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RESEARCH

Morphological characteristics and distribution of antennal sensilla of *Spodoptera litura* (Lepidoptera: Noctuidae) using scanning electron microscopy

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Abstract
Spodoptera litura Fabricius (Lepidoptera: Noctuidae) is a major agricultural pest, primarily in Asia and Oceania. Chemical odor-based trapping is a major method used to control *S. litura*, and thus understanding the antennal sensilla of *S. litura* is critical for improving the efficacy of attractants used in pest control. In the present study, the types of *S. litura* antennal sensilla were examined by low-voltage field emission scanning electron microscopy, and morphological descriptions were provided. A total of eight types and two subtypes of the antennal sensilla were identified, namely Böhm's bristles, sensilla trichodea, sensilla basiconica, sensilla chaetica, sensilla coeloconica, sensilla styloconica, sensilla squamiformia (I and II), and sensilla auricillica (I and II). Among them, sensilla squamiformia II, and sensilla auricillica II are reported for the first time in *S. litura*. This study provides morphological information to aid in future electrophysiological tests on the antennal sensilla of *S. litura*.

Keywords *Spodoptera litura* · Antennal sensilla · Scanning electron microscopy · Sensilla morphology

Introduction

Spodoptera litura Fabricius (Lepidoptera: Noctuidae) is a significant agricultural pest in Asia and Oceania (Bragard et al. 2019). As an omnivorous insect, it can feed on hundreds of plant species from 40 families, including economically important crops such as beans, crucifers, cucurbits, and others in the families Gramineae, Malvaceae, and Solanaceae (Du et al. 2022; Sharma et al. 2022). *S. litura* occurs throughout China, especially in the middle and lower reaches of the Yangtze River and South China, where it impacts primarily tobacco and cruciferous vegetables (Zhou 2009; Yang et al. 2011). Historically, chemical pesticides have been the predominant method for controlling this moth (Yushima et al. 1974; Singh and Sachan 1993; Guerrero et al. 2014). However, varying levels of pesticide resistance have developed in this insect, leading to excessive spraying and environmental pollution in some areas (Ahmad et al. 2007; Bragard et al. 2019). In recent years, many countries have begun implementing pheromone trapping to monitor and control *S. litura* (Yang et al. 2011; Sang et al. 2013). Pheromone trapping has proven to be more environmentally friendly and has led to reduced reliance on chemical pesticides. Therefore, developing more effective odor-based trapping attractants has become an important focus to improve management of *S. litura*.

Antennal sensilla are the biological sensory organs that allow insects to detect and perceive external environmental information such as air flow, air temperature, and pheromones (Galizia and Rössler 2010; Schmidt and

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Benton 2020; Li et al. 2024). Identifying the types of antennal sensilla is an important prerequisite to clarify the function of antennal sensors, and also to improve the efficacy of pheromones or other odor-based attractants. Nevertheless, relatively few studies have focused on the antennal sensilla of *S. litura*. Liu et al. (2009) conducted the first study of antennal sensilla of *S. litura* in China and recorded five types: sensilla trichodea, sensilla basiconica, sensilla chaetica, sensilla coeloconica, and sensilla auricillica. Thereafter, Aruna et al. (2019), working in India, also identified five types of antennal sensilla on *S. litura* (sensilla trichodea, sensilla chaetica, sensilla coeloconica, sensilla auricillica, and sensilla styloconica) with sensilla styloconica being newly recorded. However, the number of sensilla types reported for *S. litura* in the above two studies (6 types), is relatively low when compared to many other Noctuidae. For example, as many as 15 sensilla types have been reported for *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae) (Li et al. 2024). Therefore, it is necessary to further clarify the sensillum types of *S. litura* and describe their characteristics.

The main objective of this study was to conduct a comprehensive examination and classification of the antennal sensilla of *S. litura*, using low-voltage field emission scanning electron microscopy. For each sensilla type, we described its morphological characteristics and distribution, as well as present one or more high-resolution photos. Providing such information will facilitate future research to improve odor attractants for this major agricultural pest.

Materials and methods

Sampling insects

Newly emerged 1–2-day-old *S. litura* adults, both male and female, were used for scanning electron microscopy (SEM) observations. The use of recently-emerged adults in SEM studies was a common practice (Li et al. 2024; Xu et al. 2021). The adults were reared in the Insect Laboratory of Yunnan University. The rearing conditions were set at a temperature of 27 ± 1 °C, relative humidity of 70 ± 10%, and a light/dark cycle of L12 h:D12 h. Larvae were fed an artificial diet following the formula described by Li et al. (1998). Fully mature larvae were put individually in a circular plastic box (30 mm diameter at bottom, 40 mm diameter at top, 30 mm in height) containing sand which they entered to pupate. Newly emerged adults were transferred to plastic boxes of the same size. Adult male and female moths were provided with a diet of 10% honey water to meet their nutritional needs until they were used for the antennal sensillum studies.

Sample preparation and SEM observation

SEM observations were conducted at the Modern Analytical Testing Center of Yunnan University. Soon after moth was killed, the antennae were removed under a stereomicroscope (Nikon SMZ1500, Nikon Instrument, Japan). The treatment of the antennae was slightly modified from the steps given in Guo et al. (2022). Briefly, the dissected antennae were soaked in a 75% ethanol solution and subjected to ultrasonic cleaning for 30 s to remove surface contaminants. Afterwards, the antennae were rinsed with n-hexane for cleaning, with the process repeated three times for 15 min each. Subsequently, a series of dehydration steps were carried out using 80%, 90%, and 100% ethanol, with each step lasting 15 min. After the samples were dried, they were affixed to sample holders using conductive adhesive, and a thin layer of gold was sputter-coated on the samples using a BAL-TEC SCD005 under conditions of 30 mA for 300 s. The prepared samples were then observed and photographed using an advanced low-voltage field emission scanning electron microscope (LVSEM) (Nova NanoSEM 450, FEI, USA) operating at voltages between 3 and 10 kV and magnifications ranging from 250–60,000x.

Terminology, measurements and statistical analysis

The identification and classification of the antennal sensilla were based on the external morphology and surface features according to Schneider (1964) and Zacharuk (1980). Antennal measurements were taken on 20 intact male and 20 intact female antennae, including total length, basal diameter, and the number of subsegments. The length and basal diameter of each sensillum type were measured using Image J 1.38 software (National Institutes of Health) and reported as the mean ± SE (standard error). For each type of sensillum found, we attempted to measure 30 replicates for both males and females. However, for some sensillum types that were found beneath scales (e.g., sensilla squamiformia II), it was not possible to reach this goal.

Data analysis was conducted using SPSS 26.0 software (IBM). Differences between males and females for various sensilla measurements were statistically analyzed using Student's t-test, with an alpha level of *p*; 0.05. Similarly, size differences among the lateral sensilla chaetica (LSC), central sensilla chaetica (CSC), and dorsal sensilla chaetica (DSC) of both males and females were statistically analyzed using ANOVA and Tukey's mean separation test, with an alpha level of $p < 0.05$. Microscopic and electron microscopic images were processed using Adobe Photoshop CC 2017 software (Adobe Systems).

Results

The basic morphology of the antennae

The antennae of *Spodoptera litura* were filamentous and composed of three segments: a scape, a pedicel, and a flagellum (Fig. 1). The scape segment was connected to the head; followed by the pedicel and then the flagellum, which is major segment of the antennal sensilla distribution (Figs. 1, 2a, b and 3). Both the scape and the pedicel had muscle structure, indicating that they were able to rotate. These first two segments were totally covered by scales and had two sensilla types: Böhm's bristles (BB; also called Böhm's sensilla by others) and sensilla squamiformia II (SSQ II) (Figs. 4a, b, and 9c, d). Böhm's bristles were located at the basal portion of the scape; while sensilla squamiformia II were scattered on the surface of the pedicel. The average length and basal diameters of the scape and pedicel were significantly longer and larger in males compared to females (Table 1).

The flagellum was composed of several subsegments (Fig. 1), gradually becoming thinner towards the tip. The flagellum consisted of 83.0 ± 0.5 subsegments (n = 20) on average in females and 83.2 ± 0.6 subsegments (n = 20) in males, with no significant difference between the sexes ($t = 0.249$, df = 38, $p = 0.805$). However, there was a significant difference in flagellum length between sexes ($t = 5.51$, df = 38, $p < 0.001$), being longer on average in males than females (Table 1). At the distal end of the flagellum, there were conical structures covered with petal-like folds, and the tip was adorned with 2 or 3 small cones, which were sensilla styloconica (SS) (Fig. 2c).

