ENTOMOLOGICAL
SOCIETY OF AMERICA
SHARING INSECT SCIENCE GLOBALLY

OXFORD

Morphology and Distribution of Antennal Sensilla in an Egg Parasitoid Wasp, *Anastatus disparis* (Hymenoptera: Eupelmidae)

Jianjun Wang,[1,2,*] Pengcheng Liu,[3,*] Jianguo Wang,[2] Qingshu Luan,[2] Xu Jiang,[2] and Chuanwang Cao[1,4]

[1]College of Forestry, Northeast Forestry University, Harbin 150040, China, [2]Liaoning Provincial Key Laboratory of Forest Protection, Liaoning Academy of Forest Sciences, Shenyang 110032, China, [3]The School of Ecology and Environment, Anhui Normal University, Wuhu 241001, China, and [4]Corresponding author, e-mail: chuanwangcao@nefu.edu.cn
*Jianjun Wang and Pengcheng Liu contributed equally to the study.

Abstract

The wasp *Anastatus disparis* is an egg endoparasitoid of a number of Lepidopteran pest species. To better understand the *A. disparis* olfactory system, we observed the antennal sensilla of males and females under a scanning electron microscope and quantified their sizes and morphological characteristics. We identified the types of sensilla and counted the numbers and locations of the different types on the dorsal and ventral antennal surfaces. The antennae of *A. disparis* are geniculate, with flagella that comprise 11 subsegments in females and eight in males. The mean antenna length was 1324.10 ± 52.50 μm in females and 1323.93 ± 65.20 μm in males. Ten sensillum types were identified in both sexes: Böhm bristles (BBs), sensilla trichodea (ST, with subtypes STI and STII), sensilla chaetica (SCh), sensilla basiconica (SB, with subtypes SBI and SBII), sensilla placodea (SP), sensilla coeleoconica (SCo), sensilla grooved peg (SGP), sensilla auricillica (SAu), sensilla campaniformia (SCa), and glandular pores (GPs). The total numbers of BBs, STI, SBII, SCa, SCo, and GPs did not differ significantly between the sexes, whereas the total numbers of SCh, SBI, and SAu were significantly greater in females, and those of STII, SP, and SGP were significantly lower. The types, number, and density of antennal sensilla increased from the base to the end. The possible functions of these sensilla in host-detection behavior are discussed.

Key words: endoparasitoid, antennal sensilla, scanning electron microscopy, sexual dimorphism

Antennae are the major sensory organs of insects and are used in multiple behaviors: location of suitable hosts, identification of oviposition sites, detection of sexual partners, and avoidance of predators (Bin et al. 1989, Chiappini et al. 2001, Leal 2013, Cao and Huang 2016, Faucheux et al. 2020). Antennae contain numerous types of sensilla that perform a variety of sensory functions, including the perception of water, chemical compounds, mechanical stimuli, and temperature (Altner and Prillinger 1980, Zacharuk 1980, 1985; Chapman 1982; Altner et al. 1983; Keil 1997). The sensillum is a specific region of the exoskeleton that contains formative cells, sensory nerve cells, and sometimes auxiliary cells (Schneider 1964); the sensory cells receive various stimuli transmitted by the outer cuticular structure. Sensilla act as independent sensory units and include a number of different types, each with specific morphological features. Different species have different types of sensilla whose specific shapes and structures are related to their unique sensory tasks (Altner and Prillinger 1980, Barbarossa et al. 1998, Isidoro et al. 1999, Faucheux et al. 2020).

The wasp *Anastatus disparis* is an egg endoparasitoid of a number of Lepidopteran pest species. Among its hosts are *Odonestis pruni* (Lepidoptera: Lasiocampidae), *Actias selene ningpoana* (Lepidoptera: Saturniidae), *Antheraea pernyi* (Lepidoptera: Saturniidae), and the gypsy moth *Lymantria dispar* (Lepidoptera: Lymantriidae) (Yan et al. 1989, Li and Lou 1992), and it has been proposed as a possible biological control agent for the latter in North America (Crossman 1925, Yan et al. 1989). *A. disparis* exhibits extensive sexual dimorphism in morphology, physiology, and behavior (Liu et al. 2015, 2017, 2021).

Numerous studies have investigated antennal sensillum morphology and function in various insects, particularly Hymenoptera (Olson and Andow 1993, Onagbola and Fadamiro 2008, Zhang et al. 2015, Zheng et al. 2016, Shen et al. 2019, Sevarika et al. 2021), but to date, no reports have described the antennal sensilla of *A. disparis*. A thorough understanding of the insect olfactory system is essential for developing effective semiochemical-based control

strategies. We therefore observed the antennal sensilla of male and female *A. disparis* under a scanning electron microscope (SEM) and quantified their sizes and morphological characteristics. These data provide essential background information for future research on the behavior, physiology, and electrophysiology of *A. disparis*.

Materials and Methods

Insects

Adults of *A. disparis* were procured from a laboratory colony that was originally collected from an *L. dispar* egg mass in Xinbin Manchu Autonomous County (41.86° N, 124.43° E), Liaoning Province, China, in September 2020. The *A. disparis* adults were kept in plastic containers (20 × 10 × 6 cm) at 25 ± 1°C, 75% ± 5% RH, and a photoperiod of 12:12 (L:D) h and supplied with 20% (volume ratio) honey until used for microscopic examination.

Sample Preparation for SEM

Samples of seven male and seven female wasp antennae were prepared as described in Zheng et al. (2016). The total length of antennae and the length of each antennal segment were calculated as the average of 7 female antennae and 7 male antennae, respectively. The type and number of sensilla were calculated as 6 female antennae and 6 male antennae, while 3 left antennae, and 3 right antennae were observed for each sex of wasps. The samples were fixed in glutaraldehyde (2.5%) for 24 h at 4°C and then cleaned in an ultrasonicator twice for 5 min each in 0.1 M phosphate buffered saline. The samples were dehydrated in an acetone series (30%, 50%, 70%, 85%, and 100% for 15 min each), then dried in acetone twice for 10 min each. The cleaned and dehydrated specimens were air dried for 24 h, then mounted on copper stubs with two-sided adhesive tape in both ventral and dorsal orientations. They were sputtered-coated with gold by ion sputtering equipment (KYKY SBC-12, KYKY Technology Company Limited) and observed under a Thermo Fisher Scientific Apreo C SEM at 20 kV.

Sensilla Identification

We identified the sensilla structures on each antenna and calculated their frequencies and distributions. Sensillum types were classified as described in Altner and Prillinger (1980), Schneider (1964), and Zacharuk (1980), with reference to more recent literature on Hymenopteran antennal sensilla (Zhang et al. 2015, Zheng et al. 2016, Shen et al. 2019, Sevarika et al. 2021).

Terminology and Data Analysis

The authors calculated the number of all the sensilla observed on each segment and measured the area of the statistical region, and each segment has 6 duplicate values. However, the area of the segment was observed under the electron microscope but it is less than or equal to half of the surface area of the cylinder, and is approximately rectangular, the area is directly expressed by multiplying the length of the segment by the width of the segment. The length and width of each antennal segment and the numbers and measurements of various sensillum types were compared between males and females using independent samples t-tests (SPSS version 25.0, $P <$ 0.05). Statistical results were expressed as mean ± standard error.

Results

General Morphology of *A. disparis* and Its Antennae

The body length (length was measured from the tip of the head to the end of the abdomen) of female *A. disparis* was 3.01 ± 0.03 mm,

and the metastethidium width was 0.72 ± 0.01 mm (n = 25); these values were significantly greater (t_1 = 21.902, df_1 = 39, P = 0.000; t_2 = 8.917, df_2 = 39, P = 0.000) than those of male *A. disparis*, whose body length was 1.97 ± 0.03 mm and metastethidium width was 0.55 ± 0.02 mm (n = 16). Under the stereomicroscope, the bottom and top of the female antennae were brown and black, respectively (Fig. 1A), whereas the antennae of male *A. disparis* were completely black (Fig. 1B).

Like those of most Chalcidoidea, the antennae of male and female *A. disparis* were geniculate, comprising a radicula, a long scapula-shaped scape, a barrel-shaped pedicel, and a long flagellum. The flagellum was divided into a clava and a funicle. The flagellum of the female adults had 11 subsegments: eight funicles (F1–F8) and three clavae (C1–C3) (Fig. 1C). The top of the last segment of the female clava was truncated at an angle, forming a broadly flattened area on which were scatted numerous types of sensilla. The flagellum of the male adults had eight subsegments: seven funicles and one solid clava (Fig. 1D).

The total antenna length of female *A. disparis* was 1324.10 ± 52.50 µm. The flagellum accounted for most of the antennal length (~61.48%); the scape was the second antennomere (~28.34% of antennal length); the pedicel was the third antennomere (~6.06%), and the radicula was the shortest (~4.10%) (Table 1). The total antenna length of male *A. disparis* was 1323.93 ± 65.20 µm. Again, the flagellum accounted for most of the antennal length (~78.04%); the scape was the second antennomere (~14.65%); and the pedicel and radicula were short antennomeres (~3.81% and 3.51%, respectively) (Table 1). Total antennal length did not differ significantly between females and males (t = 0.002, df = 12, P = 0.998). The widest antennal segment in females was C1 (97.66 ± 2.35 µm), which was 2.13 times wider than the narrowest segment of the radicula. The widest antennal segment in males was F3 (94.96 ± 6.03 µm), which was 2.07 times wider than the narrowest segment of the radicula (Table 1).

Morphology of Different Antennal Sensillum Types

Ten main types of antennal sensilla were observed on male and female *A. disparis*: Böhm bristles (BBs), sensilla trichodea (ST), sensilla chaetica (SCh), sensilla basiconica (SB), sensilla placodea (SP), sensilla coeleoconica (SCo), sensilla grooved peg (SGP), sensilla auricillica (SAu), sensilla campaniformia (SCa), and glandular pores (GPs). Based on their shapes and sizes, we also identified two ST subtypes (STI and STII) and two SB subtypes (SBI and SBII).

Böhm Bristles (BBs)

BBs were conical, upright sensilla (Fig. 2A) with dullish tips and smooth-walled hairs; they were contained within a shallow inflexible cuticular socket and stood nearly perpendicular to the surface of the antennae. No pores were observed on the BBs surface (Fig. 2C). BBs were 7.86 ± 0.40 µm long with a basal diameter of 1.23 ± 0.05 µm (n = 25) in females and 7.8 5 ± 0.62 µm long with a basal diameter of 1.17 ± 0.05 µm (n = 24) in males (Table 2). The BBs were found in clusters of 3–5 on the radicula bases (Fig. 2A) and pedicel bases (Fig. 2B) in both males and females. Thus, they occur only where the head joins the scape and where the scape joins the pedicel. The mean number of BBs was 10.67 ± 1.26 in females and 9.67 ± 1.78 in males (Table 3), and BBs numbers did not differ significantly between the sexes (t = –0.459, df = 10, P = 0.656).

Sensilla Chaetica (SCh)

SCh were straight or slightly curved towards the antennal surface near the tip; they were long, thin, and sharp-tipped without a
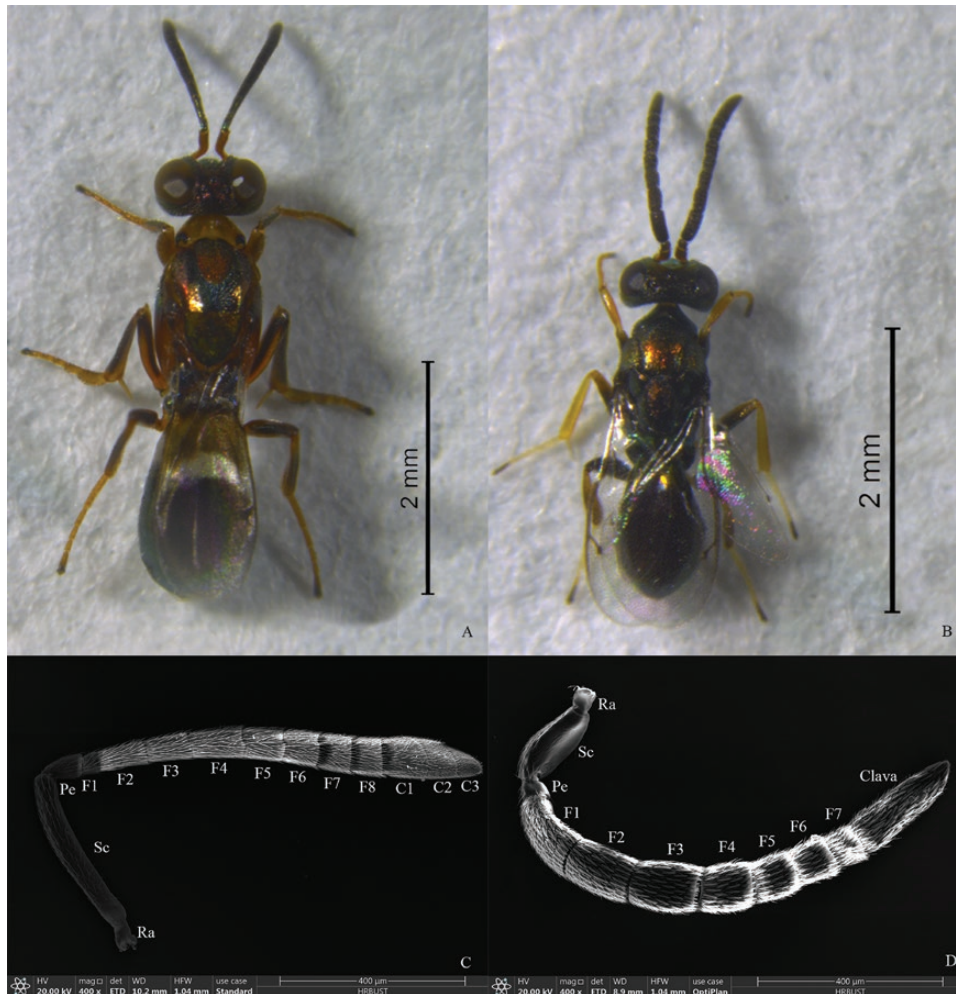
Fig. 1. Female and male adults of *A. disparis* and their antenna structures. (A): female; (B): male; (C): antenna of female; (D): antenna of male. Abbreviations: Ra: radicle; Sc: scape; Pe: pedicel; F1–F8: first to eighth funicle; C1–C3: first to third clava.

