Ultrastructure morphology of antennae and mouthparts of in-vasive pest Aethina tumida (Coleoptera: Nitidulidae)

Xiao-Xiao Chen
Gansu Agricultural University
Rui-Ling Chen
Northwest A&F University
Ding-Kun He
Northwest A&F University
Min Huang (huangmin@nwsuaf.edu.cn)
Northwest A&F University

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Abstract

The small hive beetle (SHB), as one of the six major pathogens of honeybee, has invaded China in recent years and caused serious harm to the apiculture industry of China. In order to explore the feeding mechanism of *Aethina tumida*, we used scanning electron microscopy for the first time to conduct a detailed study on the morphology and structure of antennae and mouthparts, including the distribution and abundance of sensilla. The results showed that its clavate antennae and chewing mouthparts are similar to those of other nitidulid on the structure and types of sensilla. There are 5 types of sensilla were identified on antennae: 3 subtypes of sensilla chaetica (SC), 1 type of sensilla trichodea (SP), 6 subtypes of sensilla basiconica (SB), 2 subtypes of sensilla styloconica (SS) and 1 type of Böhm bristles (BB); 8 types of sensilla on mourthparts: 1 type of SC, 8 subtypes of SB, 2 subtypes of SP, 2 subtypes of SS, 1 type of SM, 1 type of sensilla coelocinica (Sco), 2 subtypes of campaniformia (Scam) and 1 type of BB. We also compared the differences of sensilla with the only reported nitiduline species *Omosita colon* and inferred their sensory function.

1. Background

Antennae and mouthparts are important appendages with numerous sensory structures for external stimuli. Antennae are the main olfactory and tactile organs that can sense chemical and mechanical actions for foraging, mating, gathering and finding spawning groups (Na et al. 2008; Li and Chen 2010; Du et al. 2015) Mouthparts are feeding structures for detection of feeding and host plants (Li et al. 2013). The complexity and diversity of the structure of insect mouthparts and antennae are the result of evolution (Wang et al. 2019), therefore, exploring the morphology and sensilla, as well as analysing their function and differences among species are important for the understanding of insect feeding habits and their evolution, also for providing more accurate control strategies to agricultural pests (Yin and Fu 2011). So far, a great deal of researches have been done on morphology and sensilla in the antennae and mouthparts of Coleoptera on Cerambycidae (Yin and Jiang 1995; Hu et al. 2001; Zhuge et al. 2009; Zhang et al. 2011), Carabidae (Kin and Yamasaki 1996; Liu and Tian 2008; Giulioa et al. 2012), Scolytidae (Chen and Tang, 2006; Yang et al. 2010), Elateridae (Merivee 1992), Scarabaeidae (Merivee et al. 1992; Fei et al. 2012), Curculionidae (Yin et al. 2011; Smith et al. 1976; Kang et al. 2012), but few reports on Nitidulidae (Ortloff et al. 2014; Cao and Huang 2016).

The family Nitidulidae is a polyphagous insect with a wide distribution. They feed on stored crops, flowers, fungi and decayed plant and animal tissues. The nitiduline species *A. tumida* Murrary, 1867, usually called as small hive beetle (SHB), is regarded as a serious invasive pest which is a free-living predator, parasite and scavenger of honey bees (Arbogast et al. 2012; Pirk 2017). Females of *A.tumida* usually lay eggs in the small cracks, crevices and even under the cell cappings of sealed hives (Pirk 2013). The larval stage of *A. tumida*, as the main stage of damage to bee colonies, mainly feed on honey, pollen, honeybee eggs and brood, causing the death of the brood, honey fermentation and comb destruction, eventually resulting in the colony weakens and complete structural collapse of the nest (Pirk 2017; Lounsberry et al. 2010; Zhao et al. 2019).

A. tumida is native to sub-Saharan Africa and regarded as a minor pest. In 1996, it was first discovered in the United States and then spread rapidly in America and caused serious damage to the beekeeping industry (Neumann and Elzen 2019; Spiewok et al. 2007). Later, it gradually spread to Australia, America, Asia and other countries, causing different degrees of colony damage and economic loss (Zhao et al. 2019; Evans et al. 2003; Lee et al. 2017; Toufailia et al. 2017). In 2017, *A. tumida* firstly invaded into the coastal areas of China, and broken out in Hainan, Guangdong and Guangxi provinces in 2018. It can infect both Apis cerana cerana Fabricius and Apis mellifera ligustica Spinola and has caused serious damage to local bee colonies (Zhong et al. 2020). At present, many countries have listed *A. tumida* as quarantine objects and restricted the entry of bee products, species and equipment from the epidemic area. If the spread of *A. tumida* cannot be controlled in time, it will seriously affect the international trade of bee products and the healthy development of the bee industry in China (Zhao et al. 2019).

Previous paper about *A. tumida* mainly focused on traditional morphology, biology and pest control (Bernier et al. 2014; Halcroft et al 2011; Torto et al. 2010), but there is a lack of the ultrastructure morphology and sensilla studies on the important sensory organs. This study is devoted to the detailed study on the fine structure of mouthparts and antennae and the position of different types of sensilla on them by scanning electron microscope (SEM), and the possible functions of these sensilla are discussed to provide more data for further researches on the relationship between sensilla with behavior and co-evolution of insects and feeding objects.

2. Materials And Methods

2.1. Insects

Adults of A. tumida were collected from Guangzhou Province in August 2018, and preserved in 95% alcohol and stored at -20°C.

2.2. Scanning electron microscopy

Removed head from body with a dissecting needle and tweezer under a Leica M205A microscope, then dehydrated with 100% ethanol twice for 30 min each. Change different grades of tert-butanol and alcohol solutions (tert-butanol: alcohol was 3:1, 1:1, 1:3) for 15 min each time, and finally use 100% tert-butanol for 30 min. The dissected head was pasted on the sample table with double-side copper sticky tape after drying, then sputtered with gold/palladium (40/60) using a high resolution sputter coater (MSP-1S SHINKKU VD, Tokyo, Japan), lastly observed with a T-3400 SEM (Hitachi, Tokyo, Japan) operated at 15 kV or Nova Nano SEM-450 (FEI, Hillsboro, OR, USA) at 5–10 kV.

2.3. Data analysis

Photographs were observed and retouched with Adobe Photoshop CS6 (Adobe Systems, San Jose, CA, USA). Statistical analysis was performed using SPSS 19.0 (SPSS, Chicago, IL, USA). Measurements were made using Image J (win64).

2.4. Terminology

In this paper, the terminology mainly followed Schneider (1964) and also referred the published articles on Coleoptera (Merivee et al. 2001; Bartlet et al. 1999).

3. Results

3.1. Antennae

3.1.1. Gross morphology of the antennae

The antennae of A. tumida compose of 11 segments, including scape, pedicel and 9 flagellums (Figure 1). Antenna usually places in the antennal groove on the ventral surface during resting. Scape connects with head through antennifer, and with outer margin obtuse. Pedicel is cylindrical and constricted basally. Flagellums 1–6 gradually become shorter and wider, and flagellum 6 is almost disc-like. The last three segments of flagellums are swollen and gradually narrower, collectively known as uncompact antennal club. The lengths of the male and females are 975.6 ±15.0μm and 972.9±8.0μm, respectively (Table 1), and there are no significant sexual differences in the length of each segment ($P > 0.05$). Antennal club has the most abundant types and quantity of sensilla, especially on the apex of terminal segment, followed by the scape and pedicel, flagellums 1–6 are least.

3.1.2. Sensilla on antennae

5 types and 13 subtypes of sensilla were identified on antennae: 3 subtypes of sen-silla chaetica (SC), 6 subtypes of sensilla basiconica (SB), 1 type of sensilla trichodea (ST), 2 subtypes of sensilla styloconica (SS) and 1 type of Böhm bristles (BB). The division standards of antennal sensilla are presented in Table S1. The number and types of sensilla on the dorsal side of the antenna are more than those on the ventral side, and the antennae club has the most abundant types and numbers of sensilla.

Sensilla chaetica (SC) are long setae or spines, usually perpendicular to the cuticula and higher than other sensilla. They are divided into three subtypes (SC1, SC2 and SC3) ac-cording to the length and surface grooves.

Sensilla chaetica 1 (SC1) are the longest and most numerous long setae. They have sharp tips, longitudinal grooved walls and scattered into wide sockets, measure 96.86±6.24μm in length and 6.98±0.4μm in basal diameter. They are normally straight on the lateral margin of flagellum, especially the lateral and anterior margins of antennal club and curved on the outer margin of scape (Figures 2–A, C; Figure 3–A, D).

