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

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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, Iidoro 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 scattered 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 antenna 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 coeloconica (SCo), sensilla grooved peg (SGP), sensilla auricillica (SAu), sensilla campaniformia (SCa), and glandular pores (GP). Based on their shapes and sizes, we also identified two ST subtypes (ST1 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 7.85 ± 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 BB 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 ± 5.33a | 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 | 1.58 ± 0.19b | 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 ± 52.30a | 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.
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 = 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 basil 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
| Sensillum Type | Socket | Shape | Wall | Tip | Pores | Basal Diameter (μm) | Tip Length (μm) | Basal Diameter (μm) |
|---------------|--------|-------|------|-----|-------|---------------------|-----------------|---------------------|
| BB            | Inflexible | Straight | Flexible | Straight | No pore | BB 7.86 ± 0.40 | BB 7.93 ± 0.62 | BB 7.85 ± 0.62 |
| SCh           | Inflexible | Straight | Flexible | Straight | No pore | SCh 32.39 ± 0.91 | SCh 21.93 ± 0.59 | SCh 21.93 ± 0.59 |
| STI          | Inflexible | Curved | Flexible | Curved | No pore | STI 10.79 ± 1.05 | STI 12.73 ± 0.55 | STI 12.73 ± 0.55 |
| STII         | Inflexible | Curved | Flexible | Curved | No pore | STII 9.31 ± 0.63 | STII 12.17 ± 0.44 | STII 12.17 ± 0.44 |
| SBI          | Inflexible | Grooved | Flexible | Slightly curved | Pores | SBI 7.20 ± 0.33 | SBI 8.41 ± 0.64 | SBI 8.41 ± 0.64 |
| SBII         | Inflexible | Grooved | Flexible | Slightly curved | Pores | SBII 6.84 ± 0.11 | SBII 5.79 ± 0.16 | SBII 5.79 ± 0.16 |
| SP           | Inflexible | Spherical | Inflexible | - | - | SP 28.30 ± 1.45 | SP 23.88 ± 0.95 | SP 23.88 ± 0.95 |
| SGP          | Inflexible | Grooved | Inflexible | - | - | SGP 1.90 ± 0.10 | SGP 2.88 ± 0.14 | SGP 2.88 ± 0.14 |
| SAu          | Inflexible | Grooved | Slightly curved | Flexible | Pores | SAu 8.41 ± 0.64 | SAu 5.79 ± 0.16 | SAu 5.79 ± 0.16 |
| SCa          | Inflexible | - | - | - | - | SCa 1.32 ± 0.06 | SCa 1.32 ± 0.06 | SCa 1.32 ± 0.06 |
| SCa 1.32 ± 0.06 | Inflexible | - | - | - | - | SCa 1.32 ± 0.06 | SCa 1.32 ± 0.06 | SCa 1.32 ± 0.06 |
| GPs          | Inflexible | - | - | - | - | GPs 1.32 ± 0.06 | GPs 2.88 ± 0.14 | GPs 2.88 ± 0.14 |

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.

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 the flagellum in males. There were significantly fewer SGP in females (5.17 ± 1.87) than in males (19.67 ± 3.93) (t = 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 conform to 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 (11.33 ± 4.90) (Table 3).