Table 1. Measurements of antennal segments in female and male *A. disparis*

Segment of antenna		Length (μm)		Width (μm)		Flank area of cylinder (10^3 μm²)	
		♀	♂	♀	♂	♀	♂
Radicula		54.41 ± 1.44a	46.43 ± 1.36b	45.82 ± 0.97a	45.79 ± 0.74a	2.50 ± 0.10a	2.13 ± 0.07b
Scape		375.29 ± 13.11a	193.92 ± 8.55b	65.25 ± 3.64b	89.03 ± 6.08a	24.75 ± 2.29a	17.20 ± 1.25b
Pedicel		80.30 ± 5.30a	50.39 ± 1.51b	58.96 ± 2.60a	67.67 ± 3.39a	4.74 ± 0.43a	3.40 ± 0.17b
Flagellum Funicle	F1	29.34 ± 2.62b	169.86 ± 5.53a	53.70 ± 3.43b	88.92 ± 3.88a	1.58 ± 0.19b	15.09 ± 0.78a
	F2	94.25 ± 8.09b	133.59 ± 7.96a	59.83 ± 3.47b	89.01 ± 5.71a	5.71 ± 0.76b	11.94 ± 1.11a
	F3	93.40 ± 6.49b	130.74 ± 10.71a	66.22 ± 3.92b	94.96 ± 6.03a	6.23 ± 0.68b	12.55 ± 1.49a
	F4	103.77 ± 5.06a	103.81 ± 9.17a	77.96 ± 3.91b	94.60 ± 5.88a	8.10 ± 0.63a	9.86 ± 1.16a
	F5	84.95 ± 4.46a	86.28 ± 8.31a	81.35 ± 4.27a	93.86 ± 5.72a	6.93 ± 0.58a	8.03 ± 0.88a
	F6	76.31 ± 4.64a	77.17 ± 6.58a	85.71 ± 2.89a	92.86 ± 4.56a	6.55 ± 0.49a	7.14 ± 0.69a
	F7	68.34 ± 4.33a	61.84 ± 4.81a	87.85 ± 3.14a	92.24 ± 2.90a	6.02 ± 0.49a	5.68 ± 0.43a
	F8	63.26 ± 4.17	–	91.64 ± 2.70	–	5.794 ± 0.41	–
Clava	C1	78.29 ± 4.89b	269.90 ± 12.95a	97.66 ± 2.35a	90.82 ± 4.30a	7.64 ± 0.49b	24.43 ± 1.40a
	C2	59.47 ± 4.52	–	93.43 ± 4.34	–	5.60 ± 0.56	–
	C3	62.71 ± 4.86	–	83.49 ± 5.02	–	5.17 ± 0.41	–
C1–C3		200.47 ± 10.82b	269.90 ± 12.95a	–	–	18.41 ± 1.29b	24.43 ± 1.40a
F1–C3		814.09 ± 47.49b	1033.18 ± 61.72a	–	–	65.32 ± 5.22b	94.72 ± 7.23a
Total		1324.10 ± 52.50a	1323.93 ± 65.20a	–	–	97.31 ± 5.78a	117.45 ± 7.30a

Note: Data are presented as the mean ± SE. For a given segment and measurement, means followed by different letters differ significantly between males and females (*t*-test, *P*<0.05). *N* = 7 per sex. '–' indicates absence.
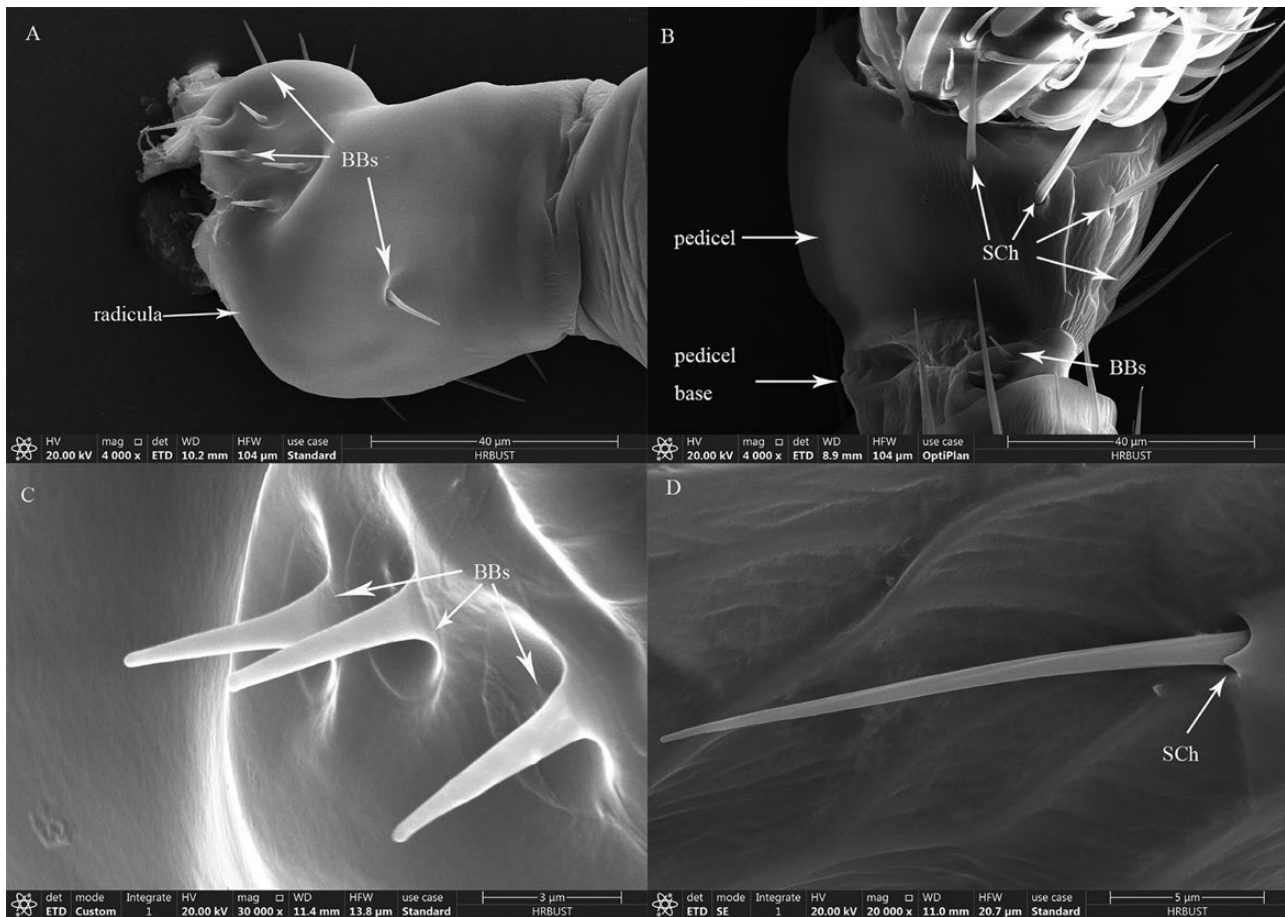
Fig. 2. Ultrastructural morphology of Böhm bristles (BBs) and sensilla chaetica (SCh) on *A. disparis* antennae. (A): BBs on the radicula; (B): BBs and SCh on the pedicel; (C): BBs and its smooth wall; (D): SCh with longitudinal lines on the side wall.

terminal pore. The shaft arose from a flexible basal socket and was characterized by longitudinal lines on the side wall and a lack of surface pores (Fig. 2B and D). SCh were 32.39 ± 0.91 µm in length with a basal diameter of 1.82 ± 0.09 µm (*n* = 20) in females and 21.93 ± 0.59 µm in length with a basal diameter of 1.23 ± 0.04 µm (*n* = 17) in males (Table 2). Sch were found on the scape and pedicel in both sexes. Females had a significantly larger number of SCh (57.00 ± 5.12) than males (21.17 ± 2.73) (*t* = 6.179, df = 10, *P* = 0.000) (Table 3).

Sensilla Trichodea (ST)
ST could be classified into two subtypes, STI and STII, based on their socket types and wall surfaces (Fig. 3A–C). STI were hair-like sensilla that tapered to a fine point (Fig. 3B). Each STI was situated in a flexible socket that was slightly elevated above the cuticle. Their sharp tips curved slightly toward the segment apex, and their longitudinally grooved shafts were aligned parallel to the long axis of the antenna (Fig. 3B); no pores were visible on the surface. STI were 10.79 ± 1.05 µm in length with a basal diameter of 2.09 ± 0.12 µm (*n* = 20) in females and 12.73 ± 0.55 µm in length with a basal diameter of 1.36 ± 0.04 µm (*n* = 45) in males (Table 2). STI were widely distributed everywhere except the radicula and were the most abundant sensillum type in both sexes. There was no significant difference in mean STI number between females (1593.50 ± 140.51) and males (1270.83 ± 148.83) (*t* = 1.576, df = 10, *P* = 0.146) (Table 3). The number of STI increased from the antennal base to the tip in females and were most numerous at the tip of the flagellum. The

number of STI first increased, then decreased, then increased again from the antennal base to the tip in males and were most numerous on the claval subsegment. The change trend of the number of STI in males is generally consistent with the change trend of the length of its segments. STI accounted for 85.65% of all sensilla in females and 67.74% in males.

STII were slightly curved hairs with a smooth surface and few pores that ended in a fine, sharp tip (Fig. 3A, C, D). STII were slightly elevated above the cuticle and lacked a socket structure (Fig. 3C). Their shafts were bent and lay approximately parallel to the surface of the antenna. STII were 9.31 ± 0.63 µm in length with a basal diameter of 1.23 ± 0.04 µm (*n* = 19) in females and 12.17 ± 0.44 µm in length with a basal diameter of 1.54 ± 0.04 µm (*n* = 31) in males (Table 2). In females, STII were found on the seventh and eighth funicular subsegments and all claval subsegments, whereas in males, they were found only on the claval subsegment. There were significantly fewer STII in females (10.17 ± 3.88) than in males (131.83 ± 34.57) (*t* = –3.498, df = 10, *P* = 0.006) (Table 3).

Sensilla Basiconica (SB)
SB were further divided into two subtypes, SBI and SBII (Fig. 4A), both of which arose from a circular, protuberant basal cuticular articulation of the antennal surface. They were straight or slightly curved and lay at an angle of 60°–85° to the antennal surface (Fig. 4A and B), with dullish tips, and several terminal pores (Fig. 4C). SBI were 7.20 ± 0.33 µm in length with a basal diameter of 0.99 ± 0.02 µm (*n* = 39) in females and 6.56 ± 0.40 µm in length with a basal

Table 2. Size and morphological characteristics of antennal sensilla on *A. disparis*

Sensillum type	Length (μm)		Basal diameter (μm)		Tip	Wall	Shape	Socket	Pores
	♀	♂	♀	♂					
BB	7.86 ± 0.40a	7.85 ± 0.62a	1.23 ± 0.05a	1.17 ± 0.05a	Dullish	Smooth	Straight	Inflexible	No pore
SCh	32.39 ± 0.91a	21.93 ± 0.59b	1.82 ± 0.09a	1.23 ± 0.04b	Sharp	Grooved	Straight	Flexible	No pore
STI	10.79 ± 1.05a	12.73 ± 0.55a	2.09 ± 0.12a	1.36 ± 0.04b	Sharp	Grooved	Curved	Flexible	No pore
STII	9.31 ± 0.63b	12.17 ± 0.44a	1.23 ± 0.04b	1.54 ± 0.04a	Sharp	Smooth	Curved	Inflexible	Pores
SBI	7.20 ± 0.33a	6.56 ± 0.40a	0.99 ± 0.02a	1.02 ± 0.03a	Dullish	Grooved	Straight or slightly curved	Flexible	Pores
SBII	6.84 ± 0.11a	5.79 ± 0.16b	1.34 ± 0.06b	1.71 ± 0.05a	Blunt	Grooved	Straight	Inflexible	Pores
SP	28.30 ± 1.45a	23.88 ± 0.95b	3.17 ± 0.08a	3.16 ± 0.06a	Blunt	Smooth	–	Inflexible	Pores
SGP	1.90 ± 0.10b	2.88 ± 0.14a	1.32 ± 0.05b	1.85 ± 0.04a	Blunt	Grooved	Straight	Inflexible	Pores
SAu	8.41 ± 0.64a	6.54 ± 0.44a	2.20 ± 0.17a	1.84 ± 0.09a	Dullish	Smooth	Slightly curved	Flexible	Pores?
SCa	–	–	4.73 ± 0.01a	3.52 ± 0.15b	–	–	–	–	No pore
SCo	1.32 ± 0.06b	2.36 ± 0.05a	0.51 ± 0.03a	0.56 ± 0.00a	–	–	–	–	Pores?
GPs	–	–	1.17 ± 0.06a	1.02 ± 0.04a	–	–	–	–	–

Note: Data are presented as the mean ± SE. Within a row, different lowercase letters indicate a significant difference between the sexes in the length or basal diameter of a sensillum type (*t*-test, $P < 0.05$). The basal diameter of SP is the widest part. The basal diameter of SGP is the diameter of the spheroid. The length of SCo is the diameter of the cuticle, and the basal diameter of SCo is the diameter of the central peg.

diameter of 1.02 ± 0.03 μm ($n = 21$) in males (Table 2). SBI was found on all flagellum subsegments except for F1 in females and males, and SBI numbers increased from the base to the tip of the antenna. The total numbers of SBI were 66.83 ± 7.75 in females and 33.00 ± 5.79 in males (Table 3).