Table 1

Length and width of antennal segments of male and female A. tumida

Sex		Scape	Pedicel	Flagellum (μm)									Total (μ
		(μm)	(μm)	1	2	3	4	5	6	7	8	9	
Male	length	213.9±0.6	116.2±1.9	102.7±0.4	54.6±1.5	49.4±1.8	40.4±0.8	43.4 ±1.9	42.7 ±1.9	81.9±0.5	76.4 ±3.0	154.1±2	
Female	length	162.1±1.9	119.5±0.8	102.3±0.8	55.5±0.3	57.2±0.6	49.5±0.5	52.5 ±2.5	49.7 ±0.5	84.8 ±3.7	84.3±0.6	155.5±1	

Sensilla chaetica 2 (SC2) are long straight setae. They have sharp tips, smooth walls and scattered into tight sockets, measure 65.1±3.6μm in length and 6.5±0.3μm in basal diameter. They are inserted on pedicel and scape (Figure 3–A and D).

Sensilla chaetica 3 (SC3) are the shortest spines, located at pedicel, flagellum 9 and basal of scape. They have blunt point tips and V-shape grooved walls, and no obvious socket at base, measure 24.0±1.6μm in length and 4.6±0.3μm in basal diameter (Figure 3–A and E).

Sensilla trichodea (ST) are long and curved hairs, gradually narrower towards apex. They have sharp tips, longitudinal grooved walls and wide sockets. They are numerous and mainly distributed on antennal club, measure 17.2±0.3μm in length and 3.6±0.1μm at basal diameter (Figure 2–B and D).

Sensilla basiconica (SB) are short and cone-shaped with the most abundance on the antennae. According to the external morphological characteristics, they can be divided into 7 subtypes (Figure 2–3).

Sensilla basiconica 1 (SB1) are long-rod shaped and have the most length among all subtypes, measure 12.1±0.5μm in length and 2.6±0.1μm at basal diameter. They are straight, thin and inserted into wide sockets with tips blunt pointed and walls smooth basally and rough apically. They are only distributed in the flagellum 9 (Figure 2–B and E).

Sensilla basiconica 2 (SB2) are short and straight. They are characterized by tips sharped, walls smooth at half base and longitudinal grooved apically and sockets tight. They only distributed at terminal segment of antennal club (Figure 2–B and F).

Sensilla basiconica 3 (SB3) are corn shaped, straight or curved. They have blunt tips and alternating grooved walls, usually inserted in tight sockets. The length is 3.7±1.6μm and the basal width is 1.6±0.3μm, and only distributed on antennal club (Figure 2–B and G).

Sensilla basiconica 4 (SB4) are typical of cuticular finger-like protuberances extending tapered from base to apex. The tips are blunt point and walls are alternating grooved. They are the least antennal sensilla which inserted in wide sockets on antennal club, measure 2.1±0.1μm in length and 1.4±0.03μm at basal diameter (Figure 2–B and I).

Sensilla basiconica 5 (SB5) are ear shaped and looking like flatted SB3. They are straight or slightly curved, and inserted in wide sockets. They are 4.1±0.3μm in length and 1.99±0.08μm in basal width and all located in flagellum 9 (Figure 2–A and J).

Sensilla basiconica 6 (SB6) are upright with smooth walls and bifurcate tips. They are inserted in wide sockets on anrennifer, measured 4.3±1.6μm in length and 2.7±0.2μm in basal diameter (Figure3–B, C and F).

Sensilla styloconica (SS) are cone shaped on raised cuticle. They are divided into 2 sub-types according to their lengths.

Sensilla styloconica 1 (SS1) are short-cone shaped. They are straight with blunt point tips and smooth walls. They are inserted in wide sockets and measure 1.7±0.1μm in length and 3.8±0.1μm in basal width, and only located in middle of antennal club (Figure 2–H).

Sensilla styloconica 2 (SS2) are figure-like, they are straight or slightly curved with blunt tips and alternating grooved walls. They are inserted in wide sockets and measure 6.0±0.2μm in length and 4.3±0.1μm in basal width, and located in the anterior margin of flagellum 7 and 8 (Figure 2–A and K).

Böhm bristles (BB) are straight and short spines, clustered at anternnifer. They have sharp tips and smooth walls, and scattered into wide sockets, measure 3.9±0.2μm in length and 2.6±0.1μm at basal diameter (Figure 3–A and C).

3.2. Mouthparts

3.2.1. Gross morphology of the mouthparts

A. tumida has typical chewing mouthparts same as other insects of Coleoptera, consisting of five parts (Figure 4–B). Labrum consists of an ossified outer lip (Figure 4–A) and a soft hairy epipharynx (Figure 7–B). It forms the upper cover of the mouthpiece to prevent food from failing off, and the anterior margin of labrum is emarginated to help feeding from the edge of food. A pair of mandibles (Figure 4–C) located behind labrum, consist of apical incisor lobes for cutting and tearing food, and basal molar lobes for grinding food. A pair of maxillae located behind mandibles, consist of cardo, stipes, galea, lacinia and maxillary palpus (Figure 5–A and B). Labium is used as the posterior wall of mouthparts to hold food and consists of postmentum, prementum, paraglossa, glossa and labial palpus. Postmentum is located at base of labium and consists of submentum and mentum. Paraglossa and glossa are collectively called lingual (Figure 6–B). Hypopharynx is located in the center of preoral cavity, helping to transport and swallow food.

3.2.2. Sensilla on mouthparts

8 types of sensilla were identified on mouthparts, including sensilla chaetica (SC), 8 subtypes of sensilla basiconica (SB), 2 subtypes of sensilla placodeum (SP), 2 type of sensilla styloconica (SS), sensilla multicobular (SM), 1 type of sensilla coelocinica (Sco), 2 subtypes of campaniformia (Scam) and 1 type of Böhm bristles (BB). The division standards of sensilla on mouthparts are presented in Table S2.

Sensilla chaetica (SC) are straight spine with sharp tips and inserted in wide sockets, with longitudinal grooved walls and measured 41.0±4.6 in length and 3.3±0.3 in basal diameter. They are distributed on lateral margin of cardo, sripes, mandile and labium (Figures 4–A, C; 5–B, F and 6–B).

Sensilla basiconica 1 (SB1) are short and upright cone-shaped. They have sharp tips and smooth walls; they are inserted in wide and deep sockets, measured 4.1±0.1μm at length and 1.5±0.2μm at basal diameter. They are only distributed on maxillary palpus (Figure 5–B, H and I).

Sensilla basiconica 2 (SB2) are finger-liked. They are straight with walls smooth; tips blunt with a small pore apically. They are 3.3±0.5μm in length and 1.9±0.7μm in basal diameter, and only distributed on sensilla region of terminal segment of maxilla and labium palpus (Figures 5–G and 6–A, C).

Sensilla basiconica 3 (SB3) are straight with smooth walls and bifurcate tips. They are measured 4.7±0.2μm in length and 1.8±0.1μm in basal diameter. They are inserted in wide sockets, and only symmetrically distribute in both sides of inner margin of epipharynx (Figure 7–A, F and I).

Sensilla basiconica 4 (SB4) are small and short cone-shaped. They are straight with smooth walls and a pore at top of blunt tips. They are inserted in wide sockets and measured in 2.1±2.0μm in length and 2.5±0.2μm at basal diameter. They are distributed on the epipharynx (Figure 7–E and K).

Sensilla basiconica 5 (SB5) are hemispherical with smooth walls and a pore at top of blunt tips. They are inserted in wide and deep sockets and measured 2.7±0.1 in length and 2.9±0.1 in basal diameter. They are distributed on the epipharynx (Figure 7–B and D).

Sensilla basiconica 6 (SB6) are hemispherical. Tips blunt with a pore, walls smooth and inserted in wide sockets. They are measured in 1.9±0.1μm in length and 2.0±0.03μm in basal diameter, and only distributed on the epipharynx (Figure 7–J, K).

Sensilla basiconica 7 (SB7) are hemispherical and straight. Tips blunt with double pores, walls smooth and inserted in wide sockets. They are measured in 1.6±0.1μm in length and 2.7±0.04μm in basal diameter, and only distributed besides SB6 (Figure 7–J, K).

Sensilla basiconica 8 (SB8) are short cylindrical with constricted apex. They are inserted in a deep socket and measured 3.3±0.1 in length and 2.1±0.2 in basal diameter. They are distributed in pairs on the lateral margin of epipharynx (Figure 7–B, C).

Sesnsilla placeodeum (SP) are long stripes that grow inside tight depressions of cuticle. They are straight with smooth walls, and are divided into two subtypes according to their lengths. Sensilla placodeum 1 (SP1) are measured 25.3±0.5μm in length and gathered symmetrically at the base of the lateral margin of the terminal segment of maxilla palpus (Figure 5–B, D). Sensilla placodeum 2 (SP2) are measured 12.9μm in length and distributed singly at the lateral margin of the terminal segment of maxilla palpus (Figure 5–B, E).

Sensilla styloconica (SS) are sensory cones and inserted in elevations of the cuticle. They are medium-sized, thick and straight with smooth walls and surrounding with Sco. There are two subtypes according to the length and shape of tips.

Sensilla stylocoica 1 (SS1) are blunt at tips and measured 2.8±0.2 in length and 2.4±0.1μm in basal diameter, and concentrated in the sensilla field at tip of terminal segment of maxillary palpus (Figrue 5–G).

