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RESEARCH

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Comparative morphology of sensilla of antennae, maxillary and labial palpi of adult *Rhyzopertha dominica* (F.) (Coleoptera: Bostrichidae), with specific reference to the typology and possible functions

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Abstract

Background The lesser grain borer *Rhyzopertha dominica* (F.) (Coleoptera: Bostrichidae) is a cosmopolitan insect pest of stored cereal grains. In this study, the fine morphology of antennae, maxillary and labial palpi as well as the typology, morphology and distribution of associated sensilla were comprehensively examined by scanning electron microscopy.

Results On antennae, six types of sensilla were identified, s. trichodea, s. chaetica, two subtypes of s. basiconica, s. ampullacea and s. styloconica, in addition of Böhm's sensilla (Bs). Sensilla trichodea and basiconica were the most abundant sensilla types in the club flagellomeres. Mouth parts of *R. dominica* were adapted for chewing; maxillary and labial palpi consisted of four and five segments, respectively. Galea of maxilla was two segments, the distal one ended with a brush like organ composed of a dense field of long s. basiconica. The sensilla of maxillary and labial palpi were long and short s. trichodea, s. basiconica, s. styloconica and s. ampullacea. Only one big sensillum digitiformium was found on the lateral side of the distal segment of the maxillary palp.

Conclusions We summarized the validated structures of different types of sensilla on antennae and palpi of *R. dominica* and proposed the potential functions of them in detection of ecologically relevant stimuli.

Keywords Antenna, Mouth parts, Sensory structures, SEM, *Rhyzopertha dominica*

Background

The lesser grain borer *Rhyzopertha dominica* (Coleoptera: Bostrichidae) is a serious pest of stored products throughout the tropics and temperate countries, either because of its ability for prolonged flight or as a result of the international trade in food products. This can cause significant economic losses in terms of nutrient depletion (Jood et al., 1996), and grain mass (Subramanyam & Hagstrum, 1995). Both larvae and adults of this insect feed on whole, sound grains and cause extensive damage (Rees, 2007). Females lay eggs on the surface of grain kernels, upon hatching; the larva enters the kernel and remains inside until maturation (Ozkaya et al., 2009). Currently, there is little information published concerning the screening of the differential structures of the sensory organs located on the antennae and mouth parts of adults of *R. dominica* responsible for detection of

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ecologically relevant stimuli lead to finding suitable habitats, food, mating opportunities and oviposition sites. However, Sawires and Elbassiouny (2019) distinguished three types of sensilla on the apical distal three segments of flagellomeres; long and short chaetica, basiconica and ampucellaceous.

Volatile semiochemicals are the principle sensory signals for insects (Mamidala et al., 2013; Wang et al., 2010). The antennae of beetles can show synergistic responses to pheromones in the presence of host plant volatiles (Giulio et al., 2012; Lopes et al., 2002; MacKay et al., 2014). The antennae of insects are the primary olfactory organ playing critical roles in food selection, intersexual communication and ovipositional site search (Zacharuk, 1985; Zhang et al., 2015). The antennal sensilla of insects have been argued to play an important role in perceiving different chemical signals related to their hosts and conspecifics (van der Goes van Naters & Carlson, 2006). It was found that the morphology and ultrastructure of antennal sensilla can be highly variable among different species of Coleoptera (Ali et al., 2016; Chi et al., 2009; Faucheux et al., 2019, 2020a, 2020b; Hao et al., 2020a; Merivee et al., 2002; Seada, 2015; Seada & Hamza, 2018). Interestingly, Chapman (2003) suggested that large numbers of sensilla should provide responses to a wider range of environmental stimuli. Previous studies investigated that the morphology and ultrastructure of antennal sensilla could be extremely variable among different species of beetles (Merivee et al., 2002; Ren et al., 2012; Volkovitsh, 2001). However, few studies have documented the structure and distribution of the antennal sensilla of beetles in the Bostrichidae, which is a large family with hundreds of species (Borowski & Wegrzynowicz, 2007; Liu & Klaus, 2011).

Understanding the feeding behavior of insects is the key to develop successful biological control programs (Wei et al., 2015). As the main feeding organs, the morphological variation of mouthparts and distribution of their sensilla is correlated with the variation of the food source as well as feeding behavior (Ma et al. 2013; Hao et al., 2020b). The sensory receptors of insect mouth parts devoted to the survival of the insect. The basic components of chewing mouthparts are the same, but they might differ due to their diverse food types and feeding preference or boring holes for laying eggs (Moon et al., 2015). Various studies have been conducted to describe the mouthpart morphology of Coleoptera (Chen et al. 2016, Hao et al., 2020a; Moon, 2015; Seada & Hamza, 2018). Characterization of the olfactory and gustatory organs of adults of *R. dominica* could provide an important starting point and valuable information for further physiological and behavioral studies, which can ultimately lead to developing practical monitoring and management strategies with semiochemicals.

Various studies have reported that the sensory complement is also relevant to a species' ecological niche and involved in feeding and reproductive behavior (Zaitseva and Elizarov 1980). The purpose of this study was to examine and compare between the distribution and fine structures of the sensorial equipment found on the antennae, maxillary and labial palpi of adult *R. dominica* that have a key role during grain selection process. The information documented here with further studies of identified chemosensitive sensilla can provide a foundation for developing semiochemical-based management strategies of adults of *R. dominica*.

Methods

Insect rearing

Approximately, 100–300 adults of *R. dominica* 3 days old collected from stored untreated cereal grains. The insects were reared for several generations in Crops Research Institute, Agricultural Research Center, Sakha, Egypt. They were placed in 850 ml glass jars containing 400 g of wheat grains as a food source. The jars openings were covered with muslin cloth, kept in a position with rubber bands. The adults of *R. dominica* were maintained in the laboratory at 28 ± 2 °C, 70 ± 5% relative humidity (RH) and light: dark photoperiod of 16: 8 h. In order to obtain adult beetles, the flour was sieved to separate the beetles.