SIBI 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 hair-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).
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    | SHI    | SBI    | SBII   | SP     | SGP    | S-Au   | SCa    | S-Co   | GP     | Total  | Density |
|---------|------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|---------|
| Radicula| ♀    | 8.33 ± 1.36a | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 8.33 ± 1.36a | 3.36 ± 0.53a |
|         | ♂    | 7.50 ± 1.18a | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 7.50 ± 1.18a | 3.48 ± 0.56a |
| Scape   | ♀    | 8.33 ± 1.36a | 0      | 3.67 ± 1.36b | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 8.33 ± 1.36a | 3.36 ± 0.53a |
|         | ♂    | 6.67 ± 1.28a | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 6.67 ± 1.28a | 3.48 ± 0.56a |
| Pedicel | ♀    | 2.33 ± 0.21a | 5.83 ± 1.64a | 27.17 ± 2.06a | 0      | 0      | 0      | 0      | 0      | 1.90 ± 0.38a | 0      | 0      | 36.83 ± 1.05a | 7.76 ± 0.59a |
|         | ♂    | 2.33 ± 0.21a | 9.33 ± 1.96a | 2.33 ± 0.33a | 0      | 0      | 0      | 0      | 0      | 1.90 ± 0.38a | 0      | 0      | 36.83 ± 1.05a | 7.76 ± 0.59a |
| Flagellum| F1   | 0      | 0      | 25.67 ± 2.29b | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 25.67 ± 2.29b | 16.29 ± 1.17a |
|         | F2   | 0      | 0      | 141.50 ± 25.52a | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 141.50 ± 25.52a | 12.97 ± 1.94a |
|         | F3   | 0      | 0      | 71.17 ± 3.49b | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 71.17 ± 3.49b | 2.50 ± 0.29a |
|         | F4   | 0      | 0      | 94.50 ± 3.06b | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 94.50 ± 3.06b | 61.67 ± 3.70b |
|         | F5   | 0      | 0      | 128.67 ± 10.37a | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 128.67 ± 10.37a | 11.10 ± 1.26a |
|         | F6   | 0      | 0      | 114.17 ± 9.09a | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 114.17 ± 9.09a | 11.10 ± 1.26a |
|         | F7   | 0      | 0      | 117.50 ± 10.42a | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 117.50 ± 10.42a | 11.10 ± 1.26a |
|         | F8   | 0      | 0      | 140.00 ± 15.22a | 2.67 ± 1.20 | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 140.00 ± 15.22a | 11.10 ± 1.26a |
| C1      | ♀    | 138.50 ± 7.87b | 3.83 ± 1.45b | 5.33 ± 1.71b | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 138.50 ± 7.87b | 21.47 ± 3.57a |
|         | ♂    | 361.67 ± 83.95a | 23.67 ± 5.15a | 21.67 ± 4.91b | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 361.67 ± 83.95a | 21.47 ± 3.57a |
| C2      | ♀    | 293.17 ± 60.99a | 5.00 ± 1.83a | 9.83 ± 0.70a | 5.33 ± 1.71b | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 293.17 ± 60.99a | 59.42 ± 10.70 |
|         | ♂    | 149.50 ± 35.69a | 0      | 1.00 ± 0.37a | 18.50 ± 2.55a | 17.17 ± 3.98b | 0      | 0      | 0      | 0      | 0      | 0      | 149.50 ± 35.69a | 10.17 ± 3.89b |
| C3      | ♀    | 405.33 ± 46.17a | 0.50 ± 0.21b | 5.00 ± 1.83a | 1.67 ± 0.42a | 0      | 0      | 0      | 0      | 0      | 0      | 0      | 405.33 ± 46.17a | 22.25 ± 1.09a |
|         | ♂    | 473.17 ± 53.95a | 0      | 0      | 1.00 ± 0.37a | 22.00 ± 5.82a | 0      | 0      | 0      | 0      | 0      | 0      | 473.17 ± 53.95a | 22.25 ± 1.09a |
| Total   | ♀    | 10.67 ± 1.26a | 57.00 ± 5.12a | 1593.50 ± 140.51a | 10.17 ± 3.89b | 66.83 ± 7.75a | 27.83 ± 10.70 | 47.83 ± 6.35b | 5.17 ± 1.87b | 35.00 ± 11.56a | 1.90 ± 0.50a | 1.00 ± 1.00b | 4.00 ± 1.34b | 1860.50 ± 156.71a | 18.46 ± 1.09a |
|         | ♂    | 9.67 ± 1.78a | 21.17 ± 2.73a | 1270.83 ± 148.83a | 131.83 ± 34.57a | 33.00 ± 5.79a | 11.33 ± 4.90a | 34.66 ± 16.35a | 10.17 ± 3.89b | 35.00 ± 11.56a | 1.90 ± 0.50a | 1.00 ± 1.00b | 4.00 ± 1.34b | 1876.00 ± 128.35a | 15.54 ± 0.96a |

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 10³ μm². '–' indicates absence.
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 $4.73 \pm 0.01 \, \mu m$ ($n = 3$) in females and $3.52 \pm 0.15 \, \mu m$ ($n = 5$) in males (Table 2). They occurred at regular intervals on the farthest distal ends of the pedicel in both females (total number $1.50 \pm 0.50$) and males ($1.67 \pm 0.21$) (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 $1.32 \pm 0.06 \, \mu m$ and $0.51 \pm 0.03 \, \mu m$ ($n = 4$) in females and $2.36 \pm 0.05 \, \mu m$ and $0.56 \pm 0.00 \, \mu m$ ($n = 3$) 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 ($1.00 \pm 1.00$) and males ($1.00 \pm 0.37$) ($t = 0.000$, df = 10, $P = 0.791$) (Table 3).

