Morphological Characterization and Distribution of Antennal Sensilla of *Mamestra brassicae* (Lepidoptera: Noctuidae) Using Scanning Electron Microscopy[1]

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Abstract The cabbage armyworm, *Mamestra brassicae* L. (Lepidoptera: Noctuidae), is a pest in cabbage crops throughout Europe and Asia. To better understand the chemical orientation of this insect toward its host products, we used scanning electron microscopy to determine the structure and distribution of antennal sensilla of *M. brassicae*. The antennae of the female and male moths were thread-like and composed of a scape, a pedicel, and a flagellum with >43 flagellomeres. Based on their morphology, sensilla chaetica (subtypes 1 and 2), sensilla trichodea (subtypes 1, 2, and 3), sensilla basiconica (subtypes 1 and 2), sensilla styloconica, Böhm bristles, sensilla coeloconica, and sensilla squamiformia were distinguished on the antennae in both sexes. The putative functions of these sensilla also were discussed with reference to their morphology, distribution, and ultrastructure. This work is a prerequisite for future electrophysiological studies of the antennal sensory system involved in intraspecific chemical communication.

Key Words *Mamestra brassicae*, antennal sensilla, scanning electron microscopy

The cabbage armyworm, *Mamestra brassicae* L. (Lepidoptera: Noctuidae), is a highly polyphagous insect. It is mainly recognized as a pest of cabbage (*Brassica oleracea* L.), but it has also been reported from a wide range of other plant species (Balachowsky 1972). Its known food plants include >70 species of 22 families, of which Brassicaceae and Chenopodiaceae are among the most preferred (Popova 1993). Several aspects of *M. brassicae* biology have been studied extensively, such as courtship and mating behavior (Birch et al. 1989, Noldus and Potting 1990, Poppy and Birch 1994) and oviposition behavior (Rojas et al. 2001). To characterize the chemical orientation of *M. brassicae* toward its host products and mates, it is necessary to know the structure of the olfactory system of the moth.

Insect antennae play an important role in detection of various external stimuli involved in finding suitable habitat and locating mates (Baker et al. 2004, Pophof et al. 2005, Sun et al. 2011). In insects, the antenna is suggested to be the principal organ carrying the olfactory receptors (Callahan 1975, Lavoie-Dornik and McNeil 1987, Schneider 1964).

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Numerous studies have been conducted to characterize antennal sensilla of various insects (Bleeker et al. 2004, Faucheux et al. 2006, Keil and Steinbrecht 1984, Liu et al. 2013, Städler 1984, Zacharuk 1980), but very few of such studies have been focused on Noctuidae (Chang et al. 2015, Hu et al. 2021, Koh et al. 1995, Malo et al. 2004, Mochizuki et al. 1992, Seada 2015). The antennal sensilla of *M. brassicae* have not been studied despite the important role they play in the life of the insect. In this study, as part of our ongoing research on mate and host location mechanisms of *M. brassicae,* we used scanning electron microscopy (SEM) techniques to characterize and determine the abundance and distribution of the antennal sensilla of this cabbage moth. This work is a prerequisite for future electrophysiological studies of the antennal sensory system involved in intraspecific chemical communication.

Materials and Methods

Insects. Pupae of *M. brassicae* were collected from cabbage crops at Changchun, Jilin Province, China. The pupae were maintained in the laboratory at 25 ± 1°C, 40% ± 10% relative humidity, and 16L:8D photoperiod. Larvae were reared on an artificial diet. Pupae were sexed and placed in separate plastic containers (20 cm high × 12 cm diameter) for adult emergence and were checked daily for emergence. Adults were fed with a 10% sugar solution dispensed on cotton wool placed on the floor of the container. Newly emerged moths were used for the SEM observations. Voucher specimens were deposited at the School of Life Sciences, Changchun Normal University (Changchun, China).

SEM. Antennae were carefully excised from the antennal sockets with fine forceps under a stereo microscope (SZX12, Olympus, Tokyo, Japan). The antennae were first kept in 70% ethanol for 24 h and then dehydrated in a graded alcohol series of 75, 80, 85, 90, and 100% in each case for 10 min each. Antennae were individually mounted with dorsal or ventral sides on aluminum stubs with double-sided sticky tape. Before examination, antennae were sputter coated with gold (20 nm) in an E-102 (Hitachi, Tokyo, Japan) high-resolution sputter coater. The specimens were examined in a Hitachi S-570 scanning electron microscope set at 20 kV. Ten antennae of each sex were examined by SEM.

Statistical analysis. The morphology and distribution of sensilla on the antennae of *M. brassicae* were examined. Sensilla on the dorsal and ventral surfaces of the antennae of both sexes were identified and measured. To characterize the sensilla, we used the nomenclature proposed by Schneider (1964) and Zacharuk (1980, 1985). The types were also compared with those described for other lepidopteran insects (e.g., Bawin et al. 2017, Castrejón-Gómez and Carrasco 2008, Chang et al. 2015, Faucheux 1997, Frank et al. 2010). Statistical results were expressed as mean (±SD) length of sensilla.

Results

General structure of the antennae. The antennae of the female and male moths were thread-like and located between the compound eyes. The antennae were composed of a basal scape, a pedicel, and a flagellum of >43 flagellomeres. The male antenna was slightly longer (mean ± SD) (8,156.7 ± 90.5 μm) than the female antenna (7,851.0 ± 56.4 μm).

