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Scanning electron microscopy study of the antennal sensilla of *Catocala remissa*

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Abstract

Catocala remissa Staudinger (Lepidoptera Noctuidae) is a defoliator of *Populus euphratica* Olivier. The present study aimed to elucidate the insect-plant and insect-insect chemical communication mechanisms involved with this process by observing the antennae and sensilla of *C. remissa* using scanning electron microscopy. In both sexes, the antennae were filiform and segmented with the three components: the scape, pedicel, and flagellum. The antennal flagellomeres of males and females were cylindrical and the dorsal surfaces had numerous overlapping scales, whereas most of the sensilla were located on the ventral surfaces. Sexual dimorphism was observed in *C. remissa* antennae. The male antennae were covered closely with scales whereas the female antennae had a loose covering of scales. Sexual dimorphism in *C. remissa* also manifested as variations in the distributions and sizes of sensilla. There were six types of sensilla on the antennae flagella: sensilla trichodea (types I, II, and III), sensilla chaetica, sensilla coeloconica, sensilla styloconica (types I and II), sensilla auricillica, and sensilla squamiformia.

Key words: antennae sensilla, scanning electron microscopy.

Introduction

Populus euphratica Olivier is the only species that can form pure forest in dry and saline deserts in NW China (Wang *et al*., 1995), where is usually grows into riparian stands. These *P. euphratica* riparian forests are of great importance for the protection of the local environment and its biodiversity as well as other environmental benefits, such as landscape preservation, wind-breaks, sand fixation, soil and riverbank protection (Westermann *et al*., 2008). In China, *P. euphratica* forests are not only important for maintaining the ecological equilibrium of Ejina but also a major tourist attraction.

Catocala remissa Staudinger (Lepidoptera Noctuidae) is a defoliator of *P. euphratica*. About 12000 hectares of *P. euphratica* forests have been damaged since 2005 and the trend year-on-year increase (Li *et al*., 2010). It has been one of the most serious forestry pests in Ejina, Inner Mongolia, China in recent years. At present, the only methods of control are chemical insecticides.

However, this approach has led to the evolution of pesticide resistance, which has severe negative impacts on human health and the environment. Thus, there is an urgent need to develop new methods to control this pest. An efficient method that is compatible with other approaches used to control different moth pests is the use of sex pheromones, which are detected by olfactory receptors on the antennae.

Insect antennae play important roles in host orientation, food selection, and oviposition site selection. The antennae vary widely in terms of their length, overall size, and the sizes of the individual segments, while their segmentation, setation, and other characteristic structures are closely related to their functions (George *et al.*, 1984). The antennae of adult insects possess various types of sensilla with different functions, which play important roles in various behaviours during adult life (Gao *et al*., 2007). Antennal sensilla are the main tools of insect chemical communications and offer many functional advantages to an insect's ability to perceive and respond to environmental signals by facilitating the detection of sensory stimuli (Derby and Steullet, 2001). These sensilla can detect various stimuli and are implicated in the recognition of food, hosts, and partners (Schneider, 1964; Onagbola *et al*., 2008). The complexity and abundance of insect antennal sensilla are linked inextricably with insect behavioural ecology (Faucheux *et al*., 2006). Numerous studies have characterized the antennal sensilla of Lepidoptera using electron microscopy techniques (Victor *et al*., 1999; 2003; 2008; Faucheux, 1990a; Faucheux *et al*., 2006; Frank *et al*., 2010; Nasra, 2008).

However, there have been no reports of the general morphology of the antennae of *C. remissa* or descriptions of the antennal sensilla of this species. Therefore, the present study used scanning electron microscopy (SEM) to characterize the antennal sensilla of male and female *C. remissa*. This basic information will provide a morphological basis for future behavioural and electrophysiological studies.

Materials and methods

Insects

C. remissa pupae were collected from a *P. euphratica* forest in Ejina, Inner Mongolia, China during early June. The pupae were segregated based on the sexual characters of abdominal tergites and maintained at 30 ± 1 °C, with 70 ± 10% relative humidity and a 14:10 L:D photoperiod. After emergence, the adult males and females were placed in separate cages (100 × 50 × 50 cm) and provided with 10% sucrose solution *ad libitum*.

Light microscopy

The antennae of both sexes (aged 48h) were immersed in 10% KOH at 80 °C for 1 h until the scales were removed and the antennae cleared. The antennae were dehydrated in 70 and 100% alcohol for 30 and 60 minutes, respectively. They were cleared with xylol and mounted in Canada balsam. Observations were using Motic microscope (20×). Motic Images Advanced 3.2 software was used to examine the images for measurements of the length of the scape, pedicel and antennal flagellum; the number of antennal flagellomeres on 30 antennae of each sex.