SBII were somewhat cylindrical in appearance; most stood upright with an angle of 80°–90° relative to the antennal surface. These straight sensilla emerged from a shallow cuticular recess with a wrinkled base; they had shallow grooves in their cuticle and a hat-like tip structure beneath which terminal pores were visible (Fig. 4A and D). SBII were 6.84 ± 0.11 μm in length with a basal diameter of 1.34 ± 0.06 μm ($n = 12$) in females and 5.79 ± 0.16 μm in length with a basal diameter of 1.71 ± 0.05 μm ($n = 6$) in males (Table 2). They were found on the second and third claval subsegments in females (total number 27.83 ± 10.70) and on the single claval subsegment in males (11.33 ± 4.90) (Table 3).

Sensilla Placodea (SP)

SP were large, elongated, plate-like sensory organs. Each emerged from a raised cuticular rim, tapered toward the tip, and contained numerous pores (Figs. 3B and 5A). They were 28.30 ± 1.45 μm in length with a basal diameter of 3.17 ± 0.08 μm ($n = 41$) in females and 23.88 ± 0.95 μm in length with a basal diameter of 3.16 ± 0.06 μm ($n = 48$) in males (Table 2). SP had a ring-like distribution on subsegments F3 to C3 of female antennae and on the whole flagellum (F1 to clava) of male antennae and were oriented parallel to the antennal axis (Table 3). They were significantly more numerous in males (366.33 ± 16.13) than in females (47.83 ± 6.35) ($t = 18.376$, df = 10, $P = 0.000$) (Table 3).

Sensilla Grooved Peg (SGP)

The SGP emerged from deep, circular, inflexible pits; each was a multiporous peg with a short, smooth stalk, and a bulbous tip (Figs. 4A and 5B) that stood nearly perpendicular to the surface of the antenna. SGP were 1.90 ± 0.10 μm in length with a bulbous head diameter of 1.32 ± 0.05 μm ($n = 13$) in females and 2.88 ± 0.14 μm in length with a bulbous head diameter of 1.85 ± 0.04 μm ($n = 24$) in males (Table 2). SGP were found on the distal portions of funicular subsegments F3–F8 and all claval subsegments in females and on the distal portions of all subsegments of the flagellum in males. There were significantly fewer SGP in females (5.17 ± 1.87) than in males (19.67 ± 3.93) ($t = -3.332$, df = 10, $P = 0.008$) (Table 3).

Sensilla Auricillica (SAu)

SAu were robust sensilla composed of two sections with a smooth surface. They were located on the distal antennae, nearly perpendicular to the antennal surface (Fig. 5C and D). The top section was club-shaped and distally coniform with a deeply concave top dorsal surface (Fig. 5C and D); it emerged from a flexible socket and was joined to the antennal wall by a short, bulging, and mortar-shaped stalk. Whether or not the SAu had cuticular pores was unclear. Some had the appearance of a newly emerged blade of grass or a rabbit's ear and arose from round pits (Fig. 5D). SAu were 8.41 ± 0.64 μm in length with a short-stalk basal diameter of 2.20 ± 0.17 μm ($n = 4$) in females and 6.54 ± 0.44 μm in length with a short-stalk basal diameter of 1.84 ± 0.09 μm ($n = 16$) in males (Table 2). They were found on the distal subsegments (C2 and C3) in females and on the single claval subsegment in males. There were significantly more SAu in females (35.00 ± 11.56) than in males (6.00 ± 1.48) ($t = 2.487$, df = 10, $P = 0.032$) (Table 3).

Table 3. Abundance and distribution of different sensillum types on the antennae of male and female *A. disparis* ($n = 6$ for each sex)

Segment	Sex	BB	SCh	STI	STII	SBI	SBII	SP	SGP	SAu	SCa	SCo	GP	Total	Density
Radicula	♀	8.33 ± 1.36a	0	0	0	0							0	8.33 ± 1.36a	3.36 ± 0.53a
Radicula	♂	7.50 ± 1.18a	0	0	0	0							0	7.50 ± 1.18a	3.48 ± 0.56a
Scape	♀	0	51.17 ± 4.32a	6.83 ± 3.36a	0	0							3.67 ± 1.12a	61.67 ± 4.45b	2.50 ± 0.29a
Scape	♂	0	11.83 ± 0.48b	22.00 ± 7.87a	0	0							3.50 ± 1.26a	37.33 ± 7.16a	2.16 ± 0.50a
Pedicel	♀	2.33 ± 0.21a	5.83 ± 1.64a	27.17 ± 2.06a	0	0					1.50 ± 0.50a		0	36.83 ± 1.05a	7.76 ± 0.59a
Pedicel	♂	2.17 ± 0.70a	9.33 ± 2.54a	2.33 ± 1.50b	0	0					1.67 ± 0.33a		0	15.50 ± 1.26b	4.74 ± 0.64b
Flagellum F1	♀	0	0	25.67 ± 2.29b	0	0		0	0				0	25.67 ± 2.29b	16.29 ± 1.17a
F1	♂	0	0	141.50 ± 25.52a	0	0		59.00 ± 3.72	2.33 ± 0.67				0	202.83 ± 29.33a	12.97 ± 1.94a
F2	♀	0	0	58.17 ± 3.53b	0	3.33 ± 0.49a		0	0				0.17 ± 0.17	61.67 ± 3.70b	11.10 ± 1.26b
F2	♂	0	0	149.67 ± 13.94a	0	1.50 ± 0.43b		44.33 ± 4.05	2.83 ± 0.60				0	198.33 ± 18.63a	16.42 ± 1.32a
F3	♀	0	0	71.17 ± 3.45b	0	3.33 ± 0.42a		1.33 ± 0.33b	0.17 ± 0.17b				0.17 ± 0.17	76.17 ± 3.20b	12.07 ± 1.03b
F3	♂	0	0	149.00 ± 17.04a	0	1.17 ± 0.48b		50.17 ± 4.23a	3.50 ± 0.56a			0.17 ± 0.17	0	204.00 ± 21.63a	16.25 ± 1.54a
F4	♀	0	0	94.50 ± 3.68b	0	4.50 ± 0.72a		4.67 ± 0.42b	0.50 ± 0.34b				0	104.17 ± 3.68b	12.53 ± 0.73b
F4	♂	0	0	124.67 ± 10.57a	0	1.00 ± 0.37b		42.17 ± 3.04a	2.67 ± 0.71a				0	170.50 ± 13.60a	17.24 ± 1.19a
F5	♀	0	0	99.33 ± 6.85a	0	5.00 ± 0.73a		5.50 ± 0.81a	0.17 ± 0.17b				0	110.00 ± 7.15b	15.17 ± 0.67a
F5	♂	0	0	117.67 ± 7.69a	0	2.00 ± 0.63b		32.17 ± 1.60a	2.50 ± 0.62a				0	154.33 ± 8.85a	19.56 ± 1.97a
F6	♀	0	0	116.17 ± 9.08a	0	5.67 ± 0.67a		5.50 ± 0.22b	0.33 ± 0.21b				0	127.67 ± 9.32a	18.82 ± 0.54a
F6	♂	0	0	106.83 ± 5.00a	0	2.00 ± 0.89b		31.00 ± 0.82a	2.00 ± 1.06a				0	141.83 ± 5.21a	20.33 ± 2.26a
F7	♀	0	0	117.50 ± 10.42a	0.83 ± 0.40a	5.67 ± 0.71a		6.00 ± 0.73b	0.17 ± 0.17b				0	130.17 ± 10.17a	21.03 ± 0.63a
F7	♂	0	0	95.50 ± 5.63a	0.17 ± 0.17	1.67 ± 0.42b		24.33 ± 0.67a	1.83 ± 0.48a				0	123.67 ± 6.45a	22.25 ± 1.69a
F8	♀	0	0	140.00 ± 15.22	2.67 ± 1.20	5.67 ± 0.88		5.67 ± 0.71	0.50 ± 0.22				0	154.50 ± 14.08	26.13 ± 1.05
F8	♂	—	—	—	—	—	—	—	—	—	—	—	—	—	—
C1	♀	0	0	138.50 ± 7.87b	3.83 ± 1.45b	5.33 ± 0.71b	0	6.67 ± 2.11b	0.33 ± 0.21a	0			0	154.67 ± 10.91b	21.47 ± 3.57a
C1	♂	0	0	361.67 ± 34.95a	131.67 ± 34.61a	23.67 ± 5.15a	11.33 ± 4.90	83.17 ± 6.48a	2.00 ± 1.06a	6.00 ± 1.48		0.83 ± 0.40	0	620.17 ± 49.18a	25.36 ± 2.48a
C2	♀	0	0	293.17 ± 60.99	1.83 ± 0.83	9.83 ± 0.70	10.67 ± 6.82	6.50 ± 1.09	1.33 ± 0.61	12.50 ± 6.00			0	335.83 ± 69.08	59.42 ± 10.70
C2	♂	—	—	—	—	—	—	—	—	—	—	—	—	—	—
C3	♀	0	0	405.33 ± 46.17	1.00 ± 0.82	18.50 ± 2.55	17.17 ± 3.98	6.00 ± 1.13	1.67 ± 0.42	22.50 ± 6.32		1.00 ± 1.00	0	473.17 ± 53.95	91.07 ± 10.62
C3	♂	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Total	♀	10.67 ± 1.26a	57.00 ± 5.12a	1593.50 ± 140.51a	10.17 ± 3.89b	66.83 ± 7.75a	27.83 ± 10.70a	47.83 ± 6.35b	5.17 ± 1.87b	35.00 ± 11.56a	1.50 ± 0.50a	1.00 ± 1.00	4.00 ± 1.34a	1860.50 ± 156.71a	18.46 ± 1.09a
Total	♂	9.67 ± 1.78a	21.17 ± 2.73b	1270.83 ± 148.83a	131.83 ± 34.57a	33.00 ± 5.79b	11.33 ± 4.90a	366.33 ± 16.13a	19.67 ± 3.93a	6.00 ± 1.48b	1.67 ± 0.21a	1.00 ± 0.37a	3.50 ± 1.26a	1876.00 ± 128.38a	15.54 ± 0.86a

Note: Data are presented as the mean ± SE. Within a column, different lowercase letters indicate significant differences between sexes in the number of each segment, total number, or density of the same type of sensillum (*t*-test, $P < 0.05$). The density is the number per $10^3 \ \mu m^2$. '-' indicates absence.
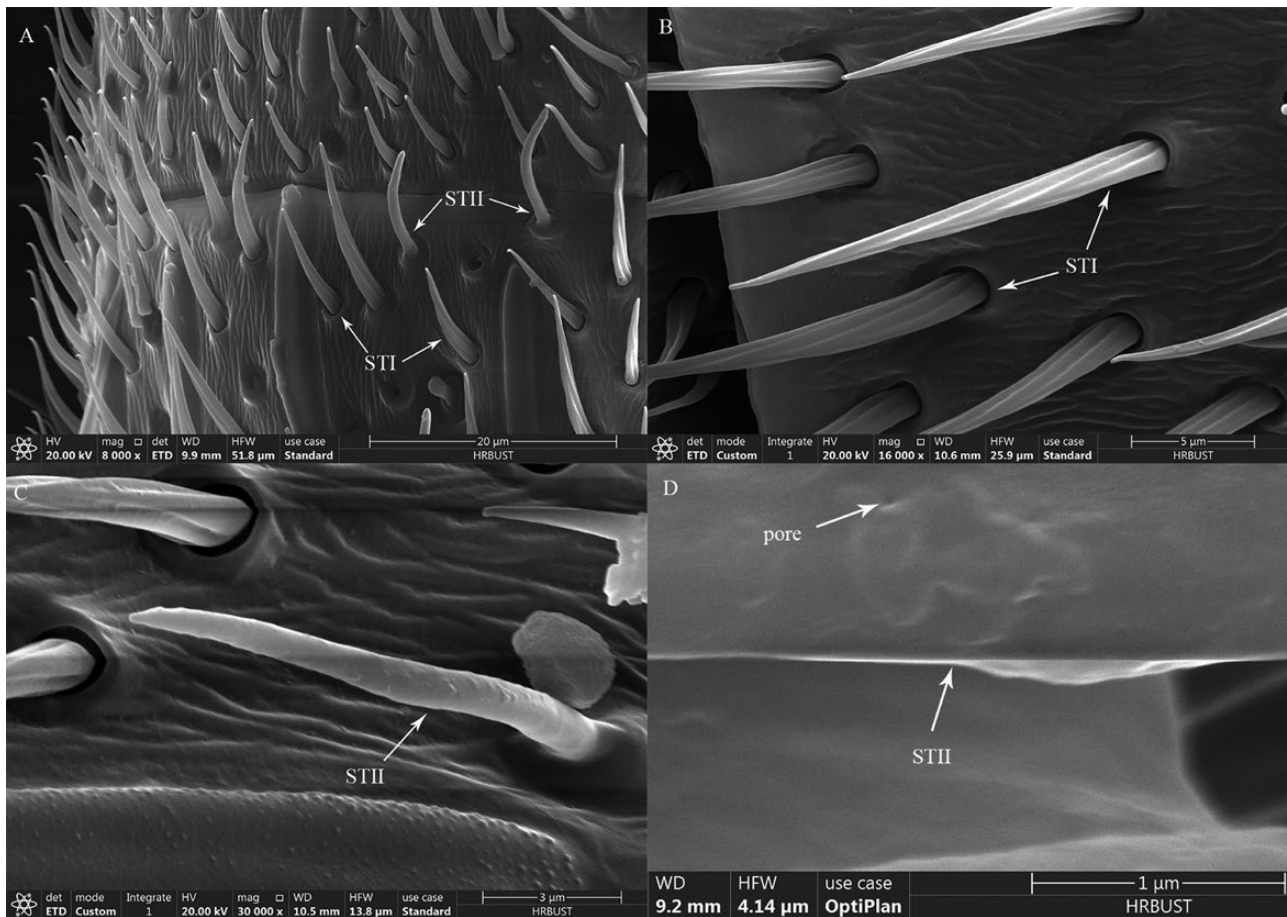
Fig. 3. Sensilla trichodea I (STI) and sensilla trichodea II (STII) of *A. disparis*. (A): STI and STII on a female antenna; (B): STI with longitudinally grooved shaft; (C): STII with smooth wall; (D): Pore on STII wall.