Types of sensilla. Based on their morphological features, we identified sensilla chaetica (SCH; subtypes 1 and 2), sensilla trichodea (ST; subtypes 1, 2, and 3), sensilla basiconica (SB; subtypes 1 and 2), sensilla styloconica (STY), Böhm bristles (BB), sensilla coeloconica (SCO), and sensilla squamiformia (SSQ). The morphological features and lengths (mean ± SD) of each antennal sensillum type are listed in Table 1.

SCH1. Each sensillum was straight, wide at the basal part, and slightly curved at the distal part where the articulation was countersunk into a central socket enclosed by a bulge (Fig. 1A). SCH1 had circumferential grooves on their surfaces (Fig. 1B). Lengths were 86.54 ± 8.47 μm (female) and 83.41 ± 8. 68 μm (male), and basal diameters were 3.35 ± 0.41 μm (female) and 3.78 ± 0.43 μm (male).

SCH2. SCH2 were oriented perpendicular to the cuticle and had a rigid needle-like appearance, with a diameter that decreased steadily from the base to the tip (Fig. 1C, D). Lengths were 35.14 ± 4.81 μm (female) and 37.82 ± 3.95 μm (male), and basal diameters were 4.98 ± 0.18 μm (female) and 4.56 ± 0.29 μm (male).

ST1. ST1 were hairs with slightly sharp tips and a helical wall and were nearly parallel to the antenna surface or slightly curved toward the antennal shaft (Fig. 2A). They became progressively more pointed from the base onward. Lengths were 44.69 ± 9.77 μm (male), and basal diameters were 1.78 ± 0.45 μm (male).

ST2. ST2 were slender hairs with a smooth surface texture at their base and a helical pattern gradually marked toward the apex (Fig. 2B, C). These hairs were inclined forward at an angle of 30–45° from the surface of the antennae. Lengths were 34.21 ± 7.34 μm (female) and 30.97 ± 4.63 μm (male), and basal diameters were 1.65 ± 0.32 μm (female) and 1.95 ± 0.32 μm (male).

ST3. High magnification images of these sensory hairs revealed that they were curved along the longitudinal axis, with a helical surface texture and a blunt tip (Figs. 2D, 3A). Lengths were 28.54 ± 4.79 μm (female) and 31.69 ± 6.05 μm (male), and basal diameters were 1.59 ± 0.27 μm (female) and 1.57 ± 0.27 μm (male).

SB1. The SB1 inserted into a shallow integumental socket and were obliquely inclined along the longitudinal axis, sometimes curving proximally or distally (Fig. 3B). The surface ornamentation on the shaft of the sensillum was very apparent; the sensillum possessed oblique ridges that fused together on one side to form a herringbone pattern, with pores present between the ridges (Fig. 3C). Lengths were 8.95 ± 2.39 μm (female) and 7.38 ± 2.38 μm (male), and basal diameters were 1.82 ± 0.29 (female) and 1.84 ± 0.42 μm (male).

SB2. The SB2 inserted into a shallow socket in the integument and were obliquely oriented to the antennal surface (Fig. 3D). Oblique and longitudinal ridges covered the surface of the sensillum, forming almost vertical rows near the base and developed into a herringbone pattern over the distal half. Pores lined the interstices between the ridges (Fig. 4A). Lengths were 16.29 ± 3.50 μm (female) and 17.42 ± 2.57 μm (male), and basal diameters were 1.35 ± 0.38 (female) and 1.30 ± 0.23 μm (male).

STY. STY lacked a flexible base and were located on a cylindrical protrusion from the antennal surface (Fig. 4B). They had two apical structures at their distal

Table 1. Length, basal diameter, and morphological characteristics of different types of antennal sensilla of *M. brassicae* ($n = 10$ per sex).

Type of Sensilla*	Sex	Mean (±SD) Length (μm)	Mean (±SD) Diameter (μm)	Morphological Characteristics			
				Tip	Wall	Shape	Pore
SCH1	Female	86.54 ± 8.47	3.35 ± 0.41	Sharp	Grooved	Strong hair	Aporous
	Male	83.41 ± 8.68	3.78 ± 0.43				
SCH2	Female	35.14 ± 4.81	4.98 ± 0.18	Sharp	Grooved	Strong hair	Aporous
	Male	37.82 ± 8.25	4.56 ± 0.29				
ST1	Male	44.69 ± 9.77	1.78 ± 0.45				
ST2	Female	34.21 ± 7.34	1.65 ± 0.32	Blunt	Smooth then helical	Strong hair	Aporous
	Male	30.97 ± 4.63	1.95 ± 0.32				
ST3	Female	28.54 ± 4.79	1.59 ± 0.27	Blunt	Smooth	Strong hair	Aporous
	Male	31.69 ± 6.05	1.57 ± 0.27				
SB1	Female	8.95 ± 2.39	1.82 ± 0.29	Blunt	Grooves drawing cones	Strong pointed hair	Multiporous
	Male	7.38 ± 2.38	1.84 ± 0.42				
SB2	Female	16.29 ± 3.50	1.35 ± 0.38	Sharp	Grooves drawing cones	Strong pointed hair	Multiporous
	Male	17.42 ± 2.57	1.30 ± 0.23				
STY	Female	16.29 ± 3.50	1.35 ± 0.38	Blunt	Smooth	Thumb-like + cone	Aporous
	Male	17.42 ± 2.57	1.30 ± 0.23				

Table 1. Continued.