Scanning electron microscopy

C. remissa antennae were freshly excised from female and male moths (aged 48h) and immersed in glutaraldehyde (2.5%) at 4 °C for > 8 h (overnight). Then the antennae were immersed in 10% KOH at 80 °C for 1 h until the scales were removed and the antennae cleared. Antennae were dehydrated using a 50, 70, 80, 90, 95, and 100% ethanol series for 30 minutes. After freeze drying, the specimens were mounted on aluminium stubs with double-sided sticky tape and coated with gold-palladium. The antennae were viewed using scanning electron microscope (S-4800; Hitachi Ltd., Tokyo, Japan) at 3 kV.

All SEM digital images were subsequently analyzed using Motic Images Advanced 3.2 software to determine the length and basal diameter of each type of sensillum. Then measurements of each type of sensillum were taken using the line function tool which allowed us to draw point-to-point line measurements along the entire length and for the basal diameter of each sensillum type. For each sex, the average length and basal diameter of the external part of each sensillum was calculated, with 30 measurements taken from photomicrographs made from both antennae from 10 individuals.

Statistical analysis

All data were analyzed using the paired samples t-test with the statistical program SPSS, version 10.0. For all comparisons between male and female antennae, the level of $P = 0.05$) was considered significant.

Results

General descriptions of antennae

The antennae of the female and male moths were threadlike in shape and were located between the compound eyes. The antennae were divided into two main areas. The dorsal surfaces had two rows of scales, where the second row overlapped the first row of the following segment. The ventral surfaces carried most of the sensilla, which belonged to various types. The antennae were divided into the scape, pedicel, and flagellum. The scape was the largest antennal segment and it was bulbous after a constriction distal to its insertion in the antennal socket. The pedicel was smaller than the scape and more elongated on the dorsal side than on the ventral surface. In male moths, the lengths of the scape and pedicel were 528.33 ± 11.2 µm and 185.97 ± 2.8 µm, respectively, which were not significantly different from those of the females, *i.e.* 537.58 ± 14.2 µm and 187.03 ± 4.4 µm, respectively ($t = 0.42$, df = 9, $P = 0.684$; $t = 0.226$, df = 9, $P = 0.826$). The mean ± SE number of flagella subsegments was 97.5 ± 1.57 for males (range 94-107), and 104.2 ± 1.48 for females (range 98-111), which was significantly different($t = 2.782$, df = 9, $P = 0.021$).The flagellum was shorter in males than in females, *i.e.* 16375.84 ± 1.8 µm and 16390.33 ± 3.1 µm, respectively. The mean total subsegment lengths of the male and female antennae were 17090.162 ± 11.5 µm and 17114.94 ± 15.3 µm, respectively (table 1).

Sexual dimorphism

The lengths of the scape and pedicel did not differ significantly between the male and female antennae (table 1). The male antennae were covered tightly by scales (figure 1A), whereas the female antennae were covered loosely (figure 1B). Long sensilla trichodea (Type I) occurred only on male antennae and other sensilla trichodea (Type II, III) occurred on male and female antennae.

Antennal sensilla types

Six major types of sensilla were observed on female and male antennal flagella: sensilla trichodea, sensilla chaetica, sensilla coeloconica, sensilla styloconica, sensilla auricillica, and sensilla squamiformia.

Sensilla trichodea

Sensilla trichodea were the most abundant of all the types of sensilla on the antennae of males and females (table 2), and were present on the ventral surface of the entire flagellum. They were multiporous with radial ridges on the surfaces (figure 2B, 2D, 2F). These sensilla were significantly more abundant on male antennae than on female antennae ($t = -79.382$, df = 9, $P < 0.001$) (table 2). The sensilla trichodea observed on the antennae of *C. remissa* belonged to three subtypes, which were designated as type I, type II, and type III based on their size (table 3).

Table 1. Mean ± SE length of the scape, pedicel and antennal flagella C. *remissa*.

Antennal location	Length (µm)		Statistics		
	Male	Female	t	df	P
Scape	528.33 ± 11.2	537.58 ± 14.2	−0.42	9	0.684
Pedicel	185.97 ± 2.8	187.03 ± 4.4	−0.226	9	0.826
Flagellum	16375.84 ± 1.8	16390.33 ± 3.1	−4.827	9	0.001
Total antenna	17090.162 ± 11.5	17114.94 ± 15.3	−1.013	9	0.338