Glandular Pores (GPs)
GPs appeared as small openings in the epidermis (Fig. 6C and D); their diameters were $1.17 \pm 0.06 \, \mu m$ in females ($n = 9$) and $1.02 \pm 0.04 \, \mu m$ 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 ($3.50 \pm 1.26$) and females ($4.00 \pm 1.34$) ($t = 0.272$, 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 GPs). 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, SP, SGP, SAu, and SCo) (Table 3).

Antennal sensilla of females and males were fewer in number and lower in density on the radicile, scape, and pedicel and higher...
in density on the flagellum. On the female antennae, the density of sensilla was lowest on the scape (2.50 ± 0.29/1,000 μm²) and highest on the claval C3 subsegment (91.07 ± 10.62/1,000 μm²). The total number of sensilla on the female antennae was 1860.50 ± 156.71, and the average density of sensilla was 18.46 ± 1.09/1,000 μm² (Table 3).

On the male antennae, the density of sensilla was lowest on the scape (2.16 ± 0.50/1,000 μm²) and highest on the claval subsegment (25.36 ± 2.48/1,000 μm²). The total number of sensilla on the male antennae was 1876.00 ± 128.38, and the average density was 15.54 ± 0.86/1,000 μm² (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, 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, Meng et al. 2012, 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 *Metaephyicus* (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...
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).

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.

Functions of Sensilla

The BBs found in A. disparis are similar to those described in Quadrastichus mendeli (Hymenoptera: Eulophidae) (Huang et al. 2018), Sclerodermus 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, Blecker 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 Sclerodermus sp. (Zhou et al. 2015). Antennal mechanoreceptors respond to vibration, touch, and air currents by drumming the surface with the
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 (Ochien et al. 2000), or sensilla basiconica type B (Navasero and Elzen 1991) in *Microplitis croceipes* (Hymenoptera: Braconidae), multiporous pitted sensilla trichodea C in *T. rubricollis* (Olson and Andow 1993), basiconica 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 Fadamiyo 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 Fadamiyo 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 Fadamiyo 2008). These sensilla have been termed basiconlic sensilla-1 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 Fadamiyo 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 Fadamiyo 2008).
SBII were morphologically distinct sensilla observed in *A. disparis* at various locations and structures 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. croceipes* (Ochieng et al. 2000), uniporous pit pore sensilla trichoida D in *T. mubilale* (Olson and Andow 1993), and sensilla basiconica in *C. naceolata* (Zhang et al. 2021). SBII are limited to the antennal apex of *A. disparis* and numerous other periomorphs, 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 parasitic 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 Chalcidioidea such as Trichogrammatidae, the SP are the antennal surface (Bleeker et al. 2004). *A. disparis* belongs to the family Eupelmidae and superfamily Chalcidoidea, and its SP morphology is similar to that of other Chalcidioidea 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 yaapiellae* (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 (Consoli et al. 1999), and work with individual sensilla demonstrated that *M. croceipes* SP were olfactory receptors that respond 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 *Symposiis sericeicornis* (Hymenoptera: Eulophidae) (Meyhöfer et al. 1997), multiporous pegs sensilla in *T. bagenoulii* (Barlin and Vinson 1981), multiporous grooved sensilla basiconica C in *T. mubilale* (Olson and Andow 1993), basicapitale peg sensilla in *P. cerealellae* (Onagbola and Fadamiro 2008), sensillum coeloconicum in *P. jaapiellae* (Zhu et al. 2021), basicapitale peg sensilla in *T. australicum* (Amornsak et al. 1998), multiporous grooved basiconica sensilla in *T. galloi* Zucchi and T. pretiosum (Consoli et al. 1999), and basicapitale sensilla in *O. phongii* and *M. parasaissetiae* (Xi et al. 2011, Zhou et al. 2013).

Here, we found pores on the swollen distal pegs of the *A. disparis* SP 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. nezaane* (Roh et al. 2019) and *M. parasaissetiae* (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, Weislo 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).

SGP 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. nezaane* (Roh et al. 2019), sensilla chaetica type 5 in *O. phongii* (Xi et al. 2011), and long sensillum basiconica in *Scherodera guani* (Hymenoptera: Bethylidae) (Li et al. 2011). In total, SGP 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). SGP were more numerous in female *A. disparis* than in males, and a previous report on *S. littoralis* indicates that SGP 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). Individual innervated SCa are found 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 (Zeng 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 (Consoli 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 *Augochlora pura* (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 mechano-receptors and/or chemoreceptors. BBs, SCh, STI, and SCa may be mechano-receptors for host location and exploration, tactile perception, air movement detection, and proprioception. STII, SBL, SBI, 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 hydrom- 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-seeking 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.

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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.

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