Type of Sensilla*	Sex	Mean (±SD) Length (μm)	Mean (±SD) Diameter (μm)	Morphological Characteristics			
				Tip	Wall	Shape	Pore
BB	Female	4.20 ± 0.85	0.54 ± 0.08	Sharp or blunt	Smooth	Spine-like	Aporous
	Male	3.90 ± 0.72	0.64 ± 0.18				
SSQ	Female	44.96 ± 7.00	1.96 ± 0.10	Sharp	Grooved	Scale-like	Aporous
	Male	49.70 ± 5.80	2.00 ± 0. 20				
SCO	Female			Blunt	Deep longitudinal	Peg in depression microtrichia	Aporous
	Male						

* SCH1: sensilla chaetica 1; SCH2: sensilla chaetica 2; ST1: sensilla trichoidea 1; ST2: sensilla trichoidea 2; ST3: sensilla trichoidea 3; SB1: sensilla basiconica 1; SB2: sensilla basiconica 2; STY: sensilla styloconica; BB: Böhm bristles; SSQ: sensilla squamiformia; SCO: sensilla coeloconica.

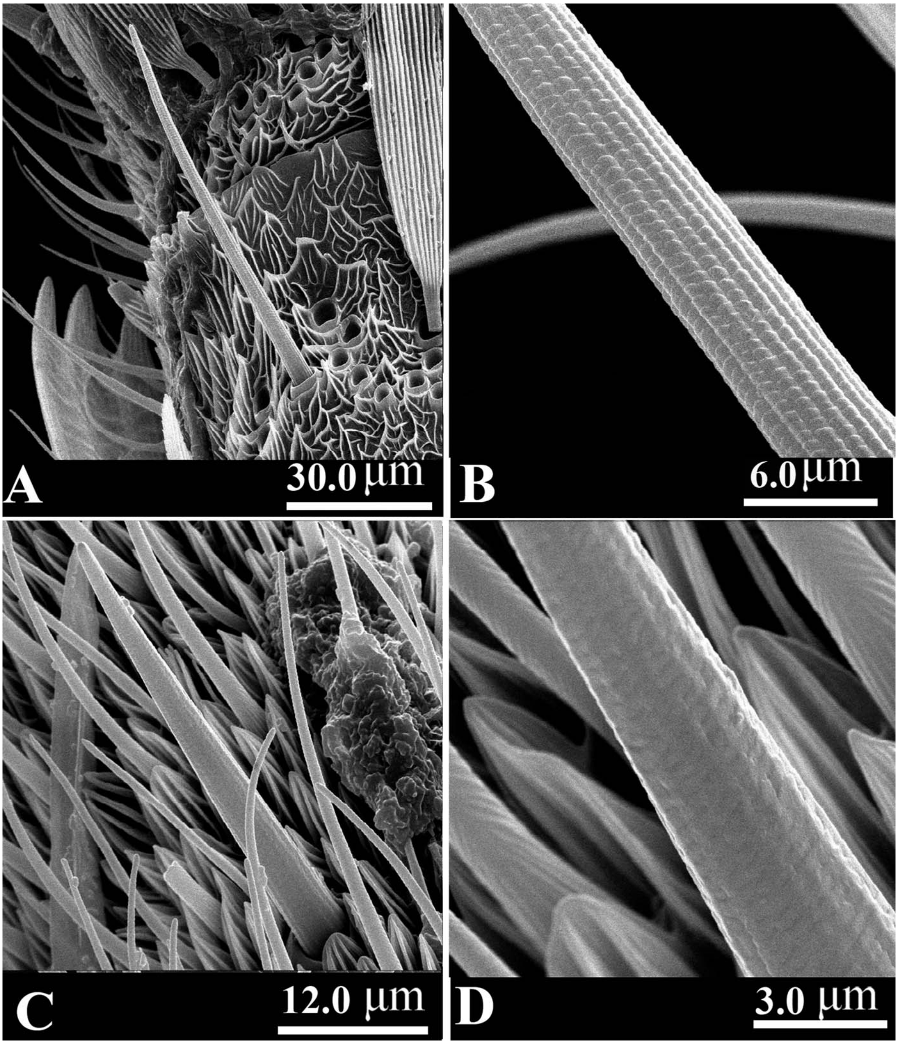

Fig. 1. Sensilla chaetica (SCH) 1 and 2 on male *M. brassicae* antennae: SC1 on the lateral side of the flagellomere (A), circumferential grooves on the wall of SC1 (B), SC2 on the dorsal side of the flagellomere (C), and the smooth surface on the wall of SC2 (D).

end. Lengths were 16.29 ± 3.50 µm (female) and 17.42 ± 2.57 µm (male), and basal diameters were 1.35 ± 0.38 µm (female) and 1.30 ± 0.23 µm (male).

BB. BB were movable spine-like structures with a smooth nonporous cuticle and recessed within cuticular depressions (Fig. 4C). These sensilla were located in clusters at the dorsal base of the scape and the pedicel near intersegmental joints. Lengths were 4.20 ± 0.85µm (female) and 3.90 ± 0.72 (male), and basal diameters were 0.54 ± 0.08 µm (female) and 0.64 ± 0.18 µm (male).