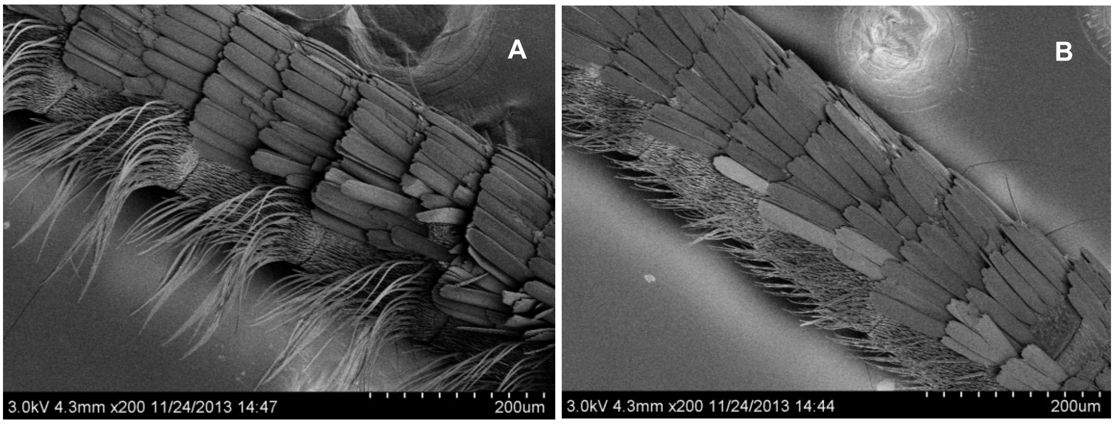

Figure 1. General morphology of antennae flagella of *C. remissa*. (A) squama assembled on flagellum of male antenna; (B) squama assembled on flagellum of female antenna.

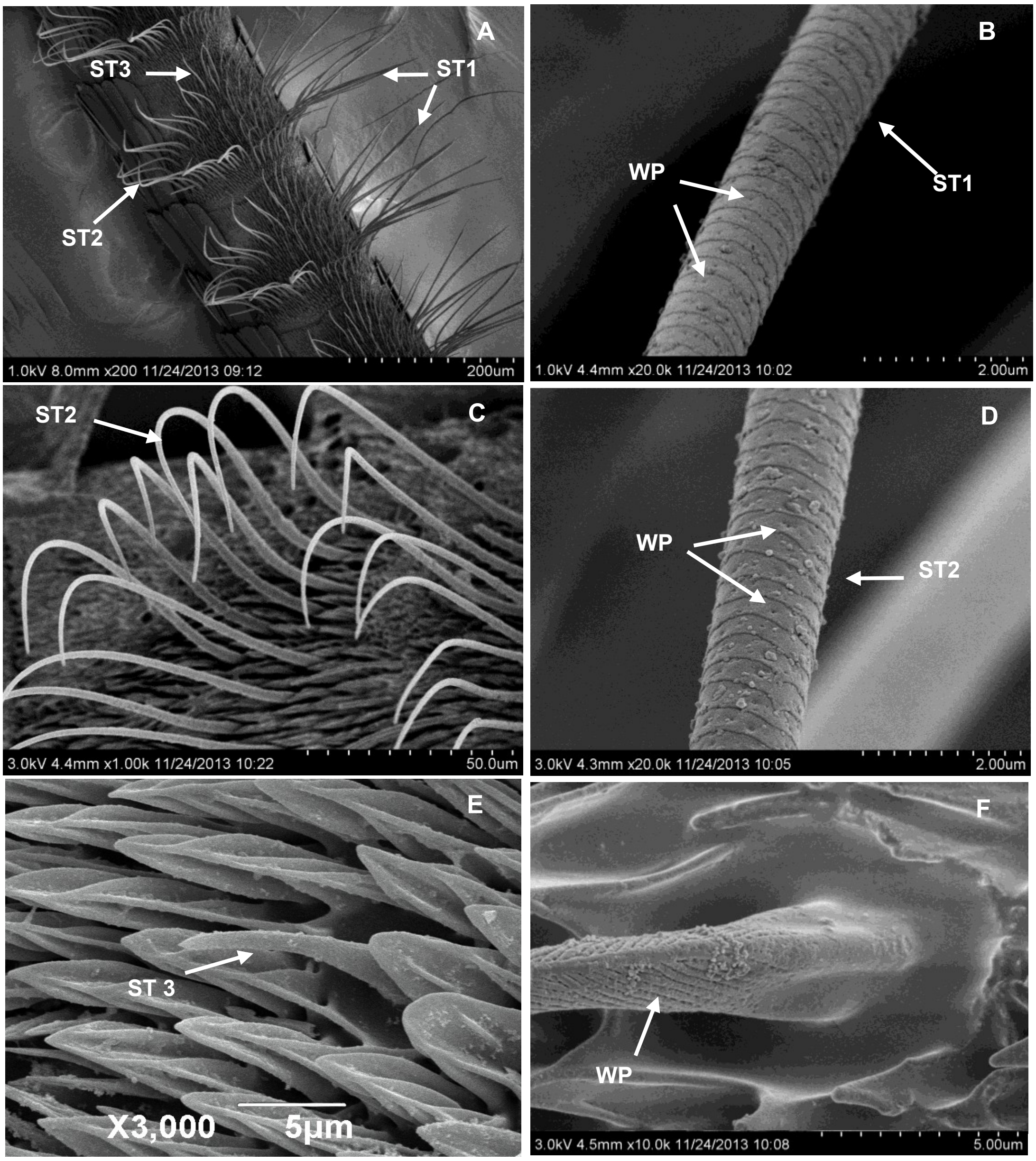

Figure 2. Scanning electron micrographs showing multiporous sensilla trichoidea. (A) male antenna flagella, showing sensilla trichoidea Type I, Type II and Type III; (B) sensilla trichoidea Type I; (C), (D) sensilla trichoidea Type II; (E), (F) sensilla trichoidea Type III. ST1, long sensilla trichoidea Type I; ST2, sensilla trichoidea Type II; ST3, sensilla trichoidea Type III; WP, wall pore.