Sensilla stylocoica 2 (SS2) are flower-like at tips and measured 7.6±0.3μm in length and 7.6±0.3 in basal diameter, and concentrated in the sensilla field at tip of terminal segment of labium palpus (Figrue 6–A, C).

Sensilla multicobular (SM) are flower-like or bract-shaped and appear to consist of many cones that curve from base to top. They have rugose walls and no obvious sockets, measured 1.3±0.6μm in length and 2.4±0.6μm at basal diameter. They are clustered and only distributed at the end of the sensilla fields at the top of terminal labium palpus (Figures 6–A, D).

Sensilla coelocinica (SCo) are nipple-like. They are short and thick with smooth walls, tips blunt with a pore. They are 2.7±0.1μm in length and 2.9±0.9μm in basal diameter. They are inserted in the pit formed by raised cuticle, distributed along the margins of sensilla fields at the top of the terminal segment of labium and maxillary palpus, and symmetrically arranged along the middle of glossa (Figures 5–G; 6–A, B, C, E).

Sensilla campaniformia 1 (SCam1) are hemispherical concave cuticle, with small projections medially. They are symmetrically located at base of epippharynx. They are measured 3.3±0.2μm in width (Figure 7–B, G).

Sensilla campaniformia 2 (SCam2) are oval concave cuticle. They are symmetrically located at apex of epippharynx. They are measured 5.1±0.4μm in width (Figure 7–B, H).

Böhm bristles (BB) are short, straight and cone shaped. They have sharp tips and smooth walls. These sensilla measured 6.9±0.3μm in length and 3.2±0.2μm at basal diameter, all of them arranged along outer margin of lacinia (Figure 5–A, C).

Table 2

Comparison of the antennal sensilla of *O. colon*, *M.* (*O.*) *chinensis* and *A. tumida*.

Species	Feed Habit	Sex	ST	SC	SB	BB	SS	SCa	SCo	Total
O. colon	Saprophagy	Male	3	2	3	1	1	1	\	6 types
(in Cao and Huang (2016))	(corpses of bovine)	Female								11 subtypes
M.(O.) chinensis	Phytophagy	Male	3	1	3	1	3	1	\	6 types
(in Li (2021))	(Host plant:									12 subtypes
	Rubus idaeus	Female	3	2	3	1	3	1	1	7 types
	flowers)									14 subtypes
A. tumida	Saprophagy	Male	1	3	6	1	2	\	\	5 types
(in this study)	(honey)	Female								13 subtypes

Table 3

Comparison of the sensilla on the mouthparts of *O. colon*, *M.* (*O.*) *chinensis* and *A. tumida*.

Species	Feed Habit	Sex	ST	SC	SB	BB	SP	SCo	SCam	SM	SS	Total
O. colon	Saprophagy	Male	1	2	7	1	2	1	2	\	\	7 types
(in Cao and Huang (2016))	(corpses of bovine)	Female										16 subtypes
M.(O.) chinensis	Phytophagy	Male	2	2	7	1	2	2	1	\	\	7 types
(in Li (2021))	(Host plant:											17 subtypes
	Rubus idaeus	Female	2	2	6	1	2	2	1	\	\	7 types
	flowers)											16 subtypes
A. tumida	Saprophagy	Male	\	1	8	1	2	1	2	1	2	8 types
(in this study)	(honey)	Female										18 subtypes

4. Discussion

4.1 Comparison of the morphology of the antennae and mouthpart of O. colon, M. (O.) chinensis and A. tumida.

Antennae of *A. tumida* are obviously shorter than its head width, the antennae are 0.8 times the width of head, while antennae of *O. colon* are longer than its head width, the antennae are 1.1 times the width of head, and antennae of *M.* (*O.*) *chinensis* are shorter than its head width, the antennae are 0.9 times the width of head. *A. tumida* has semicircular scape, flagellum 1 longest, flagellum 2–6 showed little difference in length, but flagellum 4–6 gradually widened and obviously discoid. *O. colon* has cylindrical scape, flagellum 1 longest, flagellum 1–3 obvious longer than flagellum 4–6, flagellum 4–6 not enlarged to discoid. *M.* (*O.*) *chinensis* has semicircle-like scape, flagellum 1 longest, flagellum 1-3 obvious longer than flagellum 4-6, flagellum 5-6 gradually widened and flagellum 6 obvious discoid. Antennal club of *A. tumida* is almost the same in length and width, *O. colon* with length 1.2 times as the width, and *M.* (*O.*) *chinensis* with length 1.1 times as the width.

Both phytophagous (anthophagous) nitidulid and saprophagous nitidulid have an ossified outer lip. The top of the epipharynx of *A.tumida* is partially coalescent and the overall shape is similar to that of *O.colon*. The fimbria apicale are connected to the pectin laterals, with a small number of median bristle on the middle part of the epipharynx. Bushy fimbria apicale and median bristle crest on the epipharynx of phytophagous nitidulid (*M.* (*O.*) *chinensis*), and there are thick pectin laterals on the side bristle. The top of the epipharynx of *O.colon* is almost coalescent, the fimbria apicale is dense, the median bristle crest is regressed, and pectin laterals on the side bristle are gathered in the middle to form a semi-ellipse.

The mandibles of the three species have the same structure, but differ in the num-ber of incisors and the degree of development of mandibles and molars. *O. colon* and *A. tumida* have significantly less robust mandibles, but lateral margins with developed sensory hairs. Incisors ossified, shout and bifurcated apically to form two teeth. Molars are strongly ossified and extremely thriving, protruding medially with transverse notches. Flexile prostheca links incisor and molar to coordinate their activities. *M.* (*O.*) *chinensis* have stout mandibles of similar length and width. Incisors strongly ossified, with one sharped tooth. Molars same as the former, but less developed. Prostheca are relatively developed.

The lacinia of *O. colon* and *A. tumida* are very developed with dense chaetae and similar in appearance, and the lacinia and the galea are coalescent. The stipes ventralis of them are all trapezoids with wider bases, but A. tumida's is more developed with more chaetae on the outside. The lacinia of *M.* (*O.*) *chinensis* is less developed and the galea is developed with dense chaetae apically. The stipes ventralis are curved, concave inward on one side near the palpi and convex on the other side. The maxillary palpus of all three species is composed of four segments, with the first three segments shorter and the last segment longest.

The labium all consists of five parts. All three species have developed pentagonal mentum. The whole paraglossa is nearly V-shaped, but paraglossa longest in *A. tumida* and shortest in *M.* (*O.*) *chinensis*. The paraglossa of *A. tumida* and *O. colon* are obviously more developed than that of *M.* (*O.*) *chinensis*, and with denser sensory hairs medially and apically. The labial palpus of all three species consists of three segments, but the last segment of *A. tumida* is sharply tilted, *O. colon* is slightly tilted, and *M.* (*O.*) *chinensis* is flat.

The differentiation of food habits is the result of collective long-term natural selec-tion and evolution. Insects with similar food habits have relatively similar mouthparts in morphology and structure, and vice versa. In conclusion, the mouthparts structures of the three species are similar, but *O. colon* and *A. tumida* are more similar and *M.* (*O.*) *chinensis* have obvious differences on the mandibles. On the one hand, the reason for this difference may be that both *O. colon* and *A. tumida* belong to the subfamily Nitidulinae and are more closely related, but *M.* (*O.*) *chinensis* belongs to the subfamily Meligethinae; on the other hand, it should be related to their feeding habits. Both *O. colon* and *A. tumida* are saprophagous, while *M.* (*O.*) *chinensis* is phytophagous (anthophagous). Saprophagous nitidulid (*O. colon* and *A. tumida*) mainly feed on bones, fermented pollen and honey, while *M.* (*O.*) *chinensis* is mainly feed on flowers of Rubus idaeus. When the food is infected by microorganisms and becomes rotten or fermented, its texture becomes very soft, so saprophagous nitidulid have thinner mandibles and less sharp incisors, because they don't need a sturdy mandibles to help them cut food, but well-developed molars can help them grind food.

4.2 Comparison of the Sensilla on the Antennae and Mouthparts between Saprophagous and Phytophagous nitidulid

In this study, we reported the sensilla on the antennae and mouthparts of both males and females of the invasive pest *A. tumida*. Comparing with the sensilla of the phytophagous (anthophagous) nitidulid (*M.* (*O.*) *chinensis*) reported by Li et al [54] and the saprophagous nitidulid (*O. colon*) reported by Cao and Huang (2016), there are obvious differences on the antennae and mouthparts (Table 2 and 3).

For Nitidulidae, the sensory types of antennae and mouthpart are less studied. Compared with the only reported Nitidulinae species (*O.colon*, *M.* (*O.*) *chinensis*), all of them have typical chewing mouthparts and clavate antennae and have no significant difference in the length of antennae between male and female. Due to the different feeding habits, there are differences in morphology of antennae and mouthparts, and also the differences in the type and number of sensilla, but homologous sensilla have stable distribution sites.