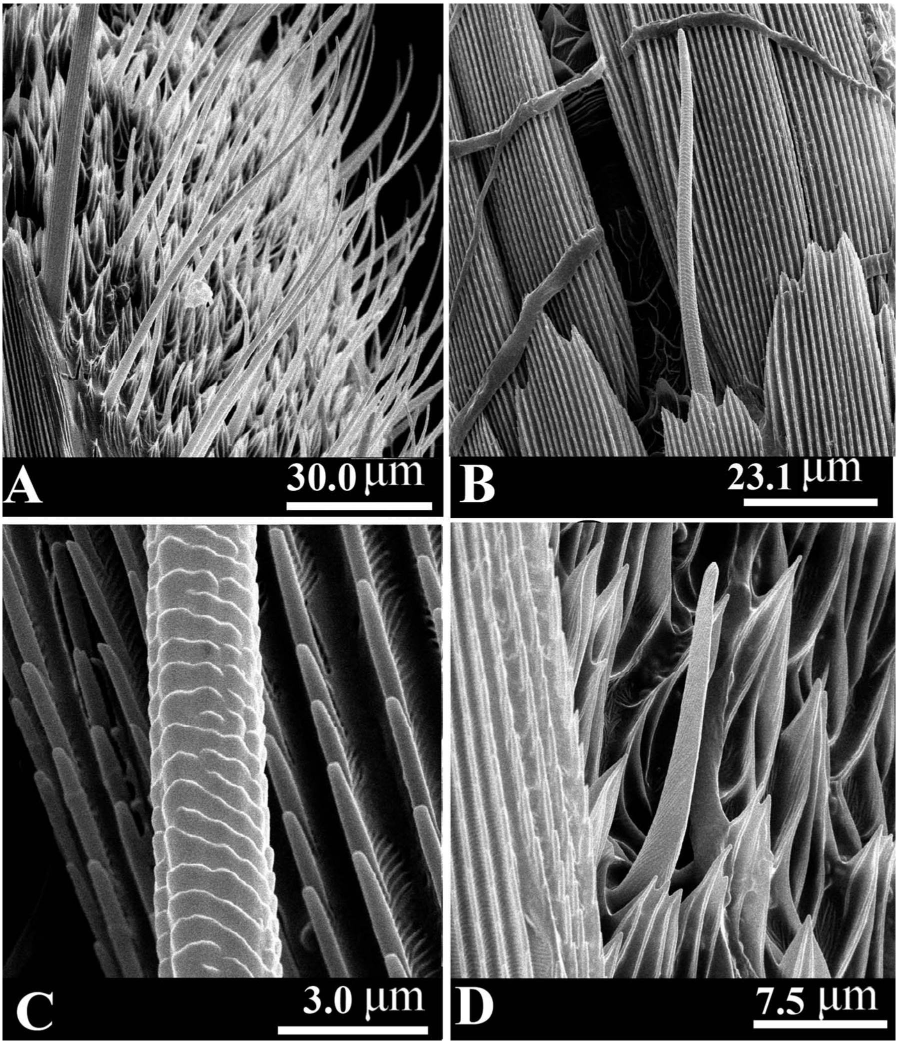

Fig. 2. Sensilla trichodea (ST) 1, 2, and 3 on *M. brassicae* antennae: ST1 are present on only male antennae in *M. brassicae* (A), ST2 are slender hairs with a smooth surface texture at their base and a helical pattern gradually marked toward the apex (B, C), ST3 (D).

SCO. SCO were small sensilla, commonly called pit pegs. A sensillum was projected from the center of a shallow cuticular pit (Fig. 4D). A fringe of 14–16 teeth could be seen along the edge of the pit. SCO were clumped at the ventral side of the flagellum (Fig. 5A).

SSQ. SSQ resembled lamellar scales but were shorter and finer and possessed slender distal ends (Fig. 5B). Lengths were 44.96 ± 7.00 µm (female) and