Fine structure and scanning electron microscopy

For scanning electron microscopy (SEM), whole adult insects were immersed in 70% ethanol overnight at 4 °C. Specimens were put in a series of graded solution of ethanol, from 70 to 100%, mounted on SEM stubs with double sided sticky tapes and sputter coated with gold–palladium (3:2) in a JEOL ion sputter JFC-1100E. The specimens were visualized using a scanning electron microscope (JSM-5300, UK).

The number, distribution, and morphometric characters of each sensillum type were analyzed from SEM micrographs of five individuals with imageJ program (https://imagej.nih.gov/ij/). The lengths of all types of sensilla were then analyzed from SEM micrographs. All data were reported as means and standard error of means.

Results

General morphology of the antennae

The length of antenna of the adult lesser grain borer *R. dominica* was 197 ± 9.4 µm. The antenna consisted of a scape (the 1st antennomere), a pedicel, and a flagellum. The flagellum was composed of eight flagellomeres,

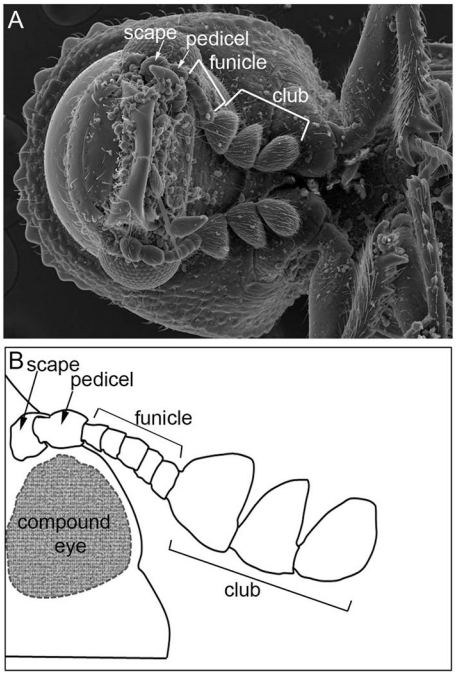

Fig. 1 Whole antenna of adult *Rhyzopertha dominica*. **A** Scanning electron micrograph (SEM) of head and the projected antennae; flagellomeres were arranged as a proximal narrow funicle (fl1–fl5) and a distal wide club (cl1–cl3), pe—pedicel, sc—scape; scale bar = 50 µm. **B** Schematic drawing of the whole antenna showing the proximal funicle and distal club

Table 1 Mean ± (SE) of the length (µm) and basal width (µm) of the scape, pedicel and all flagellomeres of the funicle (fl1–fl5) and club (cl1–cl3) of the antenna of adult *Rhyzopertha dominica*, ($n = 5$)

	Length (µm)	Width (µm)
Scape	20.29 ± 0.61	15.98 ± 0.55
Pedicel	20.11 ± 0.49	16.36 ± 0.68
fl1	12.82 ± 0.50	11.78 ± 0.21
fl2	10.52 ± 0.36	12.13 ± 0.25
fl3	8.79 ± 0.26	13.22 ± 0.30
fl4	10.80 ± 0.25	14.08 ± 0.25
fl5	9.48 ± 0.49	14.48 ± 0.49
cl1	32.47 ± 0.99	19.02 ± 0.89
cl2	28.96 ± 0.26	20.40 ± 0.40
cl3	42.93 ± 0.85	22.29 ± 0.95

distinguished into narrow proximal funicle (fl1–fl5) and wide distal club (cl1–cl3) (Fig. 1A–B, Table 1). Two clusters of Böhm's sensilla located at the basal part of the scape and pedicel were also detected (Fig. 2A and D and Table 2).

Antennal sensillum types and distribution

Based on the morphological features, the antennal sensilla of the adult *R. dominica* could be identified into six types: one type of s. trichodea, one type of s. chaetica, two subtypes of s. basiconica (short coned sb1 and elongated sb2), one type of s. ampullacea, in addition of Böhm's sensilla (Bbs) (Figs. 1, 2, 3, Table 2). The density of sensilla increases from proximal to distal parts of antenna but all types of sensilla were found only on the distal three antennal club flagellomeres. The dominant types of sensilla were s. trichodea and s. basiconica, especially on the distal club flagellomeres (Figs. 1, 2, 3, 4). Sensilla trichodea were detected along all flagellar segments (Fig. 2A).

Sensilla trichodea

Sensilla trichodea were pointed hairs surrounded by a deep ditch in the cuticle and tapering only at the distal end (Length = 18.4 ± 0.26 µm and basal width = 0.69 ± 0.02 µm) (Fig. 2 and Table 2). They were randomly located on all flagellar segments and the most abundant antennal sensilla type in the last club flagellar segments of antennae ($n = 98.7 \pm 3.6$) (Figs. 1, 2, 3, 4, Table 2). The density on the first five proximal flagellar segments (funicle) was low and increased toward the distal end of the flagellum (Figs. 3 and 4).

Sensilla basiconica

There were two subtypes of s. basiconica, bs1 and bs2, predominantly scattered along the three club flagellar segments and intermittent between s. trichodea (Figs. 3A–D and 4, Table 2).