Sensilla Campaniformia (SCa)

SCa were slightly elevated, smooth, circular structures with no pores and were located in depressed cuticular cavities connected to corrugated membrane structures (Fig. 6A). The basal diameters of SCa were 4.73 ± 0.01 µm (*n* = 3) in females and 3.52 ± 0.15 µm (*n* = 5) in males (Table 2). They occurred at regular intervals on the farthest distal ends of the pedicel in both females (total number 1.50 ± 0.50) and males (1.67 ± 0.21) (Table 3).

Sensilla Coeloconica (SCo)

The SCo were cake-shaped sensory structures, and the ambient cuticle was protuberant. The tiny central peg of each was slightly embedded in a shallow, open cuticular cavity, or growing over it (Fig. 6B). The diameters of the cuticle and central peg were 1.32 ± 0.06 µm and 0.51 ± 0.03 µm (*n* = 4) in females and 2.36 ± 0.05 µm and 0.56 ± 0.00 µm (*n* = 3) in males (Table 2). SCo were found on the last funicular subsegment (dorsolateral surface) in both males and females. The total number of SCo did not differ significantly between females (1.00 ± 1.00) and males (1.00 ± 0.37) (*t* = 0.000, df = 10, *P* = 1.000) (Table 3).

Glandular Pores (GPs)

GPs appeared as small openings in the epidermis (Fig. 6C and D); their diameters were 1.17 ± 0.06 µm in females (*n* = 9) and 1.02 ± 0.04 µm in males (*n* = 5) (Table 2). GPs were found on the scape and on subsegments F2–F3 in females and on the scape subsegment in males. The total number of GPs did not differ significantly between

males (3.50 ± 1.26) and females (4.00 ± 1.34) (*t* = 0.272, df = 10, *P* = 0.791) (Table 3).

Distribution of Sensillum Types on Antennal Segments of *A. disparis*

The numbers and types of sensilla increased from the base to the apex of the antennae in both sexes (Table 3). There were relatively few sensilla and a limited number of sensillum types on the basal antennal segments of female and male antennae. The radicula contained only BBs. The scape segment contained three sensillum types (STI, SCh, and GPs), and the pedicel segments contained four (BBs, STI, SCh, and SCa).

In female antennae, the first funicle segment (F1) contained only STI; F2 had three types (STI, SBI, and GPs); and F3 had five (STI, SBI, SP, SGP, and GPs). F4, F5, and F6 of the female antennae contained the same four sensillum types (STI, SBI, SP, and SGP); F7, F8, and C1 contained the latter four sensillum types and also contained STII. In addition to these five sensillum types, C2 also contained SBII and SAu. C3 shared all the types present on C2 and also contained SCo (Table 3).

In male antennae, there were 3 types of sensillum on the F1 subsegment (STI, SP, and SGP). Subsegments F2–F7 all contained STI, SBI, SP, and SGP. The claval subsegment is the top of the male antennae; it contained the largest number of sensilla and sensillum types (STI, STII, SBI, SBII, SP, SGP, SAu, and SCo) (Table 3).

Antennal sensilla of females and males were fewer in number and lower in density on the radicle, scape, and pedicel and higher
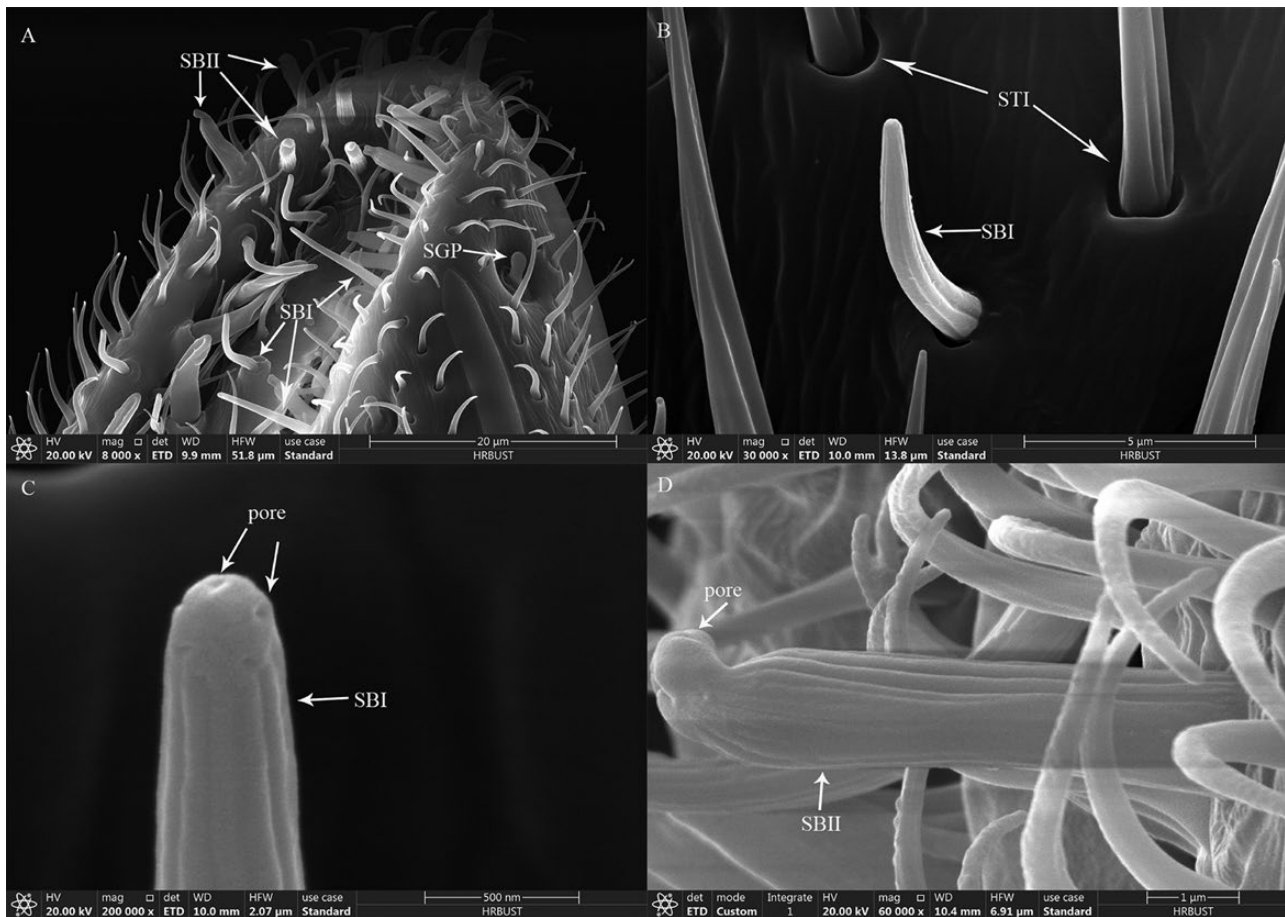
Fig. 4. Sensilla basiconica I (SBI), sensilla basiconica II (SBII), sensilla trichodea I (STI), and sensilla grooved peg (SGP) of *A. disparis*. (A): SBI, SBII, and SGP at the end of a female antenna; (B): STI and SBI; (C): Terminal pore on SBI; (D): Terminal pore on SBII.

in density on the flagellum. On the female antennae, the density of sensilla was lowest on the scape ($2.50 \pm 0.29/1,000$ μm^2) and highest on the claval C3 subsegment ($91.07 \pm 10.62/1,000$ μm^2). The total number of sensilla on the female antennae was 1860.50 ± 156.71, and the average density of sensilla was $18.46 \pm 1.09/1,000$ μm^2 (Table 3). On the male antennae, the density of sensilla was lowest on the scape ($2.16 \pm 0.50/1,000$ μm^2) and highest on the claval subsegment ($25.36 \pm 2.48/1,000$ μm^2). The total number of sensilla on the male antennae was 1876.00 ± 128.38, and the average density was $15.54 \pm 0.86/1,000$ μm^2 (Table 3).

Discussion

Morphology of *A. disparis* Antennae

Like most Hymenopteran parasitoids, *A. disparis* has sexually monomorphic, geniculate antenna made up of four basic segments, the radicula, scape, pedicel, and flagellum. The radicula is the most proximal segment and joins the antenna to the head; the radiculae of both sexes were consistent in morphology with those of other parasitoid wasps (Amornsak et al. 1998, Onagbola and Fadamiro 2008, Meng et al. 2012, Roh et al. 2019, Wong et al. 2021, Zhang et al. 2021, Zhu et al. 2021). The wasp radicula is generally considered a separate segment, as it is wholly separate from the scape and contains different types of sensilla (Onagbola and Fadamiro 2008, Roh et al. 2019, Wong et al. 2021, Zhang et al. 2021, Zhu et al. 2021). Nonetheless, use of the term '"segment"' is typically limited to structures with their own musculature, and additional research

would be required to verify that the *A. disparis* radicula is indeed a separate segment (Chapman 1998). Plate-like dilation of the scape has a protective role in Encyrtidae (Trjapitzin 1977), but according to Storozheva (1991), the same dilation is unlikely to serve a protective function in Eulophinae. The dilated male scape may serve to excite the antennae of the female (Dahms 1984, Zheng et al. 2016), a possibility that is consistent with *A. disparis* courtship behavior, in which males move the inside portion of the scape along the outer portion of the female flagellum.

Sexual dimorphism is commonly reported in the antennal sensilla of Hymenopteran parasitoids, including the superfamily Chalcidoidea (Navasero and Elzen 1991, Isidoro et al. 1996, Onagbola and Fadamiro 2008). In *Metaphycus* (Hymenoptera: Encyrtidae) and *Ooencyrtus phongi* (Hymenoptera: Encyrtidae), e.g., the clavae of females are segmented, whereas those of males are solid (Guerrieri and Noyes 2000, Xi et al. 2011). In other species, males have shorter antennae than females; examples include *Pteromalus cerealellae* (Hymenoptera: Pteromalidae), *Spathius agrili* (Hymenoptera: Braconidae), and *Trichogramma australicum* (Hymenoptera: Trichogrammatidae) (Amornsak et al. 1998, Onagbola and Fadamiro 2008, Wang et al. 2010).