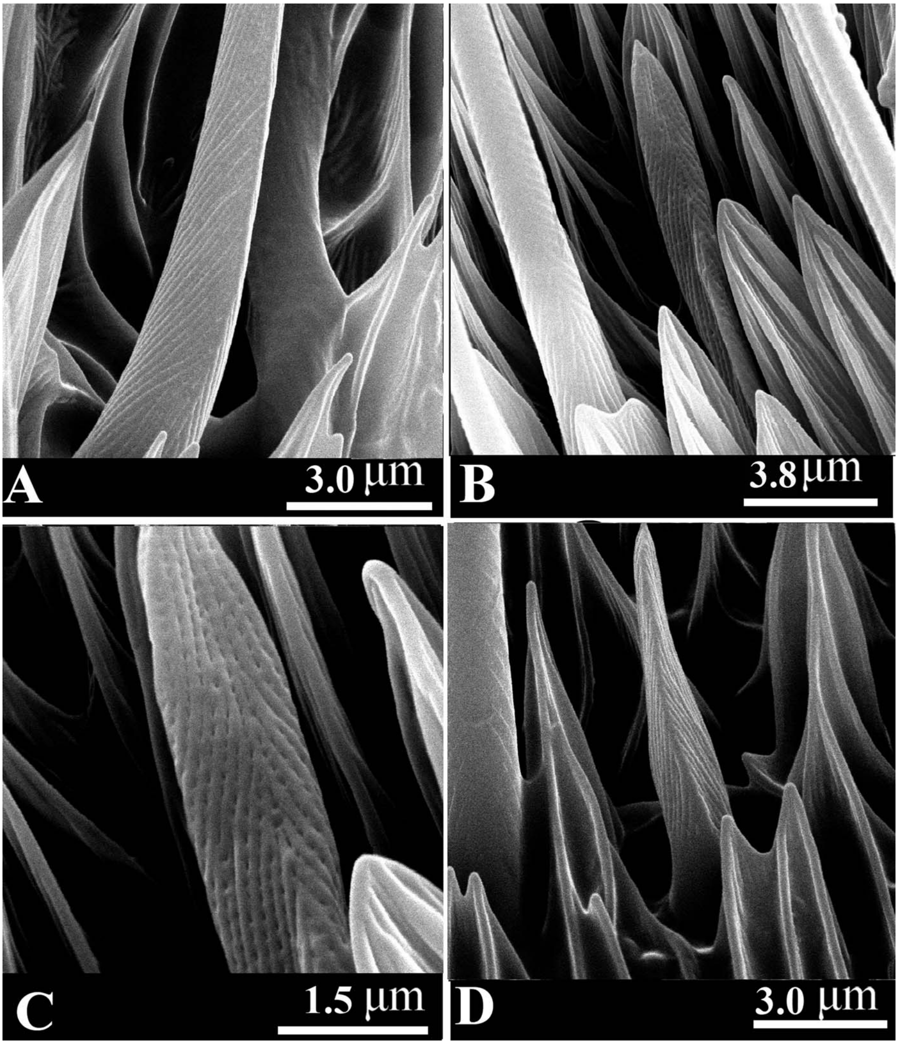

Fig. 3. Sensilla trichodea (ST3) and sensilla basiconica (SB) 1 and 2 on *M. brassicae* antennae: surface pores of ST3 (A), SB1 (B), numerous pores present between the ridges on the cuticle of SB1 at higher magnification (C), and SB2 (D).

49.70 ± 5.80 μm (male), and basal diameters were 1.96 ± 0.10 μm (female) and 2.00 ± 0. 20 (male).

Abundance and distribution of antennal sensilla. Three to seven SCH1 were found on each flagellar segment in both sexes, except that the penultimate segment had more than seven. These sensilla were found on the antennae of both sexes. The ST were the most abundant sensilla and were widely distributed on the antennae of both sexes. They were mainly found on the ventral side of the antennae but lacked the specialized sunken socket at the base. SB were present in both males and females along the ventral and lateral surfaces of the lateral branches, although the approximate density was significantly higher in females than in males. STY were always found in the upper middle region of the ventral surface of each flagellar subsegment in both sexes. BB aggregated only on the base of the scape and the internode junction of the antennal scape and pedicel and were almost perpendicular to the surface of the antenna. One to five SCO were distributed on the ventral surfaces of the distal edge of flagellomeres. Two or three SSQ were found along the scape, pedicel, and flagellum, especially on the dorsolateral side of each flagellomere but were absent toward terminal flagellomeres.

Discussion

The general shape and structure of the antennae of male and female *M. brassicae* are similar to those reported for other species of Lepidoptera (Bawin et al. 2017, Castrejón-Gómez et al. 1999, Koh et al. 1995, Zheng et al. 2014, Zheng et al. 2023). The antennal flagellomeres of males and females are cylindrical and most of the sensilla are located on the ventral surface, whereas the dorsal surface possesses numerous overlapping scales (Fig. 5D). Functions of the antennal scales have been described as protecting the antenna (Koh et al. 1995), contributing to the detection of stimulus direction (Van der Pers et al. 1980), and trapping and concentrating odorous molecules (Wall 1978); however, these hypotheses have not been tested. Based on morphological criteria and according to the published scientific reports, we inferred the function of the sensilla in *M. brassicae* described here.

SCH1 are similar in shape to those reported for *Spodoptera exigua* Hübner (Jefferson et al. 1970), *Noctua pronuba* L. (Faucheux 1990), and *Catocala remissa* Staudinger (Zheng et al. 2014) but differ in length. SCH2 are similar in morphology and location to those reported on *Spodoptera frugiperda* (J.E. Smith) (Malo et al. 2004), *Synanthedon scitula* (Harris) (Frank et al. 2010), and *Nyctemera annulata* Boisduval (Mark et al. 2018). Several researchers have suggested that SCH have both a contact chemo- and mechanoreceptive function because they arise from a socket and possess a terminal pore (Altner and Prillinger 1980, Van der Pers et al. 1980). Jørgensen et al. (2007) noted that SCH of *Heliothis virescens* (F.) possess one mechanosensory neuron and four gustatory receptor neurons that aid in the detection and discrimination of noxious and edible food sources. A similar function seems likely in *M. brassicae,* particularly because SCH1 and SCH2 tend to extend beyond the antennal surface, thus allowing increased contact with the substrate. In studies of sesiid species, the presence of a terminal pore has not been documented, and the primary function of these sensilla was considered mechanoreceptive (Karalius 1994, Sellier 1977). Although the presence of a terminal pore on SCH2 of the *M. brassicae* could not be confirmed, the behavior of females suggests that the role of these sensilla may involve both mechano- and contact chemoreception.