The sensilla basiconica I (sb1, $n = 38 \pm 3.8$) were short, curved, rod-like hairs (Length = 3.74 ± 0.03, basal width = 1.63 ± 0.02 µm) and abundant mainly at the dorsal side of club flagellomeres (Fig. 3A–D). They were parallel to the cuticle of the antenna and end with blunt tip but did not have basal sockets (Fig. 3B–D). The sensilla basiconica II, sb2 ($n = 26.7 \pm 2.7$) were longer than s. basiconica I. They were thin, finger like hairs (Length = 5.29 ± 0.06, basal width = 0.94 ± 0.01 µm) with blunt tip, smooth cuticle and without basal socket (Figs. 3B–D and 4 and Table 2). They were distributed at the distal end of each club flagellomere (Fig. 3A–D).

Sensilla ampullacea

Each s. ampullacea was a prominent elliptical depression and central opening (basal diameter = 1.3 ± 0.05 µm). Ampullacea sensilla were found exclusively at the distal end of the third club flagellar segment (cl3) (Fig. 3C–D). Only small apertures were visible, but they could not be counted. These sensilla

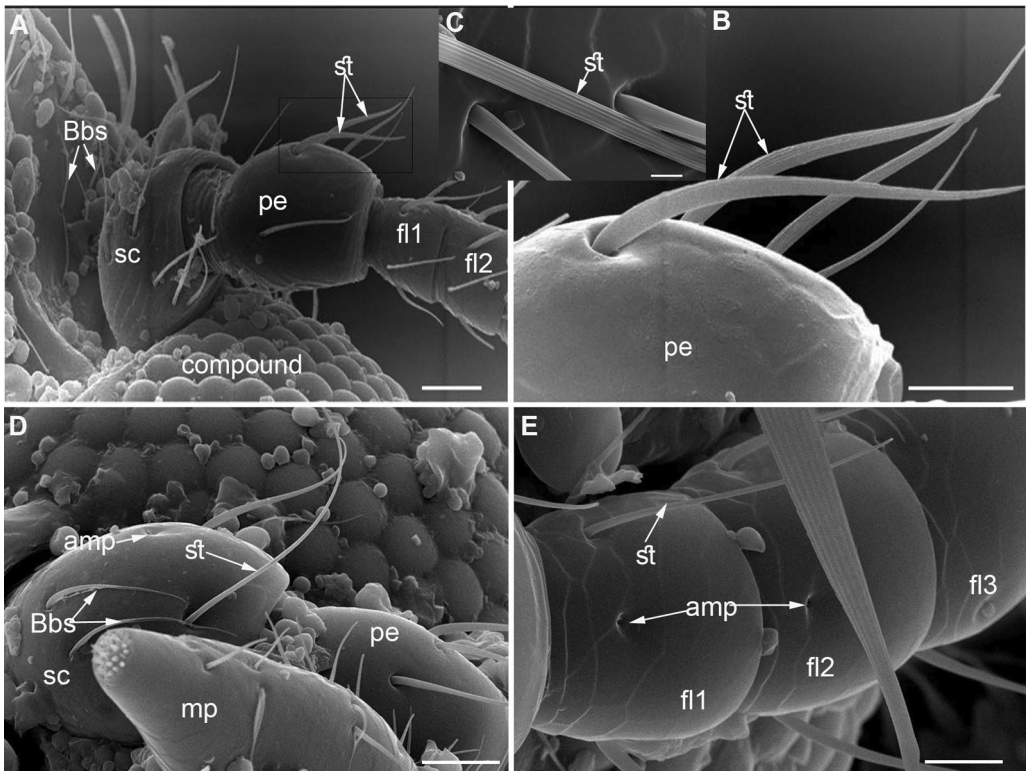

Fig. 2 Scanning electron micrographs of the basal part of the antenna of adult *Rhyzopertha dominica*. **A** The scape (sc) bears a group of s. trichodea (st) and Böhm's sensilla (Bbs), pedicel (pe) and two basal flagellomeres (fl1 and fl2) bears grooved sharp tipped s. trichoid sensilla (st). **B** The pedicel (pe) with s. trichodea (st) fit into depressed cuticle. **C** Enlarged part of s. trichodea showing the longitudinally grooved shafts. **D** Scape (sc) and pedicel (pe), showing one dorsal s. ampullacea (amp) on the scape. **E** The three basal flagellomeres (f1-f3) of the flagellum carrying s. trichodea (st) and ampullacea (amp). Scale bars: **A** and **B** 10 µm; **C** 2 µm; **D** 20 µm; **E** 10 µm

Table 2 Mean number ± (SE) of different types of sensilla found on the scape, pedicel and flagellomeres of the funicle (fl1–fl5) and club (cl1–cl3) of the antenna of adult *Rhyzopertha dominica* ($n = 10$)

	Bbs	st	sb1	sb2	sch	amp
Scape	6 ± 0.68	6.8 ± 0.63	–	–	–	1
Pedicel	3.5 ± 0.35	6.6 ± 0.55	–	–	–	–
fl1–fl5	–	6.3 ± 0.48	–	–	–	1
cl1	–	92.5 ± 8.54	31.7 ± 3.8	21.7 ± 1.44	8.7 ± 0.8	nc
cl2	–	100 ± 8.54	37.5 ± 3.6	27.5 ± 1.44	9 ± 0.7	nc
cl3	–	104.5 ± 3.88	45 ± 2.5	31 ± 2.65	9.67 ± 1.1	nc

(–): sensilla were not found and (nc): sensilla could not be counted

appear as small round openings on the cuticular surface externally (Fig. 3B–D).

Sensilla chaetica

The sensilla chaetica ($n = 9 \pm 0.33$ per each club flagellomere) were long, thick and curved rods with longitudinal warts recessed in depressed cuticle (Length = 10.27 ± 0.27 µm, basal width = 1.29 ± 0.02 µm) (Table 2). The external surface of s. chaetica was slightly rough whereas the base of these sensilla was inserted slightly depressed into the cuticle and end with blunt tips which suggesting the gustatory function (Fig. 4). They were distributed at the periphery of each club flagellomere (Fig. 4).