Here, we found that male and female *A. disparis* adults exhibited sexual dimorphism in the numbers, sizes, and types of their antennal segments and sensilla. The male and female antennae were of similar size, but the female antennae contained a larger number of flagellomeres. The male flagellum had eight subsegments, whereas the female flagellum had 11. There were 10
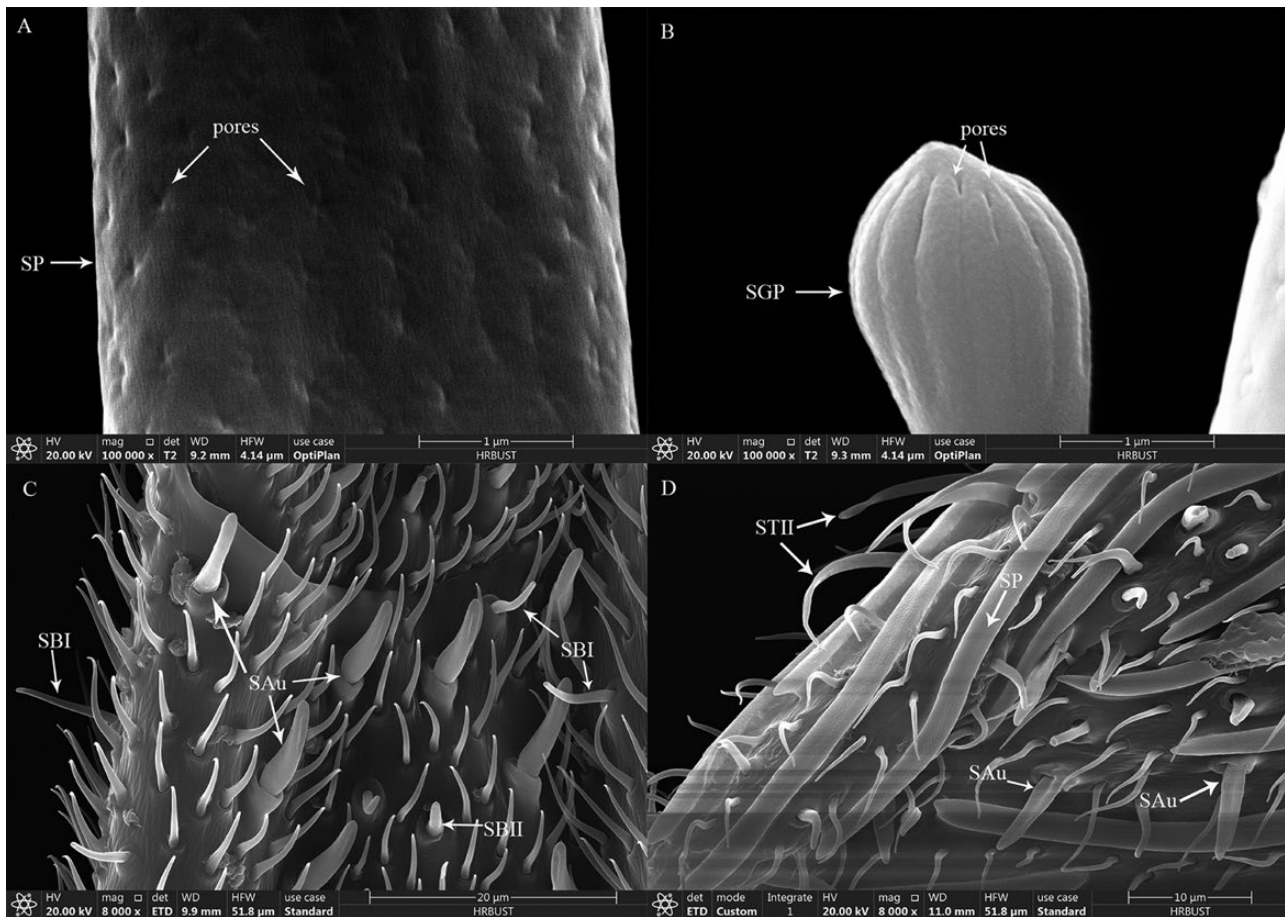
Fig. 5. Sensilla placodea (SP), sensilla grooved peg (SGP), and sensilla auricillica (SAu) of *A. disparis*. (A): SP with numerous pores; (B): SGP with pores; (C): SAu, SBI, and SBII on a female antenna; (D): SAu, SP, and STII on a male antenna.

morphologically distinct sensillum types, all of which were found on both male and female antennae. Most have been described previously in other parasitoid wasps, albeit with some differences in specific nomenclature (Olson and Andow 1993, Isidoro et al. 1996, Amornsak et al. 1998, Pettersson et al. 2001). The sensilla of both sexes were very similar in terms of external morphology, but their abundance and distribution on the antenna differed (Table 3).

Functions of Sensilla

The BBs found in *A. disparis* are similar to those described in *Quadrastichus mendeli* (Hymenoptera: Eulophidae) (Huang et al. 2018), *Sclerodermu*s sp. (Hymenoptera: Bethylidae) (Zhou et al. 2015), and *Omosita colon* (Coleoptera: Nitidulidae) (Cao and Huang 2016) with the same nomenclature. BBs have also been described using the terms sensilla chaetica type Ra in *O. phongi* (Xi et al. 2011), aporous type 4 sensilla trichodea in *P. cerealellae* (Onagbola and Fadamiro 2008), sensilla chaetica nonporous in *P. puparum* (Dweck 2009), sensilla chaetica-2 in *M. parasaissetiae*, and sensilla chaetica on radicula in *Trichospilus pupivorus* (Hymenoptera: Eulophidae) (Silva et al. 2016). Here, BBs were found only on the radicula and at the scape-pedicel junction in *A. disparis*, suggesting a role in proprioception of antennal movement and position (Dweck 2009, Zhou et al. 2013, Silva et al. 2016, Huang et al. 2018) or in sensing antennal position at an optimal angle for obtaining accurate host signals (Merivee et al. 2002, Zhou et al. 2015).

SCh have been described in a number of different Hymenopteran families, and those characterized here for *A. disparis* are similar in structure and description to those reported previously (van Baaren et al. 1996, 1999; Amornsak et al. 1998; Pettersson et al. 2001; Marques-Silva et al. 2006; Zhou et al. 2013; Huang et al. 2018). SCh were distributed around the scape and pedicel in both male and female *A. disparis*, and females had significantly more than males. Previous TEM observations of *Q. mendeli* indicated that sensory neurons were not present in the SCh lumen (Huang et al. 2018). As tactile mechanoreceptors, SCh enable the wasp to assess the position of its antennae relative to the environment (Ochieng et al. 2000, Xu et al. 2000), and previous work indicates that SCh may participate in host discrimination and examination (Isidoro et al. 1996, Onagbola and Fadamiro 2008). It is likely that SCh function similarly in the host exploration behavior of *A. disparis*.

STI are thought to function as mechanoreceptors, and their different morphological features have been characterized in many Hymenopteran families (Olson and Andow 1993, Isidoro et al. 1996, Amornsak et al. 1998, Ochieng et al. 2000, Pettersson et al. 2001, Bleeker et al. 2004, Roux et al. 2005, Gao et al. 2007, Dweck and Gadallah 2008, Onagbola and Fadamiro 2008, Zhang et al. 2021). Our results showed that STI were the most numerous and widespread sensilla on the *A. disparis* antenna. The total number of STI was higher in females than in males, similar to previous reports for *P. cerealellae* (Onagbola and Fadamiro 2008) and *Sclerodermu*s sp. (Zhou et al. 2015). Antennal mechanoreceptors respond to vibration, touch, and air currents by drumming the surface with the
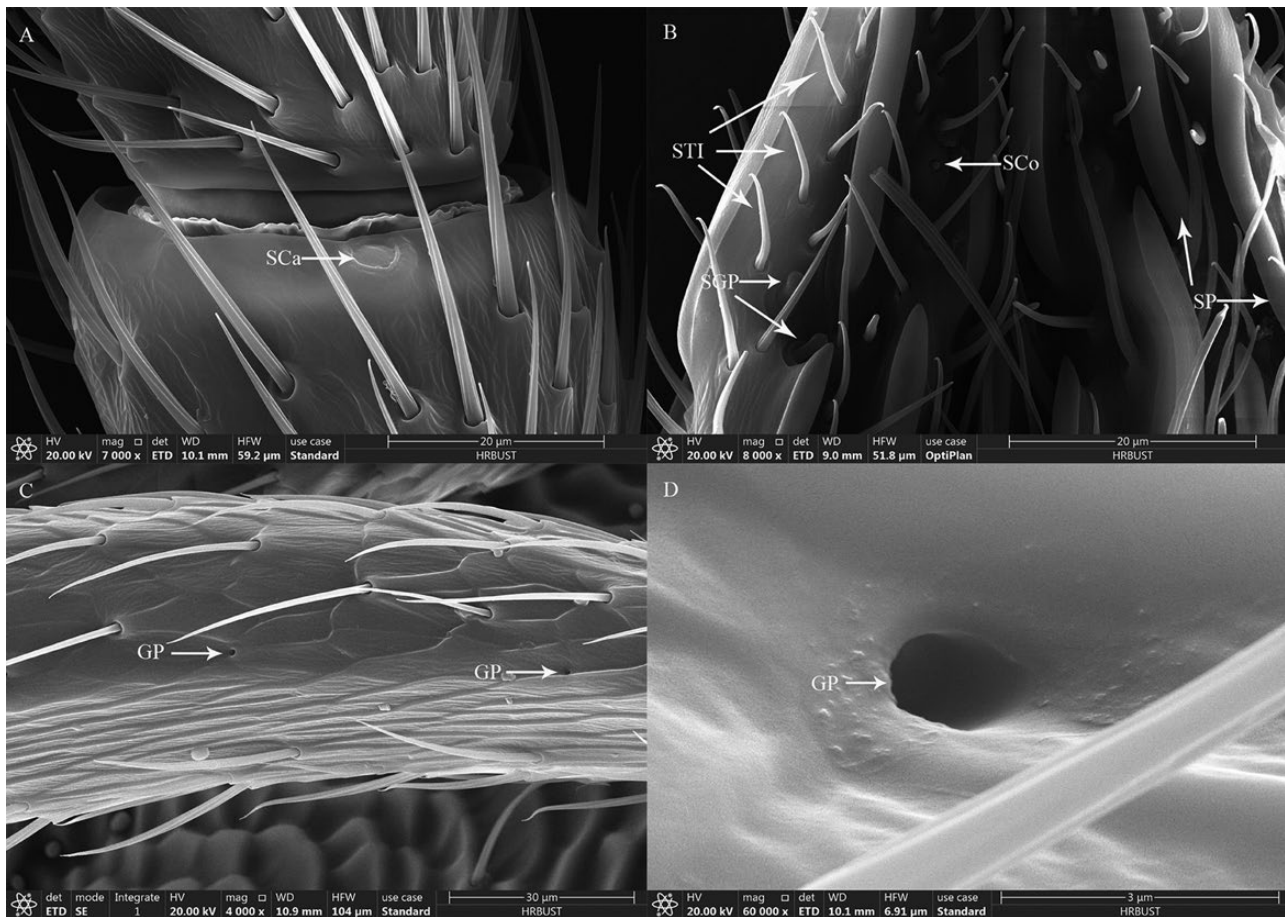
Fig. 6. Sensilla campaniformia (SCa), sensilla coeloconica (SCo), and glandular pores (GPs) of *A. disparis*. (A): SCa on a female antenna; (B): SCo, STI, SGP, and SP on a male antenna; (C): GPs on a scape; (D): GP.

apicoventral portion of the antennal club that contains such sensilla (van Veen and van Wijk 1985). Internal examination of these socketed, nonporous STI in *Tetrastichus howardi* (Hymenoptera: Eulophidae) and *T. hagenowii* suggested that they were mechanoreceptors (Barlin and Vinson 1981, Zheng et al. 2016). Here, the STI emerged from flexible sockets, and their shafts lacked pores and exhibited a longitudinal groove. These features are consistent with those reported previously, suggesting that the STI are likely to be mechanoreceptors.

The STII observed here were similar in distribution and morphology to sensilla that have been described previously by a number of different names: trichoid sensilla in *Rhopalicus tutela* (Hymenoptera: Pteromalidae) (Pettersson et al. 2001), basiconica type 2 sensilla (Ochieng et al. 2000), or sensilla basiconica type B (Navasero and Elzen 1991) in *Microplitis croceipes* (Hymenoptera: Braconidae), multiporous pitted sensilla trichodea C in *T. nubilale* (Olson and Andow 1993), multiporous sensilla trichodea type 5 in *P. puparum* (Dweck 2009), thin-walled chemoreceptors in *Nasonia vitripennis* (Hymenoptera: Pteromalidae) (Slifer 1969) and *Peridesmia discus* (Hymenoptera: Pteromalidae) (Miller 1972), sensilla trichodea in *R. tutela* (Pettersson et al. 2001), long single-walled sensilla in *Neodiprion sertifer* (Hymenoptera: Diprionidae) (Hallberg 1979), and multiporous type III sensilla trichodea in *P. cerealellae* (Onagbola and Fadamiro 2008). *A. disparis* STII were found mainly on the last three subsegments in females and the last subsegment in males. Antennal STII in many insects are thought to function as olfactory receptors (Steinbrecht 1997, Bleeker et al. 2004, Dweck 2009). For example, STII of *R. tutela* is proposed to be

a pheromone receptor (Pettersson et al. 2001), and STII of *N. sertifer* has been verified as a sex pheromone receptor by electrophysiological studies (Hallberg 1979, Hansson et al. 1991). STII were more abundant on male than female antennae of *A. disparis*, perhaps indicating a role in female sex pheromone detection for mate location, as described previously in other parasitoids (Barlin and Vinson 1981, Bleeker et al. 2004, Onagbola and Fadamiro 2008, Zhou et al. 2013, Zhu et al. 2021). Because STII have long shafts and are highly abundant, they offer a large surface area on which to receive signals from female conspecifics.