Type I sensilla (range 129.98-151.23 μm) were the longest with a length of 139.88 ± 2.30 μm and a diameter of 3.13 ± 0.10 μm at the base. They were slightly bent and perpendicular to the antennae (figure 2A) and present only on male antennae. Type II sensilla were 30.09-94.32μm and had a basal width of 3.26-5.98 μm (figure 2C). Type III sensilla were 10.43-24.58μm long and had a basal width of 3.47-5.88μm (figure 2E). Type II and Type III were present on males and females antennae.

Sensilla chaetica

The sensilla chaetica had circumferential grooves on their surfaces (figure 3C, 3D). 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 (figure 3E). There were 3-7 sensilla chaetica on each flagellar segment in both sexes, except the penultimate segment had > 7 (figure 3B). They were significantly more abundant on the female antennae (t = 3.066, df = 9, P = 0.013).

Sensilla styloconica

The styloconica sensilla lacked a flexible base and were located on a cylindrical protrusion from the antennal surface. These sensilla were always found in the upper middle region of the ventral surface of each flagellar subsegment in both sexes. A single sensillum of this type was often present on each segment in males and females. These sensilla were 15.4-41 μm long with a basal width of 3.98-6.5 μm. The mean number of these sensilla was similar in both sexes (t = 0.978, df = 9, P = 0.353). These sensilla were divided into two subtypes based on the presence or absence of apical structures. Type I were smooth and lacked apical structures on their tips (figure 4A), whereas type II had 1–3 apical structures at their distal end (figure 4B, 4C, 4D).

Sensilla coeloconica

Each sensillum comprised a depression surrounded by 10 or 13 cuticular "spines" of different sizes and a pit peg, both of which had longitudinal striations on their surfaces (figure 5A, 5B). These sensilla were 5.1-10.9 μm in diameter. The number of sensilla coeloconica were not significant different in both sexes (t = 0.978, df = 9, P = 0.353) (table 3). In general, the sensilla coeloconica were present on the ventral surfaces of the antennae of males and females. Some sensilla coeloconica were also observed on the dorsal surfaces.

Sensilla squamiformia

The sensilla squamiformia resembled lamellar scales, but they were shorter and finer than the scales and possessed slender distal ends (figure 5C). These sensilla were 39.3-49.9 μm long and had a basal width of 1.99-3.12 μm. Sensilla squamiformia were significantly more aboundant on male antennae (t = −3.498, df = 9, P = 0.007) (table 3).These sensilla were present on the dorsal parts of the antenna among the scales.

Sensilla auricillica

The sensilla auricillica usually had a typical rabbit-ear shape. They occur primarily on the ventral side of antennal flagella (figure 5D) and their distribution on each flagellomere was random. These sensilla were the second most abundant type on the antennae of males and females (table 2). They were 8.85-10.21 μm and had a basla width of 2.73-3.15 μm. Sensilla auricillica were significantly more abundant on females than on males (t = 21.664, df = 9, P < 0.001) (table 2).

Table 2. Mean ± SE number of sensilla in male and female antennae of *C. remissa*.

Type of sensilla	Number of sensilla	
	Male	Female
Trichodea	9558.20 ± 15.58a	5069.80 ± 12.90b
Chaetica	806.4 ± 10.98a	844.40 ± 6.28b
Styloconica	100.80 ± 1.37a	101.80 ± 0.78a
Coeloconica	504.00 ± 6.86a	509.00 ± 3.93a
Squamiformia	20.40 ± 1.03a	19.30 ± 0.99b
Auricillica	1173.00 ± 11.56a	1555 ± 10.58b

Means across rows followed by the same letter are not significantly different.

Table 3. Mean ± SE dimensions of the sensilla (μm) on the antennae of C. *remissa*.

Type of sensilla	Male		Female	
	Length	Width	Length	Width
Trichodea Type I	139.88 ± 2.30	3.13 ± 0.10		
Trichodea Type II	82.96 ± 2.86a	4.69 ± 0.26a	46.73 ± 2.62b	4.35 ± 0.20b
Trichodea Type III	19.02 ± 1.04b	4.55 ± 0.19b	16.54 ± 1.39a	4.76 ± 0.23a
Chaetica	88.91 ± 3.00a	4.36 ± 0.18a	96.51 ± 2.53b	4.33 ± 0.15b
Styloconica	19.44 ± 0.81b	4.79 ± 0.21b	33.51 ± 1.79a	4.84 ± 0.24a
Coeloconica	4.32 ± 0.64a	1.75 ± 0.08b	4.33 ± 0.15a	1.74 ± 0.09a
Squamiformia	41.71 ± 0.99a	2.54 ± 0.12a	40.61 ± 0.25a	2.32 ± 0.03b
Auricillica	9.73 ± 0.143b	3.07 ± 0.06a	9.51 ± 0.148a	3.13 ± 0.03b

Values comparing sexes within the same row followed by the same letter are not significantly different.