Böhm's sensilla

Böhm's sensilla were spine-like cuticular structures, similar to trichoid sensilla in shape but these sensilla were

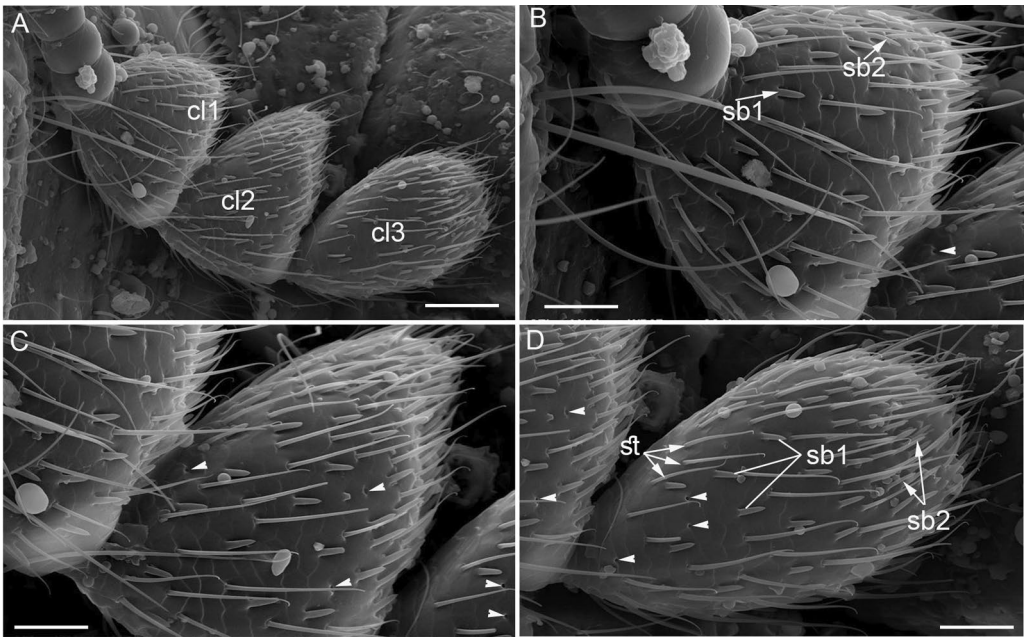

Fig. 3 Scanning electron micrographs of the distal part of the antenna of adult *Rhyzopertha dominica*. **A** The three flagellomeres of the club (cl1–cl3) and their sensilla. Scale bar = 50 µm. **B–D** The spatial distribution of sensilla of club flagellomeres; cl1 (**B**), cl2 (**C**), cl3 (**D**) which densely packed with numerous sharp tipped s. trichodea (st), short blunt tipped s. basiconica (sb1 and sb2) and s. ampullacea (amp) (arrow heads)

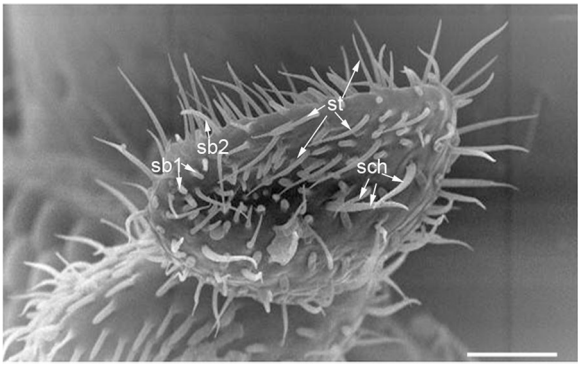

Fig. 4 Scanning electron micrograph (SEM) of a close-up view of the distal antennal flagellomere (Cl3) of adult *Rhyzopertha dominica* showing the most numerous sensilla; trichodea (st) and basiconica (sb1 and sb2) and sparsely distributed s. chaetica (sch) which were distinguished by its characteristic arch shaped shafts with longitudinal warts and emerging from a depressed cuticle. Scale bar = 10 µm

sharper and much shorter in length and found in clusters without wall pores on the surface or at the tip (Fig. 2A and D). They were distributed in one or two clusters at the bases of scape and pedicel (Table 2).

Sensory organs of the mouth parts

Mouth parts of adult *R. dominica* are adapted for chewing and consisted of prolonged labrum, two unjointed prolonged mandibles (labrum and mandibles are forming a beak like structure), two symmetrical maxillae with a pair of four segmented maxillary palps and two double segmented galea, and one labium with a lateral pair of five segmented labial palps (Fig. 5A–D). The sensory field of the chemosensory sensilla was found to be mainly concentrated at the tip of the distal segments of both maxillary and labial palps (Fig. 5B–D).

Sensilla of labial palp

The five segments of the labial palp of adult *R. dominica* had numerous s. trichodea divided into two subtypes; short (st1) and long (st2) distributed around the periphery of all segments (Fig. 5A). The sensilla of the basal labial segment could not be investigated. The second segment had both subtypes of s. trichodea (st1: length = 4.4 ± 0.44 µm and $n = 6 \pm 0.4$ and st2; length = 18.29 µm and $n = 2.5 \pm 0.29$), in addition of many microtrichea (mt) (Fig. 5A–B). The third segment of labial palp had only short s. trichodea (st1: length = 9.93 ± 0.27 µm and $n = 1.25 \pm 0.25$) (Table 3). Even though, the fourth segment of the labial palp had both subtypes of s. trichodea (st1: length = 6.2 ± 1.89 µm, $n = 3.33 \pm 0.33$ and st2: length = 25.5 ± 2.46 µm, $n = 8.5 \pm 1.3$) (Fig. 5A–B). Furthermore, the labial palp had the longer s. trichodea than maxillary palp (Fig. 5A–B). The distal segment of the labial palp was elongated, conical shaped and terminated with an apical