Scales were the most prominent structures on the antennal surface, covering the entire surface of the scape and the pedicel, as well as the dorsal side of the flagellum, occupying almost 50% of the antennal surface area (Fig. 2a, b and d). Most of the sensilla found on *S. litura* were primarily distributed on the ventral side of the flagellum, with a few sensilla located under the scales (Fig. 3a). Each subsegment had two rows of scales arranged in an overlapping tile pattern, where the scales of the previous subsegment covered the base of the next subsegment (Fig. 2d). The scales looked shield-like with parallel vertical ridges on their surfaces (Fig. 2d). The average length of scales was significantly different between the sexes, being 71.01 ± 0.91 µm in females and 80.99 ± 1.15 µm in males ($t = 6.95$, df = 58, $p < 0.001$).

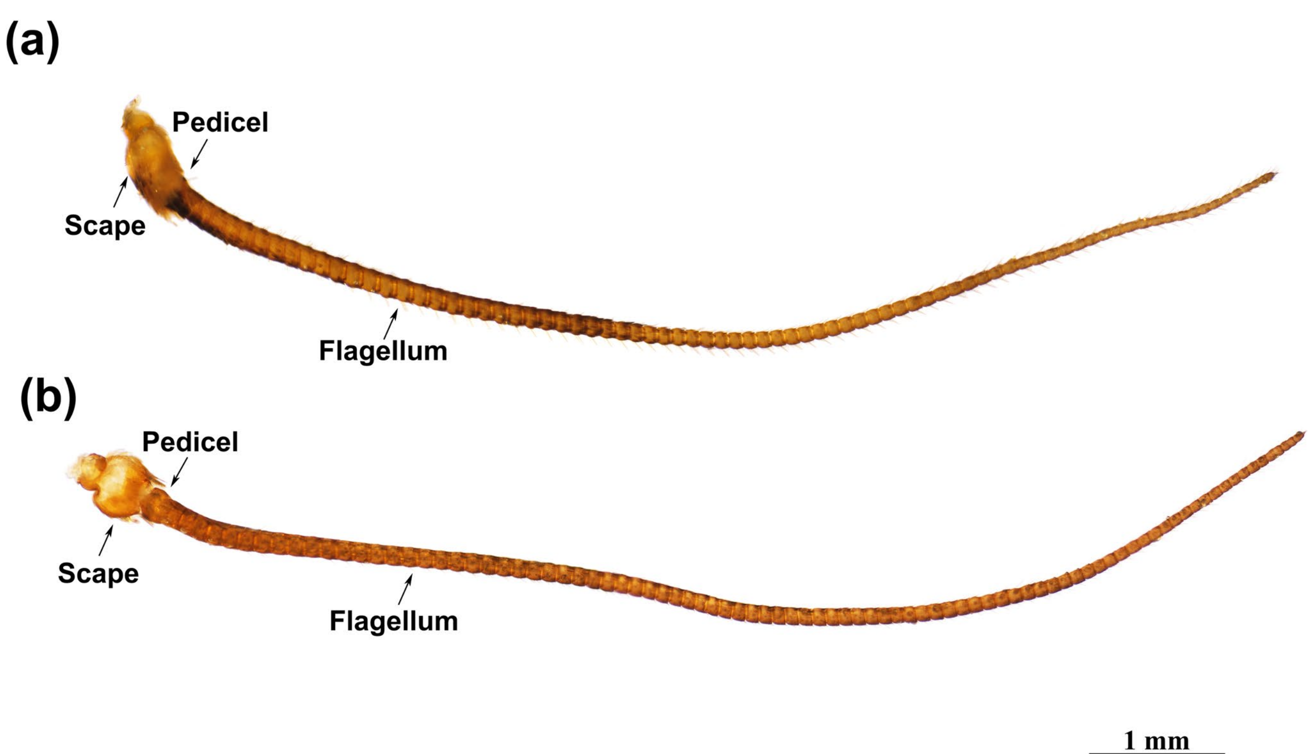

Fig. 1 Typical appearance of the adult antennae from *Spodoptera litura* moths: **a** male and **b** female

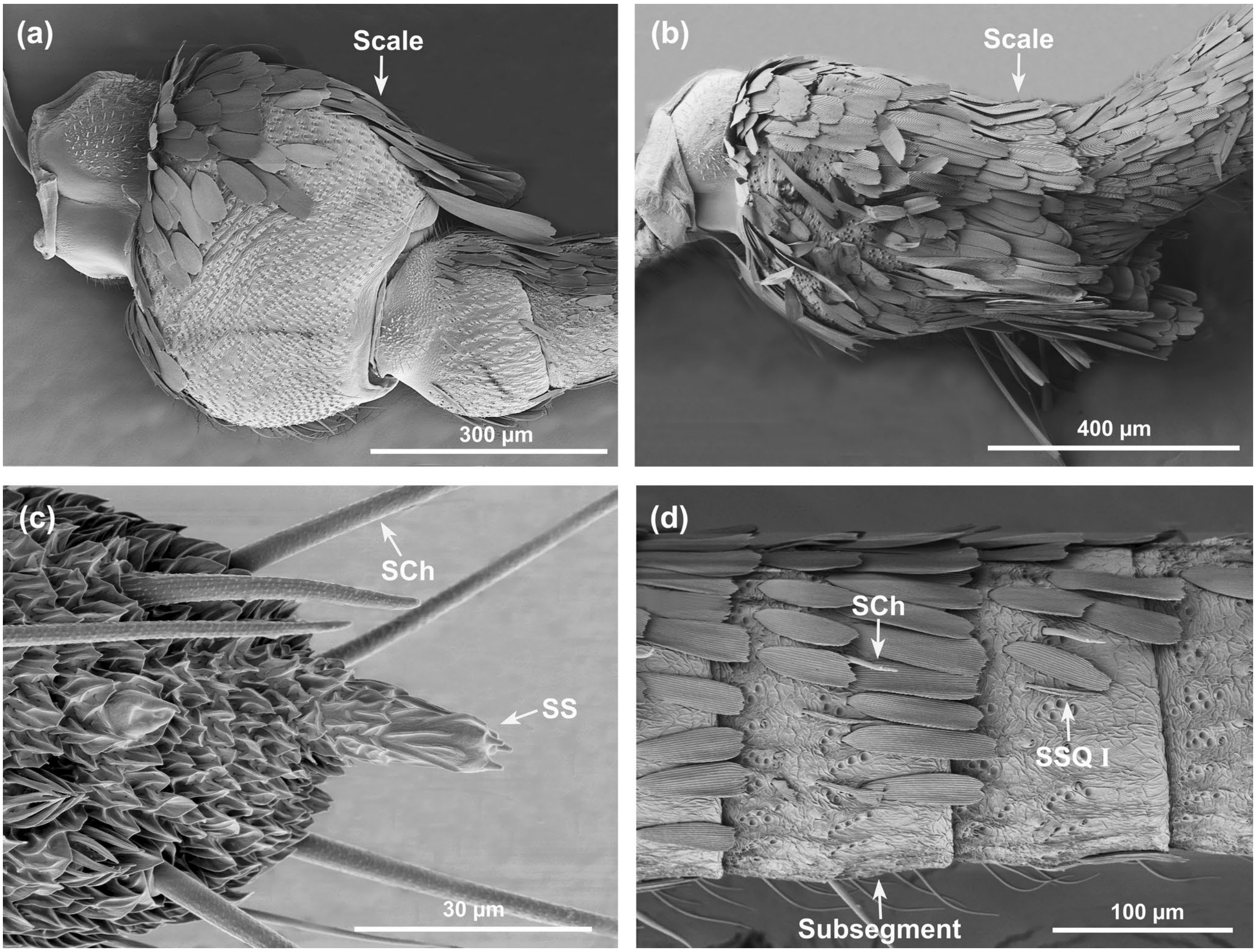

Fig. 2 Scanning electron micrographs of the antennal scape, pedicel and flagellum of *Spodoptera litura*: **a** the scape and pedicel after removing some scales, **b** the scape and pedicel with scales present, **c** the tip of the flagellum and **d** scale arrangement on flagellum subsegments. *SCh* sensilla chaetica; *SS* sensilla styloconica and *SSQ I* sensilla squamiformia I