Cao and Huang (2016) found six types of sensilla on the antennae of both males and females of *O. colon*, including sensilla trichodea (ST; three subtypes), sensilla chaetica (SC; two subtypes), sensilla basiconica (SB; three subtypes), Böhm bristles (BB), sensilla styloconica (SS), and sensilla cavity (SCa). Li et al (2021) found six types of sensilla on the antennae of males and seven types of sensilla on the antennae of females of *M.* (*O.*) *chinensis*, including sensilla trichodea (ST; three subtypes), sensilla chaetica (SC; one subtype on males, two subtypes on females), sensilla basiconica (SB; three subtypes), Böhm bristles (BB), sensilla styloconica (SS), sensilla cavity (SCa) and sensilla coeloconica (SCo) which is only present in females. In this study, we found that five other sensilla types except sensilla cavity and sensilla coeloconica are also present in the antennae of males and females. There are also significant differences in the sensilla subtypes. In this study, we found the Böhm bristles-like sensilla (SB6) on the antennifer that have not previously been reported in Coleoptera until now; the finger-like sensilla basiconica (SB4) on an-tennal club; the corn shaped sensilla basiconica (SB3) on antennal club; and the ear shaped sensilla basiconica (SB5) which looks like flatted SB3 on the flagellum nine. Although the number of these newly described sensilla subtypes in Nitidulidae is very small, the position of the same kind of sensilla subtypes is very concentrated.

Cao and Huang (2016) found seven types of sensilla on the mouthparts of *O. colon*, including sensilla trichodea (ST), sensilla chaetica (SC; two subtypes), sensilla basiconica (SB; seven subtypes), sensilla coeloconica (SCo), sensilla placodea (SP; two subtypes), Böhm bristles (BB), and sensilla campaniformia (SCa; two subtypes). Li et al. (2021) found seven types of sensilla on the mouthparts of M. chinensis, including sensilla trichodea (ST; two subtypes), sensilla chaetica (SC; two subtypes), sensilla basiconica (SB; seven subtypes on males, six subtypes on females), sensilla coeloconica (SCo; two subtypes), sensilla placodea (SP; two subtypes), Böhm bristles (BB), and sensilla campaniformia (SCa). In this study, we found that the six types of sensilla on the mouthparts of *A. tumida* are the same as those of *O. colon* and *M.* (*O.*) *chinensis* except sensilla trichodea, and there are two types of sensilla only present in *A. tumida*. Among them, sensilla placodea and Böhm bristles have almost no difference in morphological characteristics in the three Nitidulidae, but there is no sensilla trichodea on the mouthparts of *A. tumida*. Sensilla campaniformia found in *M.* (*O.*) *chinensis* are long, and the sockets are deeper than others. Sensilla campaniformia of *O. colon* are located on a sunken area of the cuticula and are symmetrically distributed on the epipharynx, while Scam of *A. tumida* are small projections located in hemispherical concave cuticle. The subtypes of sensilla basiconica and sensilla coeloconica are significantly different in *A. tumida*, *M.* (*O.*) *chinensis* and *O. colon*. For instance, the sensilla basiconica with one or two pores at the tops of blunt tips (SB5, SB6 and SB7) are found in the *A. tumida* only, and the flower-like or bract-shaped sensilla multicobular with rugose walls. SB5, SB6, SB7 and SM are not found in *M.* (*O.*) *chinensis* and *O. colon*.

4.3 Sensory function and feeding behavior of A. tumida

Similar to other Coleoptera, BB was widely distributed at the base of antennifer (Merivee et al. 2001; Bartlet et al. 1999) and assumed to function as gravity receptor allowing a response to gravity when insects experience mechanical stimulation (Schneider 1964). In addition, BB is also distributed on lacinia, and its morphology is similar to that on antennae, so it can be inferred that it has a similar function of keeping the maxilla palp in a proper position when the insect moves or changes position, which is also consistent with its ability to sense mechanical stimuli. However, on the antennifer of A. tumida, there are several BB-like sensilla called SB6 in this study that have the same function as BB.

SC are significantly higher than other sensilla, making them more sensitive to environmental changes. Barlet et al. (1999) found that sensilla chaetica could respond to hostplant chemicals, so these sensilla might be regarded as gustatory sensors. SC2 have smooth walls and distribute on pedicel and scape, they were surrounded by SC1, and so they might have the same function as SC1. SC3 are located on pedicel, flagellum 9 and basal of scape and they might have the function of sensing the position of antennae relative to the head. On the mouthparts, SC are mainly distributed in anterior margin of labium, outer margin of mandible, maxillary palp and labial palp. When foraging, SC may help them sense external mechanical stimuli and quickly locate food (Cao and Huang 2016).

SB have the most abundant sensory subtypes and rich in sensory nerve organs, which play an important role in host seeking and risk avoidance behavior (Chen et al. 2013; Zhang et al. 2012). They are divided into two types based on whether there are pores in the top. The pore enables them to communicate with the external environment for chemical signals and feel the smell of the host plant when searching for food, so as to stimulate the directional movement of insects and determine whether food can be accepted under the stimulus of olfactory and gustatory. SB with a pore in Vanessa cardui and porous in Homoeosoma nebulella, both are olfactory sensillum (Faucheux 1995). So on the mouthparts, SB2, SB4, SB5, SB6, SB8 with a pore and SB7 with two poles apically may all olfactory sensillum, and different subtypes may be used to identify different chemicals. SB1 and SB3 without pore may be mechanical sensillum.

SB on antennae are all without pores. SB1 are the most abundant and also found in other insects (Zhang et al. 2012; Ma and Du 2000). SB3 are similar to SB2 of Chrysolina aeruginosa (Zhang et al. 2013). SB1 and SB3 might have general functions as gustatory sensors (Bartlet et al. 1999; Ma and Du 2000). SB2 are similar to Sco of Chrysolina aeruginosa and SB3 of Phyllotreta striolata (Zhang et al. 2013; Zhang et al. 2013), which generally regarded as sensors that recognize changes in humidity and temperature (Bartlet et al. 1999). There are no reports about SB4 on the antenna in Coleoptera of previous study. They are the least antenna sensilla, and their alternating grooved walls suggested that these sensilla might have the functions of olfactory. SB5 are similar to SB5 of Phyllotreta striolata, and their distributions suggest that these sensilla might be having a vital role in host plant detection for oviposition (Zhang et al. 1026). SB6 are similar to BB in this study and they distributed around BB in a small amount. There have been no reports about SB6 on the antenna in Coleoptera of previous study. Based on their similarity with BB and their distributions, we believe that they might have the same function as BB.

Studies have shown that SS on the antennae are rich in nerve cells, which can sense temperature, humidity, olfaction and gustation (Ma and Du 2000). SS1 on the antenna resemble the sensilla styloconica of Chrysolina aeruginosa and Psylliodes chrysocephala, whose functions are similar to SB2 on the antennae in this study, both of which are identifying changes in the humidity and temperature (Bartlet et al. 1999). SS2 locate in the anterior margin of flagellum 7 and 8, and have the same distribution position as SB3 of Dacne picta and SB1 of O. colon, sug-gesting that these sensillum may be gustatory or humidity receptor (Cao and Huang 2016; Li et al. 2012). Many insects have SS on maxillary palp and labium palp (Zhang et al. 2013), so SS1 and SS2 on mouthparts may have the same function, and the flower-shaped tips help increasing the contact area for better gustatory function (Hallberg 1982).

ST are numerous and mainly distributed in antennal club, and they are regarded as common olfactory sensors.

SP are similar to the “poreless sensilla” on I. typographus (Hallberg 1982), "sensilla aperture" on Apriona germari (Zhuge et al. 2009) and SP on Asias halodendir (Xiao and Liu 2011) and O. colon (Cao and Huang 2016). Richerson found that SP have microporous structures and confirmed that this type of sensor is the olfactory sensor.

Terminal segment of maxilla palp and labial palp have abundant sensilla, especially at the top, forming a sensor region surrounded with Sco along outer margin. Sco similar to sensilla twig basiconica 6 in Cryptorrhynchus lapathi (Yang et al. 2019) and Sco in O. colon (Cao and Huang 2016). Sco are innervated by four dendrites, which are morphologically similar to no-pore sensilla, suggesting that they are also the thermo- and hygro- receptors (Li et al. 2012).

Scam has relatively stable cuticle appearance, circular arch shape or bell shape, and is thought to be an ontological mechanoreceptor that senses and responds to the tension created by the insect's exoskeleton (Shields 2008).

5. Conclusion

This is the first detailed study of the morphology and sensilla of the mouthpart and antennae of *A. tumida*. The results showed that *A. tumida* have typical chewing mouth-parts and clavate antennae similar to other Nitidulidae species. 5 types of 13 subtypes of sensilla on antennae and 8 types of 18 subtypes of sensilla on mouthparts were found. The sensilla basiconica are the most abundant in subtypes and sensilla chaetica are the most abundant in numbers. Compared with other structures of the mouthpart and an-tennae, antennal club, maxilla palp and labium palp have more abundant sensilla which function as mechanorecepter and chemoreceptor playing an important role in searching food and selecting habita.

Declarations

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Author contributions Conceptualization: XC and MH. Methodology: XC, RC. Investigation: XC, RC. DK, Data acquisition: XC, RC. Data analysis: MH, XC, RC. Writing–original draft preparation: MH, XC. Writing–review and editing: all authors. Funding acquisition: MH.