ST1 are longer than the other ST subtypes and are present on only male antennae in *M. brassicae*. This sensillum is similar in structure to those reported for other moths (Castrejón-Gómez et al. 2003, Frank et al. 2010, Ndomo-Moualeu et al. 2014). In codling moths, the long ST houses highly sensitive pheromone-detecting olfactory receptor

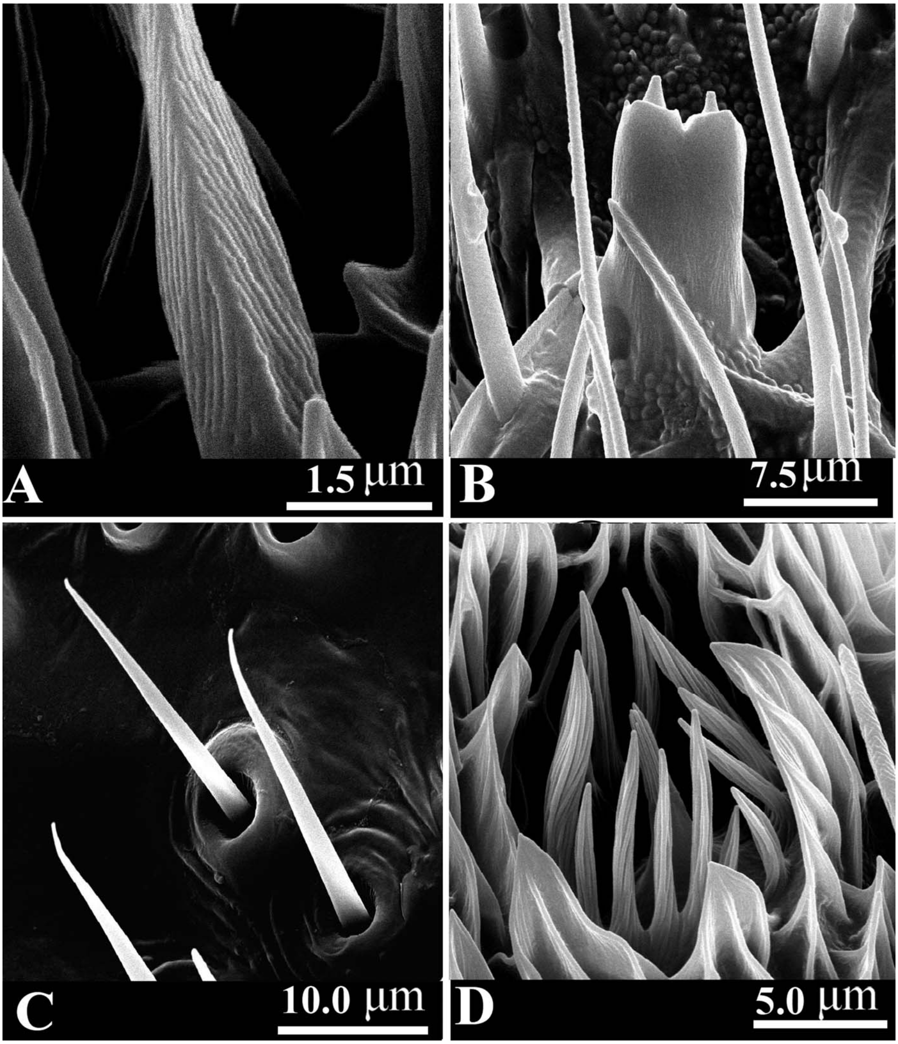

Fig. 4. Surface of sensilla basiconica 2 (A), sensilla styloconica (B), Böhm bristles on the base of the scape (C), and sensilla coeloconica (D).

neurons (Ebbinghaus et al. 1997). In several moth species, the long ST on male antennae responds to female sex pheromones (Baker et al. 2004, Cossé et al. 1998, Faucheux et al. 2006, Hansson 1995). Thus, the ST in *M. brassicae* also might be responsible for the reception of sex pheromones. The response of ST1 to conspecific female sex pheromones in *M. brassicae* could be studied via single sensillum recording.

ST2 resemble "sensilla trichodea I" in two tortricid moths, *Cydia pomonella* (L.) and *Cydia succedana* (Denis and Schiffermüller) (Roh et al. 2016) and in the defoliating moth, *Phauda flammans* (Walker) (Liu et al. 2018). ST3 located on the