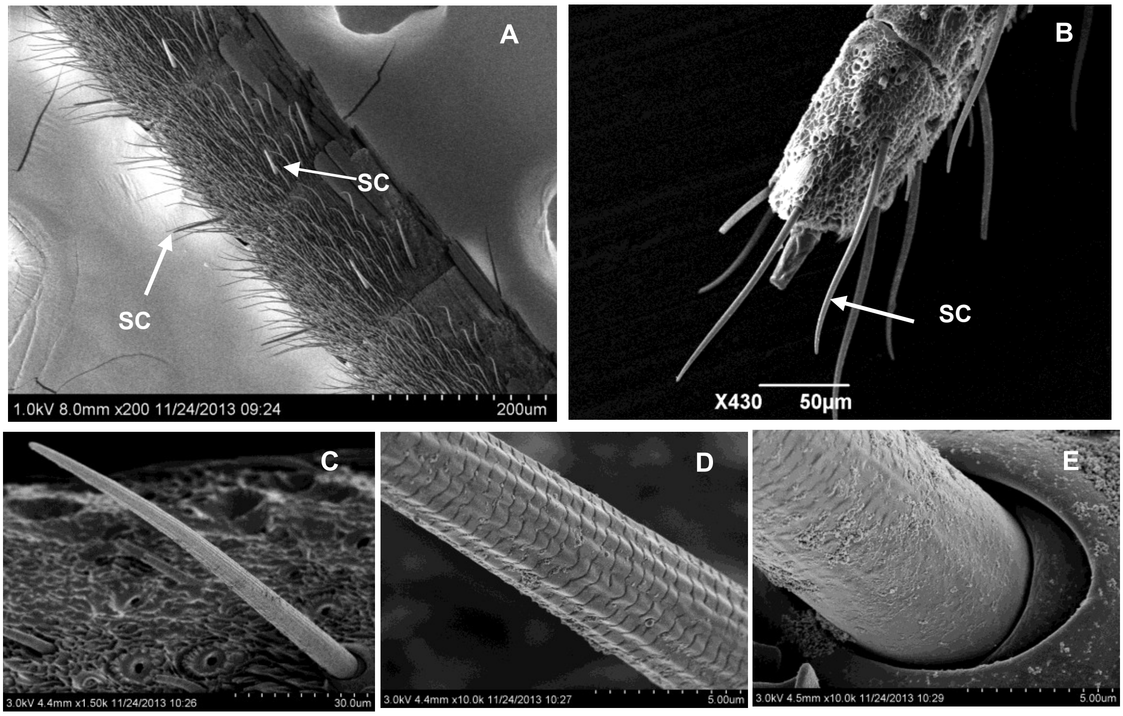

Figure 3. Scanning electron micrographs showing sensilla chaetica, SC. (A) male antenna flagella; (B) apical and penultimate segment of the antenna; (C) (D) (E) details of a sensilla chaetica.