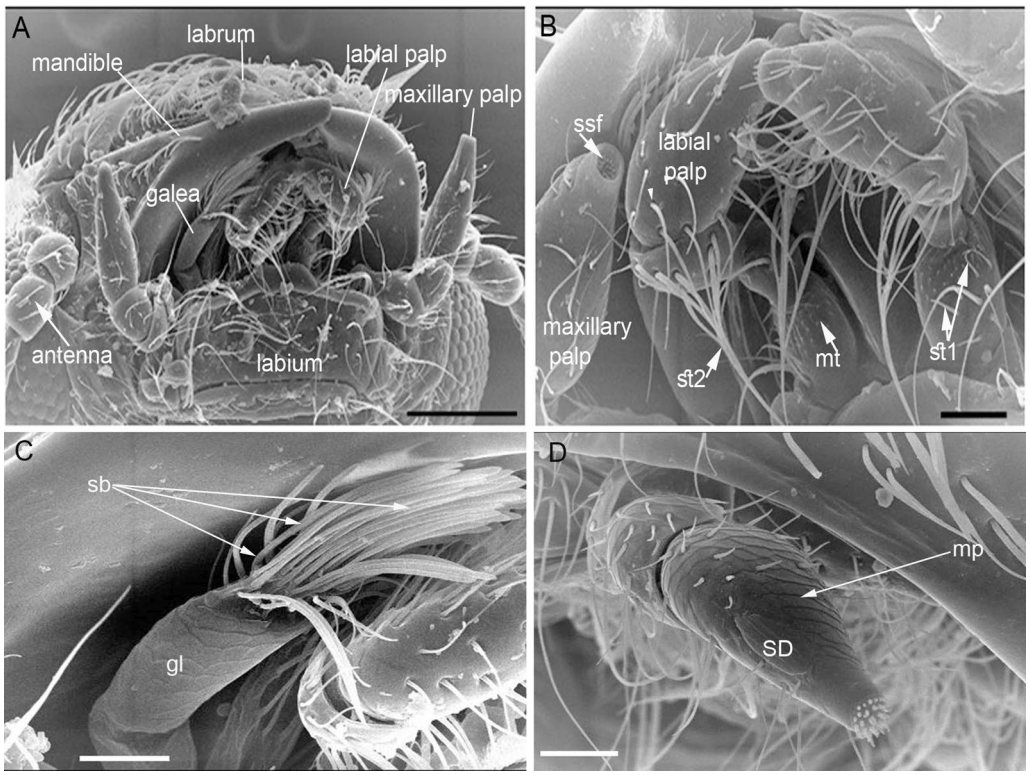

Fig. 5 Scanning electron micrographs (SEM) of the ventral view of the mouth parts of adult *Rhyzopertha dominica* with associated sense organs. **A** Mouth parts showing the labrum, mandibles, maxillae carry two four-segmented maxillary palps and lateral galea fringed with a dense comb of large basiconic sensilla, and the labium with two five-segmented labial palps. **B** Higher magnification of the labial palp showing the sensory field of their distal segments having numerous short and long s. trichodea (st1 and st2); note that the second segment of labial palp carried many cone shaped microtrichea (mt). **C** Galea of maxilla (gl) fringed with a dense field of long s. basiconica (sb) and the distal segment of the maxillary palp (mp) surrounded with numerous long s. trichodea (st2). **D** Lateral view of the head showing antenna (ant), labrum (lb), mandible (md) and labial palp (lp). scale bars: **A** 50 µm; **B–D** 10 µm

Table 3 Mean ± (SE) of the length (µm) and width (µm) of the segments of the maxillary and labial papli and galea of maxilla of adult *Rhyzopertha dominica* ($n = 5$) and the number of their associated sensilla ($n = 10$)

	Length (µm)	Width (µm)	No. of sensilla				
Labial palp			**st1**	**st2**	**sb**	**sst**	**amp**
Segment 1	5.9 ± 0.20	8.7 ± 0.33	–	–	–	–	–
Segment 2	15.4 ± 0.32	13.4 ± 0.34	6 ± 0.4	2.5 ± 0.3	–	–	–
Segment 3	5.4 ± 0.29	6.1 ± 0.31	–	1.3 ± 0.3	–	–	–
Segment 4	6.1 ± 0.52	10.7 ± 0.81	3.3 ± 0.3	8.5 ± 1.3	–	–	–
Segment 5	22.3 ± 1.39	13.2 ± 0.57	18.8 ± 1.9	–	nc	nc	nc
Maxillary palp							
Segment 1	11.7 ± 0.49	16.3 ± 0.65	nc	nc	–	–	–
Segment 2	28.6 ± 0.88	21.2 ± 0.86	–	17 ± 1.07	–	–	–
Segment 3	11.6 ± 0.68	15.5 ± 0.77	10.7 ± 0.7	–	–	–	–
Segment 4	49.3 ± 1.87	19 ± 0.62	18 ± 1.38	–	–	–	–
Ssf			–	–	12.8 ± 0.7	10.8 ± 0.9	2
Galea							
Segment 1	13.31 ± 0.4	11.43 ± 0.2	–	–	–	–	–
Segment 2	21.6 ± 0.39	11.9 ± 0.34	–	–	42.3 ± 2.3	–	–

(–): sensilla were not found and (nc): sensilla could not be counted

disc. The apical disc consisted of a sensory field fringed with many s. basiconica and s. styloconica which could not be investigated as they were obscured. In addition of short s. trichodea at the external periphery of it (st1: length = 12.1 ± 2.38 µm, n = 18.8 ± 1.85) (Fig. 5A–B).