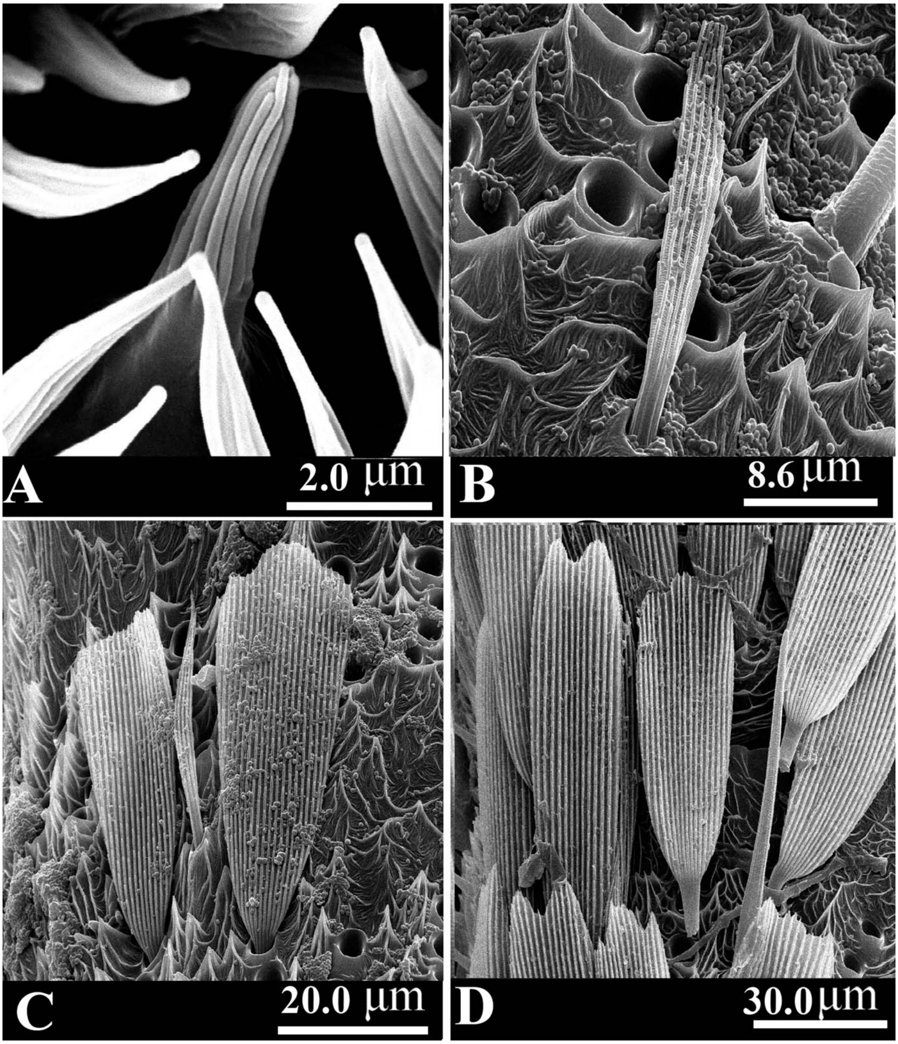

Fig. 5. Sensilla coeloconica longitudinally grooved projection (referred to as a peg) (A), sensilla squamiformia (B), sensilla squamiformia distributed among the lamellar scales on the scape (C), scales on the antennal surface (D).

flagellomere of *M. brassicae* are very similar to the “ridgeless-type trichoidea” in the beet armyworm, *S. exigua* (Mochizuki et al. 1992) and the “sensilla trichoidea Type III” of *C. remissa* (Zheng et al. 2014). Sensilla trichodea subtypes II and III were more abundant in females than in males. We do not know at present the functions of ST2 and ST3 on female antenna of *M. brassicae*. Subtypes of females may be able to detect their own sex pheromones and plant volatile compounds for female-specific behaviors. For example, antennae on females of

Spodoptera littoralis (Boisduval) (Ljunberg et al. 1993) and *Trichoplusia ni* (Hübner) (Birch 1977) responded to conspecific sex pheromones. The short ST of female antennae in *S. littoralis* and *Cactoblastis cactorum* (Berg) (Lepidoptera: Pyralidae) detected plant volatiles (Anderson et al. 1995, Pophof et al. 2005). Functions of ST2 and ST3 needed to be studied in regard to responses of the females to their own sex pheromones and host plant volatiles.

Two types of SB were identified on both sexes in this study. SB1 were found on flagellomeres of *M. brassicae* as in other moths (Faucheux 1999, Faucheux et al. 2006, Razowski and Wojtusiak 2004, Sun et al. 2011). The SB1 were lined up longitudinally in *M. brassicae* (our study) and in moths of the Oecophoridae (Faucheux 1978), Tortricidae (Cuperus 1985), and Pyralidae (Faucheux 1991). SB2 in *M. brassicae* appear to be identical to the "sensilla basiconica type 4" in *N. annulata* (Mark et al. 2018). SB are important olfactory setae that are structurally adapted to the recognition of plant odors in phytophagous insects (Laue et al. 1994, Schneider 1964, Steinbrecht et al. 1995). Scanning and transmission electron microscopy studies of SB in the coleopteran *Phoracantha semipunctata* (F.) (Cerambycidae) revealed such structure, and single sensory cell recordings revealed responses to plant odors with no difference between males and females (Lopes et al. 2002). In other studies, olfactory neurons housed in SB responded to plant-associated odorants in *S. littoralis* (Binyameen et al. 2012) and *Manduca sexta* (L.) (Ghaninia et al. 2014). The surface of SB in this study (Fig. 3C) was multiporous, suggesting that SB are olfactory receptors used to detect volatile plant odors (Pophof et al. 2005).