SBI morphology in *A. disparis* was similar to that of sensilla described previously in many parasitoid wasps (Navasero and Elzen 1991, Olson and Andow 1993, Isidoro et al. 1996, Bleeker et al. 2004, Onagbola and Fadamiro 2008). These sensilla have been termed basiconic sensilla-2 in *M. parasaissetiae* (Zhou et al. 2013), sensilla trichodea TP in *Cotesia glomerata* (Hymenoptera: Braconidae) and *C. rubecula* (Bleeker et al. 2004), uniporous chaetica sensilla in *P. cerealellae* (Onagbola and Fadamiro 2008), and sensilla chaetica I and II in *Copidosomopsis nacoleiae* (Hymenoptera: Encyrtidae) (Zhang et al. 2021). SBI are distinguished by the presence of cuticular fingers and numerous apical pores; they have been suggested to function as gustatory chemoreceptors for host recognition and to participate in contact chemoreception (Altner and Prillinger 1980, Olson and Andow 1993, Pettersson et al. 2001, Roux et al. 2005), including gustatory functions (Isidoro et al. 1996, Barbarossa et al. 1998, Gao et al. 2007, Onagbola and Fadamiro 2008).

SBII were morphologically distinct sensilla observed in *A. disparis* whose locations and structure were similar to those of basiconic sensilla-3 in *M. parasaissetiae* (Zhou et al. 2013), sensillum chaetica type 4 in *Anaphes victus* (Hymenoptera: Mymaridae) and *A. listronoti* (van Baaren et al. 1999), sensilla basiconica type 1 in *M. croceipe* (Ochieng et al. 2000), uniporous pit pore sensilla trichodea D in *T. nubilale* (Olson and Andow 1993), and sensilla basiconica in *C. nacoleiae* (Zhang et al. 2021). SBII are limited to the antennal apex of *A. disparis* and numerous other pteromalids, indicating that they are likely to function as contact chemoreceptors (Weseloh 1972, Amornsak et al. 1998) involved in host recognition and acceptance (Roux et al. 2005, Zhou et al. 2013, Zhang et al. 2015).

SP have been reported on the antennae of almost all parasitoid wasps, although their specific morphologies differ among families (Miller 1972, Butterfield and Anderson 1994, Ochieng et al. 2000, Bleeker et al. 2004, Roux et al. 2005, Bourdais et al. 2006, Gao et al. 2007, Dweck and Gadallah 2008, Onagbola and Fadamiro 2008, Dweck, 2009). In Chalcidoidea such as Trichogrammatidae (Cönsoli et al. 1999), Mymaridae (van Baaren et al. 1999), and Ptermalidae (Pettersson et al. 2001, Onagbola and Fadamiro 2008), SP are not embedded in the flagellomere but are elevated directly above the antennal surface (Pettersson et al. 2001). By contrast, in Braconidae, SP are embedded in the flagellomere and only slightly elevated above the antennal surface (Bleeker et al. 2004). *A. disparis* belongs to the family Eupelmidae and superfamily Chalcidoidea, and its SP morphology was similar to that of other Chalcidoidea wasps. Our finding that antennal SP were significantly more abundant in male *A. disparis* than in females was consistent with reports on *C. rubecula* and *C. glomerata* (Bleeker et al. 2004), *M. croceipes* (Navasero and Elzen 1991, Ochieng et al. 2000), and *A. victus* and *A. listronoti* (van Baaren et al. 1999), but it contrasted with findings in several other hymenopterans, including *P. cerealellae* (Onagbola and Fadamiro 2008), *T. pupivorus* (Silva et al. 2016), *M. parasaissetiae* (Zhou et al. 2013), and *Pseudotorymus jaapiellae* (Hymenoptera: Torymidae) (Zhu et al. 2021). SP are considered to be olfactory organs (Bleeker et al. 2004, Roux et al. 2005, Zhang et al. 2015), and the multiple SP wall pores of many species are consistent with an olfactory function (Barlin and Vinson 1981, Ochieng et al. 2000, Bleeker et al. 2004, Roux et al. 2005, Marques-Silva et al. 2006, Gao et al. 2007, Das et al. 2011). Previous work suggests that they may enable *Trichogramma galloi* to orient towards its host over long distances (Cönsoli et al. 1999), and work with individual sensilla demonstrated that *M. croceipes* SP were olfactory receptors that responded to plant volatiles in a dose-dependent manner (Ochieng et al. 2000). SP are thus likely to act as pheromone detectors in *A. disparis*. Dimorphism in SP may be related to behavioral differences between the sexes (e.g., mate and host location, host utilization) that involve the perception of physical, volatile, and contact chemical signals from mates or substrates (Zhou et al. 2013). Female *M. croceipes* have been shown to detect plant volatiles via SP early in the search for potential oviposition hosts, whereas male wasps may use them to locate mates based on plant-based chemical signals, perhaps together with female sex pheromones (Whitman and Eller 1992, Alborn et al. 1995, Pophof et al. 2005).

SGP are commonly found in hymenopteran parasitoids. They have been termed peg-like sensilla in *Sympiesis sericeicornis* (Hymenoptera: Eulophidae) (Meyhöfer et al. 1997), multiporous pegs sensilla in *T. hagenowii* (Barlin and Vinson 1981), multiporous grooved sensilla basiconica C in *T. nubilale* (Olson and Andow 1993), basiconic capitate peg sensilla in *P. cerealellae* (Onagbola and Fadamiro 2008), sensillum coeloconicum in *P. jaapiellae* (Zhu et al. 2021), basiconic capitate peg sensilla in *T. australicum* (Amornsak et al. 1998), multiparous grooved basiconica sensilla in *T. galloi* Zucchi and *T. pretiosum* (Cönsoli et al. 1999), and basiconic sensilla in *O. phongi* and *M. parasaissetiae* (Xi et al. 2011, Zhou et al. 2013). Here, we found pores on the swollen distal pegs of the *A. disparis* SGP and observed that their stalks emerged upright from inflexible circular pits, suggesting that they can receive environmental stimuli through narrow apertures. Sex-related differences in SGP numbers have previously been observed in *O. nezarae* (Roh et al. 2019) and *M. parasaissetia* (Zhou et al. 2013). Here, SGP were significantly more numerous on male than female antennae of *A. disparis*. They are thought to function mainly as olfactory (van Baaren et al. 1996, Pophof et al. 2005), hygro-, thermo-, or mechano-receptors (Altner et al. 1983, Wcislo 1995, Zhu et al. 2021) or in the perception of CO_2 (Stange and Stowe 1999), suggesting that they may serve dual roles as thermo- and chemo-receptors (Altner et al. 1981, Altner and Loftus 1985; Isidoro et al. 1996, 1999).

SAu have been described previously in *Protophormia terraenovae* (Diptera: Calliphoridae) (Setzu et al. 2011) and four species of *Gasterophilus* (Diptera: Gasterophilidae) (Zhang et al. 2016), in which they were characterized as spoon- or ear-like structures with a sunken or concavely indented distal surface. In location and structure, they are comparable to the finger-like sensilla of *M. parasaissetiae* (Zhou et al. 2013) and *O. nezarae* (Roh et al. 2019), sensilla chaetica type 5 in *O. phongi* (Xi et al. 2011), and long sensilla basiconica in *Scleroderma guani* (Hymenoptera: Bethylidae) (Li et al. 2011). In total, SAu observed here had partly sunken cuticular surfaces, perhaps reflecting the deflation and shrinkage that may accompany dehydration for SEM, a finding that has been noted previously (Zhang et al. 2016). SAu were more numerous in female *A. disparis* than in males, and a previous report on *S. littoralis* indicates that SAu may have an important role during female host location for oviposition (Seada 2015). Because of their large surface area, a number of studies have proposed that these sensilla may perceive stimuli from the host substrate (Zhou et al. 2013, Roh et al. 2019).

SCa have been characterized previously in a number of Hymenopterans (Amornsak et al. 1998, Zheng et al. 2016, Roh et al. 2019, Sevarika et al. 2021) and Coleopterans (Faucheux and Kundrata 2017). Individually innervated SCa with thick walls and a smooth, domed cuticular structure were observed in *Tetrastichus* sp. (Hymenoptera: Eulophidae) (Schneider 1964, Wong et al. 2021). Here, SCa of *A. disparis* appeared as nonporous caps positioned in the joints of the antennae. Previous work suggests that stretching and muscular contractions of the pedicel, as well as external pressures, alter the shape of the SCa sensory dome. SCa are therefore thought to be proprioceptors, enabling mechanical deformation of the cuticle (Zheng et al. 2016, Faucheux and Kundrata 2017) and may also participate in antennal gland secretion (Bin et al. 1989).

Antennal SCo have previously been reported in other parasitoids, including Braconidae and Trichogrammatidae (Cönsoli et al. 1999, Roux et al. 2005). They were the least abundant sensillum type on *A. disparis* and have previously been described as pit organs, as they are found within deep pits in *Augochloru puru* (Hymenoptera: Apoidea) (Wcislo 1995); they have also been termed coeloconic sensilla in *P. cerealellae* (Onagbola and Fadamiro 2008), sensilla coeloconica type-II in *Dryocosmus kuriphilus* (Hymenoptera: Cynipidae) (Sevarika et al. 2021), and coeloconic sensillum type II in *C. glomerata* and *C. rubecula* (Bleeker et al. 2004). The specific functions of SCo are currently unclear, although it has been suggested that, like SGP, they participate in thermo- and hygroperception (Altner et al. 1983, Bleeker et al. 2004, Onagbola and Fadamiro 2008). SCo have shown similar ultrastructural features in most species examined: three sensory neurons are typically observed, with

two unbranched dendrites that extend into the peg lumen and a final lamellated dendrite that terminates at the peg base (Altner and Loftus 1985). However, a separate study reported a similar sensillum in which none of the three dendrites were branched (Schneider et al. 2018). Previous research indicates that GPs have an olfactory function and are highly sensitive to sex pheromone (Zhou et al. 2011), and a large amount of paste was found around the GPs of the drone after mating (Lu et al. 2006).

In *A. disparis*, there were more sensillum types on the antennal tips than on other antennomeres: six types of sensillum in total (SP, SGP, SB, SAu, ST, and SCo), including the most common sensillum types of Chalcidoidea parasitoids. The antennal tips are thought to be centers of exploration. When female parasitoids intensely antennated host surfaces, they made contact with only the tips of their antennae, scanning for chemical cues or movement of air particles in the boundary layer around the host (Casas et al. 1998). *A. disparis* has also displayed such antennal tapping movements, and *Aprostocetus prolixus* (Hymenoptera: Eulophidae) has been shown to receive chemical information from eggs of *Apriona germari* Hope (Coleoptera: Cerambycidae) through similar behavior. The numerous antennal tip sensilla may therefore have an important role in signal perception for host detection at close range (Huang et al. 2018).

Conclusion

Here, we observed sexual dimorphism in the external morphology of *A. disparis* antenna. The same types of sensilla were found on both sexes, some of which were putative mechanoreceptors and/or chemoreceptors. BBs, SCh, STI, and SCa may be mechanoreceptors for host location and exploration, tactile perception, air movement detection, and proprioception. STII, SBI, SBII, SP, SAu, SCo, and GPs may be chemoreceptors for olfactory perception during behaviors such as food acquisition, mating, or host searching. SGP may be antennal hydro- and thermo-receptors.

Male parasitoid wasps frequently have more olfactory sensilla, as they are attracted to female conspecifics by sex pheromones in many species (Tagawa 1977, Tagawa and Kitano 1981, Chapman 1982, Field and Keller 1993). Our findings were consistent with this higher olfactory sensitivity of males, as they bore larger numbers of SP on their antennae. Such dimorphism provides a morphological basis for understanding specific, sex-related behaviors mediated by antennal perception in *A. disparis* and related species. In parasitic Hymenoptera, olfactory cues are used to direct a number of female behaviors, including habitat searching; host detection, location, examination, discrimination, and acceptance; and oviposition (Weseloh 1972, Bin et al. 1989, Isidoro et al. 2001). By contrast, the olfactory systems of males participate mainly in female recognition (Bin et al. 1999, Battaglia et al. 2002).

This examination of the abundance, distribution, and external morphology of various antennal sensillum types in *A. disparis* provides insight into olfactory mechanisms used for intra- and inter-specific chemical communication. It provides basic information for the future use of Y-tube olfactometer bioassays to investigate host-searching mechanisms. Further research on the functional morphology of *A. disparis* sensilla could make use of confocal and transmission electron microscopy, as well as electrophysiological recordings, to verify the expression location of specific odorant binding proteins and provide additional evidence for the sensillum functions suggested here (Silva et al. 2016, Zheng et al. 2016, Wong et al. 2021). Next, we will try to master the gene information corresponding to various important olfactory sensilla

and their roles in locating hosts, mating, oviposition, etc., so as to improve their ability to locate, mate or parasitize through gene manipulation.

Author Contributions

JJ Wang, PC Liu and CW Cao conceived and designed the experiments; JJ Wang, JG Wang and CW Cao performed the experiments and writing original draft; PC Liu, QS Luan and X Jiang edited the paper. All authors have read and agreed to the published version of the manuscript.