Sensilla of maxillary palp

The first three segments of the maxillary palp of adult *R. dominica* were cylindrical in shape (Fig. 5A, C and D), while the distal segment was conical in shape and their cuticular walls presented striations resembling 'fishbone' patterns (Fig. 5D).

The sensilla of the basal segment of the maxillary palp were difficult to investigate. The second segment of the maxillary palp had long s. trichodea (st2: length = 23.35 ± 3.2 µm, width = 0.9 ± 0.3 µm, n = 17 ± 1.07) (Fig. 5A, B and D). The third segment had ventral s. trichodea (st1: length = 7.58 ± 0.69 µm, width = 0.67 ± 0.2 µm, n = 10.7 ± 0.7). The distal segment of the maxillary palp had short s. trichodea (st1: length = 10.23 ± 0.5 µm, width = 0.72 ± 0.1 µm, n = 18 ± 1.38) (Fig. 6 A). In addition of a single big sensillum digitiformium at the dorsal region (length = 9.28 ± 0.04 µm, middle width = 4.28 ± 0.01 µm) (Fig. 5D, 6A and C). The s. digitiformium was rabbit ear-shaped with cuticular surface showed a shallow concavity, with small longitudinal grooves in the cuticle (Fig. 6A, C and D). It was parallel to the dorsal region of the distal segment of the maxillary palp on the distal extremity.

Sensilla trichodea were distributed at the ventral region of the maxillary palp, they were hairs sharply tapering at the tip and recessed in a depression in the cuticle (Fig. 6C).

The apical tip of the distal segment of the maxillary palp was a concave disc carried a sensory field (ssf) consisted of s. basiconica (length = 0.9 ± 0.07 µm, width = 0.34 ± 0.01 µm, n = 12.8 ± 0.7) and s. styloconica (length = 0.49 ± 0.07 µm, width = 1.05 ± 0.15 µm, n = 10.8 ± 0.9). Sensilla basiconica (sb) and styloconica (sst) were intermingled and distributed around the perimeter of the sensory field (Fig. 6B). Sensilla basiconica were pegs tapered from the base to the apex and the apical extremity formed a triangular shape (Fig. 6B), their structure may dedicate the olfactory or gustatory functions. Sensilla styloconica were peg-like structures, set on top of conical cuticular styles attached to the cuticle ended with apical nipples, with a basal diameter of 2.18 ± 0.3 µm (Fig. 6B). In addition, two sensilla ampulacea at the periphery of the sensory field of the apical segment of the maxillary palp were detected.

The galea of maxilla consisted of two segments (Fig. 5A and C), the distal one was fringed with a tuft of long s. basiconica (length = 20.4 ± 1.13 µm, basal diameter = 0.87 ± 0.01 µm, n = 42.3 ± 2.28). These sensilla were thick, smooth and curved rods with blunt tips.

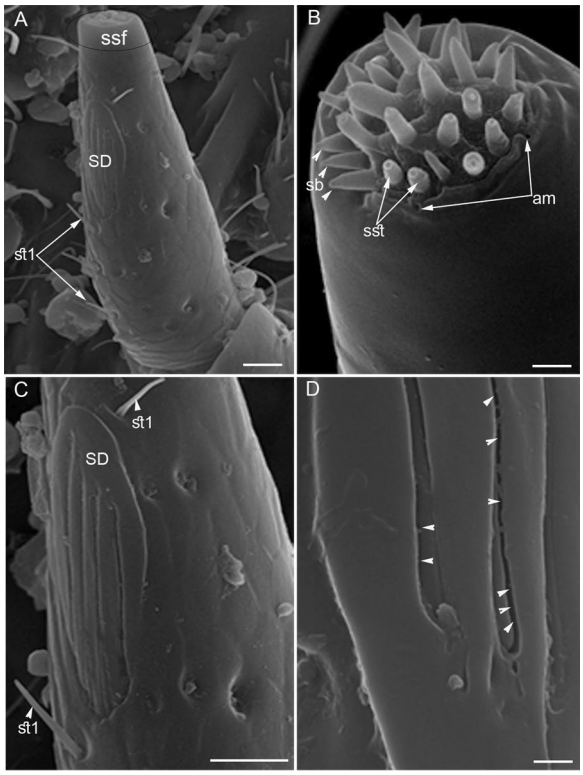

Fig. 6 Scanning electron micrographs (SEM) of close up view of the distal segment of the maxillary palp of adult *Rhyzopertha dominica* and their associated sense organs. **A** Distal segment of the maxillary palp with numerous short s. trichodea (st1) and single large s. digitiformium (SD), note that the apical tip of the palp carry an apical sensory field (ssf); scale bar = 10 µm. **B** Enlarged view of the apical part of the maxillary palp carried s. styloconica (sst), s. basiconica (sb) and s. ampullacea. Scale bar = 2 µm. **C** Close up view of s. digitiformium showing longitudinal gutters. Scale bar = 10 µm. **D** enlarged view of the base of s. digitiformium showing internal pores inside the longitudinal gutters (arrow heads). Scale bars: **A** 10 µm; **B** 2 µm; **C** 10 µm; **D** 1 µm

Discussion

In this study, we focused on the morphology, structure as well as the distribution pattern of the sensilla found on antennae, maxillary and labial palpi of the adult lesser grain borer, *R. dominica*. These organs were significantly equipped with more sensory sensilla which are involved in the chemical communication during its life. Interspecific and intraspecific chemical interactions are generally mediated by pheromones and allelochemicals (Song et al., 2017). Stored grain pests, including *R. dominica* mainly depend on the chemical cues to detect, infest and ingest their food (Oehlschlager et al., 1988).

