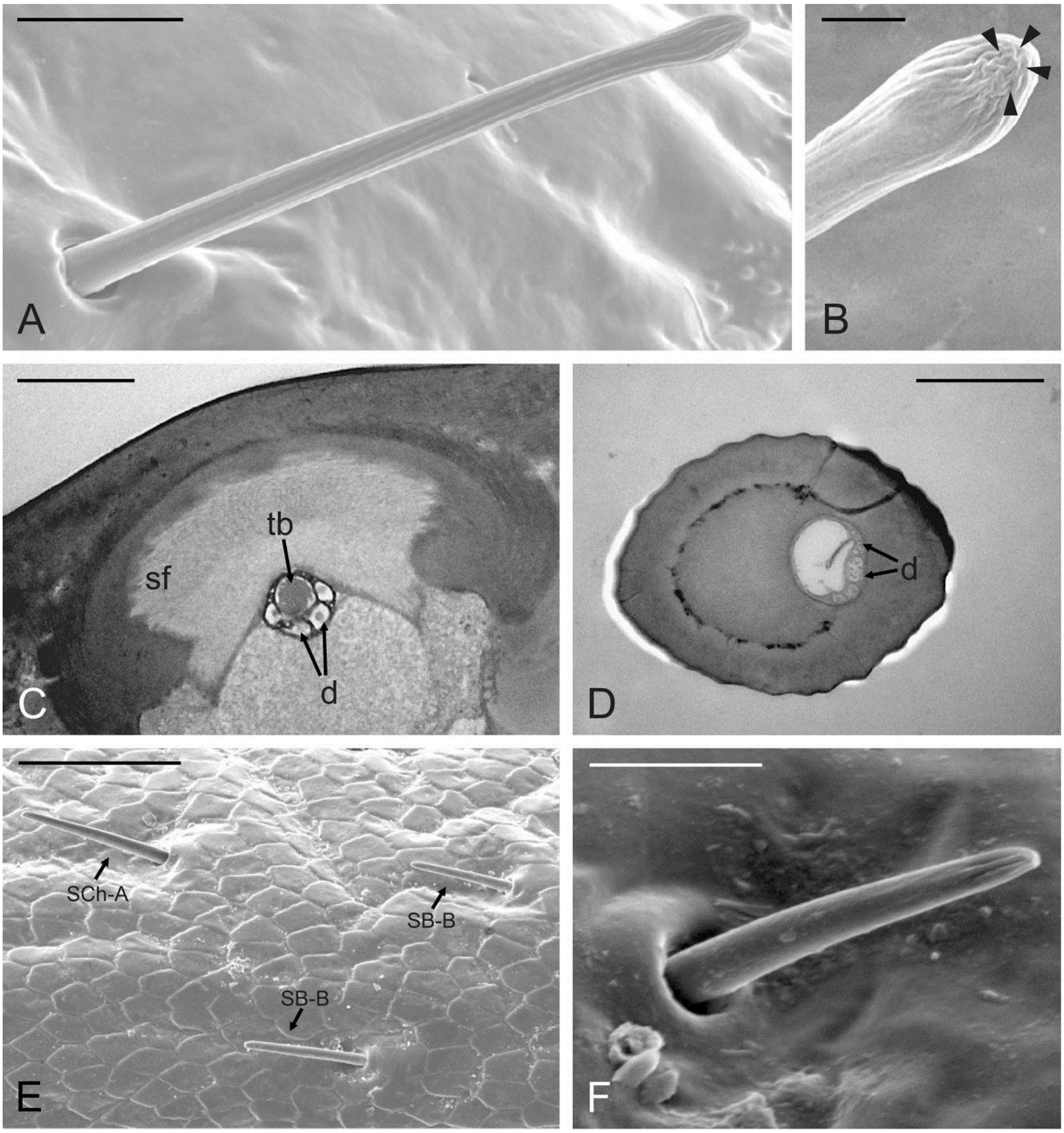

Figure 3. *H. halys* sensilla basiconica types A and B. (**A-D**) basiconic sensilla type A (SB-A). (**A**) sensillum, with a club shaped tip, on the pedicel of a 5th instar nymph. (**B**) close-up view of a SB-A showing longitudinal grooves along the shaft, depressions and numerous pores at the tip (black arrowheads). (**C**) cross section at the basal level part of SB-A, with the suspension fibers (sf), dendrites (d) and a tubular body (tb). (**D**) cross section of SB-A cuticular shaft showing four dendrites (d). (**E-F**) basiconic sensilla type B (SB-B). (**E**) two sensilla on the pedicel of a male (**F**) sensillum with longitudinal grooves on its apical part inserted in a well-defined socket. SCh-A, sensillum chaeticum. A, B, E, F (SEM); C, D (TEM). Scale bars: A= 10 μm; B, C = 2 μm; D = 1 μm; E = 40 μm, F = 5 μm.

and inner) in this region, with three dendrites housed in a narrow lumen (figure 4C-D). SB-C are inserted in inflexible socket and are only present on the flagellomeres (predominantly on Fl2) of adults and 5th instar nymphs.

Sensilla basiconica type D (SB-D)

SB-D are 15-20 µm long, with a constant diameter of 1.5-2.0 µm, except for the distal part that tapers to terminate in a pore (figure 4E-F). The base of the sensillum is smooth and bent towards the tip of the antennae, and the rest of the cuticular shaft is ribbed with longitudinal grooves. These sensilla are set into a tight inflexible socket, most of them are standing almost parallel to the antennal surface and they sometimes occur in groups of 4-7 (figure 4G). SB-D are found exclusively on the flagellomeres of adults and 5th instar nymphs; predominantly on the Fl2 (table 2, table S1).