References Cited

Alborn, H. T., W. J. Lewis, and J. H. Tumlinson. 1995. Host-specific recognition kairomone for the parasitoid *Microplitis croceipes* (Cresson). *J. Chem. Ecol.* 21: 1697–1708. doi:10.1007/BF02033670

Altner, H., and R. Loftus. 1985. Ultrastructure and function of insect thermo and hygroreceptors. *Annu. Rev. Entomol.* 30: 273–295. doi:10.1146/annurev.en.30.010185.001421

Altner, H., and L. Prillinger. 1980. Ultrastructure of invertebrate chemo-, thermo-, and hygroreceptors and its functional significance. *Int. Rev. Cytol.* 67: 69–139. doi:10.1016/S0074-7696(08)62427-4

Altner, H., C. Routil, and R. Loftus. 1981. The structure of bimodal chemo-, thermo-, and hygroreceptive sensilla on the antenna of *Locusta migratoria*. *Cell Tissue Res.* 215: 289–308. doi:10.1007/BF00239116

Altner, H., L. Schaller-Selzer, H. Stetter, and I. Wohlrab. 1983. Poreless sensilla with inflexible sockets: a comparative study of a fundamental type of insect sensilla probably comprising thermo- and hygroreceptors. *Cell Tissue Res.* 234: 279–307. doi:10.1007/BF00213769

Amornsak, W., B. Cribb, and G. Gordh. 1998. External morphology of antennal sensilla of *Trichogramma australicum* Girault (Hymenoptera: Trichogrammatidae). *Int. J. Insect Morphol. Embryol.* 27: 67–82. doi:10.1016/S0020-7322(98)00003-8

Barbarossa, I. T., P. Muroni, M. Dardani, P. Casula, and A. M. Angioy. 1998. New insight into the antennal chemosensory function of *Opius concolor* (Hymenoptera: Braconidae). *Ital. J. Zool.* 65: 367–370. doi:10.1080/11250009809386775

Barlin, M. R., and S. B. Vinson. 1981. The multiporous plate sensilla and its potential use in braconid systematic (Hymenoptera: Braconidae). *Can. Entomol.* 113: 931–938.

Battaglia, D., N. Isidoro, R. Romani, F. Bin, and F. Pennacchio. 2002. Mating behavior of *Aphidius ervi* (Hymenoptera: Braconidae): the role of antennae. *Eur. J. Entomol.* 99: 451–456. doi:10.14411/eje.2002.057

Bin, F., S. Colazza, N. Isidoro, and S. B. Vinson. 1989. Antennal chemosensilla and glands, and their possible meaning in the reproductive behaviour of *Trissolcus basalis* (Woll.) (Hym.: Scelionidae). *Entomologica*. 24: 33–97. doi:10.15162/0425-1016/623

Bin, F., F. Wäckers, R. Romani, and N. Isidoro. 1999. Tyloids in *Pimpla turionellae* (L.) are release structures of male antennal glands involved in courtship behavior (Hymenoptera: Ichneumonidae). *Int. J. Insect Morphol. Embryol.* 28: 61–68. doi:10.1016/S0020-7322(99)00015-X

Bleeker, M. A. K., H. M. Smid, A. C. van Aelst, J. J. A. van Loon, and L. E. M. Vet. 2004. Antennal sensilla of two parasitoid wasps: a comparative scanning electron microscopy study. *Microsc. Res. Tech.* 63: 266–273. doi:10.1002/jemt.20038

Bourdais, D., P. Vernon, L. Krespi, J. Le Lannic, and J. B. van. 2006. Antennal structure of male and female *Aphidius rhopalosiphi* DeStefani-Peres (Hymenoptera: Braconidae): description and morphological alterations after cold storage or heat exposure. *Microsc. Res. Tech*. 69: 1005–1013. doi:10.1002/jemt.20378

Butterfield, A., and M. Anderson. 1994. Morphology and ultrastructure of antennal sensilla of the parasitoid, *Trybliographa rapae* (Westw.) (Hymenoptera: Cynipidae). *Int. J. Insect Morphol. Embryol*. 23: 11–20. doi:10.1016/0020-7322(94)90012-4

Cao, Y. K., and M. Huang. 2016. A SEM study of the antenna and mouthparts of *Omosita colon* (Linnaeus) (Coleoptera: Nitidulidae). *Microsc. Res. Tech*. 79: 1152–1164. doi:10.1002/jemt.22770

Casas, J., S. Baclier, J. Tautz, R. Meyhofer, and D. Pierre. 1998. Leaf vibrations and air movements in a leafminer-parasitoid system. *Biol. Control*. 11: 147–153. doi:10.1006/bcon.1997.0593

Chapman, R. F. 1982. Chemoreception: the significance of receptor numbers. *Adv. Insect Physiol*. 16: 247–356. doi:10.1016/S0065-2806(08)60155-1

Chapman, R. F. 1998. Nervous system, pp. 533–735. *In The insects structure and function*, 4th ed. Cambridge University Press, UK.

Chiappini, E., C. Solinas, and M. Solinas. 2001. Antennal sensilla of *Anagrus atomus* (L.) (Hymenoptera: Mymaridae) female and their possible behavioural significance. *Entomologica*. 35: 51–76. doi:10.15162/0425-1016/731

Cönsoli, F. L., E. W. Kitajima, and J. R. P. Parra. 1999. Sensilla on the antenna and ovipositor of the parasitic wasps *Trichogramma galloi* Zucchi and *T. pretiosum* Riley (Hym., Trichogrammatidae). *Microsc. Res. Tech*. 45: 313–324. doi:10.1002/(SICI)1097-0029(19990515/01)45:4<313::AID-JEMT15>3.0.CO;2-4

Crossman, S. S. 1925. Two imported egg parasites of the gipsy moth, *Anastatus bifasciatus* Fonsc and *Schedius kuvanae* Howard. *J. Agric. Res*. 30: 75. https://naldc.nal.usda.gov/download/IND43966953/PDF.

Dahms, E. C. 1984. A review of the biology of species in the genus *Melittobia* (Hymenoptera: Eulophidae) with interpretations and additions using observations on *Melittobia australica*. *Mem. Queensl. Mus*. 21: 337–360. doi:10.17082/J.2204-1478.21-2.1984.1984-05

Das, P., L. Chen, K. R. Sharma, and H. Y. Fadamiro. 2011. Abundance of antennal chemosensilla in two parasitoid wasps with different degree of host specificity may explain sexual and species differences in their response to host-related volatiles. *Microsc. Res. Tech*. 74: 900–909. doi:10.1002/jemt.20974

Dweck, H. K. M. 2009. Antennal sensory receptors of *Pteromalus puparum* female (Hymenoptera: Pteromalidae), a gregarious pupal endoparasitoid of *Pieris rapae*. *Micron*. 40: 769–774. doi:10.1016/j.micron.2009.07.012

Dweck, H. K. M., and N. S. Gadallah. 2008. Description of the antennal sensilla of *Habrobracon hebetor*. *BioControl*. 53: 841–856. doi:10.1007/s10526-007-9145-6

Faucheux, M. J., and R. Kundrata. 2017. Comparative antennal morphology of male Drilini with special reference to the sensilla (Coleoptera: Elateridae: Agrypninae). *Zool. Anz*. 266: 105–119. doi:10.1016/j.jcz.2016.11.002

Faucheux, M. J., T. Németh, and R. Kundrata. 2020. Comparative antennal morphology of *Agriotes* (Coleoptera: Elateridae), with special reference to the typology and possible functions of sensilla. *Insects*. 11: 137. doi:10.3390/insects11020137

Field, S. A., and M. A. Keller. 1993. Courtship and intersexual signaling in the parasitic wasp *Cotesia rubecula* (Hymenoptera: Braconidae). *J. Insect Behav*. 6: 737–750. doi:10.1007/BF01201673

Gao, Y., L. Z. Luo, and A. Hammond. 2007. Antennal morphology, structure and sensilla distribution in *Microplitis pallidipes* (Hymenoptera: Braconidae). *Micron*. 38: 684–693. doi:10.1016/j.micron.2006.09.004

Guerrieri, E., and J. S. Noyes. 2000. Revision of European species of genus *Metaphycus* Mercet (Hymenoptera: Chalcidoidea: Encyrtidae), parasitoids of scale insects. *Syst. Entomol*. 25: 147–222. doi:10.1046/j.1365-3113.2000.00099.x

Hallberg, E. 1979. The fine structure of the antennal sensilla of the pine saw fly *Neodiprion sertifer* (Insecta: Hymenoptera). *Protoplasma*. 101: 111–126. doi:10.1007/BF01293440

Hansson, B. S., J. N. Van der Pers, H. E. Högberg, E. Hedenstrom, O. Anderbrant, and J. Lofqvist. 1991. Sex pheromone perception in male pine sawflies, *Neodiprion sertifer* (Hymenoptera, Diprionidae). *J. Comp. Physiol. A*. 168: 533–538. doi:10.1007/BF00215075

Huang, Z. Y., Y. J. Zhang, J. Y. Liu, Z. D. Yang, W. Lu, and X. L. Zheng. 2018. Ultrastructure of female antennal sensilla of an endoparasitoid wasp, *Quadrastichus mendeli* Kim and La Salle (Hymenoptera: Eulophidae: Tetrastichinae). *Microsc. Microanal*. 24: 431–441. doi:10.1017/S1431927618012424

Isidoro, N., F. Bin, S. Colazza, and S. B. Vison. 1996. Morphology of antennal gustatory sensilla and glands in some parasitoid hymenoptera with hypothesis on their role in sex and host recognition. *J. Hymenopt. Res*. 5: 206–239. doi:10.5962/BHL.PART.28120

Isidoro, N., F. Bin, R. Romani, J. Pujade-Villar, and P. Ros-Farré. 1999. Diversity and function of male antennal glands in Cynipoidea (Hymenoptera). *Zool. Scr*. 28: 165–174. doi:10.1046/j.1463-6409.1999.00013.x

Isidoro, N., R. Romani, and F. Bin. 2001. Antennal multiporous sensilla: their gustatory features for host recognition in female parasitic wasps (Insecta, Hymenoptera: Platygastroidea). *Microsc. Res. Tech*. 55: 350–358. doi:10.1002/jemt.1183

Keil, T. A. 1997. Functional morphology of insect mechanoreceptors. *Microsc. Res. Tech*. 39: 506–531. doi:10.1002/(SICI)1097-0029(19971215)39:6<506::AID-JEMT5>3.0.CO;2-B

Leal, W. S. 2013. Odorant reception in insects, roles of receptors, binding proteins, and degrading enzymes. *Annu. Rev. Entomol*. 58: 373–391. doi:10.1146/annurev-ento-120811-153635

Li, B. J., and J. X. Lou. 1992. Preliminary studies on *Anastatus disparis* (Hymenoptera: Eupelmidae), an egg parasitoid of gypsy moth. *Chin. J. Biol. Control*. 8: 144. doi:10.16409/j.cnki.2095-039x.1992.03.018. in Chinese

Li, X., D. Lu, X. Liu, Q. Zhang, and X. Zhou. 2011. Ultrastructural characterization of olfactory sensilla and immunolocalization of odorant binding and chemosensory proteins from an ectoparasitoid *Scleroderma guani* (Hymenoptera: Bethylidae). *Int. J. Biol. Sci*. 7: 848–868. doi:10.7150/ijbs

Liu, P. C., D. J. Hao, W. Hu, J. R. Wei, and J. J. Wang. 2021. Life history of aggression in *Anastatus disparis* (Hymenoptera: Eupelmidae) with extreme male–male combat. *Bull. Entomol. Res*. 111: 146–152. doi:10.1017/S0007485320000413

Liu, P. C., J. Men, B. Zhao, and J. R. Wei. 2017. Fitness-related offspring sex allocation of *Anastatus disparis*, a gypsy moth egg parasitoid, on different-sized host species. *Entomol. Exp. Appl*. 163: 281–286. doi:10.1111/eea.12579

Liu, P. C., J. R. Wei, J. J. Wang, J. X. Liu, and L. J. Dong. 2015. Relationship between the environmental temperatures and development of *Anastatus disparis* (Ruschka) (Hymenoptera: Eupelmidae) and the sex ratio control of the offspring. *Forest Pest Disease*. 34: 9–14. (in Chinese with English summary). https://en.cnki.com.cn/Article_en/CJFDTOTAL-SLBC201502003.htm.

Lu, J. F., Y. Li, H. Q. Qiu, B. J. Shen, and W. J. Fu. 2006. Scanning electron micrographs studies of antennal sensilla in male *Tetrastichus* sp. *Nat. Enemies Insects*. 28: 71–75. (in Chinese). https://kns.cnki.net/kcms/detail/detail.aspx?FileName=KCTD200602005&DbName=CJFQ2006.

Marques-Silva, S., C. P. Matiello-Guss, J. H. C. Delabie, C. S. F. Mariano, J. C. Zanuncio, and J. E. Serrao. 2006. Sensilla and secretory glands in the antennae of a primitive ant: *Dinoponera lucida* (Formicidae: Ponerinae). *Microsc. Res. Tech*. 69: 885–890. doi:10.1002/jemt.20356

Meng, Z. J., S. C. Yan, C. P. Yang, and C. C. Ruan. 2012. Asymmetrical distribution of antennal sensilla in the female *Anastatus japonicus* Ashmead (Hymenoptera: Eupelmidae). *Microsc. Res. Tech*. 75: 1066–1075. doi:10.1002/jemt.22032

Merivee, E., A. Ploomi, M. Rahi, J. Bresciani, H. P. Ravn, A. Luik, and V. Sammelselg. 2002. Antennal sensilla of the ground beetle *Bembidion properans* Steph. (Coleoptera, Carabidae). *Micron*. 33: 429–440. doi:10.1016/S0968-4328(02)00003-3

Meyhöfer, R., J. Casas, and S. Dorn. 1997. Mechano- and chemoreceptors and their possible role in host location behavior of *Sympiesis sericeicornis* (Hymenoptera: Eulophidae). *Ann. Entomol. Soc. Am*. 90: 208–219. doi:10.1093/aesa/90.2.208

Miller, M. C. 1972. Scanning electron microscope studies of the flagellar sense receptors of *Peridesmia discus* and *Nasonia vitripennis*

(Hymenoptera: Pteromalidae). *Ann. Entomol. Soc. Am.* 65: 1119–1124. doi:10.1093/aesa/65.5.1119

Navasero, R. C., and G. W. Elzen. 1991. Sensilla on the antennae, foretarsi and palpi of *Microplitis croceipes* (Cresson) (Hymenoptera: Braconidae). *Proc. Entomol. Soc. Wash.* 93: 737–747. https://www.biodiversitylibrary.org/part/55549.