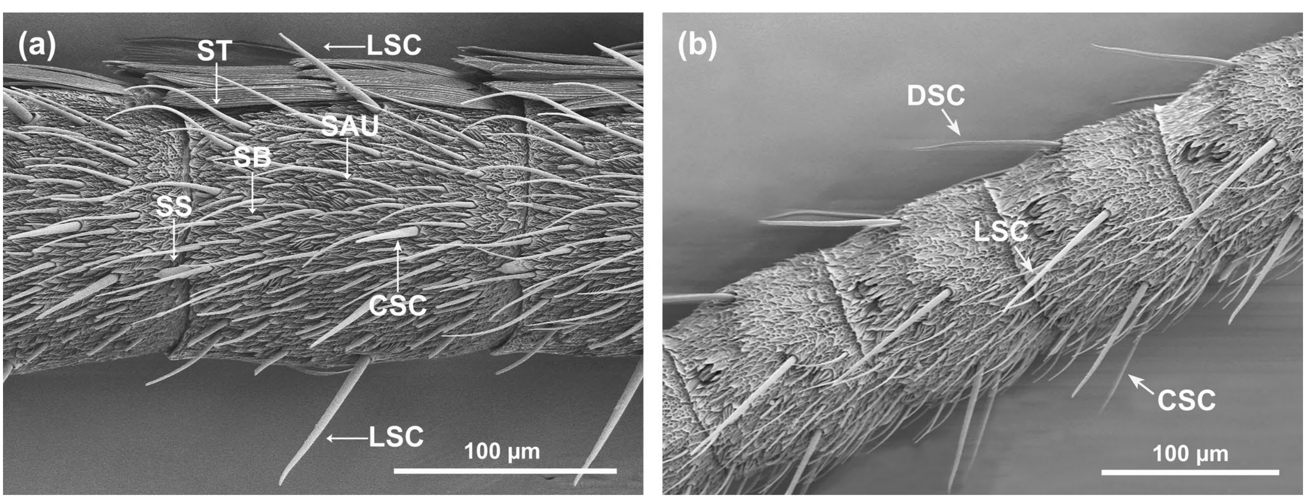

Fig. 3 Morphological characteristics and distribution of various sensilla on the flagellum of *Spodoptera litura*: **a** ventral side of flagellum and **b** lateral side of flagellum. *ST* sensilla trichodea; *SB* sensilla basiconica; *LSC* lateral sensilla chaetica; *CSC* central sensilla chaetica; *DSC* dorsal sensilla chaetica; *SAU* sensilla auricillica and *SS* sensilla styloconica

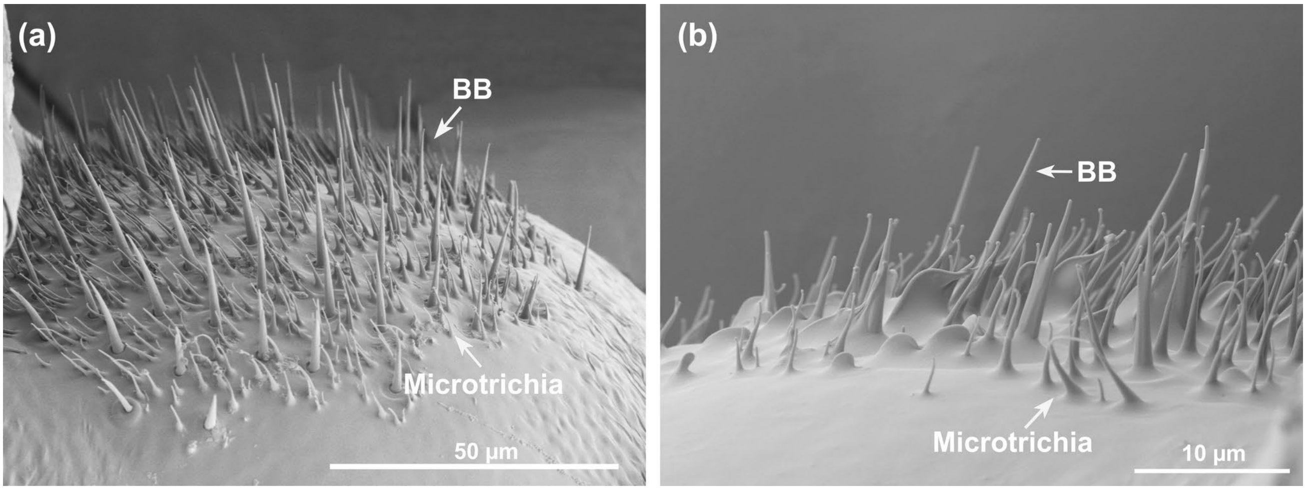

Fig. 4 Morphological characteristics and distribution of Böhm's bristles on the antennae of *Spodoptera litura*: **a** *BB* Böhm's bristles and **b** microtrichia

Table 1 Mean (SE) length and basal diameter of the antennal segments of male (N = 20) and female (N = 20) *Spodoptera litura*

Antennal segments	Mean lengths		Mean basal diameters (µm)	
	Female	Male	Female	Male
Scape	350.50 ± 7.58 (µm) b	393.35 ± 10.85 (µm) a	260.30 ± 7.75 a	278.25 ± 5.93 a
Pedicel	171.05 ± 4.88 (µm) b	187.50 ± 4.46 (µm) a	197.95 ± 3.31 b	222.00 ± 6.40 a
Flagellum	8.89 ± 1.70 (mm) b	9.86 ± 0.66 (mm) a	NA	NA
Total	9.38 ± 0.17 (mm) b	10.45 ± 0.07 (mm) a	NA	NA

For length and diameter measurements separately, values comparing sexes within a row followed by different letters were significantly different (paired t-test, $p < 0.05$)

Types of antennal sensilla

Eight types of antennal sensilla and two subtypes were identified in the present study, namely Böhm's bristles (BB), sensilla trichodea (ST), sensilla basiconica (SB), sensilla chaetica (SC), sensilla coeloconica (SCO), sensilla styloconica (SS), sensilla squamiformia I and II (SSQ I and SSQ II), and sensilla auricillica I and II (SAU I and SAU II).

Böhm's bristles

Böhm's bristles (BB) were only found on the surface of the scape and pedicel, distributed in clusters at the base of the two segments, near the intersegmental region (Fig. 4a). These sensilla looked like thorns in appearance, arising from a socket-like depression, gradually tapering from the base to the tip, and ending in a sharp point. They had a smooth surface without surface pores, suggesting their role was mostly mechanical (Fig. 4b; Table 2). Average BB basal diameter was not significantly different between the sexes ($t = 1.22$, df = 58, $p = 0.227$); while the mean BB length was significantly ($t = 5.54$, df = 58, $p < 0.001$) longer in males than in females (Table 3).

Numerous microtrichia were observed around BB (Fig. 4b). The microtrichia did not have structures or a socket-like depression at their base, were angled with the surface at approximately 90 degrees, and were shorter and much slender compared to BB (Fig. 4b).

Sensilla trichodea

Sensilla trichodea (ST) were the most abundant sensilla type found on the antennae of *S. litura*, accounting for approximately 70% of all sensilla found. The ST were primarily located on the ventral side of the flagellum (Figs. 3a and 5a). ST gradually tapered from base to tip, ending with a rounded and blunt apex (Fig. 5b). The ST angled away from the antenna surface and had helical ridges along their length (Fig. 5a, b; Table 2). Average ST length ($t = 5.75$, df = 58, $p < 0.001$) and basal diameter ($t = 5.50$, df = 58, $p < 0.001$) were significantly larger in males than females (Table 3).

Table 2 Morphological features and location of the antennal sensilla observed on *Spodoptera litura* adult moths

Sensilla types	Shape	Wall surface	Pores	Locations[a]
Böhm's bristles, BB	Thorn	Smooth	Aporous	S, P
Sensilla trichodea ST	Slender hair	Helical ridges	Multiporous	Flv
Sensilla basiconica, SB	Small cone	Longitudinal ridges	Multiporous	Flv
Sensilla chaetica, SCh	Upright spine	Striped	Uniporous	Fld, Flv, Fll, Flt
Sensilla coeloconica, SCO	Chrysanthemum-like	Longitudinal ridges	Multiporous	Flv, Flt
Sensilla styloconica, SS	Cylindrical	Intricate ridges	Aporous	Flv, Flt
Sensilla squamiformia I, SSQ I	Narrow willow leaf	Longitudinal grooves	Aporous	Fld
Sensilla squamiformia II, SSQ II	Spindle	Vertical stripes	Aporous	S, P
Sensilla auricillica I, SAU I	Rabbit ear-like	Longitudinal ridges	Multiporous	Flv
Sensilla auricillica II, SAU II	Enlarged ear-like	Smooth	Multiporous	Flv

[a]*S* scape, *P* pedicel, *Fld* dorsal side of flagellomeres, *Flv* ventral side of flagellomeres, *Fll* lateral side of flagellomeres, *Flt* terminal flagellomere

Table 3 Mean length and basal diameter of the antennal sensilla present on adult female and male *Spodoptera litura* moths