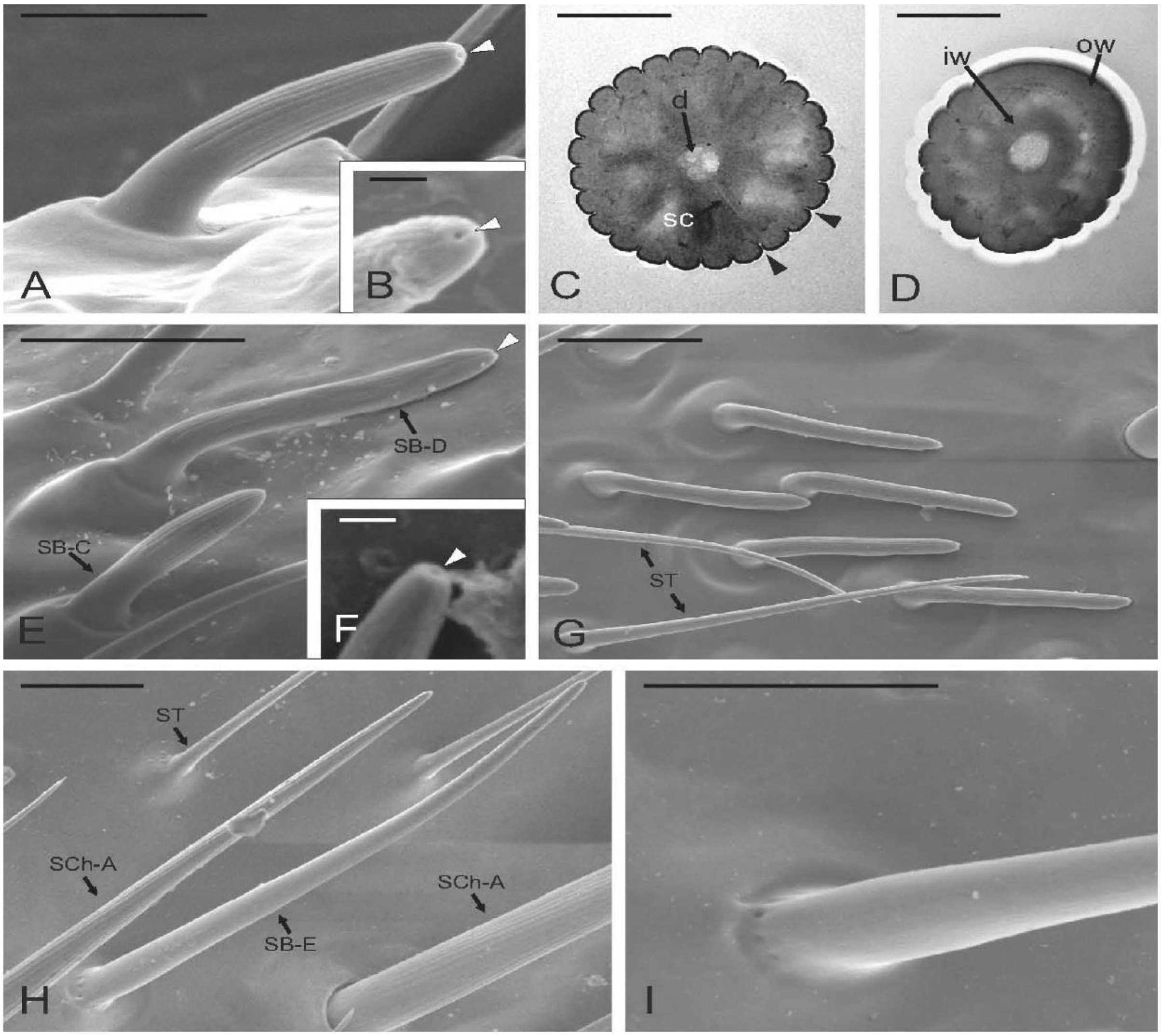

Figure 4. *H. halys* sensilla basiconica types C, D and E. (**A-D**) double-walled sensillum basiconica type C (SB-C). (**A**) sensillum with longitudinal grooves and an apical moulting pore at the tip (white arrowhead). (**B**) tip of the sensillum with an apical moulting pore (white arrowhead). (**C-D**) cross sections of the same sensillum SB-C taken at two different levels. (**C**) middle region of the shaft, with dendrites (d) located within the small lumen, and a few spoke channels (sc) connecting the external pores (black arrowheads) with the internal lumen. (**D**) more basal section, showing the typical double-walled organization with the outer wall (ow) and the inner wall (iw). At this level, part of the outer wall becomes smooth since longitudinal grooves are lacking at the basal region. (**E-G**) sensilla basiconica type D (SB-D). (**E**) single elongated sensillum with a pore at the tip (white arrowhead). (**F**) tip of the sensillum with a pore (white arrowhead). (**G**) cluster of five SB-D located on the flagellum 2 (Fl2) of a female. (**H-I**) sensilla basiconica type E (SB-E). (**H**) sensillum with smooth surface (**I**) base of the sensillum with pores. ST, sensilla trichoidea. SCh-A, sensilla chaetica type A. A-B, E-I (SEM); C, D (TEM). Scale bars: A = 5 μm; B-D, F = 1 μm; E, G-I = 10 μm.

Sensilla basiconica type E (SB-E)

SB-E are straight sensilla but curved near the apical region and composed of a shaft that tapers slightly from the base to a rounded tip (figure 4H-I). Their surface appears to be smooth, lacking pores and longitudinal grooves. They are 30-40 µm in length (3.3-4.5 in basal diameter) and are inserted into inflexible sockets. The base of the sensilla is surrounded by 7-10 pores; the latter might either be the openings of exocrine antennal glands or moulting pores (figure 4I). SB-E outnumber the other types of sensilla basiconica present on the antennae. None of them are recorded on the scape, very few on the pedicels, while the majority are present on the flagellomeres of adults and 5th instar nymphs (table 2, table S1). The 5th instar nymphs have a lower number of SB-E in the Fl1 with respect to females (p = 0.003) and males (p = 0.002).