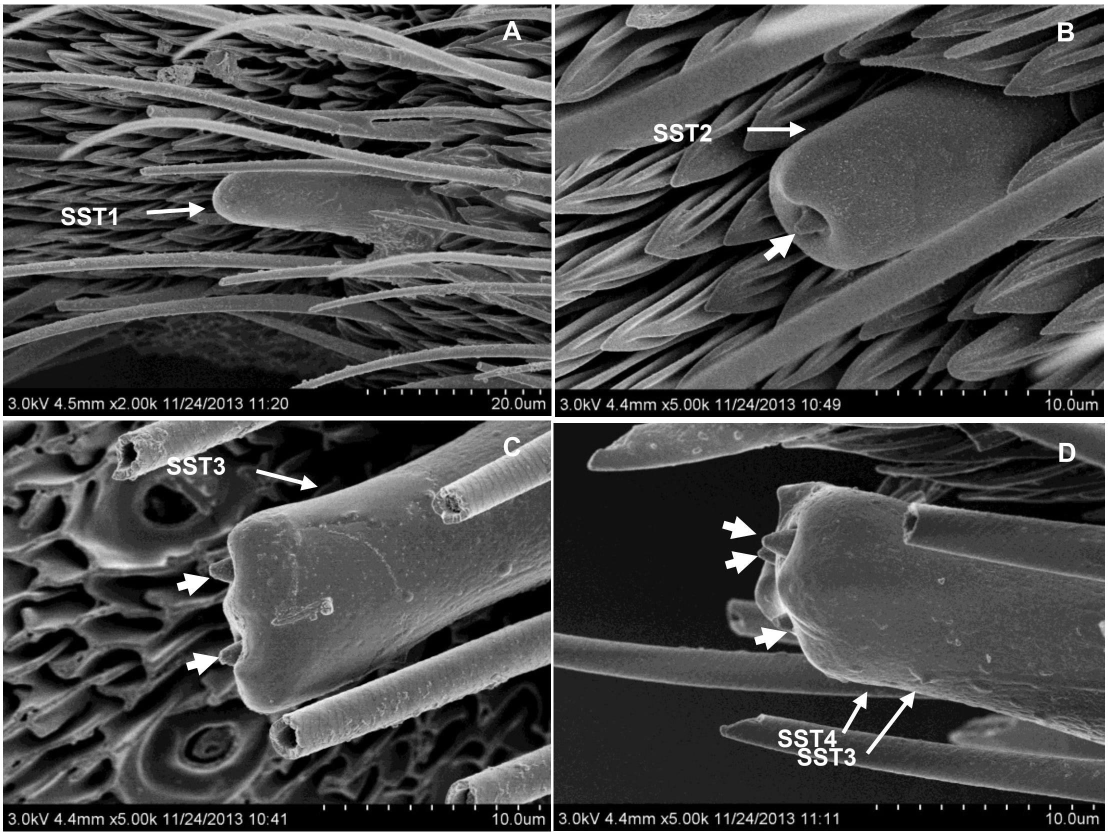

Figure 4. Scanning electron micrographs showing sensilla styloconica. (A) SST1, the sensilla of no peak on the tip; (B) SST2, the sensilla of one peak on the tip; (C) SST3, the sensilla of two peaks on the tip; (D) SST4, sensilla of three peaks on the tip. The enhanced arrow indicates the peaks.

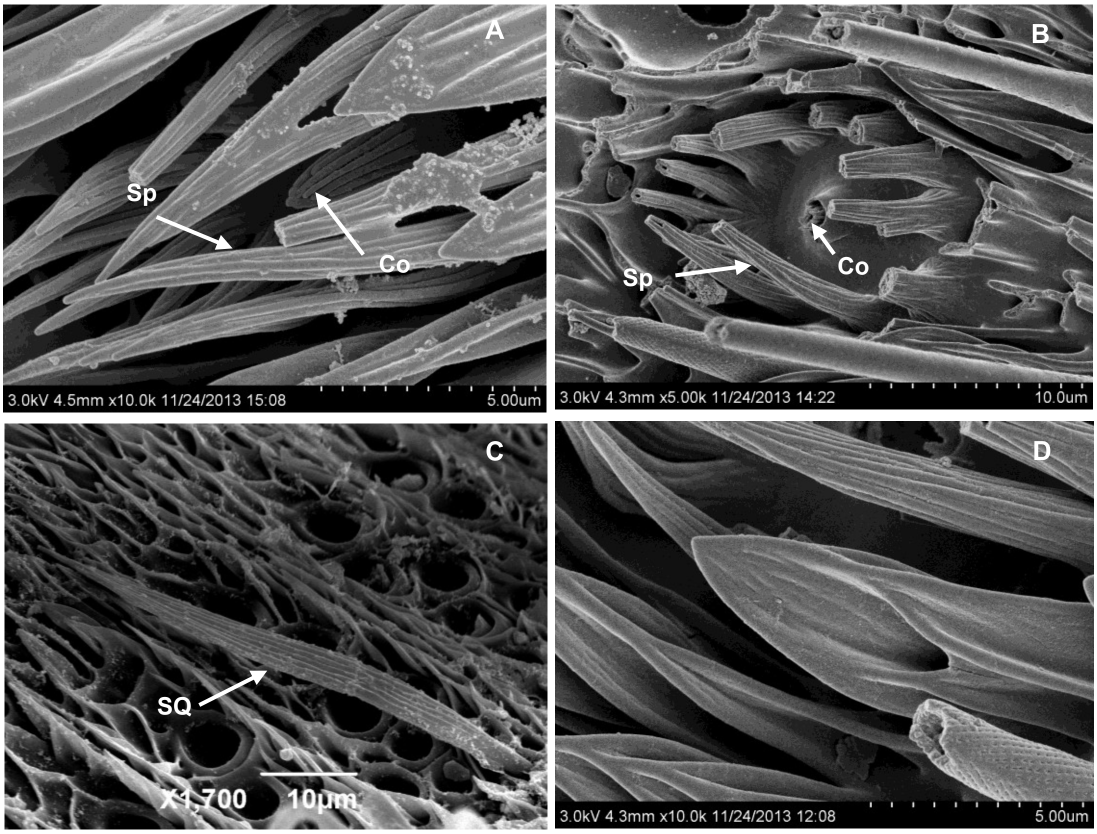

Figure 5. Scanning electron micrographs showing several sensillum types. (A) coeloconica sensilla (Co, sensillum coeloconicum; Sp, spines); (B) The cross section of coeloconica sensilla; (C) SQ, sensilla squamiformia; (D) sensilla auricillica.