Compliance with ethical standards

Conflict of interest: All authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and institutional guidelines for the care and use of animals were followed. No endangered species or animals from protected areas were used for this study. This article does not contain any studies with human participants performed by any of the authors.

References

1. Arbogast RT, Torto B, Willms S, Fombong AT, Duehl A, Teal PEA (2012) Estimating Reproductive Success of *Aethina tumida* (Coleoptera: Nitidulidae) in Honey Bee Colonies by Trapping Emigrating Larvae. Environmental Entomology 41(1): 152–158.
2. Bartlet E, Romani R, Williams IH, Isidoro N (1999) Functional anatomy of sensory structures on the antennae of *Psylliodes chrysocephala* L. (Coleoptera, Chrysomelidae). International Journal of Insect Morphology and Embryology 28: 291–300.
3. Bernier M, Fournier V, Eccles L, Giovenazzo P (2014) Control of *Aethina tumida* (Coleoptera: Nitidulidae) using in-hive traps. Canadian Entomologist 147: 97–108.
4. Cao YK, Huang M (2016) A SEM study of the antenna and mouthparts of *Omosita colon* (Linnaeus) (Coleoptera: Nitidulidae). Microscopy Research & Technique 79: 1152–1164.
5. Chen H, Li ZB, Tang M (2006) Scanning electron microscope observation on antenna of *Dendroctonus armandi* (Coleoptera: Scolytidae). Science silvae sinicae 42(11): 156–159.
6. Chen X. Ultrastructures study of antennal sensillae of ten Bruchuidae storage pests. Harbin: Northeast Normal University, 2013, 77pp.
7. Du X, Cao S, Zhang GY, Lu JJ, Wu JX, Li YP (2015) Ultrastructure comparison of the antennal sensilla of three scarabs (Coleoptera: Scarabaeidae). Acta Agriculture Boreali-occidentalis 24(5):48–156.
8. Evans JD, Pettis JS, Hood WM (2003) Shimanuki, H. Tracking an invasive honey bee pest: mitochondrial DNA variation in North American small hive beetles. *Apidologie* 34: 103–109.
9. Faucheux MJ (1995) Sensilla on the larval antennae and mouthparts of the European sunflower moth, *Homoeosoma nebulella* Den. and Schiff. (Lepidoptera: Pyralidae). International Journal of Insect Morphology and Embryology 24 (4): 391–403.
10. Fei RL, Li KB, Xiao C, Yi J, Cao YZ (2012) Ultrastructure of the antennal sensilla of *Holotrichia parallel*. Plant Protection 38(4): 63–67.
11. Giglio A, Ferrero EA, Perrotta E, Talarico FF, Brandmayr TZ (2010) Sensory structures involved in prey detection on the labial palp of the ant-hunting beetle *Siagona europaea* Dejean 1826 (Coleoptera,Carabidae). Acta Zoologica 91: 328–334.
12. Giulioa AD, Maurizia E, Stacconi MVR (2012) Functional structure ofantennal sensilla in the myrmeeophilous beetle *Paussus favieri* (Coleoptera Carabidae Paussini). Micron 43: 705–719.
13. Halcroft M, Spooner-Hart R, Neumann P (2011) Behavioral defense strategies of the stingless bee, *Austroplebeia australis*, against the small hive beetle, *Aethina tumida*. Insectes Sociaux 58:245–253.
14. Hallberg E (1982) Sensory organs in *Ips typographus* (Insecta: Coleoptera) Fine structure of the sensilla of the maxillary and labial palps. Actu Zoologicu 63(4):191–198.

15. Hu J, Li YL, Liu JH, Zheng RL, Yang F (2001) Scanning Electron Microscope Study on the Adult Sensors of *Cosinesthes salicis* Gressitt. Journal of Chinese Electron Microscopy Society 20(4): 499–500.
16. Kang GJ, Zhu ZR, Cheng JA, Way MO (2012) Antennal sensilla of parthenogenetic and bisexual *Lissorhoptrus oryzophilus* (Coleoptera Curetdionidae). Florida Entomologist 95(1): 8–15.
17. Kim JL,Yamasaki T (1996) Sensilla of *Carabus* (*Isiocarabus*) *fiducarius saishutoicus* Csiki (Coleoptera: Carabidae). International Journal of Insect Morphology and Embryology 25(1–2): 153–172.
18. Lee S, Hong KJ, Yun SC, Yong SC, Yoo MS, Lee S (2017) Review of the subgenus *Aethina* Erichson s. str. (Coleoptera: Nitidulidae: Nitidulinae) in Korea, reporting recent invasion of small hive beetle, *Aethina tumida*. Journal of Asia-Pacific Entomology 20: 553–558.
19. Li J, Ren GD, Dong JZ, Wang YY (2012) Antennal sensilla of adult *Dacne picta* observed with scanning electron microscope. Chinese Journal of Aplied Entomology 49(3): 762–765.
20. Li QH, Chen LY, Liu MK, Wang WK, Sabatelli S, Giulio AD, Audisio P (2021) Scanning Electron Microscope Study of Antennae and Mouthparts in the Pollen-Beetle *Meligethes* (*Odonthogethes*) *chinensis* (Coleoptera: Nitidulidae: Meligethinae) Insects 12: 659.
21. Li Z, Chen L (2010) Advances in the application of antennal sensory features to insect classification. Entomotaxonomia 32:113–118.
22. Li XM, Ren GD, Wang XP (2013) Fine structures of the antennal sensilla from sexually dimorphic antenna of *Cerocoma schreberi* (Colepotera Meloidae). Journal of Hebei University(Natural Science Edition) 33(4): 408–412.
23. Li ZK, Zhou XW, Yang FL, Niu CY (2013) The mouthparts of *Bactrocera minax* by scanning electron microscope. Plant quarantine 27: 57–59.
24. Liu GQ, Tian MY (2008) Scanning electron microscopic observation of *Carabus prodigus* antennae and their electroan tennographic responses. JournalofSouthChinaAgriculturalUniversity 29(2): 50–58.
25. Lounsberry Z, Spiewok S, Pernal SF, Sonstegard TS, Hood WM, Pettis J, Neumann P, Evans JD (2010) Worldwide Diaspora of *Aethina tumida* (Coleoptera: Nitidulidae), a Nest Parasite of Honey Bees. Annals of the Entomological Society of America 103(4): 671–677.
26. Ma RY, Du JW (2000) Antenna sensors of insects. Entomological Knowledge 37(3): 179–183.
27. Merivee E (1992) Antennal sensila of the female and male elaterid beetle *Agriotes obscurus* L. (Coleoptera: Elateridae). Proceedings of the Estonian Academy of Sciences 41: 189–215.
28. Merivee E, Ploomi A, Luik A, Rahi M, Sammelselg V (2001) Antennal sensilla of the ground beetle *Platynus dorsalis* (Pontoppidan, 1763) (Coleoptera, Carabidae). Microscopy research and technique 55: 339–349.Merivee E, Rahi M, Bresciani J, Ravn HP, Luik A (1998) Antennal sensilla of the click beetle, *Limonius aeruginosus* (Olivier) (Coleoptera: Elateridae). International Journal of Insect Morphology and Embryology 27(4): 311–318.
29. Na J, Yu WX, Li YP, Dong X, Jiao J (2008) Types of antennal sensilla in insects and their physiological and ecological significance. Journal of S henyang Normal University (Natural Science) 26: 213–216.
30. Neumann P, Elzen PJ (2004) The biology of the small hive beetle (*Aethina tumida*, Coleoptera: Nitidulidae): Gaps in our knowledge of an invasive species. Apidologie 35: 229–247.
31. Ortloff A, Zanetti N, Centeno N, Silva R, Bustamante F, Olave Á (2014) Ultramorphological characteristics of mature larvae of *Nitidula carnaria* (Schaller 1783) (Coleoptera: Nitidulidae), a beetle species of forensic importance. Forensic Science International 239: e1–e9.
32. Pirk CWW (2017) Small Hive Beetles (*Aethina tumida* Murray) (Coleoptera: Nitidulidae). 143–155.
33. Pirk CWW, Neumann P (2013) Small Hive Beetles are Facultative Predators of Adult Honey Bees. Journal of Insect Behavior 26:796–803.
34. Schneider D (1964) Insect antennae. Annual Review of Entomology 9: 103–122.
35. Shields VDC (2008) Ultrastructure of insect sensilla. New York: Encyclopedia of Entomology pp. 4009–4023.
36. Smith CM, Frazier JL, Coons LB, Knight WE (1976) Antennal sensilla of the Clover head weevil *Hypera meles* (F) (Coleoptera: Curculionidae). International Journal of Insect Morphology and Embryology 5(6): 349–355.
37. Spiewok S, Pettis JS, Duncan M, Spooner-Hart R, Westervelt D, Neumann P (2007) Small hive beetle, *Aethina tumida*, populations I: Infestation levels of honeybee colonies, apiaries and regions. Apidologie 38(6), 595–605.
38. Torto B, Fombong AT, Arbogast RT, Teal PE (2010) Monitoring *Aethina tumida* (Coleoptera: Nitidulidae) with baited bottom board traps: occurrence and seasonal abundance in honey bee colonies in Kenya. Environmental Entomology 39: 1731–1736.
39. Toufailia HA, Alves DA, Bená DC, Bento JMS, Iwanicki NSA, Cline AR, Ellis JD, Ratnieks FLW (2017) First record of small hive beetle, *Aethina tumida* Murray, in South America. Journal of Apicultural Research 56(1): 76–80.
40. Wang Y, Li L, Dai W (2019) Fine Morphology of the Mouthparts in *Cheilocapsus nigrescens* (Hemiptera: Heteroptera: Miridae) Reflects Adaptation for Phytophagous Habits. Insects 10: (143).
41. Xiao FS, Liu Q (2011) The type and characteristic of olfaction sensilla in *Asias halodendri*. Chinese Journal of Applied Entomology 48(3): 680–687.
42. Yang QF, Han JL, Li Q (2010) Antennal sensilla of *Xylosandrus germanus* adult observed with scanning electron microscope. Chinese Bulletin of Entomology 47(3): 520–524.
43. Yang YC, Ren LL, Xu LL, Wang T, Zong SX (019) Comparative morphology of sensilla on the antennae, maxillary and labial palps in different larval instars of *Cryptorrhynchus lapathi* (Linnaeus) (Coleoptera: Curculionidae). Zoologischer Anzeiger 283: 93–101.
44. Yin H, Fu YT, Guan N (2011) Observation on mouthpart sensilla of Acridoidea (Orthoptera: Acridoidea) with scanning Electron Microscope. Sichuan Journal of Zoology 30: 740–742.
45. Yin XM, Jiang SN (1995) SEM observations of main antennal sensilla and receptors of Maxipalp and Labipalpo of *Philus antennatus* larvae. Acta Agriculturae Universitatis Henanensis 4: 374–377.