Sensilla coeloconica (SCo)

SCo consist of short straight pegs with blunt tip protruding from a pit, however not projecting out of it (figure 5A). They are inserted in a cuticular aperture having a diameter of 1.5-2.5 µm. SCo are the shortest and least abundant sensilla type recorded on the antennae of

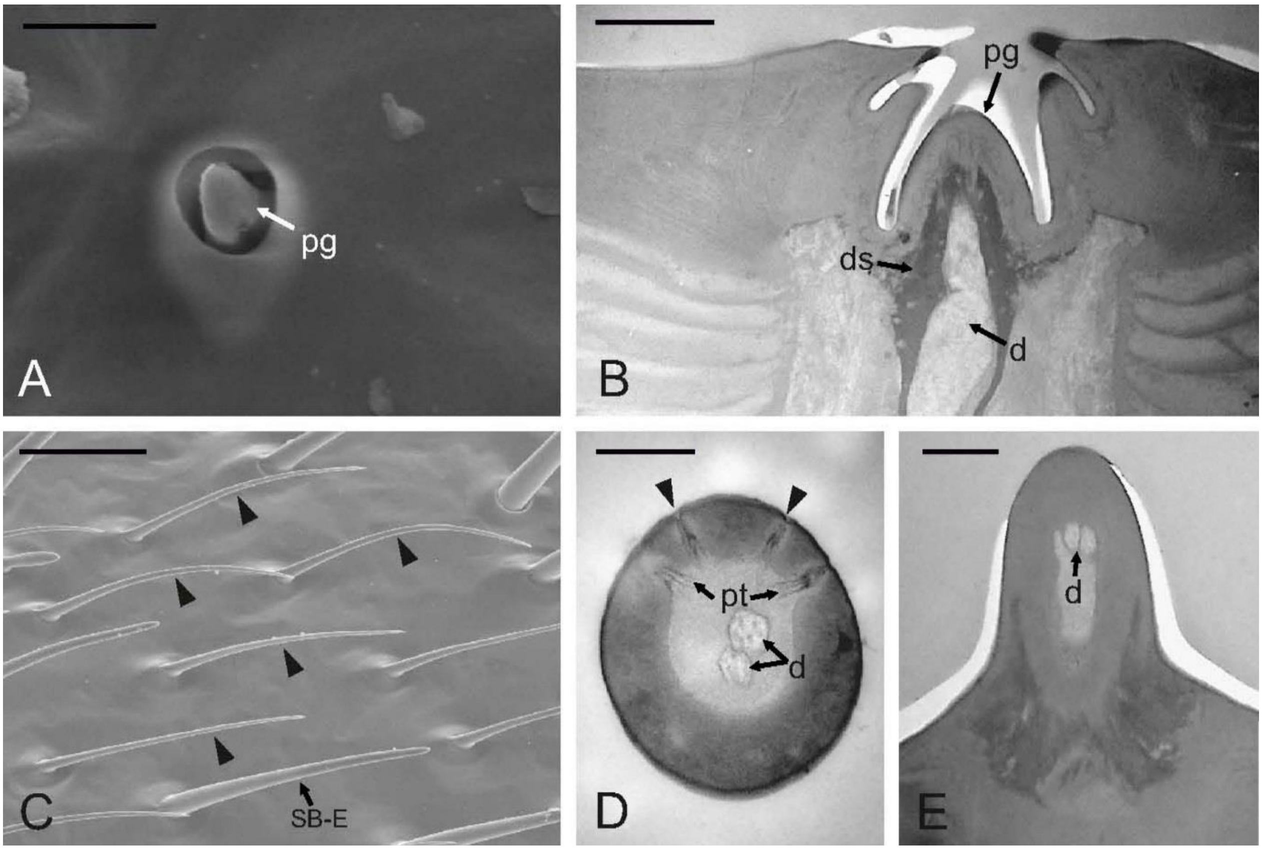

Figure 5. *H. halys* sensilla coeloconica and trichoidea (**A-B**) sensillum coeloconica (SCo). (**A**) the peg (pg) inserted into a pit. (**B**) longitudinal section of SCo near the base showing the peg (pg) located just below the cuticular opening. A thick dendrite sheath (ds) enveloping the distal part of the dendrites (d) is visible. (**C-E**) Sensilla trichoidea (ST). (**C**) ST (black arrowheads) on the Fl1 of a female. (**D**) a cross -section of the middle portion of the cuticular shaft with pores (black arrowheads), pore tubules (pt) and dendrites (d). (**E**) Oblique section through the base of the sensillum showing the dendrites (d). SB-E, sensillum basiconicum type E. A, C (SEM); B, D, E (TEM). Scale bars: A, B = 2 µm; C = 20 µm; D = 0.5 µm; E = 1 µm.

H. halys (table 2, table S1). A longitudinal section through the sensillum shows the absence of pores on the peg that is surrounded by finger-like projections and is concealed in the cavity of a cuticle inside a tight socket (figure 5B). They are scattered on the whole antennae of both adults and 5th instar nymphs.

Sensilla trichoidea (ST)

ST are curved slender hair-like structures (1.5-2.0 µm in basal diameter), with a sharp tip and are 35-40 µm long (figure 5C). Oblique sections through the inflexible socket reveal the presence of a single porous thick wall, whereby each pore opens through a tubule to reach the hair lumen (figure 5D). The latter houses two dendrites (figure 5D-E). ST are present solely on the flagellomeres (predominantly on the Fl2) and are the most abundant sensory structures on the antennae of *H. halys* (table 2, table S1).