Ochieng, S. A., K. C. Park, J. W. Zhu, and T. C. Baker. 2000. Functional morphology of antennal chemoreceptors of the parasitoid *Microplitis croceipes* (Hymenoptera: Braconidae). *Arthropod Struct. Dev.* 29: 231–240. doi:10.1016/S1467-8039(01)00008-1

Olson, D. N., and D. A. Andow. 1993. Antennal sensilla of female *Trichogramma nubilale* (Ertle and Davis) (Hymenoptera: Trichogrammatidae) and comparisons with other parasitic Hymenoptera. *Int. J. Insect Morphol. Embryol.* 22: 507–520. doi:10.1016/0020-7322(93)90037-2

Onagbola, E. O., and H. Y. Fadamiro. 2008. Scanning electron microscopy studies of antennal sensilla of *Pteromalus cerealellae* (Hymenoptera: Pteromalidae). *Micron.* 39: 526–535. doi:10.1016/j.micron.2007.08.001

Pettersson, E. M., E. Hallberg, and G. Birgersson. 2001. Evidence for the importance of odour-perception in the parasitoid *Rhopalicus tutela* (Walker) (Hym., Pteromalidae). *J. Appl. Entomol.* 125: 293–301. doi:10.1046/j.1439-0418.2001.00550.x

Pophof, B., G. Stange, and L. Abrell. 2005. Volatile organic compounds as signals in a plant-herbivore system: electrophysiological responses in olfactory sensilla of the moth *Cactoblastis cactorum*. *Chem. Senses.* 30: 51–68. doi:10.1093/chemse/bji001

Roh, G. H., Y. J. Lee, J. J. Zhu, and C. G. Park. 2019. Morphology and distribution of antennal sensilla in egg parasitoid, *Ooencyrtus nezarae* (Hymenoptera: Encyrtidae). *Microsc. Res. Tech.* 82: 972–982. doi:10.1002/jemt.23244

Roux, O., J. van Baaren, C. Gers, L. Arvanitakis, and L. Legal. 2005. Antennal structure and oviposition behavior of the *Plutella xylostella* specialist parasitoid: *Cotesia plutellae*. *Microsc. Res. Tech.* 68: 36–44. doi:10.1002/jemt.20220

Schneider, D. 1964. Insect antennae. *Annu. Rev. Entomol.* 9: 103–122. doi:10.1146/annurev.en.09.010164.000535

Schneider, E. S., C. J. Kleineidam, G. Leitinger, and H. Römer. 2018. Ultrastructure and electrophysiology of thermosensitive sensilla coeloconica in a tropical katydid of the genus *Mecopoda* (Orthoptera, Tettigoniidae). *Arthropod Struct. Dev.* 47: 482–497. doi:10.1016/j.asd.2018.08.002

Seada, M. A. 2015. Antennal morphology and sensillum distribution of female cotton leaf worm *Spodoptera littoralis* (Lepidoptera: Noctuidae). *J. Basic Appl. Zool.* 68: 10–18. doi:10.1016/j.jobaz.2015.01.005

Setzu, M. D., S. Poddighe, and A. M. Angioy. 2011. Sensilla on the antennal funiculus of the blow fly, *Protophormia terraenovae* (Diptera: Calliphoridae). *Micron.* 42: 471–477. doi:10.1016/j.micron.2011.01.005

Sevarika, M., M. V. Rossi Stacconi, and R. Romani. 2021. Fine morphology of antennal and ovipositor sensory structures of the gall chestnut wasp, *Dryocosmus kuriphilus*. *Insects.* 12: 231. doi:10.3390/insects12030231

Shen, S. F., W. Wu, Z. Zhang, Y. M. Wang, X. B. Kong, F. Liu, and S. F. Zhang. 2019. Morphological analysis of sensilla on different organs in *Pachyneuron aphidis*, a hyperparasitoid of *Myzus persicae*. *Microsc. Res. Tech.* 82: 1810–1818. doi:10.1002/jemt.23347

Silva, I. M., K. S. Pereira, T. Spranghers, J. C. Zanuncio, and J. E. Serrão. 2016. Antennal sensilla and sexual dimorphism of the parasitoid *Trichospilus pupivorus* (Hymenoptera: Eulophidae). *Microsc. Microanal.* 22: 913–921. doi:10.1017/S1431927616011314

Slifer, E. H. 1969. Sense organs on the antenna of a parasitic wasp, *Nasonia vitripennis* (Hymenoptera, Pteromalidae). *Biol. Bull-US.* 136: 253–263. doi:10.2307/1539818

Stange, G., and S. Stowe. 1999. Carbon-dioxide sensing structures in terrestrial arthropods. *Microsc. Res. Tech.* 47: 416–427. doi:10.1002/(SICI)1097-0029(19991215)47:6<416::AID-JEMT5>3.0.CO;2-X

Steinbrecht, R. A. 1997. Pore structures in insect olfactory sensilla: a review of data and concepts. *Int. J. Insect Morphol. Embryol.* 26: 229–245. doi:10.1016/S0020-7322(97)00024-X

Storozheva, N. A. 1991. Morphology and evolutionary transformations of the antennae of *Eulophine* wasps (Hymenoptera, Eulophidae). *Entomol. Obozr.* 70: 168–182.

Tagawa, J. 1977. Localization and histology of the female sex pheromone-producing gland in the parasitic wasp *Apanteles glomeratus*. *J. Insect Physiol.* 23: 49–56. doi:10.1016/0022-1910(77)90108-1

Tagawa, J., and H. Kitano. 1981. Mating behaviour of the braconid wasp, *Apanteles glomeratus* L. (Hymenoptera: Braconidae) in the field. *Appl. Entomol. Zool.* 16: 345–350. doi:10.1303/AEZ.16.345

Trjapitzin, V. A. 1977. Characteristic traits of morphology of adult encyrtids (Hymenoptera, Chalcidoidea, Encyrtidae) and their systematic significance. *Tr. Vses. Entomol. O-va.* 58: 145–199.

van Baaren, J., R. Barbier, and J. P. Nénon. 1996. Females antennal sensilla of *Epidinocarsis lopezi* and *Leptomastix dactylopii* (Hymenoptera: Encyrtidae), parasitoids of pseudococcid mealybugs. *Can. J. Zool.* 74: 710–720. doi:10.1139/z96-080

van Baaren, J., G. Boivin, J. Le Lannic, and J. P. Nénon. 1999. Comparison of antennal sensilla of *Anaphes victus* and *A. listronoti* (Hymenoptera, Mymaridae), egg parasitoids of Curculionidae. *Zoomorphology.* 119: 1–8. doi:10.1007/s004350050076

van Veen, J. C., and M. L. E. van Wijk. 1985. The unique structure and functions of the ovipositor of the non-paralyzed ectoparasitoid *Colpoclypeus florus* Walk. (Hym., Eulophidae) with special reference to antennal sensilla and immature stages. *J. Appl. Entomol.* 99: 511–531. doi:10.1111/j.1439-0418.1985.tb02019.x

Wang, X. Y., Z. Q. Yang, and J. R. Gould. 2010. Sensilla on the antennae, legs and ovipositor of *Spathius agrili* Yang (Hymenoptera: Braconidae), a parasitoid of the emerald ash borer *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae). *Microsc. Res. Tech.* 73: 560–571. doi:10.1002/jemt.20795

Wcislo, W. T. 1995. Sensilla numbers and antennal morphology of parasitic and non-parasitic bees (Hymenoptera: Apoidea). *Int. J. Insect Morphol. Embryol.* 24: 63–81. doi:10.1016/0020-7322(94)E0006-B

Weseloh, R. M. 1972. Sense organs of the hyperparasite *Cheiloneurus noxius* (Hymenoptera: Encyrtidae) important in host selection processes. *Ann. Entomol. Soc. Am.* 65: 41–46. doi:10.1093/aesa/65.1.41

Whitman, D. W., and F. J. Eller. 1992. Orientation of *Microplitis croceipes* (Hymenoptera: Braconidae) to green leaf volatiles: dose-response curves. *J. Chem. Ecol.* 18: 1743–1753. doi:10.1007/BF02751099

Wong, S. S., C. S. Tee, P. A. C. Ooi, and W. Wong. 2021. Sexual dimorphism of antennal and ovipositor sensilla of *Tetrastichus* sp. (Hymenoptera: Eulophidae). *J. Asia-Pac. Entomol.* 24: 1313–1325. doi:10.1016/j.aspen.2021.08.018

Xi, Y. Q., X. M. Yin, C. D. Zhu, E. Guerrieri, and Y. Z. Zhang. 2011. Scanning electron microscopy studies of antennal sensilla of *Ooencyrtus phongi* (Hymenoptera: Encyrtidae). *Microsc. Res. Tech.* 74: 936–945. doi:10.1002/jemt.20979

Xu, Y., J. Hong, and C. Hu. 2000. Ultrastructural studies on the antennal sensilla of *Pteromalus puparum* L. (Hymenoptera: Pteromalidae). *J. Zhejiang Univ. - Agric. Life Sci.* 26: 394–398. (in Chinese with English summary). https://kns.cnki.net/kcms/detail/detail.aspx?FileName=ZJNY200004010&DbName=CJFQ2000.

Yan, J. J., C. H. Xu, W. C. Gao, G. W. Li, D. F. Yao, and P. Y. Zhang. 1989. *Parasites and predators of forest pest.* China Forestry Publishing House, Beijing.

Zacharuk, R. Y. 1980. Ultrastructure and function of insect chemosensilla. *Annu. Rev. Entomol.* 25: 27–47. doi:10.1146/annurev.en.25.010180.000331

Zacharuk, R. Y. 1985. Antennae and sensilla, pp. 1–70. *In* G. A. Kerkut and L. I. Gilbert (eds.), *Comparative insect physiology, biochemistry and pharmocology,* vol. 6. Pergamon Press, Oxford.

Zhang, Y. J., D. Y. Chen, X. T. Chao, Z. S. Dong, Z. Y. Huang, X. L. Zheng, and W. Lu. 2021. Ultrastructure of antennal sensilla of *Copidosomopsis nacoleiae* (Eady) (Hymenoptera: Chalcidoidea: Encyrtidae), a parasitoid of *Diaphania angustalis* (Snellen) (Lepidoptera: Crambidae). *Microsc. Res. Tech.* 84: 2149–2165. doi:10.1002/jemt.23770

Zhang, L., Y. Q. Feng, L. L. Ren, Y. Q. Luo, F. Wang, and S. X. Zong. 2015. Sensilla on antenna, ovipositor and leg of *Eriborus applicitus* (Hymenoptera: Ichneumonidae), a parasitoid wasp of *Holcocerus insularis* Staudinger (Lepidoptera: Cossidae). *Acta Zool. (Stockholm).* 96: 253–263. doi:10.1111/azo.12073

Zhang, D., X. Y. Li, X. H. Liu, Q. K. Wang, and T. Pape. 2016. The antenna of horse stomach bot flies: morphology and phylogenetic implications (Oestridae, Gasterophilinae: *Gasterophilus* Leach). *Sci. Rep.* 6: 34409. doi:10.1038/srep34409

Zheng, Y. H., L. X. Zheng, Y. L. Liao, and W. J. Wu. 2016. Sexual dimorphism in antennal morphology and sensilla ultrastructure of a pupal endoparasitoid *Tetrastichus howardi* (Olliff) (Hymenoptera: Eulophidae). *Microsc. Res. Tech*. 79: 374–384. doi:10.1002/jemt.22640

Zhou, C. X., X. Sun, F. Mi, J. Y. Chen, and M. Q. Wang. 2015. Antennal sensilla in the parasitoid *Sclerodermus* sp. (Hymenoptera: Bethylidae). *J. Insect Sci*. 15: 36. doi:10.1093/jisesa/iev024

Zhou, H., W. J. Wu, Z. F. Zhang, and Y. Zhang. 2011. Antennal sensilla of *Apanteles cypris* Nixon (Hymenoptera: Braconidae), a larval endoparasitoid of *Cnaphalocrocis medinalis* Guenée (Lepidoptera: Pyralidae). *Microsc. Res. Tech*. 74: 1199–1208. doi:10.1002/jemt.21016

Zhou, H., W. J. Wu, F. P. Zhang, and Y. G. Fu. 2013. Scanning electron microscopy studies of the antennal sensilla of *Metaphycus parasaissetiae* Zhang & Huang (Hymenoptera: Encyrtidae). *Neotrop. Entomol*. 42: 278–287. doi:10.1007/s13744-013-0113-9

Zhu, X., S. Liu, C. Q. Xu, K. Guo, R. Xu, H. L. Qiao, and J. Chen. 2021. Morphology and distribution of sensilla on the antennae and ovipositor of the Hymenopteran parasitoid *Pseudotorymus jaapiellae* Yang et Chen. *Microsc. Res. Tech*. 84: 1873–1886. doi:10.1002/jemt.23744