Discussion

The general shape and structure of the antennae of male and female *C. remissa* were similar to those reported for other species of Lepidoptera (Victor *et al*., 1999; 2003; 2008; Faucheux, 1990a; Faucheux *et al*., 2006; Frank *et al*., 2010; Nasra, 2008). The antennal flagellomeres of males and females were cylindrical and most of the sensilla were located on the ventral surface, whereas the dorsal surface possessed numerous overlapping scales. This arrangement has been reported in several Lepidoptera families, including Sesiidae (Karalius, 1994), Noctuidae (Faucheux, 1990a; Mochizuki *et al*., 1992; Koh *et al*., 1995), Pyralidae (Faucheux, 1991; Hansson *et al*., 1995; Castrejón- Gómez *et al*., 2003), and Tortricidae (Castrejón-Gómez and Carrasco, 2008). This arrangement may protect the antennae and their sensilla from damage (Koh *et al*., 1995). Alternatively, the scales might not protect the sensilla from mechanical damage, but the distribution of the sensilla and scales on the antennae may allow insects to detect the direction of a stimulus (Van Der Pers *et al*., 1980). It has also been suggested that the scales are a mechanism for trapping and concentrating odour molecules (Wall, 1978).

The antennae of *C. remissa* exhibited sexual dimorphism. The male antennae were covered tightly with scales whereas the female antennae were loosely covered. Although they were similar in size to the male antennae, the antennae of female *C. remissa* possessed more antennal flagellomeres. In *C. remissa*, the sexually dimorphic characteristics were mainly related to variations in the distribution and size of sensilla.

In the present study, six types of sensilla were identified on the antennae flagella of female and male *C. remissa* moths. The types and distributions of the different sensilla on the antennae of *C. remissa* were similar to those present on the antennae of other noctuid species (Jefferson *et al*., 1970; Faucheux, 1990a; Ljungberg *et al*., 1993; Monti *et al*., 1995). The uniporous pegs associated with sensilla auricillica in some Noctuidae families (Faucheux, 1993; 1999) are not observed in *C. remissa*. Estimates of the sensilla on the antennae of male and female *C. remissa* showed that sensilla trichodea were the most abundant of the different types of sensilla identified. Flower and Helson (1971; 1974) suggested that all of the trichoidea sensillum types were present in some form on the noctuid moths they examined, so they are capable of perceiving broadly similar stimuli in their surroundings.

Three distinct subtypes of sensilla trichodea were differentiated based on their size on the antennae of *C. remissa.* The male antennae possessed large numbers of long trichoid sensilla (type I sensilla), which were absent from female antennae. The presence of these sensilla has also been reported in other species of Noctuidae, *i.e*., *Trichoplusia ni* (Hubner), *Helicoverpa zea* (Boddie), *Spodoptera ornithogalli* Guenee, and *Spodoptera exigua* (Hubner) (Jefferson *et al*., 1970), *Noctua* *pronuba* (L.) (Faucheux, 1990a). In several moths, the long trichoid sensilla on male antennae are receptors for female sex pheromones (Boekh *et al*., 1965; Schneider and Steinbrecht, 1968; Van Der Pers and Den Otter, 1978; Kaissling, 1979; Zacharuk, 1985; Renou, 1991; Zhang *et al*., 2001). The functions of the type II and type III sensilla trichoidea are unknown on the male and female antennae of *C. remissa*. In *Mamestra thalassina* Hufnagel and *Mamestra suasa* (Denis et Schiffermuller), some hairs of the type II sensilla trichodea respond to the same compounds as the type I (Renou 1991; Lucas and Renou, 1991). Various studies show that female moths with sensilla trichodea can detect their own sex pheromones and they react in different ways, e.g. females of *T. ni* aggregate to increase the chance of mating (Birch, 1977), females of *Helicoverpa armigera* (Hubner) and *H. zea* move away from calling females (Saad and Scott, 1981), whereas females of *Choristoneura fumiferana* (Clemens) are stimulated to oviposit (Palanaswamy and Seabrook, 1978).

More sensilla chaetica were observed on the antennae of female *C. remissa* (table 2), but the presence of numerous large sensilla trichodea near the proximal ends of the male antennae may have obstructed the view of additional sensilla chaetica on those flagellomeres, so they may have been underestimated in males. In *C. remissa*, the structure of the sensilla chaetica was similar to that reported in other noctuids (Jefferson *et al*., 1970; Liu and Liu, 1984; Faucheux, 1990a). The terminal pore of sensilla chaetica is described in *N. pronuba* (Faucheux, 1990a) and in the pyralid *Homoeosoma nebulella* (Denis et Schiffermuller) (Faucheux, 1991). In some lepidopteran families, it has been suggested that these sensilla also function as contact chemoreceptors (Schneider, 1964; Hallberg *et al*., 1994). Several studies suggest that sensilla chaetica function as contact chemoreceptors and mechanoreceptors because they arise from a socket and possess a terminal pore (Altner and Prillinger, 1980; Van der Pers *et al*., 1980, Faucheux, 1990a).