Sensilla chaetica type A (SCh-A)

SCh-A are characterized by a blunt conical apex and a grooved wall (figure 6A-B). They are produced from a flexible socket at the base, and their length varies greatly between 30 µm and 120 µm (3.8-7.5 µm in basal diameter). They are the longest sensilla recorded on *H. halys* antennae, and their diameter decreases steadily from the base to the apex. In cross-section, they show a thin cuticular wall perforated by numerous pores irregularly distributed along its length. Each pore opens inward forming pore tubules that extend into the hair lumen, where around 50 dendritic branches are housed (figure 6C-D). SCh-A are present on all antennomeres with the highest density on the flagellomeres in adults, but in the 5th instar nymphs, Fl2 has more SCh-A than Fl1 (table 2, table S1).

Sensilla chaetica type B (SCh-B)

These sensilla are 25-50 µm in length and 2.5-4.0 µm in diameter at the base tapering to 1.5-2.0 µm near the tip. They are characterized by a smooth surface, protruding between 50° and 70° from the antennae, and there is no evidence of the existence of pores neither grooves (figure 6E). SCh-B are found on all the antennal segments; however, they are less abundant than SCh-A (table 2, table S1).

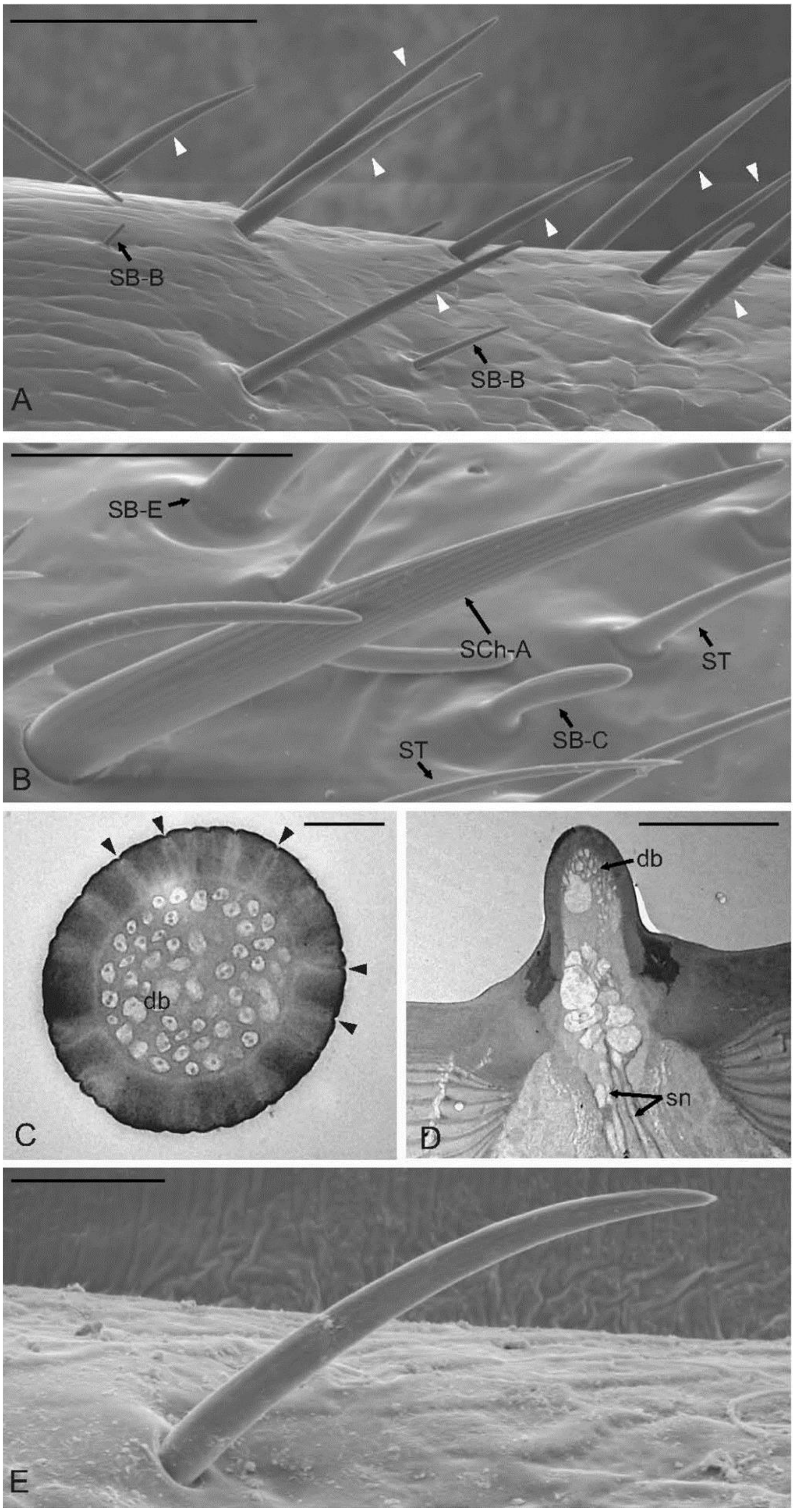

Figure 6. *H. halys* sensilla chaetica types A and B. (**A-D**) sensillum chaeticum (SCh-A). (**A**) SCh-A (white arrowheads) on the Fl1 of a female (**B**) sensillum with longitudinal grooves. (**C**) cross-section of the cuticular shaft with numerous pores (black arrowheads), and the sensillum lumen filled with dendritic branches (db). (**D**) longitudinal cross section through the base of the sensillum showing a thin cuticular wall where sensory neurons (sn) start to divide into several dendritic branches (db). (**E**) sensillum chaeticum type B (SCh-B) with smooth surface. SB-B, basiconic sensilla type B. A, B, E (SEM); C, D (TEM). Scale bars: A = 50 μm; B = 20 μm; C = 0.5 μm; D = 5 μm; E = 10 μm.