Sensilla types	Mean lengths (µm)		Mean basal diameters (µm)	
	Female	Male	Female	Male
Böhm's bristles, BB	16.77 ± 0.36 b	22.72 ± 0.62 a	2.18 ± 0.05 a	2.28 ± 0.53 a
Sensilla trichodea ST	67.17 ± 1.12 b	81.60 ± 3.00 a	2.98 ± 0.08 b	3.76 ± 0.11 a
Sensilla basiconica, SB	12.46 ± 0.51 a	13.42 ± 0.54 a	2.38 ± 0.47 b	2.60 ± 0.08 a
Sensilla Chaetica, Central, CSC	74.34 ± 1.02 a3	75.65 ± 1.63 a2	4.54 ± 0.08 b2	5.17 ± 0.17 a2
Sensilla Chaetica, Dorsal, DSC	79.62 ± 1.44 a2	79.86 ± 1.09 a2	4.22 ± 0.99 b2	4.78 ± 0.11 a2
Sensilla Chaetica, Lateral, LSC	87.05 ± 1.29 b1	102.49 ± 2.38 a1	5.36 ± 0.12 b1	6.77 ± 0.14 a1
Sensilla coeloconica, SCO	NA[a]	NA	9.84 ± 0.19 b	10.68 ± 0.97 a
Sensilla styloconica, SS	21.83 ± 0.35 a	22.55 ± 0.40 a	6.20 ± 1.15 a	6.28 ± 0.19 a
Sensilla squamiformia I, SSQ I	49.37 ± 0.51 b	53.32 ± 0.68 a	2.07 ± 0.05 a	2.21 ± 0.05 a
Sensilla squamiformia II, SSQ II	66.27 ± 2.25 a	70.81 ± 1.96 a	2.01 ± 0.07 a	2.13 ± 0.06 a
Sensilla auricillica I, SAU I	14.13 ± 0.74 a	14.47 ± 0.75 a	2.60 ± 0.11 a	2.86 ± 0.12 a
Sensilla auricillica II, SAU II	12.18 ± 0.17 a	12.37 ± 0.29 a	NA[a]	NA

Values comparing sexes within a row for either length or basal diameter and followed by different letters were significantly different (paired t-test, $p < 0.05$). Mean values within a column for CSC, DSC and LSC followed by the same letter were not significantly different (ANOVA and Tukey mean separation test, $p < 0.05$). [a]NA = Not available. The mean lengths of SCO and basal diameters of SAU II were not measured

Sensilla basiconica

Sensilla basiconica (SB) were the second most abundant sensilla type, being located on the ventral side of the flagellum, with 5–12 SB per subsegment. The SB were widest at their base, short, and with a slender and blunt tip (Fig. 6a, b). The SB surface was characterized by longitudinal ridges with numerous pores between ridges (Fig. 6b; Table 2). Average SB length did not differ significantly between the sexes ($t = 1.30$, df = 58, $p = 0.201$); however, average SB basal diameter was greater in males than females ($t = 2.40$, df = 58, $p = 0.021$) (Table 3).

Sensilla chaetica

Sensilla chaetica (SCh) resembled an upright spine, with its base arising from a socket-like depression, then tapering slightly and ending with a blunt, rounded, uniporous sensilla (Fig. 7a, b) (Table 2). SCh were distributed on all subsegments of the flagellum, with slightly longer SCh being located near the flagellum tip. There were 6 SCh per subsegment near the middle of flagellum in both females and males (n = 15 females and 15 males). Pores were clearly visible at the SCh tip (Fig. 7c, d). Based on their location around each subsegment, SCh are often classified as lateral sensilla

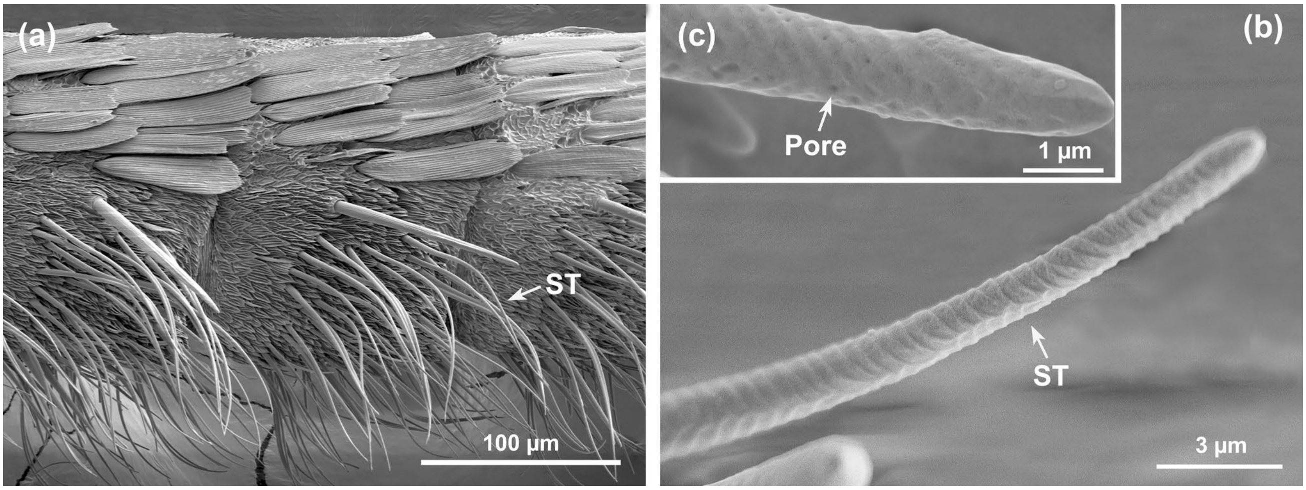

Fig. 5 Morphological characteristics of sensilla trichodea of *Spodoptera litura*: **a** overall appearance and basal structure of sensilla trichodea and **b** the morphological characteristics of sensilla trichodea. *ST* sensilla trichodea

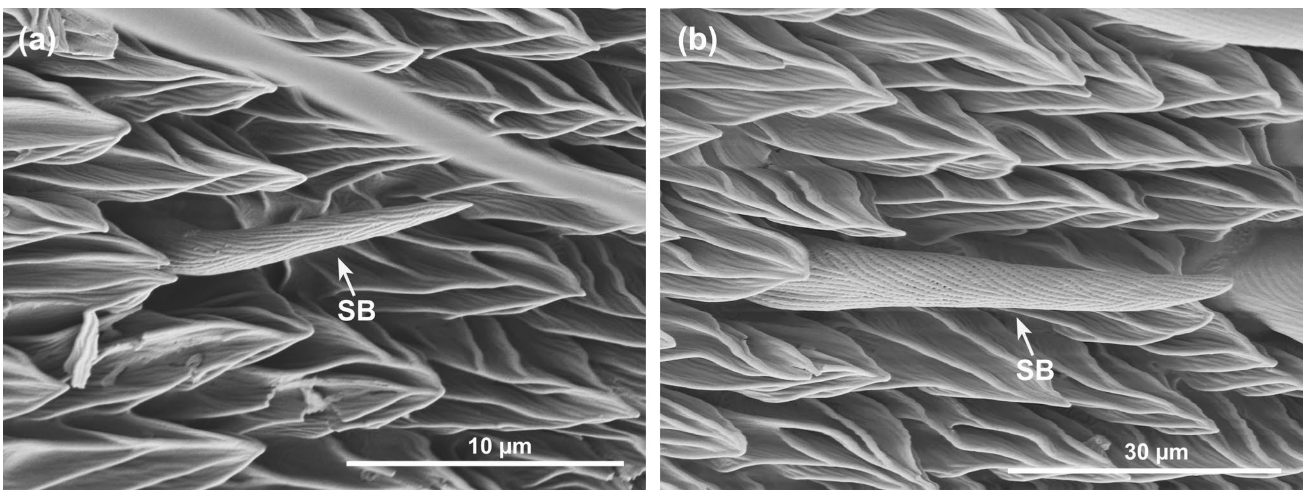

Fig. 6 Morphological characteristics of sensilla basiconica of *Spodoptera litura*: **a** overall appearance and morphological characteristics of sensilla basiconica and **b** the morphological characteristics of sensilla basiconica at greater magnification. *SB* sensilla basiconica

chaetica (LSC), central sensilla chaetica (CSC), and dorsal sensilla chaetica (DSC) (Fig. 3a, b; Table 3) (Gargi et al. 2022; Li et al. 2024). Average length (F = 65.596, df = 2, $p < 0.001$) and basal diameter (F = 54.818, df = 2, $p < 0.001$) differed significantly among LSC, CSC and DSC in males. For example, in males, average LSC length was significantly longer than either CSC or DSC, with no significant difference found between CSC and DSC) (Table 3). Similarly, average LSC basal diameter was significantly wider than either CSC or DSC, with no significant difference found between CSC and DSC. In females, average LSC length was significantly longer than either DSC or CSC, and DSC were longer than CSC (Table 3; F = 25.697, df = 2, $p < 0.001$). Likewise, in females, average LSC basal diameter was significantly wider than both CSC and DSC, with no significant difference found between CSC and DSC (Table 3; F = 35.266, df = 2, $p < 0.001$).