In general, sensilla coeloconica belong to two subtypes: with or without spines. Those with spines are found in Lepidoptera such as *Chlunetia transversa* Walker (Mo and Zhao, 2006), *H. armigera* (Wang *et al*., 2002), and *Plutella xylostella* (L.) (Yang *et al*., 2001) and numerous other moths (Faucheux, 1999). The subtype that lacks spines possesses a form similar to that found in Neopseustidae (Faucheux *et al*., 2006). It has been suggested that the spines protect the cones from physical damage in the environment. Some insects possess both types of sensilla, e.g. *N. pronuba* (Faucheux, 1990a), *Micropterix calthella* (L.) (Faucheux, 1997), *Manduca sexta* (L.) (Shields and Hildebrand, 1999) and *Loxostege sticticalis* (L.) (Yin *et al*., 2004). In the present study, only sensilla coeloconica with spines were found on the female and male antennae. It has been suggested that these sensilla are sensitive to humidity (Altner *et al*., 1977), but their ultrastructure suggests that they are olfactory receptors and they may be sensitive to the volatile odours of plants (Van der Pers, 1981).

Sensilla styloconica are widely distributed on the antennae of Noctuidae (Castrejón-Gómez *et al*., 1999) and Torticidae (Wall, 1978). In the present study, these sensilla were divided into two subtypes based on the presence or absence of apical structures. Type I are smooth with no apical structures on their tips, whereas type II have 1-3 apical structures at their distal ends. Sensilla styloconica with double or triple apical structures are common in noctuids, e.g. *T. ni*, *H. zea*, *S. ornithogalli*, *S. exigua* (Jefferson *et al*., 1970), *Mythimna unipuncta* (Haworth) (Lavoie and McNeil, 1987), and *Mamestra configurata* Walker (Liu and Liu, 1984). Sensilla styloconica function as thermo-hygroreceptors in moths (Steinbrecht and Muller, 1991).

Sensilla squamiformia are frequent in Lepidoptera, including *M. unipuncta*, *N. pronuba, Agathiphaga vitiensis* Dumbleton, *Copitarsia consueta* (Walker), *Zamagiria dixolophella* Dyar, *Opogona sacchari* (Bojer), (Lavoie and McNeil, 1987; Faucheux, 1990a; 1990b; Castrejón-Gómez *et al*., 1999; 2003; Shen *et al*., 2005). This type of sensillum may be related to the protection of the terminus of the antenna, but this has not been confirmed. However, these sensilla are involved in tactile mechanoreception (Faucheux, 1999).

In *C. remissa*, the sensilla auricillica were morphologically similar to those described in other Lepidoptera (Hallberg, 1981; Hallberg *et al*., 1994; Subchev, 1980; Faucheux, 1999). The sensilla auricillica found on the antennal surface of *C. remissa* had morphological features that indicated olfactory functions, since they belong to the single-walled, wall-pore sensilla (Altner, 1977). In physiological studies, similar sensilla possessed neurons that responded to plant odours (Anderson *et al*., 2000). In *S. exigua,* the sensilla auricillica respond to a floral odour, phenylethyl alcohol (Mochizuki *et al*., 1992), whereas responses to potential sex pheromones were recorded in *Cydia pomonella* (L.) (Ebbinghaus *et al*., 1998).

Conclusion

C. remissa is a genus of owlet moths which are commonly known as underwings. Information on the natural behaviour and ecology of this genus is scarce because of their cryptic coloration and resting habits. *C. remissa* has high specificity to its host plants and cannot complete its life-cycle without *Populus* spp. The elucidation of the chemical communication that occurs between this moth and its host plant will provide new insights into their behavioural interactions. Thus, chemo-ecological studies should provide a theoretical basis for the integrated management of *C. remissa*. To the best of our knowledge, this is the first study to describe the detailed morphology of the antennal sensilla of *C. remissa.* Several chemoreceptive, mechanoreceptive, and thermohygroreceptive sensilla were identified in this study. Sensilla trichodea, auricillica and coeloconica are generally accepted to be the main olfactory sensilla in many insect species and their functions are related to plant odours, pheromones, and other chemical stimulants (Faucheux, 1999). There were some difficulties with the description and nomenclature of *C. remissa* sensilla because different standards are available. The presence or absence of pores on the sensillum wall is indeed indispensable prerequisites in a study seeking to define different types of sensilla. Future studies should obtain more detailed descriptions and elucidate the functions of the antennal sensilla of *C. remissa* using transmission electron microscopy, as well as electrophysiological and behavioural experiments, to confirm the functions of the different types of sensilla described in the present study.

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