Discussion

The antenna of *H. halys* adults is filiform and based on the nomenclature of Schuh and Slater (2007), it consists of five segments; scape, pedicel 1, pedicel 2, flagellum 1 and flagellum 2, whereas fifth instar nymphs have a single pedicel segment, and consequently a shorter antenna. The same authors highlighted that additional sclerites may occur during postembryonic development in many pentatomids causing the subdivision of the pedicel, which can explain the absence of pedicel 2 in nymphal stages. All the pentatomids studied so far were reported to have 5-segmented antennae like *H. halys*. These include both predatory: *Perillus bioculatus* (F.), *Eocanthecona furcellata* (Wolff), *Canthecona furcellata* (Wolff), *Arma chinensis* (Fallou) and *Podisus maculiventris* (Say), and phytophagous species: *Dolycoris indicus* (Stal), *Plautia crossota* (Dallas), *Nezara viridula* (L.), *Cyclopelta siccifolia* (Westwood), *Chrysocoris purpurea* (Westwood), *Euschistus heros* (F.), *Piezodorus guildinii* (Westwood), *Edessa meditabunda* (F.) (Rani and Madhavendra, 1995; 2005; Sinitsina and Krutov, 1996; Brézot *et al*., 1997; Silva *et al*., 2010; Ahmad *et al*. 2016; Barsagade and Gathalkar, 2016).

Both male and female of *H. halys* show no differences in antennal size, neither in types nor in numbers of antennal sensilla. Moreover, we report a lower density of sensilla on the antenna of *H. halys* nymphs when compared to adults. This difference in the number of sensilla is not a novel observation, for it was reported in other hemipterans (Rani and Madhavendra, 1995; Chinta *et al*., 1997; Brézot *et al*., 1997). In her seminal study, Catalá (1997) concluded that insects have a general tendency to increase the number of receptors in the adult stage, especially chemoreceptors such as basiconic and trichoid sensilla. According to Chapman (1982), this phenomenon may be related to a differing chemical communication between adults and nymphs. Given that in *H. halys* both life stages occupy the same habitat and feed on the same hosts, this increase in adults might reflect the need for additional sensorial requirements essential for the sexual maturity of adults and/or their dispersive capacity. For instance, the mating behaviour of *H. halys*, described by Mazzoni *et al*. (2017) and in *Halyomorpha mista* Uhler (synonym of *H. halys*) by Kawada and Kitamura (1983), involves antennation by males of the posterior end of sexually-responsive females; the step preceding copula formation. Other pentatomids exhibiting this behaviour include *E. meditabunda* (Silva *et al*., 2012) and *Murgantia histrionica* (Hahn) (Lanigan and Barrows, 1977). Likewise, many authors investigated the important role of hemipteran antennae in localizing suitable oviposition sites, such as the case in *Neomegalotomus parvus* (Westwood) (Alydidae) (Ventura and Panizzi, 2000), *Rhinocoris bicolor* (F.) and *Rhinocoris tropicus* (Herrich-Schaeffer) (Reduviidae) (Parker, 1969) and *Thyanta pallidovirens* (Stal) (Pentatomidae) (Wang and Miller, 1997). In addition, *H. halys* adults show greater capacity for active dispersal and colonization of new habitats when compared to the wingless nymphal stages (Lee *et al*., 2014; Lee and Leskey, 2015).

There are five main types of sensilla on the antennae of *H. halys* adults and fifth instar nymphs: basiconica, (types A, B, C, D and E), coeloconica, trichoidea and chaetica (types A and B). The density of sensilla increased from proximal to distal ends, and the dominant type was by far sensilla trichoidea, located especially on the flagellomeres.

Chemo- and mechanosensory sensilla

Olfaction

Olfaction is one of the most fundamental insect sensory modalities, mediating intra- and interspecific communication; including but not limited to foraging, host location, mate finding and aggregation. In *H. halys*, sensilla basiconica types C and D (SB-C and SB-D), trichoidea (ST) and chaetica type A (SCh-A) are presumed to possess olfactory roles, based on their morphological characteristics.

Both basiconic sensilla (types C and D) are inserted into inflexible sockets and have a single pore at the tip with longitudinal grooves running along their surface; features generally shared among olfactory sensilla. These sensilla are similar in appearance to other basiconic sensilla described in *D. indicus*, *P. crossota*, *E. furcellata* and *P. bioculatus* (termed “SBsh” by Ahmad *et al*., 2016), in *N. viridula* (termed “type 4 sensillum” by Brézot *et al*., 1997) and in *C. siccifolia* and *C. purpurea* (termed “s.b. II” by Rani and Madhavendra, 2005).

ST in *H. halys* are found only in the flagellomeres and are characterized by the presence of pores on the cuticular wall, with two sensory neurons innervating each sensillum; rendering their olfactory role plausible. Further validation of our assumption of ST sensilla as olfactory can be deduced from the study of Toyama *et al*. (2006), who observed that the ablation of the terminal flagellomere of *H. halys* reduced but did not completely inhibit aggregate formation. However, both antennectomy and the removal of the two flagellomeres totally inhibited this behaviour (Toyama *et al*., 2006), indicating that the sensory structures present on these segments are necessary for perceiving the aggregation pheromone. The authors referred to these structures as “hair-shaped sensilla” and suggested the interference of olfactory and/or tactile cues in their performance. Moreover, the morphology and presumable role of ST are in accordance with similar findings in *N. viridula* (termed “type 1 sensilla” by Brézot *et al*., 1997), in *E. heros*, *E. meditabunda* and *P. guildinii* (termed “ST2” by Silva *et al*., 2010) and in *A. chinensis* (termed “ST1” by Zhang *et al*., 2014a). Whereas, Ahmad *et al*. (2016) assumed a mechanosensory function of sensilla trichodea found on the flagellum of *D. indicus*, *P. crossota*, *P. bioculatus* and *E. furcellata* due to the presence of flexible sockets at the base of their aporous walls.