46. Zhang C, Wang ZY, He KL, Bai SX (2012) Scanning electron microscopy studies of antennal sensilla of *Monolepta hieroglyphica*. Journal of Applied Entomology 49(3): 756–761.
47. Zhang GH, Li BL, Li CR (2016) Morphology and distribution of antennal sensilla of female *Phyllotreta striolata* (Fabricius) (Coleoptera: Chrysomelidae). Microscopy Research & Technique 79: 219–226.
48. Zhang J, Guan L, Ren BZ (2011) Fine structure and distribution of antennal sensilla of longicorn beetles *Leptura atcuata* Panzer and *Leptura aethiops* (Coleoptera; Cerambycidae). Annals of the Entomological Society of America 104(4):778–787.
49. Zhang L, Ren LL, Luo YQ, Zong SX (2013) Scanning electron microscopy analysis of the cephalic sensilla of *Chrysolina aeruginosa* Fald. (Coleoptera, Chrysomelidae). Microscopy Research & Technique 76: 423–431.
50. Zhao HX, Chen DF, Hou CS, Wang HT, Huang WZ, Ji CH, Ren Q, Xia XS, Zhang XF (2019) Biological characteristics, invasion hazards and control strategies of bee hive small beetles. Journal of bee 1: 8–11.
51. Zhong YH, Han WS, Zhao DX, Zhao S, Wang SJ, Liu JF, Gao JL (2020) Risk assessment for the introduction of small hive beetle, *Aethina tumida*, into China. Plant quarantine 34(2): 48–51.
52. Zhuge PP, Ge HM, Wang MH, Wu SB, Luo SL, Zhang GA (2009) Observation of sensilla on the cephalic appendage of *Apriona germari* with scanning electron microscopy. Chinese Journal of Aplied Entomology 46(2): 238–243.

Figures

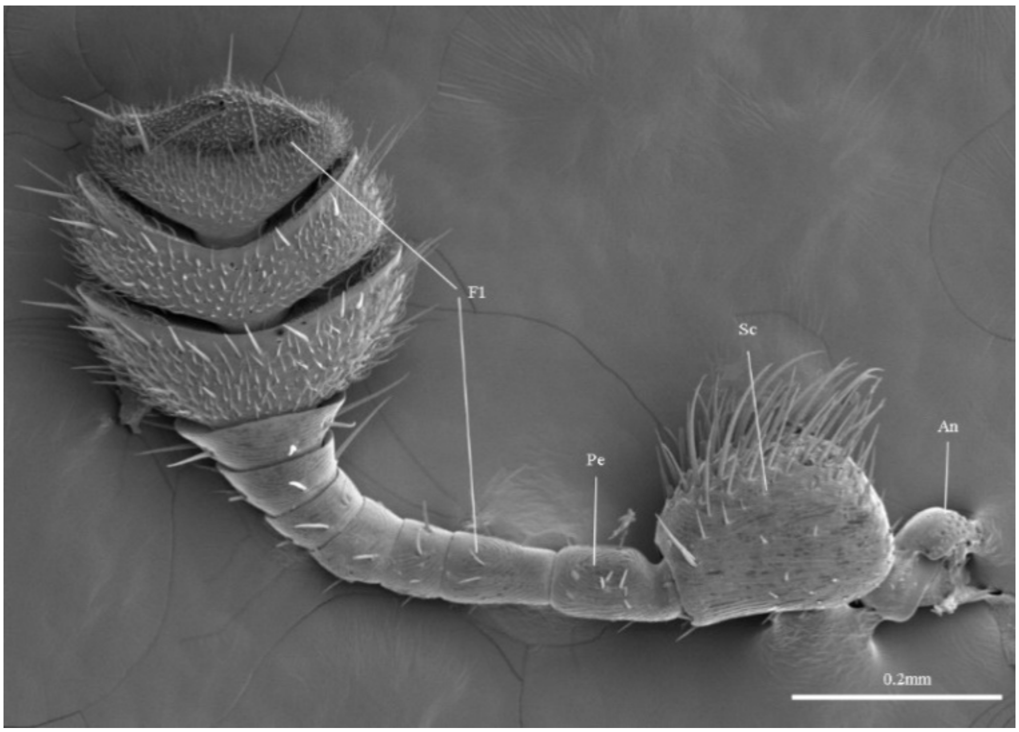

Figure 1

Antenna of A. tumida. Fl, flagellum; Pe, pedicel; Sc, scape; An, anrennifer.

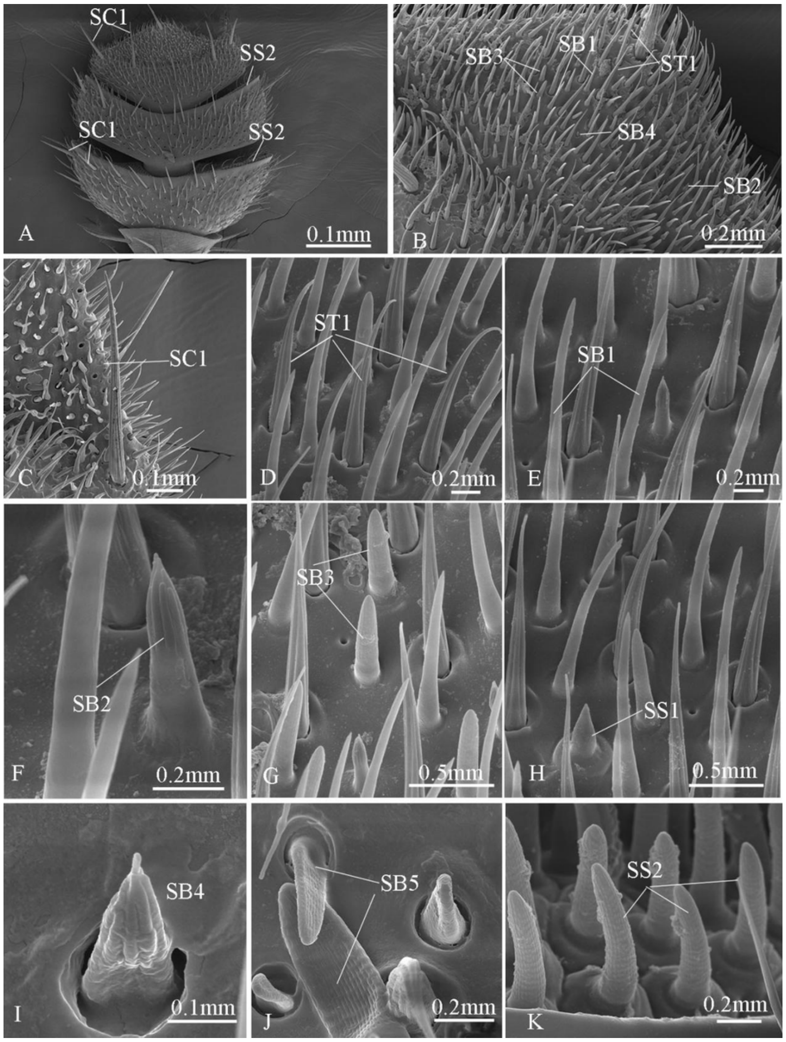

Figure 2

Antennal sensilla in *A. tumida*. A. Antennal club; B. antennal club; C. sensilla chaetica 1 (SC1); D. sensilla trichodea 1 (ST1); E. sensilla basiconica 1 (SB1); F. sensilla basiconica 2 (SB2); G. sensilla basiconica 3 (SB3); H. sensilla styloconica 1 (SS1); I. sensilla basiconica 4 (SB4); J. sensilla basiconica 5 (SB5); K. sensilla styloconica 2 (SS2).