Sensilla of antennae

In this study, five types of sensilla, including s. trichodea, two subtypes of s. basiconica, s. chaetica, s. ampullacea and Böhm's bristles, were identified in details in adult *R. dominica* by scanning electron microscope (SEM). The antennal sensilla are important sensory organs for insect communication and survival, and they are in direct contact with their environment (Nakanishi et al., 2009). The relative number and diversity of sensilla found in antennae of *R. dominica* are close in magnitude to those reported previously for other members of Coleoptera, such as *Agrilus mali* (Coleoptera: Buprestidae) (Yi et al., 2016), *Callosobruchus chinensis* (L.), *C. maculatus* (F.) (Coleoptera: Bruchidae) (Hu et al., 2009) and *Tribolium castenium* (Coleoptera: Tenebrionidae) (Seada & Hamza, 2018).

In the present study, Böhm's sensilla (BBs) were found only on the first two segments of the antennae which was in accordance with other studies. They had a typical feature of mechano-sensitive receptors that perceive the common pressure on the cuticle produced by the movement of the antennae (Hao et al., 2020a; Merivee et al., 2002). Böhm's sensilla were classified by Schneider (1964) as s. chaetica, but these setae were shorter and sharper than s. chaetica which were arranged in clusters at the base of the scape and pedicel.

The s. trichodea of antennae of adult *R. dominica* were abundant at the three distal club flagellar segments, suggesting that these sensilla were serving as olfactory receptors. They were widely believed to be olfactory sensilla (Yang et al., 2009). Typically, *Hippodamia convergens* (Coccinellidae) did not respond to odors when their s. trichodea were removed, which deduced their responsibility for long-range olfactory reception (Hamilton et al., 1999). In *Rhynchophorus palmarum* (Coleoptera: Carabidae), s. trichodea were described as chemoreceptors to sex or aggregation pheromone (Merivee et al., 2002). Sensilla trichodea were common types in antennae of different beetles and densely located on the tip of the flagellum (Chi et al., 2009; Srivastava & Omkar, 2003). Sensilla similar to s. trichodea of this study had been described in different beetles, e.g. *Bembidion lampros* (Hbst.), *Dastarcus helophoroides* (Fairmaire), and *Agrilus mali* (Ploomi et al., 2003; Ren et al., 2012; Yi et al., 2016).

In the current study, s. basiconica (sb1-sb2) were the second most frequent type found in the three club flagellar segments (cl1–cl3) of adult *R. dominica*. In contrary to s. trichodea, both subtypes of s. basiconica were found only on the dorsal side of all club flagellar segments. Basiconic sensilla of antennae of *R. dominica* were straight and smooth walled with blunt (sb1) or sharp tips (sb2) without setting in basal sockets. Based on the porous characteristics and previous publications, the two subtypes of s. basiconica of *R. dominica* may perform a chemo-receptive function (Lopes et al., 2002; Zacharuk, 1985). Commonly, aporous sensilla work as mechanoreceptors, thermoreceptors, or hygroreceptors receptors while porous sensilla work as chemoreceptors (e.g. olfactory and gustatory) (Keil, 1999; McIver, 1985). Similarly, antennal s. basiconica of *Tetrigus lewisi* and *Callosobruchus chinensis* considered to play critical roles in odor sensing for searching relevant habitat and food resources (Ren et al., 2014; Wang et al., 2018).

Indeed, the structure characteristics of s. basiconica vary greatly among different insect groups, however, all s. basiconica share common features; i.e. lower in height and have much more wall pores in comparison to trichoid sensilla (Shields, 2004). The basiconic sensilla in this study were similar in external morphology to some basiconic sensilla found in other beetles, i.e. *Agrilus mali*, *A. planipennis*, and *Dastarcus helophoroides* (Fairmaire) (Ren et al., 2012; Yi et al., 2016). The basiconic sensilla of *Phoracantha semipunctata* (Coleoptera: Cerambycidae) were found to be tuned and specialized for a particular set of host and non-host volatiles (Lopes et al., 2002). Ali et al. (2016) reported that the basiconic sensilla of distal three flagellar segments of *Tribolium castaneum* (Coleoptera: Tenebrionidae) play a major role in the fast location of food sources, whereas the removal of the last three flagellar segments increased the time spent in making a choice.

As the most abundant among all sensilla classes in our study, external structure of trichoid and basiconic sensilla might represent the major portion of the olfactory repertoire on the antennae of *R. dominica.* Thus, they could be important for long-range chemosensory perception of environmental cues. Typically, s. trichodea and s. basiconica were the basic types that distributed on the antennae of all studied coleopteran species (Hao et al., 2020a).

In the current study, s. ampullacea were recessed in a pit at the dorsal region of the scape and flagellum of antennae of *R. dominica* and their morphology was noticeably distinct from other sensilla types. This is not optimal for receiving chemical stimuli, but is likely a necessary adaptation to prevent desiccation (Kristoffersen et al., 2006). Accordingly, s. ampullacea might also participate in the processes of hygro- and thermoreception (Kleineidam & Tautz, 1996; Ruchty et al., 2010) and the perception of CO2 (Kleineidam & Roces, 2000). Correlated to the abundance of hair sensilla, s. ampullacea have been found in low numbers on the antennal club of *R. dominica* (Sawires & Elbassiouny, 2019) and other insects as well (Renthal et al., 2003; Romani et al., 2010). Hao et al. (2020a) found that s. coeloconica of *Hippodamia variegata* (Coleoptera: Coccinellidae) were small pit organs, which were similar to s. ampullacea that were

observed in our study. Similarly, sensilla cavity in *Callosobruchus septempunctata* (Srivastava & Omkar, 2003) and *C. chinensis* (Wang et al., 2018) have the same structure of s. ampullacea of *R. dominica*.