Sensilla coeloconica

Sensilla coeloconica (SCO) were the most complex sensilla found in *S. litura*, consisting of a central cone (CP), surrounded by multiple spines (SP) (Fig. 8a). The central cone (CP), was conical in shape with longitudinal ridges on its surface and a very deep depression which looked like a pore at the tip, and was surrounded by approximately 12–15 spines (Fig. 8a; Table 2). The spines (SP) had longitudinal ridges and were significantly longer than the central cone, bending inward from their base and forming a dome-like structure that enveloped the central cone, similar to a

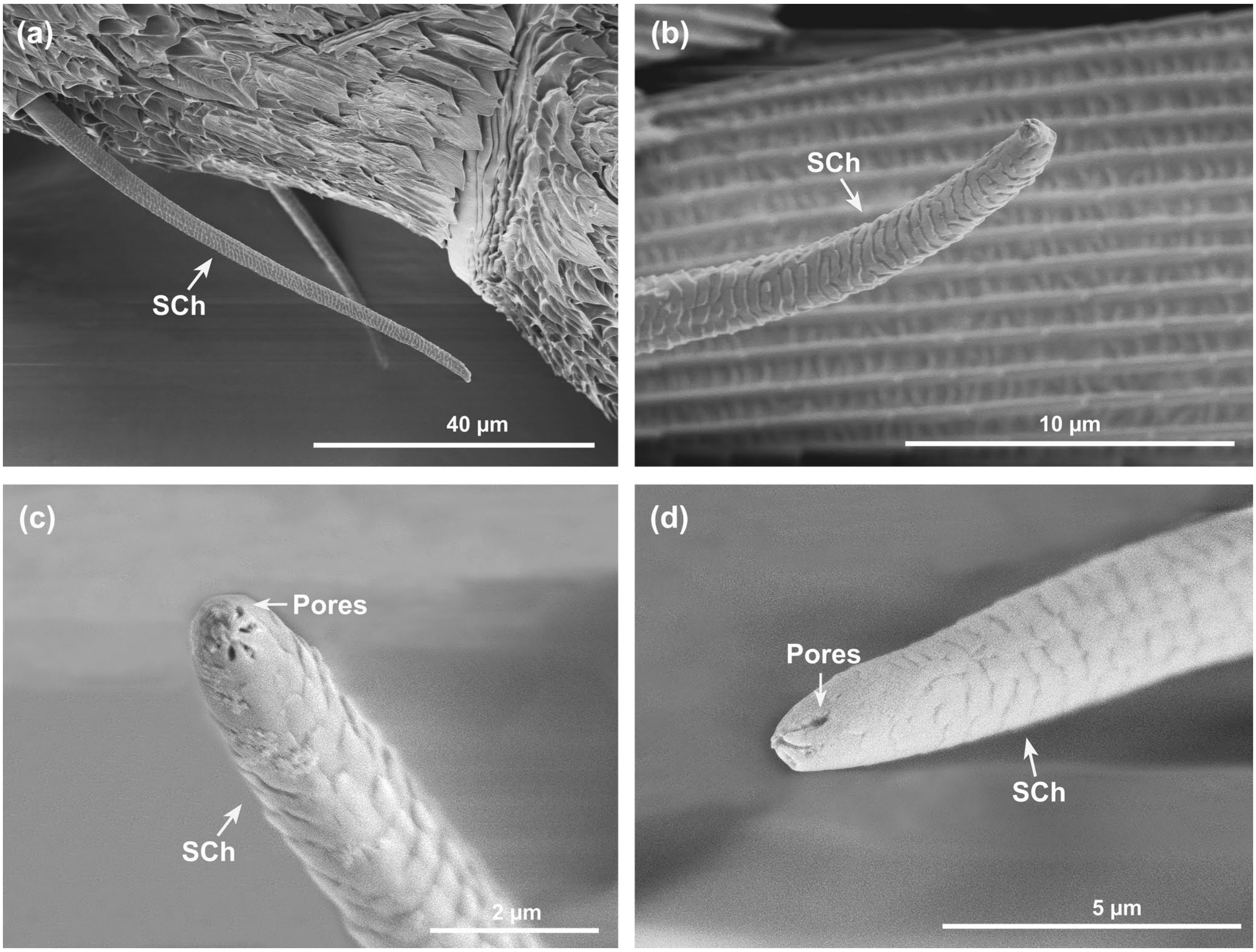

Fig. 7 Scanning electron micrographs of sensilla chaetica of *Spodoptera litura*: **a** overall appearance of sensilla chaetica, **b** morphological characteristics of sensilla chaetica, **c** tip detail of sensilla chaetica and **d** detail of the tip of sensilla chaetica. *SCh* sensilla chaetica

chrysanthemum flower (Fig. 8a). Two to eight SCO were present on the ventral side of each flagellum subsegment and at the terminal end (Table 2). The size of SCO varied significantly between the sexes, with the basal diameter being significantly larger in males than females ($t=3.90$, df = 58, $p<0.001$) (Table 2).

Sensilla styloconica

Sensilla styloconica (SS) were present at the distal end of each subsegment, usually one per subsegment along the ventral side (Figs. 3a and 8b). The SS were cylindrical in shape, with 1–3 blunt protrusions at the tip that were angled at about 45 degrees to the surface (Fig. 8b–d; Table 2). SS with three blunt protrusions were found only in the terminal subsegments, while SS with 1–2 blunt protrusions appeared in the other subsegments. Several small pores were irregularly distributed on the surface of SS (Fig. 8d). There were no significant differences between sexes in average SS length ($t=1.35$, df = 58, $p=0.181$) or basal diameter ($t=0.33$, df = 58, $p=0.745$) (Table 3).

Sensilla squamiformia I

Sensilla squamiformia I (SSQ I) were found in all subsegments of the flagellum, located in socket-like depressions that appeared to be connected with the antenna through the membrane within the depression. SSQ I were widest near their center, gradually narrowing towards the base and tip (Fig. 9a, b). The SSQ I surface had a serrated longitudinal ridge structure (Fig. 9a). No pores were detected on SSQ I (Fig. 9a; Table 2). There were 3–5 SSQ I on each subsegment of the flagellum, primarily on the dorsal side (Fig. 9b). The base of each SSQ I was covered by scales, with just the upper part appearing above the scales. The average length of SSQ I was significantly longer in males than females ($t=4.68$, df = 58, $p<0.001$), while average