Electrophysiological studies by Zhang *et al*. (2014b) have shown that *H. halys* adults and nymphs can detect various essential oils thanks to the presence of olfactory receptors on their antennae. Furthermore, Zhong *et al*. (2017) discovered that (E)-2-decenal functions as an alarm pheromone for *H. halys*, repelling both males and females at higher doses. Also, green leaf volatiles (GLVs) were shown to be key foraging cues for *H. halys* adults (Morrison *et al*., 2018). Such results provide more evidence to the major role of the olfactory sensilla mentioned above in the chemical signaling, perception and behaviour of this pest. This knowledge can be exploited for establishing a more efficient management strategy based on the employment of improved lures, repellents and attract-and-kill techniques.

Mechano-olfaction

SB-B in *H. halys* share with the above discussed olfactory sensilla the presence of longitudinal grooves, however the fact that they are inserted in flexible sockets suggests a dual function: a mechano-olfactory role. This function might explain the observations of Toyama *et al*. (2006), who noticed that bugs encountering aggregations frequently contacted the settled bugs with their antennae prior to joining them. Justus and Mitchell (1996) suggested that the movement of the antennae might create a wind vortex around it, facilitating the contact of odour molecules with the sensilla. Nevertheless, the role of SB-B cannot be stated with definite certainty, given first their position on the pedicel, and second the lack of respective TEM micrographs. Additional morphological and electrophysiological investigation is needed to clarify their exact role.

Mechano-gustation

The presence of a tubular body and dendrites extending along the shaft in the cross sections of SB-A and its insertion in flexible sockets suggest a possible double gustatory-mechanosensory function. A similar type of sensillum was previously recorded on the flagellum of adults and fifth instar nymphs of two other pentatomid species: *E. heros* and *E. meditabunda* (Silva *et al*., 2010). Such sensilla possessed longitudinal grooves and two apical pores, which are indicative of chemoreceptive sensilla. The SB-A we observed in *H. halys* are probably responsible for providing gustatory cues for fifth instar nymphs from their surrounding food sources. SEM micrographs suggest that pores are present at the tip of the sensillum and provide easy passage for substances from the exterior to the dendrites.

Thermo-hygrosensory sensilla

According to Altner and Prillinger (1980), hygroreceptors occur together with thermoreceptors in pegs that show no pore systems. The absence of pores in the sensillum wall of SCo precludes any olfactory function; these sensilla are thought to be involved in thermo- and hygro-reception, detecting wetness, dryness and changes in air temperature. Sensilla coeloconica were reported in other pentatomids: *N. viridula* (Brézot *et al*., 1997), *C. purpurea* (Rani and Madhavendra, 2005) and *P. guildinii* (Silva *et al*., 2010), where they were assigned to various presumed roles ranging from hygro-, thermo- to chemosensory reception.

The function of sensilla basiconica type E (SB-E) remains vague. Ventura and Panizzi (2005) described bristle sensilla with a curved extremity, bearing pores on the base and without flexible sockets on the last flagellomere of *N. parvus*. Similar sensilla were also observed on the last segment of the antennae of *Lygaeus kalmii* Stal (Hemiptera Lygaeidae) (Slifer and Sekhon, 1963). An olfactory function was assigned in both species. However, in *H. halys* the lack of pores on SB-E limits such an olfactory assumption; their function can be elucidated through further investigations.

Knowing the structure and function of the sensory system is necessary to characterize how the communication modalities interact in *H. halys* behaviour. The results of this study enhance our understanding of the sensory reception processes involved in the host plant selection and other behaviours of *H. halys*, which will indirectly help in developing more efficient tools to control this economically important pest.

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References

Ahmad A., Parveen S., Brożek J., Dey D., 2016.- Antennal sensilla of phytophagous and predatory pentatomids (Hemiptera: Pentatomidae): a comparative study of four genera.- *Journal of Comparative Zoology*, 261: 48-55.

Altner H., Prillinger L., 1980.- Ultrastructure of invertebrate chemo-, thermo-, and hygroreceptors and its functional significance.- *International Review of Cytology*, 67: 69-139.

Barsagade D. D., Gathalkar G. B., 2016.- First predation record of *Canthecona furcellata* (Wolff.) (Hemiptera: Pentatomidae) on spinning stage silkworm *Antheraea mylitta* (Drury).- *Entomological Research*, 46: 236-245.

Berg J., Schmidt K., 1997.- Comparative morphology and molting of sensilla basiconica of *Lepisma saccharina* Linnaeus (Zygentoma: Lepismatidae) and *Machilis* sp. (Archaeognatha: Machilidae).- *International Journal of Insect Morphology and Embryology*, 26: 161-172.

Brézot P., Tauban D., Renou M., 1997.- Sense organs on the antennal flagellum of the green stink bug, *Nezara viridula* (L.) (Heteroptera: Pentatomidae): sensillum types and numerical growth during the post-embryonic development.- *International Journal of Insect Morphology and Embryology*, 25: 427-441.

Catalá S., 1997.- Antennal sensilla of Triatominae (Hemiptera, Reduviidae): a comparative study over five genera.- *International Journal of Insect Morphology and Embryology*, 26: 67-73.