STY of *M. brassicae* possess several general features in common with STY of many other lepidopterans, namely, the presence of a stylus and a sensory cone and the distal distribution on the lateral branches (Faucheux 1997, 1999). These sensilla were considered thermo- and hygrosensitive in *Bombyx mori* (L.) (Steinbrecht 1989) and members of the Pyralidae (Hallberg et al. 1994, Hansson 1995); however, the presence of an apical pore in the Tortricidae suggested a contact chemoreceptive function (Castrejon-Gomez and Carrasco 2008, Wall 1978). Apoporous STY have been demonstrated to be thermo- and hygroreceptors containing two antagonistic hygroreceptive cells and one thermoreceptive cell responding to cold in *B. mori* (Steinbrecht 1989, Steinbrecht and Müller 1991) and *Antheraea* species (Gödde and Haug 1990, Haug 1985). An apical pore was not found on STY of *M. brassicae* (Fig. 4B), suggesting that these STY may have a thermo- and hygrosensory function.

BB of *M. brassicae* antennae are similar in morphology to those on the scape and pedicel of *Micropterix calthella* L. (Faucheux 1997), *Clostera anastomosis* L. (Liu et al. 2013) and *Plodia interpunctella* (Hübner) (Ndomo-Moualeu et al. 2014). BB location is as reported by Schneider (1964): "a typical bristle is always found in areas opposite the intersegmental membrane between head and scape, as well as between scape and pedicel on the scape and pedicel, respectively." The functions attributed to these sensilla are ambiguous. Schneider (1964) suggested that these hair plates may play a mechanosensitive role. Results of recent studies suggest that they mediate antennal positioning in moths during flights (Krishnan et al. 2012). The BB located in the pedicel respond to changes in location and vibration of the whole antenna, whereas those located near the scales–pedicel boundary transfer information about the position of the antenna (rather than its movement) to the brain (Krishnan et al. 2012). Some studies of these sensilla on *Cnaphalocrocis medinalis* (Guenée) (Lepidoptera: Pyralidae) revealed sporulated walls, suggesting an olfactory function (Sun et al. 2011). Therefore, further research, especially single sensilla recordings, are needed with the BB in *M. brassicae* to determine their precise function.

The SSQ in *M. brassicae* also are frequently found in many lepidopterans, where these sensilla are distributed among the lamellar scales (Faucheux 1999). Typically, this sensilla type is characterized by slender lamellar scales (Fig. 5B), although some variation in morphology exists (e.g., Liu et al. 2013, Yang et al. 2009). SSQ observed in *M. brassicae* are of the more conventional form and bear particular resemblance to those sensory structures seen in male *Zamagiria dixolophella* Dyar (Castrejón Gómez et al. 2003) and in a number of skipper butterflies (Yuan et al. 2014). SSQ in *M. brassicae* are similar in morphology and location to those reported on other moth species such as *P. interpunctella* (Ndomo-Moualeu et al. 2014) and *Z. dixolophella* (Castrejón Gómez et al. 2003). Sexual dimorphism of SSQ has been described in some species (e.g., Castrejón Gómez et al. 2003, Zheng et al. 2014), although the functional significance of this dimorphism is unknown. No sexual dimorphism was apparent in the morphology of SSQ in *M. brassicae*; however, because the SSQ density could not be estimated accurately, a difference between males and females cannot be ruled out. SSQ are thought to have a mechanoreceptive function (Faucheux 1999), and their location on the dorsal side of the antennal spindle in *M. brassicae* suggests that in this species they likely have the same function.

SCO present on the antenna of *M. brassicae* are similar to those described in members of the Pyralidae such as *Hypsipyla grandella* (Zeller) (Callahan 1975), *Homoeosoma nebulella* Denis and Schiffermüller (Faucheux 1991), *Ostrinia nubilalis* (Hübner) (Hallberg et al. 1994), *Ostrinia furnacalis* (Guenée) (Jung et al. 1999), and *Z. dixolophella* (Castrejón-Gómez et al. 2003). Similar results were reported in some members of the Tortricidae such as *Argyrotaenia velutiana* (Walker) (Callahan 1975), *Cydia nigricana* (F.) (Wall 1978) and some members of the Noctuidae such as *Pseudaletia unipuncta* (Haw) (Lavoie-Dornik and McNeil 1987). The function of SCO might be olfactory (Yang et al. 2009). Two types of SCO have been found in some insects (Roux et al. 2005), whereas only one type has been found in others (Gao et al. 2007, Steinbrecht 1984). In the present study, only one type was found in the antennae of both sexes of *M. brassicae,* and these grooved pegs may function as chemo- or thermoreceptors. SCO that are recessed below the antennal surface and located within cavities may be involved in the perception of humidity, temperature, heat, or CO_2 (Altner et al. 1983, Steinbrecht 1984), may play a role in preventing desiccation (Kristoffersen et al. 2006), and may have an olfactory function (Gao et al. 2007, Keil 1999, Ochieng et al. 2000, Roux et al. 2005, Steinbrecht 1997). Results of a transmission electron microscopic study of the tobacco hornworm, *Manduca sexta* L. (Lepidoptera: Sphingidae) suggested that olfactory molecules entered through the grooves in SCO (Shields and Hildebrand 2001). In the SCO of *M. brassicae,* the presence of deep longitudinal grooves on the surface of central and circumferential pegs also suggests their olfactory function (Fig. 5A).

We identified and characterized nine types of antennal sensilla of *M. brassicae* and discussed their probable functions. These results provide necessary background information for our ongoing study of the chemical ecology of *M. brassicae*. Future studies on the functional morphology of the antennal sensilla by use of transmission electron microscopy coupled with electrophysiological recordings will likely confirm the functions of the sensilla identified in this study.

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