In the present study, s. chaetica found on the antennae of adult *R. dominica* were mainly distributed on the distal region of the club flagellomeres (cl1–cl3) with a few number and surrounded by a deep and thick circular furrow coupled with a wall around. Characterized by their thick wall and specific distal location might suggest a contact-chemoreceptive function (Ryan, 2002). Similarly, s. chaetica of *Psylliodes chrysocephala* were suggested to be contact chemosensilla responded to chemicals presented in plant surface waxes (Isidoro, 1998). Borg and Norris (1971) assumed that s.chaetica found on the antennae of *Scolytus multistriatus* were mechanoreceptors allowing the insect to explore the position of the antenna in relation to the surrounding. Sensilla chaetica were also common on the antennae of many other insects (Chi et al., 2009; Hao et al., 2020a; Seada & Hamza, 2018; Wei et al., 2015).

palpi

It is worth noting that, there is a great species diversity and very broad range of trophic relations and modes of feeding in Coleoptera. In our study, both maxillary and labial palps of adult *R. dominica* have similar sets of numerous sensilla; however the labial palp carried more longer sensilla trichodea. Similarly, the sensory organs of the maxillary and labial palps of Dytiscidae and Dermestidae have very similar groups of sensilla (Alekseev et al., 2006). An increase in the number of sensilla in the sensory organs should apparently facilitate a better perception of information from the surrounding (Merivee et al., 2002). Various studies described the morphology of the mouthparts of Coleoptera insects (Hao et al., 2020b; Moon, 2015; Seada & Hamza, 2018), but no reports have focused on *R. dominica*.

The data of the current study revealed that sets of sensilla present on both maxillary and labial palpi of adult *R. dominica* had different types of sensilla, among them, two subtypes of s. trichodea (st1 and st2), which were more widespread and abundant all around the palpal segments. In addition, specialized sensory apical area at the last distal segment of the maxillary and labial palpi had different kinds of s. basiconica, s. styloconica and ampullacea. Despite, they have been distinguished but could not be counted in the labial palp as they were concealed inside. In contrast, there was only one big sensillum digitiformium on the lateral side of the distal segment of the maxillary palp. External structure of trichoid sensilla; sharp tips and flexible sockets might dedicate the mechanosensory function. Seo and Youn (2000) found that the maxillary and labial palpi of *Hippodamia variegata* (Coleoptera: Coccinellidae) were mainly used as mechanoreceptors. Furthermore, s. trichodea in this species appeared to be identical to those found on the labial palp of *Pyrrhocoris sibiricus* (Wang & Dai, 2017). However, the similarity of the s. digitiformium to morphologically or physiologically characterized s. auricillica in other insects might suggest the olfactory function. Sensilla digitiformium have been described in different insect species, i.e. on the tip of the ovipositor of *Dyseriocrania subpurpurella* (Lepidoptera: Eriocraniidae) (Faucheux, 2008), on the labial palps of *Ctenicera destructor* (Coleoptera: Elatridae) which responded electrophysiologically to contact and vibratory stimuli (Zacharuk et al., 1977). Furthermore, sensilla digitiformia were suggested to be sensitive to temperature (Devitt & Smith, 1982). In *Helicoverpa armigera* caterpillars the digitiformia sensilla on the maxillary palp was probable candidate for the CO2-receptor (Keil, 1996). It has been also found also on the maxillary palp of larvae of *spodoptera littoralis* (Awad et al., 2015).

The galea of maxillae of *R. dominica* had a dense tuft of long s. basiconica these sensilla were curved with blunt tips and smooth surfaces which assume a gustatory or olfactory functions. Zacharuk (1985) proposed that s. basiconica and s. styloconica correspond to the uniporous sensilla with a sculptured porous point through the cuticle. Behavioral investigations on herbivorous insects indicated the significance of the gustatory sensilla of the galea of maxillae on the feeding process (de Boer, 2006). In contrast, a single type of an olfactory basiconicum sensillum on the last distal segment of the maxillary palp of adult *Toxorhynchites brevipalpis* (Diptera: Culicidae) had been found (McIver & Siemicki, 1984).

Correspondingly, the species that have a limited range of diet like *R. dominica* have a smaller number of sensilla on the palpi. In preceding studies, functional types of olfactory and gustatory sensilla were found on the palpi of different insects (Guo et al., 2018; Zhao et al., 2013).

Conclusions

This study is the first to characterize the sensilla found on mouth parts of an important invasive beetle; *R. dominica*. Differences in the numbers and distribution of various sensilla in different organs of the beetle like antennae, the main organ for olfaction, and palpi which responsible for the taste of food were also evaluated. Such studies would clarify the expected functional roles of various insect sensilla in sensing pheromones, and host and non-host chemicals, which could ultimately lead to developing novel efficient control strategies.

Abbreviations

amp	Sensilla ampullaceal
ant	Antenna
Bbs	Böhm's sensilla
cl1–cl3	Distal club flagellomeres
gl	Galea of maxilla
fl1–fl5	Basal flagellomeres
lb	Labrum
lp	Labial palp
md	Mandible
mp	Maxillary palp
mt	Microtrichea
pe	Pedicel
sb1 and sb2	Sensilla basiconica
sc	The scape
SD	Sensilla digitiformium
SEM	Scanning electron microscopy
st1 and st2	Sensilla trichodea
ssf	Sensory field
sst	Sensilla styloconica

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MAS and AMH had the idea for the article, conducted, analyzed, and wrote the manuscript. The first draft of the manuscript was written by MAS. All authors read and approved the final manuscript.

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Declarations

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