CESARI M., MAISTRELLO L., PIEMONTESE L., BONINI R., DIOLI P., LEE W., PARK C. G., PARTSINEVELOS G. K., REBECCHI L., GUIDETTI R., 2018.- Genetic diversity of the brown marmorated stink bug *Halyomorpha halys* in the invaded territories of Europe and its patterns of diffusion in Italy.- *Biological Invasions*, 20: 1073-1092.

CHAPMAN R. F., 1982.- Chemoreception: the significance of sensillum numbers.- *Advances in Insect Physiology*, 16: 247-356.

CHINTA S., DICKENS J. C., BAKER G. T., 1997.- Morphology and distribution of antennal sensilla of the tarnished plant bug, *Lygus lineolaris* (Palisot de beauvois) (Hemiptera: Miridae).- *International Journal of Insect Morphology and Embryology*, 26: 21-26.

EPPO, 2018.- *EPPO Global Database*.- [online] URL: https://gd.eppo.int (accessed, 2 May 2018).

FOGAIN R., GRAFF S. 2011.- First records of the invasive pest, *Halyomorpha halys* (Hemiptera: Pentatomidae), in Ontario and Quebec.- *Journal of the Entomological Society of Ontario*, 142: 45-48.

GONZAGA-SEGURA J., VALDÉZ-CARRASCO J., CASTREJÓN-GÓMEZ V. R., 2013.- Sense organs on the antennal flagellum of *Leptoglossus zonatus* (Heteroptera: Coreidae).- *Annals of the Entomological Society of America*, 106: 510-517.

HAYE T., GARIEPY T., HOELMER K., ROSSI J. P., STREITO J. C., TASSUS X., DESNEUX N., 2015.- Range expansion of the invasive brown marmorated stinkbug, *Halyomorpha halys*: an increasing threat to field, fruit and vegetable crops worldwide.- *Journal of Pest Science*, 88: 665-673.

HOEBEKE E. R., CARTER M. E., 2003.- *Halyomorpha halys* (Stål) (Heteroptera: Pentatomidae): a polyphagous plant pest from Asia newly detected in North America.- *Proceedings of the Entomological Society of Washington*, 105: 225-237.

JUSTUS K. A., MITCHELL B. K., 1996.- Oviposition site selection by the diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae).- *Journal of Insect Behavior*, 9: 887-898.

KAWADA H., KITAMURA C., 1983.- The reproductive behavior of the brown marmorated stink bug, *Halyomorpha mista* Uhler (Heteroptera: Pentatomidae) I. Observation of mating behavior and multiple copulation.- *Applied Entomology and Zoology*, 18: 234-242.

KEIL T. A., 1999.- Morphology and development of the peripheral olfactory organs, pp. 5-47. In: *Insect olfaction* (HANSSON B. S., Ed.).- Springer, Berlin, Germany.

KIM J., PARK K. C., ROH H. S., KIM J., OH H. W., KIM J. A., PARK C. G., 2016.- Morphology and distribution of antennal sensilla of the bean bug *Riptortus pedestris* (Hemiptera: Alydidae).- *Microscopy Research and Technique*, 79: 501-511.

LANIGAN P., BARROWS E., 1977.- Sexual behavior of *Murgantia histrionica* (Hemiptera: Pentatomidae).- *Psyche: A Journal of Entomology*, 84. 191-197.

LEE D. H., 2015.- Current status of research progress on the biology and management of *Halyomorpha halys* (Hemiptera: Pentatomidae) as an invasive species.- *Applied Entomology and Zoology*, 50: 277-290.

LEE D. H., LESKEY T., 2015.- Flight behavior of foraging and overwintering brown marmorated stink bug, *Halyomorpha halys* (Hemiptera: Pentatomidae).- *Bulletin of Entomological Research*, 105: 566-573.

LEE D. H., NIELSEN A., LESKEY T., 2014.- Dispersal capacity and behavior of nymphal stages of *Halyomorpha halys* (Hemiptera: Pentatomidae) evaluated under laboratory and field conditions.- *Journal of Insect Behavior*, 27: 639-651.

MAISTRELLO L., DIOLI P., DUTTO M., VOLANI S., PASQUALI S., GILIOLI G., 2018.- Tracking the spread of sneaking aliens by integrating crowdsourcing and spatial modeling: the Italian invasion of *Halyomorpha halys*.- *BioScience*, 68: 979-989.

MALEK R., TATTONI C., CIOLLI M., CORRADINI S., ANDREIS D., IBRAHIM A., MAZZONI V., ERIKSSON A., ANFORA G., 2018.- Coupling traditional monitoring and citizen science to disentangle the invasion of *Halyomorpha halys*.- *International Journal of Geo-Information*, 7: 171.

MAZZONI V., POLAJNAR J., BALDINI M., STACCONI M. V. R., ANFORA G., GUIDETTI R., MAISTRELLO L., 2017.- Use of substrate-borne vibrational signals to attract the brown marmorated stink bug, *Halyomorpha halys*.- *Journal of Pest Science*, 90: 1219-1229.

MISSBACH C., DWECK H. K., VOGEL H., VILCINSKAS A., STENSMYR M. C., HANSSON B. S., GROSSE-WILDE E., 2014.- Evolution of insect olfactory receptors.- *Elife*, 3: 1-22.

MORRISON III W. R., ALLEN M., LESKEY T., 2018.- Behavioral response of the invasive *Halyomorpha halys* (Hemiptera: Pentatomidae) to host plant stimuli augmented with semiochemicals in the field.- *Agricultural and Forest Entomology*, 20: 62-72.