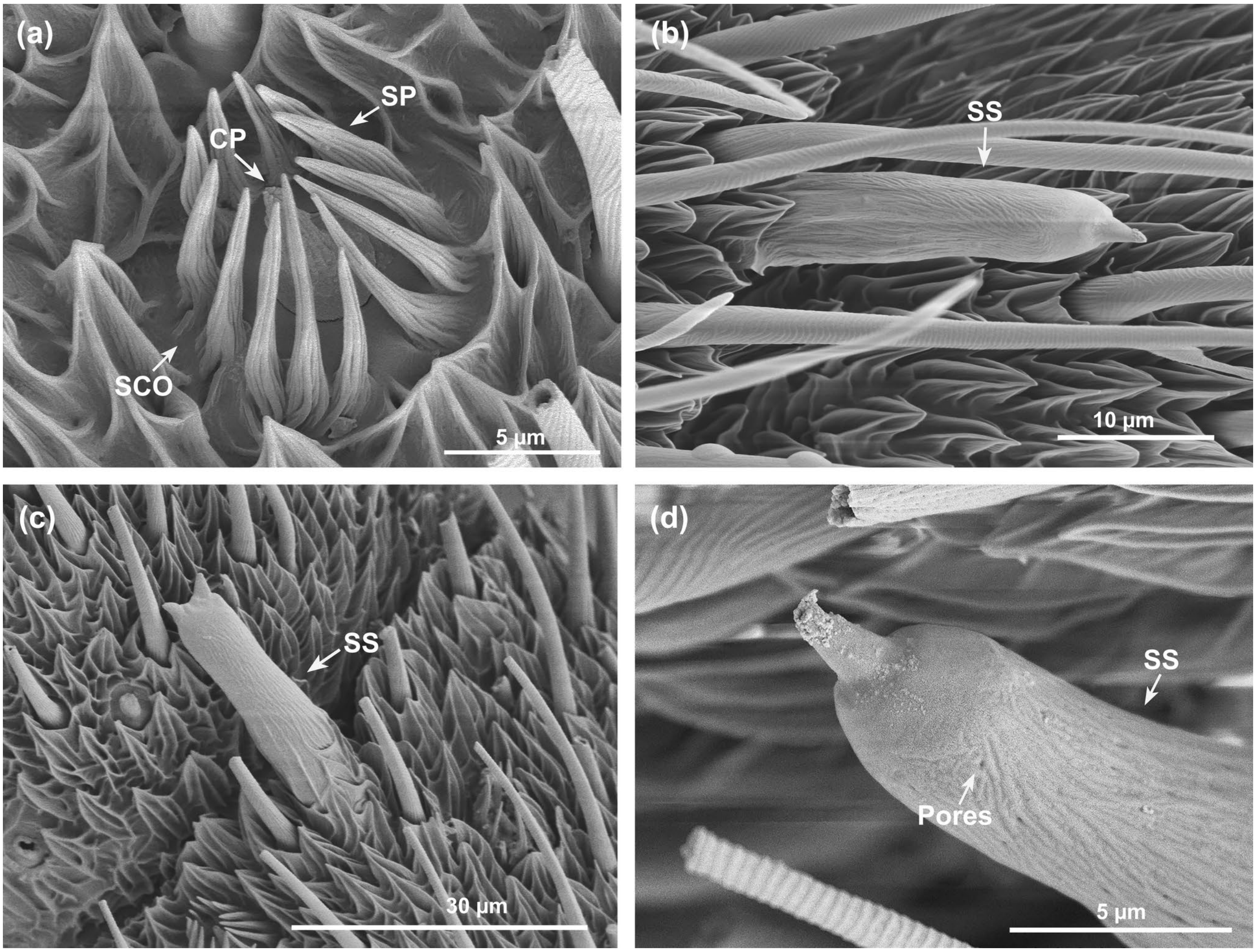

Fig. 8 Scanning electron micrographs of two sensilla of *Spodoptera litura*: **a** overall appearance of sensilla coeloconica (SCO), with surrounding spines (SP) and central peg (CP), **b** sensilla styloconica with one pointed cone, **c** sensilla styloconica with two blunt protrusions and **d** cuticular (no sensory) pores on the stylus of sensilla styloconica. *SCO* sensilla coeloconica; *SS* sensilla styloconica; *SP* spine; *CP* central peg

basal diameter did not differ significantly between the sexes ($t=1.92$, df $=58$, $p=0.06$).

Sensilla squamiformia II

Sensilla squamiformia II (SSQ II) was another subtype of sensilla detected on *S. litura* (Fig. 9c). SSQ II were similar in morphology to SSQ I, but different in their distribution and size. SSQ II were abundant and distributed over the entire scape but found only sparsely on the lateral sides of the pedicel; whereas, SSQ I were present only on the subsegments of the flagellum (Fig. 9d) (Table 2). In addition, SSQ II had longitudinal ridges similar to SSQ I, but the SSQ II were slenderer with a slightly curved tip (Fig. 9a, c; Table 2). Moreover, the average length of SSQ II was significantly longer than SSQ I in both males ($t=9.907$, df $=47$, $p<0.001$) and females ($t=8.935$, df $=47$, $p<0.001$) (Table 3). However, there were no significant differences between the sexes regarding SSQ II average length ($t=1.52$, df $=36$, $p=0.137$) or average basal diameter ($t=1.27$, df $=36$, $p=0.211$).

Sensilla auricillica I

Sensilla auricillica I (SAU I) originated from socket-like depressions and had the shape of a rabbit's ear (Fig. 10a). There were pores on the SAU I surface. Average SAU I length ($t=1.66$, df $=58$, $p=0.103$) and basal diameter ($t=0.33$, df $=58$, $p=0.743$) did not differ significantly between the sexes (Table 3). There was a large depression in these sensilla that gradually narrowed toward the tip (Fig. 10a). There were longitudinal ridges along the length of these sensilla (Fig. 10a). The pores on SAU I

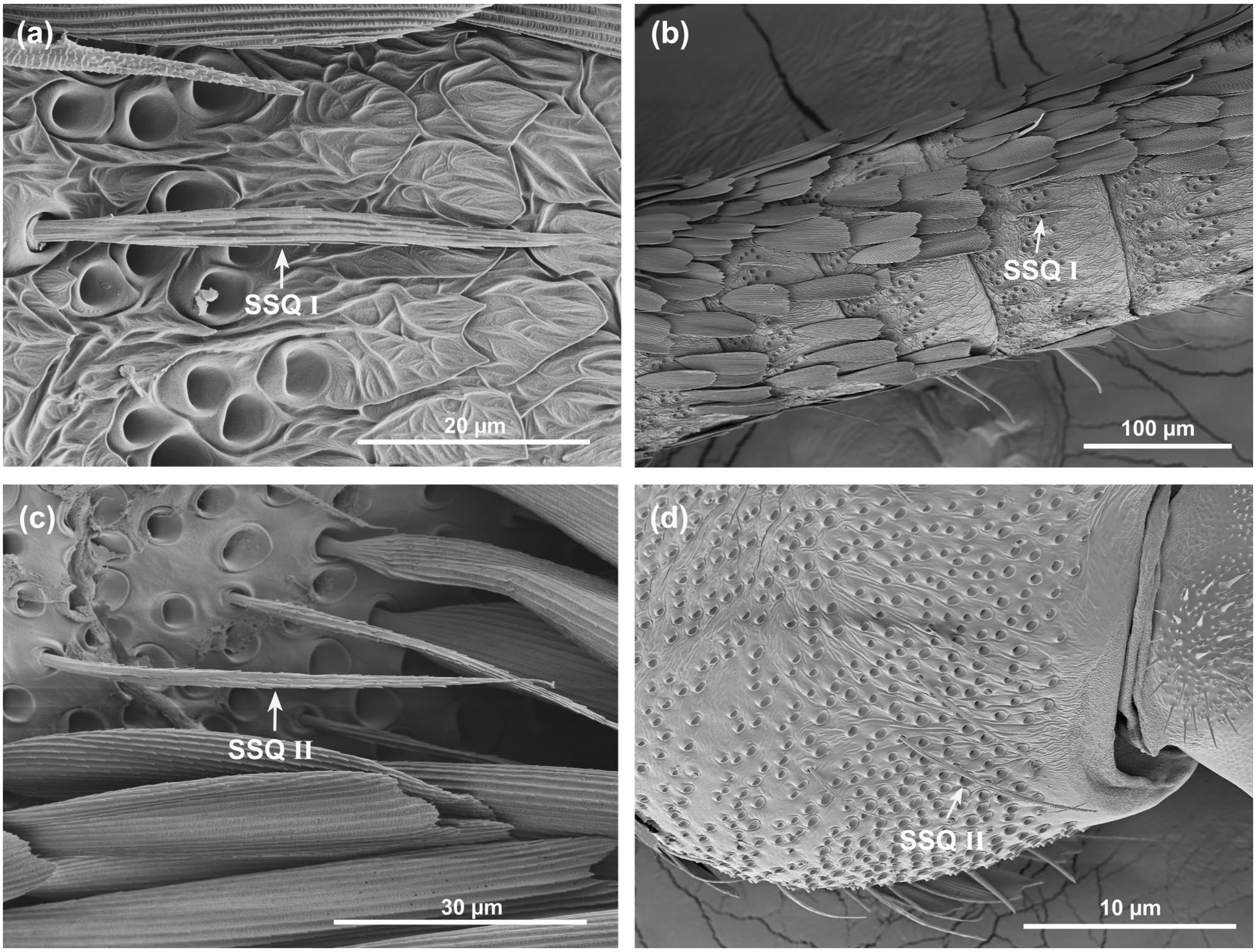

Fig. 9 Scanning electron micrographs of sensilla squamiformia of *Spodoptera litura*: **a** morphological characteristics of sensilla squamiformia I, **b** distribution and overall appearance of sensilla squamiformia I, **c** morphological characteristics of sensilla squamiformia II and **d** distribution and overall appearance of sensilla squamiformia II. *SSQ I* sensilla squamiformia I and *SSQ II* sensilla squamiformia II