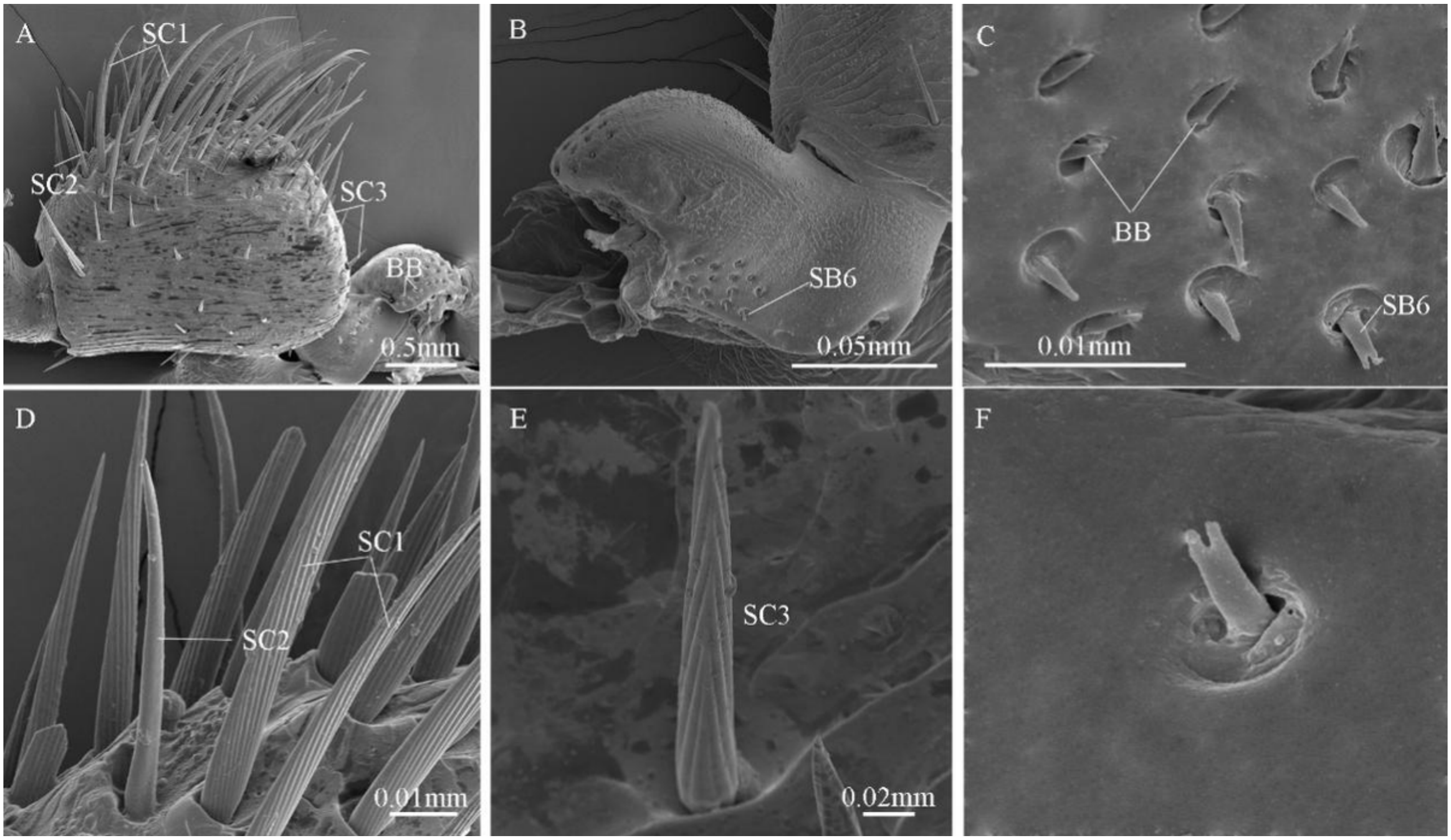

Figure 3

Antennal sensilla in *A. tumida*. A. medial view of scape; B. lateral view of antennifer; C. sensilla basiconica 6 (SB6) and Bohm bristles (BB); D. sensilla chaetica 2 (SC2); E. sensilla chaetica 3 (SC3); F. sensilla basiconica 6 (SB6).

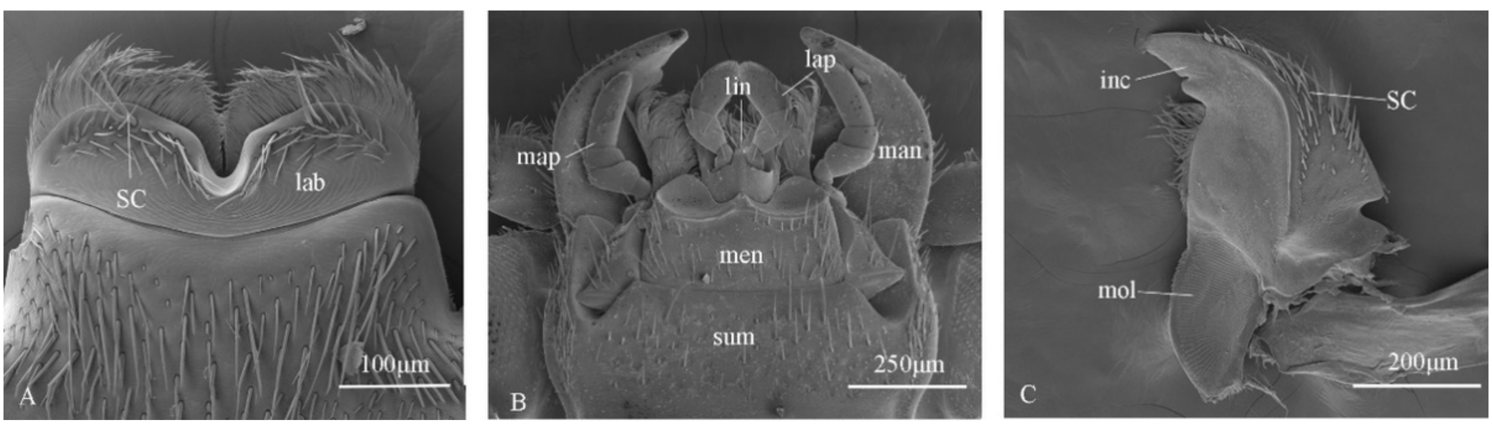

Figure 4

Head and mouthparts of *A. tumida*. A. dorsal view; B. ventral view; C. mandible, dorsal view. Lab, labrum; lin, lingual; lap, labrum palpu; man, mandible; map, mandible pulp; men, mentum; sum, submentum; inc, incisor lobe; mol, molar lobe.