NIELSEN A., HAMILTON G., MATADHA D., 2008.- Developmental rate estimation and life table analysis for *Halyomorpha halys* (Hemiptera: Pentatomidae).- *Environmental Entomology*, 37: 348-355.

ODA, 2013.- Pest Alert: Brown Marmorated Stink Bug *Halyomorpha halys*.- Oregon Department of Agriculture Fact Sheets and Pest Alerts, Salem, OR, USA. [online] URL: http://www.oregon.gov/ODA/Pages/default.aspx (accessed, 6 May 2018)

OLSON J., MOON R., KELLS S., MESCE K., 2014.- Morphology, ultrastructure and functional role of antennal sensilla in off-host aggregation by the bed bug, *Cimex lectularius*.- *Arthropod Structure and Development*, 2014: 1-6.

PARKER A. H., 1969.- The predatory and reproductive behaviour of *Rhinocoris bicolor* and *R. tropicus* (Hemiptera: Reduviidae).- *Entomologia Experimentalis et Applicata*, 12: 107-117.

PAULA D. P., TOGAWA R. C., COSTA M. M. C., GRYNBERG P., MARTINS N. F., ANDOW D. A., 2016.- Identification and expression profile of odorant-binding proteins in *Halyomorpha halys* (Hemiptera: Pentatomidae).- *Insect Molecular Biology*, 25: 580-594.

RANI P. U., MADHAVENDRA S. S., 1995.- Morphology and distribution of antennal sense organs and diversity of mouthpart structures in *Odontopus nigricornis* (Stall) and *Nezara viridula* L. (Hemiptera).- *International Journal of Insect Morphology and Embryology*, 24: 119-132.

RANI P. U., MADHAVENDRA S. S., 2005.- External morphology of antennal and rostral sensillae in four hemipteran insects and their possible role in host plant selection.- *International Journal of Tropical Insect Science*, 25: 198-207.

ROMANI R., ROSSI STACCONI M. V., 2009.- Mapping and ultrastructure of antennal chemosensilla of the wheat bug *Eurygaster maura*.- *Insect Science*, 16: 193-203.

SCHUH R. T., SLATER J. A., 2007.- *True bugs of the world: classification and natural history*.- Cornell University Press, New York, USA.

SILVA C. C., DE CAPDEVILLE G., MORAES M. C. B., FALCAO R., SOLINO L. F., LAUMANN R. A., SILVA J. P., BORGES M., 2010.- Morphology, distribution and abundance of antennal sensilla in three stink bug species (Hemiptera: Pentatomidae).- *Micron*, 41: 289-300.

SILVA C. C., LAUMANN R. A., FERREIRA J. B. C., MORAES M. C. B., BORGES M., ČOKL A., 2012.- Reproductive biology, mating behavior, and vibratory communication of the brown-winged stink bug, *Edessa meditabunda* (Fabr.) (Heteroptera: Pentatomidae).- *Psyche: A Journal of Entomology*, 2012: 1-9.

SINITSINA E. E., KRUTOV V. V., 1996.- Antennal and labial sense organs in a bug *Podisus maculiventris* (Hemiptera, Pentatomidae).- *Zoologichesky Zhurnal*, 75: 1167-73.

SLIFER E. H., SEKHON S. S., 1963.- Sense organs on the antennal flagellum of the small milkweed bug, *Lygaeus kalmii* Stål (Hemiptera, Lygaeidae).- *Journal of Morphology*, 112: 165-193.

TOYAMA M., IHARA F., YAGINUMA K., 2006.- Formation of aggregations in adults of the brown marmorated stink bug, *Halyomorpha halys* (Stål) (Heteroptera: Pentatomidae): the role of antennae in short-range locations.- *Applied Entomology and Zoology*, 41: 309-315.

VENTURA M. U., PANIZZI A. R., 2000.- Oviposition behavior of *Neomegalotomus parvus* (West.) (Hemiptera: Alydidae): daily rhythm and site choice.- *Anais da Sociedade Entomológica do Brasil*, 29: 391-400.

VENTURA M. U., PANIZZI A. R., 2005.- Morphology of olfactory sensilla and its role in host plant recognition by *Neomegalotomus parvus* (Westwood) (Heteroptera: Alydidae).- *Brazilian Archives of Biology and Technology*, 48: 589-597.

WANG Q., MILLAR J., 1997.- Reproductive behavior of *Thyanta pallidovirens* (Heteroptera: Pentatomidae).- *Annals of the Entomological Society of America*, 90: 380-388.

ZACHARUK R. Y., 1985.- Antennae and sensilla, pp. 1-69. In: *Comprehensive insect physiology, biochemistry and pharmacology* (KERKUT G. A., GILBERT L. I., Eds), Vol. 6 Nervous system: sensory.- Pergamon Press, Oxford, UK.

ZHANG J., ZHANG X. J., LIU C. Y., MENG L., ZHOU Y., 2014a.- Fine structure and distribution of antennal sensilla of stink bug *Arma chinensis* (Heteroptera: Pentatomidae).- *Entomologica Fennica*, 25: 186-198.

ZHANG Q. H., SCHNEIDMILLER R., HOOVER D., ZHOU G., MARGARYAN A., BRYANT P., 2014b.- Essential oils as spatial repellents for the brown marmorated stink bug, *Halyomorpha halys* (Stål) (Hemiptera: Pentatomidae).- *Journal of Applied Entomology*, 138: 490-499.

ZHONG Y. Z., ZHANG J. P., REN L. L., TANG R., ZHAN H. X., CHEN G. H., ZHANG F., 2017.- Behavioral responses of the egg parasitoid *Trissolcus japonicus* to volatiles from adults of its stink bug host, *Halyomorpha halys*.- *Journal of Pest Science*, 90: 1097-1105.

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