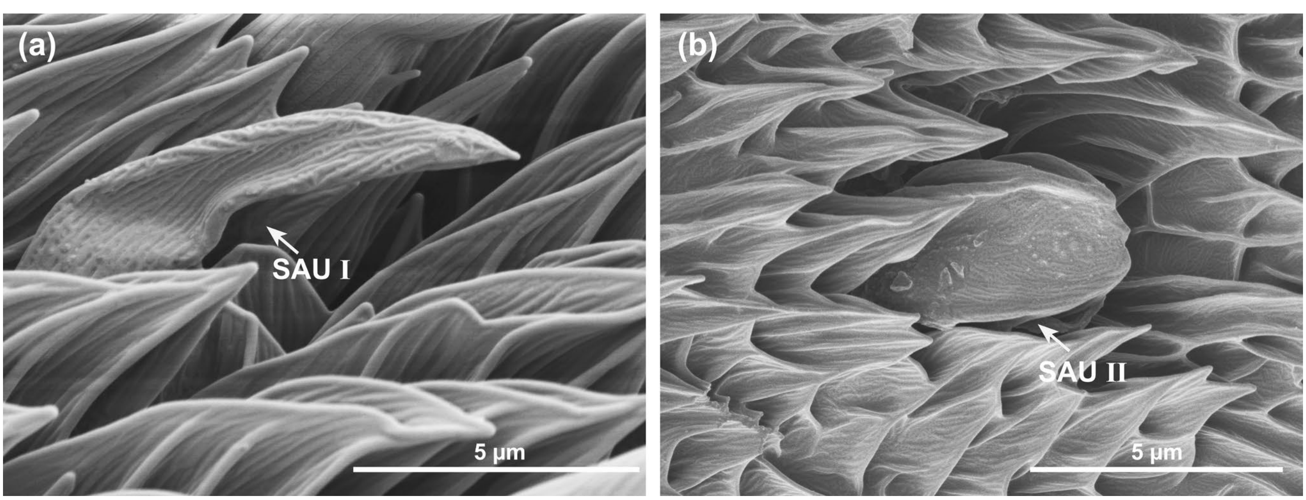

Fig. 10 Scanning electron micrographs of sensilla auricillica of *Spodoptera litura*: **a** morphological characteristics of sensilla auricillica I and **b** morphological characteristics of sensilla auricillica II. *SAU I* sensilla auricillica I and *SAU II* sensilla auricillica II

were scattered sparsely on the ventral side of the sensilla (Fig. 10a; Table 2).

Sensilla auricillica II

Sensilla auricillica II (SAU II) showed obvious differences in morphology and distribution from SAU I (Fig. 10; Table 2). The SAU II had an overall tongue-like shape, with its tip being only slightly narrower than its central region, and having 3 small protrusions at the tip (Fig. 10b). SAU II had some longitudinal ridges on their surface but they were not as prominent as on SAU I (Fig. 10b). SAU II were present in all subsegments of the flagellum, near the junction of the ventral and lateral surfaces, and usually with 1–4 SAU II being found in each subsegment. Average SAU II length did not differ significantly between the sexes ($t = 0.57$, df $= 58$, $p = 0.569$) (Table 3).

Discussion

Antennal sensilla are important sensory organs for insects, allowing them to receive and perceive external information, locate host plants, avoid predators, and seek mates (Schneider 1964; Chapman 1982; Nation 2001). The needs of insects to perceive these various types of external information promoted the evolution of the complex variety of insect antennal sensilla types (Schneider 1964; Chapman 1982; Li et al. 2024). Identifying the types of the antennal sensilla on a given insect facilitates our understanding of the mechanisms by which an insect can sense environmental stimuli, as well as possibly contributing to the development of innovative odor attractants, which can be used in insect pest control (Malo et al. 2004; Ansebo et al. 2005).

Prior to the present study, six types of the antennal sensilla had been recorded in *Spodoptera litura*, namely sensilla trichodea, sensilla basiconica, sensilla chaetica, sensilla coeloconica, sensilla styloconica, and sensilla auricillica (Liu et al. 2009; Aruna et al. 2019). In the current study, we identified a total of eight antennal sensilla and two subtypes, of which sensilla squamiformia II, and sensilla auricillica II were recorded for the first time.

From an evolutionary perspective, the types of antennal sensilla present on a given insect species are often similar, but not necessarily the same, as those found on closely related species (Schneider 1964). Our study focused on *S. litura* that were originally collected in Yunnan, China. We assume that sensilla morphology is highly stable across the geographic range of an insect. Meanwhile, in the current study, larvae were reared under uniform conditions, and antennae were taken from newly emerged 1–2-day-old adults. In this way, the study may minimize the effects of larval diets, adult age, and mating status on the morphology of antennal sensilla, if any.

In the moth family Noctuidae, nine types of antennal sensilla have been recorded to date: Böhm's bristles, sensilla trichodea, sensilla chaetica, sensilla coeloconica, sensilla styloconica, sensilla squamiformia, sensilla auricillica, sensilla basiconica, and uniporous peg sensilla. These types of antennal sensilla have been observed in *Athetis lepigone* (Noctuidae) (Hu et al. 2021), *Copitarsia consueta* (Noctuidae) (Castrejón-Gómez et al. 1999), *Helicoverpa armigera* (Noctuidae) (Rani et al. 2021a), *H. assulta* (Noctuidae) (Koh et al. 1995), *Mythimna separata* (Noctuidae) (Chang et al. 2015), *Noctua pronuba* (Faucheux 1990), and *S. frugiperda* (Noctuidae) (Malo et al. 2004; Li et al. 2024) and *S. littoralis* (Seada 2015). The antennal sensilla recorded in the current study were shared with many of the above noctuids, except for sensilla squamiformia II and sensilla auricillica II. This similarity in the antennal sensilla types among several Noctuidae moths indicates a common evolutionary origin and similar requirements for receiving and perceiving external information.

The sensilla and scales are the most obvious features on the antennal surface in *S. litura*. The antennal sensilla are primarily distributed on the ventral side of the flagellum, with the scales being the most widespread and abundant non-sensory structures present, being found on the scape, pedicel, and dorsal side of the flagellum. This distribution pattern of sensilla and scales in the antenna of *S. litura* is consistent with many other Noctuidae (Faucheux 1990; Koh et al. 1995; Chang et al. 2015; Roh et al. 2016; Yang et al. 2017; Zhang et al. 2019; Hu et al. 2021; Rani et al. 2021a). Koh et al. (1995) proposed that the arrangement of scales helps prevent mechanical damage to the antenna and the antennal sensilla. Others have suggested that the scales help capture and concentrate odors, thus enhancing the insect's ability to perceive and accurately locate the odor (Van der Pers et al. 1980; Faucheux 1990; Castrejón-Gómez et al. 1999).

In terms of function, the antennal sensilla of *S. litura* can be classified into three categories: mechanical sensilla, chemical sensilla, and temperature and humidity sensilla. Both Böhm's bristles and sensilla squamiformia are considered mechanical sensilla, responsible for detecting mechanical stimuli derived from the external environment (Schneider 1964; Kristensen 2003). Böhm's bristles are mainly found on the intersegmental membranes between the scape and pedicel, allowing for adjustment in antenna orientation (Schneider 1964; Koh et al. 1995; Castrejón-Gómez et al. 1999). Böhm's bristles are considered proprioceptors by some researchers (Faucheux 1999), mainly found on the intersegmental membranes between the scape and pedicel, allowing for the orientation of the antenna to be adjusted (Schneider 1964; Koh et al. 1995; Castrejón-Gómez et al.

1999). Numerous microtrichia were also observed around Böhm's bristles (Fig. 4b) and are generally considered to have no sensory function (Hu et al. 2021; Rani et al. 2021a).

Sensilla squamiformia, another mechanical sensilla, has been widely recorded in species of Noctuidae, such as *A. lepigone* (Hu et al. 2021), *H. armigera* (Rani et al. 2021a), *M. separata* (Chang et al. 2015), *N. pronuba* (Faucheux 1990), *S. frugiperda* (Malo et al. 2004; Li et al. 2024) and *S. littoralis* (Seada 2015). Because sensilla squamiformia are in sockets with no surface pores, some researchers suggested that these sensilla may sense air vibrations rather than perceive chemical molecules (Steinbrecht 1997; Bawin et al. 2017). Sensilla squamiformia I and sensilla squamiformia II were similar in shape but were significantly different in size in the present study. Considering that sensilla squamiformia I and II were located on different parts of the antenna (Table 2; Fig. 9b, d), we classified sensilla squamiformia II as a separate subtype of sensilla squamiformia.

The chemosensory antennal sensilla identified in *S. litura* include sensilla trichodea, sensilla basiconica, sensilla chaetica, sensilla coeloconica, and sensilla auricillica. Pores on the surface of the antennal sensilla are the key feature that defines these sensilla as having a chemosensory function, given that they serve as channels for external chemicals to enter and interact with internal sensory receptors (Schneider 1964; Zacharuk 1980).

Sensilla trichodea are one of the most common antennal sensilla types found in Lepidoptera (Faucheux 1999; Malo et al. 2004; Seada 2015; Roh et al. 2016; Zhang et al. 2019; Rani et al. 2021b). Sensilla trichodea can perceive sex pheromones and plant odors, indicating that these sensilla are essential for insects to locate mates and their host plants (Faucheux 1999; Seada 2015; Roh et al. 2016; Yang et al. 2017; Zhang et al. 2019; Rani et al. 2021a). Pores on the surface of sensilla trichodea have been recorded in several moths species such as *Cydia pomonella* (Tortricidae) (Roh et al. 2016), C. *succedana* (Tortricidae) (Roh et al. 2016), *Diaphania angustalis* (Crambidae) (Zhang et al. 2019), *Dioryctria rubella* (Pyralidae) (Xu et al. 2021), *H. armigera* (Rani et al. 2021a), *M. separata* (Chang et al. 2015), *N. pronuba* (Faucheux 1990) and *S. littoralis* (Seada 2015). In our study, numerous pores were observed on the surface of sensilla trichodea (Fig. 5c), indicating that they likely serve as chemosensory organs.