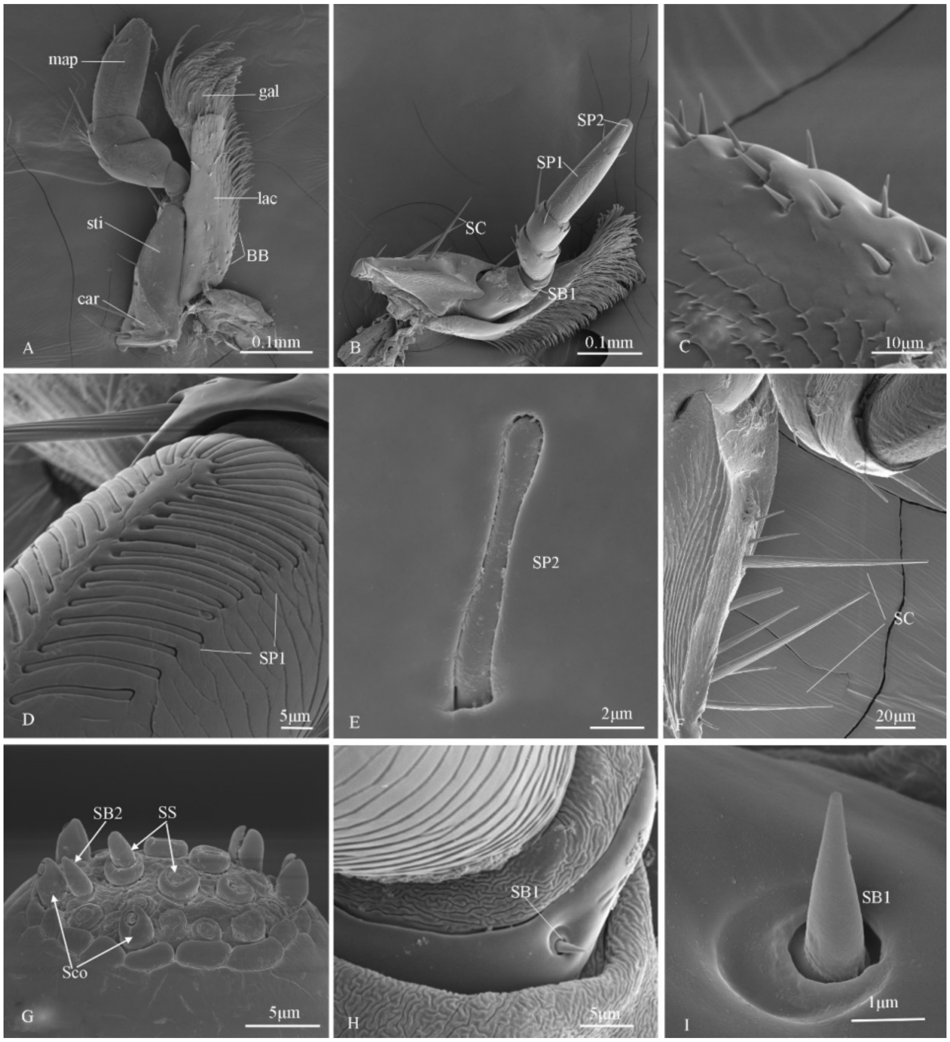

Figure 5

Sensilla on the maxillae palp of *A. tumida*. A. ventral view; B. lateral view; C. Bohm bristles (BB); D. Sensilla placodea 1 (SP1); E. Sensilla placodea 2 (SP2); F. sensilla chaetica (SC); G. sensilla coeloconica (Sco), sensilla styloconica 1 (SS1) and sensilla basiconica 2 (SB2) on the top of maxillary palps; H, I. sensillia basiconica 1 (SB1). Map, maxillary palpus; gal, galea; lac, lacinia; car, cardo; sti, stipes.

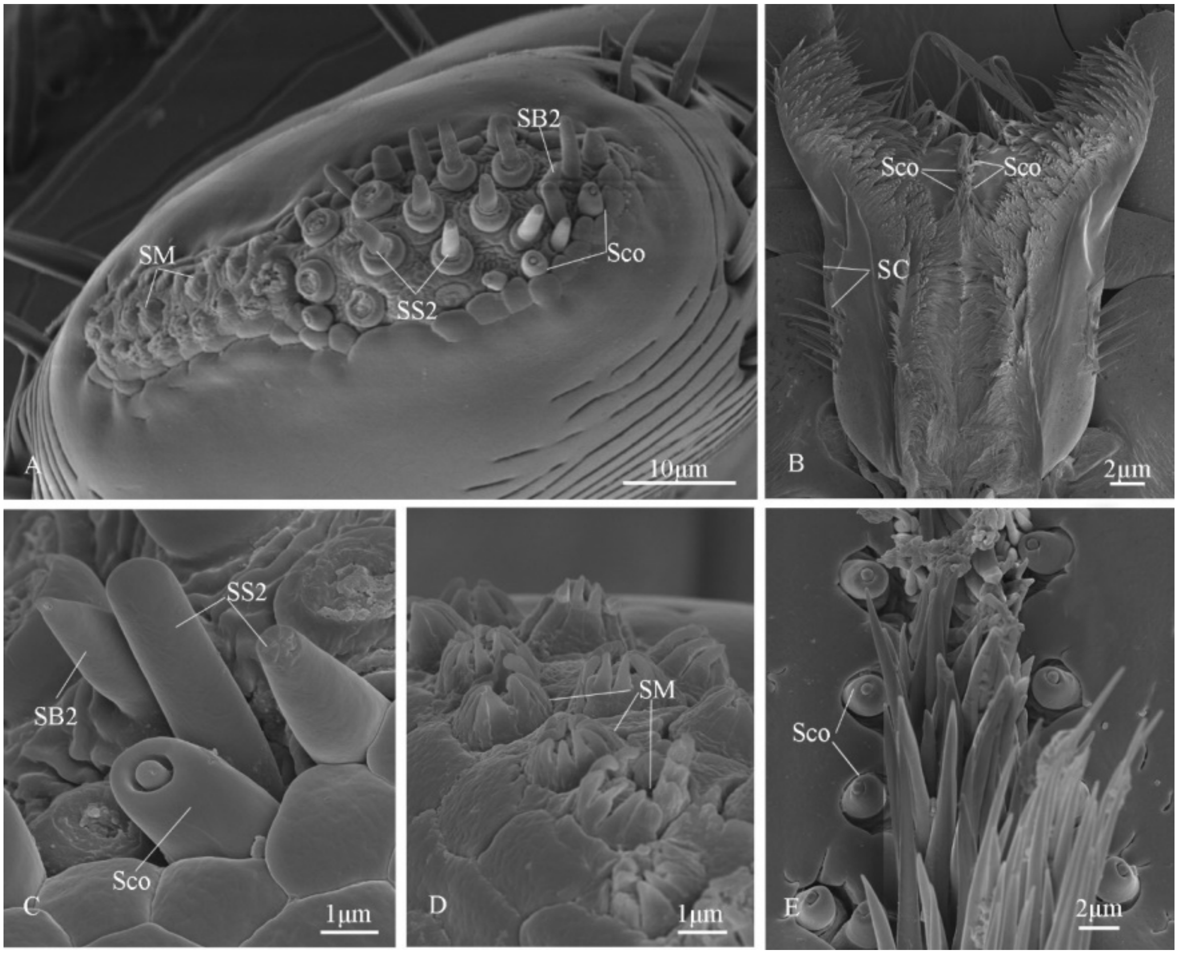

Figure 6

Sensilla on labium palp of *A. tumida*. A. terminal segmrnt of labium palp; B, glossa, ventral view; C. sensilla coelocinica (Sco), sensilla styloconica 2 (SS2), sensilla basiconica 2 (SB2); D. sensilla multilobular (SM); E. sensilla coeloconica (Sco).

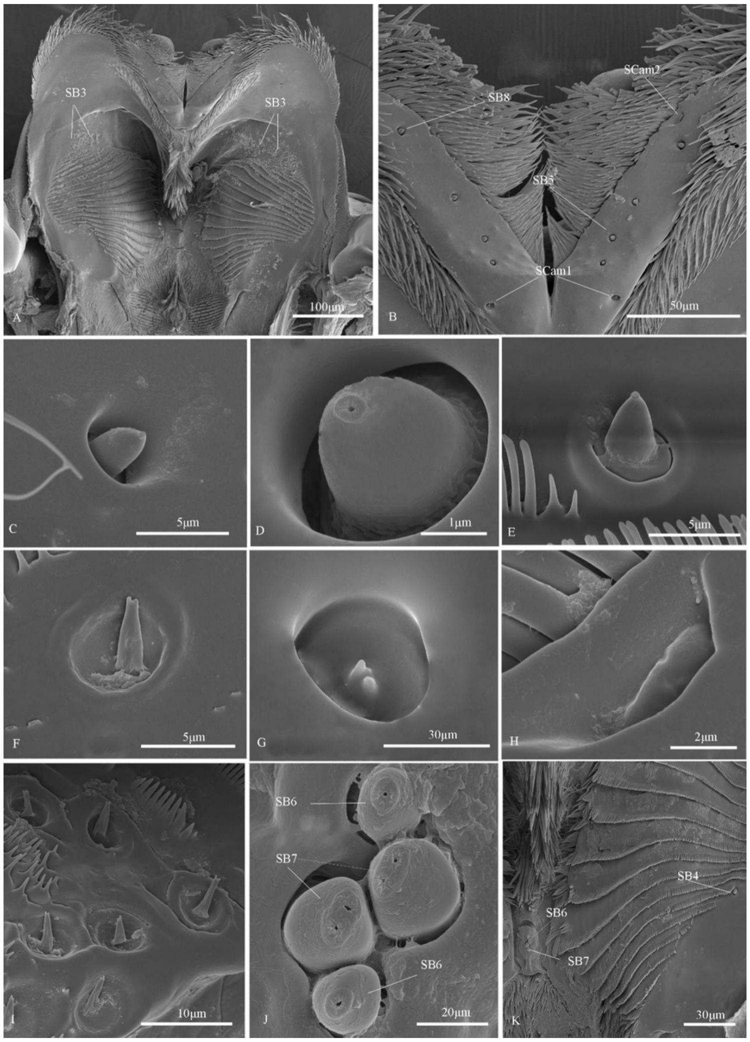

Figure 7

Sensilla on the epipharynx of *A. tumida*. A. epipharynx, ventral view; B. sensilla basiconica 5 (SB5), sensilla basiconica 8 (SB8), sensilla campaniformia 1 (SCam1) and 2 (SCam2); C, sensilla basiconica 8 (SB8); D. sensilla basiconica 5 (SB5); E. sensilla basiconica 4 (SB4); F, I. sensilla basiconica 3 (SB3); G. sensilla campaniformia 1 (Scam1); H. Sensilla campaniformia 2 (Scam2).