Sensilla basiconica have been recorded in almost all Lepidoptera with filiform antennae, and their distribution pattern on the antennal surface is generally the same in all Noctuidae studied to date (Liu and Liu 1984; Faucheux 1990; Chang et al. 2015; Rani et al. 2021a). The surface of sensilla basiconica is characterized by numerous small pores and grooves, suggesting that these sensilla have an olfactory function such as pheromone and plant odor detection (Liu and Liu 1984; Faucheux 1999; Chang et al. 2015; Zhang et al. 2019; Rani et al. 2021a). Koh et al. (1995) reported that the sensilla basiconica of *H. assulta* are porous, fluted, and thin-walled, and have a role in odor detection.

Sensilla chaetica are very common in the antennae of the noctuid moths, being found in each subsegment of the flagellum (Faucheux 1990; Malo et al. 2004; Seada 2015; Hu et al. 2021). These sensilla had the widest distribution on the antennae of *S. litura* compared to the others types found, being present on the dorsal, lateral and ventral sides of the flagellum. In some studies, sensilla chaetica are referred to as central chaetica, lateral chaetica, and dorsal chaetica according to their locations on the surface of the flagellum (Malo et al. 2004; Gargi et al. 2022; Li et al. 2024). This naming method was adopted in our study. The size, shape and distribution of sensilla chaetica are similar among all Noctuidae studied to date, suggesting they have a similar perception function among species (Faucheux 1990, 1999; Chang et al. 2015; Yuan et al. 2017; Hu et al. 2021; Rani et al. 2021b). In several studies of Lepidoptera, sensilla chaetica have been the longest of all sensilla detected (Faucheux 1991, 1999; Chang et al. 2015; Rani et al. 2021a, b; Li et al. 2024). Some authors have proposed that sensilla chaetica help protect other sensilla on the same antenna (Faucheux 1991, 1999; Chang et al. 2015; Rani et al. 2021a), while others have suggested that they may have a taste function (Popescu et al. 2013; Seada 2015; Bawin et al. 2017; Li et al. 2024). The presence of terminal pores in *N. pronuba* (Faucheux 1990) and *S. litura* (this paper) characterizes gustative sensilla (Zacharuk 1980).

Sensilla coeloconica exhibit a distinctive morphology among the many types of antennal sensilla of Lepidoptera, characterized by a central cone surrounded by numerous spines (Flower and Helson 1974; Faucheux 1999; Bawin et al. 2017; Rani et al. 2021a). Sensilla coeloconica have been mostly found on the ventral surface of the flagellum, but their number and shape vary among moth species (Malo et al. 2004; Chang et al. 2015; Seada 2015; Rani et al. 2021b). For example, sensilla coeloconica of *S. frugiperda* have a distinct petal-like structure that encloses the sensilla in a cavity, and the upper part of the spines bends more inward to form a distinct dome-like structure (Li et al. 2024). Many authors have suggested that the surrounding spines serve to protect the central cone from mechanical damage (Yang et al. 2009; Rani et al. 2021a). In addition, Binyameen et al. (2012) suggested that sensilla coeloconica have an olfactory function in *S. littoralis*. Moreover, in several recent studies, sensilla coeloconica were considered multifunctional, i.e., capable of perceiving temperature, humidity, water vapor, pheromones, and plant odors (Seada 2015; Yang et al. 2017; Zhang et al. 2019; Rani et al. 2021a, b).

Sensilla auricillica have been widely reported in Lepidoptera (reviewed in Faucheux 1990), including *Earias vittella* (Nolidae) (Rani et al. 2021b), *Athetis lepigone* (Hu et al. 2021), *Cydia succedana* (Tortricidae) (Roh et al. 2016), and *S. frugiperda* (Li et al. 2024). Two subtypes of sensilla auricillica were observed in our study of *S. litura*. These two subtypes have been also recorded in the tortricids *C. pomonella* and *C. succedana* (Roh et al. 2016). Sensilla auricillica are porous sensilla and considered involved in detection of host volatiles and pheromones (Faucheux 2006). Hu et al. (2021) also proposed that sensilla auricillica had an olfactory function in *A. lepigone*. Electrophysiological studies have demonstrated that sensilla auricillica of the tortricid *C. pomonella* can respond to phytochemicals and sex pheromones (Ansebo et al. 2005).

Sensilla styloconica are commonly found on the filiform antennae of Lepidoptera (Faucheux 1999; Koh et al. 1995; Castrejón-Gómez et al. 1999; Malo et al. 2004; Chang et al. 2015; Seada 2015; Aruna et al. 2019; Rani et al. 2021a; Li et al. 2024). Sensilla styloconica have usually been found on the ventral distal portion of each subsegment of the flagellum. Overall, the number, morphological characteristics and distribution of sensilla styloconica are similar in the Noctuidae (Faucheux 1990; Castrejón-Gómez et al. 1999; Malo et al. 2004; Chang et al. 2015; Seada 2015; Aruna et al. 2019; Rani et al. 2021a; Gargi et al. 2022; Li et al. 2024). The blunt protrusions at the tip of sensilla styloconica are a distinguishing feature of this sensilla type. The number of blunt protrusions in *S. litura* varied from one to three in our study, which was also consistent with the report by Aruna et al. (2019). A similar pattern has been reported in other Noctuidae (Faucheux 1999; Koh et al. 1995; Castrejón-Gómez et al. 1999; Malo et al. 2004; Chang et al. 2015; Hu et al. 2021; Rani et al. 2021a, Li et al. 2024). Based on the number of the blunt protrusions Rani et al. (2021a), Zheng et al. (2014), classified these sensilla into two subtypes, but others have not used the number of blunt protrusions as a morphological feature to assign subtype classification (Faucheux 1990, 1999; Koh et al. 1995; Castrejón-Gómez et al. 1999; Malo et al. 2004; Galizia and Rössler 2010; Zheng et al. 2014; Chang et al. 2015; Seada 2015; Aruna et al. 2019; Hu et al. 2021; Rani et al. 2021a; Li et al. 2024). Although we noted variation in the number of blunt protrusions in the present study, we did not classify sensilla styloconica into subtypes.

Sensilla styloconica on antennae are categorized as humidity and temperature sensing sensilla, given that no pores are generally observed on their surface (Faucheux 1999; Roh et al. 2016; Yang et al. 2017; Rani et al. 2021b). In our study of *S. litura*, pores were observed to be irregularly distributed on the surface of the stylus of sensilla styloconica (Fig. 8d). However, we are not certain if they are sensory pores. In general, on the antennae of Lepidoptera, sensilla styloconica are always aporous sensilla, whereas on the proboscis of Lepidoptera, sensilla styloconica are uniporous sensilla (having a terminal pore) with a gustative function (Faucheux 1999).

Our study documented some differences in the size of antennal sensilla between male and female *S. litura*. Generally, except for the SSQ II, SAU I and SAU II, both the mechanosensilla and chemosensilla on males were either longer in the length (as SSQ I), or wider in the basal diameter (as SB, CSC, DSC, and SCO), or both longer in the length and wider in the basal diameter (as SB and LSC) than those on females; while temperature and humidity sensilla (SS) did not differ between sexes. Similarly, for other Noctuidae, the number and size of chemosensitive sensilla on antennae of males were generally larger than those on females (Castrejón-Gómez 1999; Hu et al. 2021; Li et al. 2024). This size difference in male and female sensilla may reflect differences in the size of male and female antennae, given that the antennae of males are generally larger than those of females.

Conclusion

Our study demonstrated that *Spodoptera litura* possess eight types and two subtypes of the antennal sensilla: Böhm's bristles, sensilla trichodea, sensilla basiconica, sensilla chaetica, sensilla coeloconica, sensilla styloconica, sensilla squamiformia (I and II), and sensilla auricillica (I and II). Sensilla squamiformia II and sensilla auricillica II were reported for the first time. Detailed low-voltage field emission scanning electron microscope images and descriptions were provided for each sensillum type. This study provided the morphological information to aid in future neurophysiological testing of the antennal sensilla of *S. litura*.

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Data availability All data are presented in this study. Raw images or raw data of all taken measurments can be made available upon reasonable request to the corresponding author.

Declarations

Conflict of interest The authors declare no competing interests.

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