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RESEARCH ARTICLE

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

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Abstract

The fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae), is a globally significant agricultural pest, causing severe damage to corn production in China. Chemical odor-based trapping is a major approach for FAW control, making it essential to understand the FAW antennal sensillum types to enhance development of effective chemical odor attractants. In this study, we comprehensively examined the antennal sensilla types of FAW, identifying eight types and two subtypes, including Böhm's bristles, sensilla trichoidea, sensilla chaetica (I and II), sensilla coeloconica, sensilla styloconica, sensilla squamiformia (I and II), sensilla auricillica, and sensilla basiconica. Sensilla chaetica II, and sensilla squamiformia II are reported for the first time for FAW in this study. Detailed low-voltage field emission scanning electron microscope (LVSEM) images and descriptions are provided for each sensillum type. This study provides the morphological information to aid in conducting antennal sensillum neurophysiological tests on FAW.

Research Highlights

- The types of sensilla of fall armyworm were examined, identifying eight types and two subtypes, including Böhm's bristles, sensilla trichoidea, sensilla chaetica (I and II), sensilla coeloconica, sensilla styloconica, sensilla squamiformia (I and II), sensilla auricillica, and sensilla basiconica.
- Detailed low-voltage field emission scanning electron microscope images and descriptions were provided for each sensillum type.

KEYWORDS

antennal sensilla, scanning electron microscopy, sensilla morphological characteristics, *Spodoptera frugiperda*

1 | INTRODUCTION

The fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae), is a significant migratory pest of global concern (FAO, 2018, 2020; Overton et al., 2021). This insect is native to the Americas, and was recently reported as established in Africa (Goergen et al., 2016), and Asia (Sharanabasappa et al., 2018). FAW is currently distributed in over 80 countries in the Americas, Africa, Asia, and Oceania (Goergen et al., 2016; Sharanabasappa et al., 2018; Sun et al., 2021; Wu et al., 2021). In January 2019, FAW was found in southwestern China, apparently having migrated from Myanmar, and rapidly expanded its range to 26 Chinese provinces or autonomous

TABLE 1 Antennal sensilla of the *Spodoptera frugiperda* reported in the literature.

Sensilla type and code	Country where reported[a]	Presumed major role	Morphological traits	References[b]
Böhm bristles, BB	CN IN	Mechanoreception	Aporous, socket	1, 2, 4, 5
Sensilla trichoidea, ST	CN EG IN MX	Chemoreception	Multiporous, socket	1, 2, 3, 4, 5, 6
Sensilla chaetica, SCh	CN EG IN MX	Chemo- and mechano-reception	Uniporous, socket	1, 2, 3, 4, 5, 6
Sensilla coeloconica, SCO	CN EG IN MX	Chemo-, thermo- and hygro-reception	Multiparous, socket	1, 2, 3, 4, 5, 6
Sensilla styloconica, SS	CN EG IN MX	Thermo- and hygro-reception	Aporous, no socket[c]	1, 2, 3, 4, 5, 6
Sensilla auricillica, SAU	CN EG IN MX	Chemoreception	Multiporous, socket	1, 3, 4, 5, 6
Sensilla basiconica, SB	CN EG IN MX	Chemoreception	Multiporous, no socket	1, 2, 3, 4, 5, 6
Sensilla squamiformia, SSQ	CN EG IN MX	Mechanoreception	Aporous, socket	1, 2, 3, 4, 5, 6
Sensilla gemmiformium, SG	CN	Unknown	Aporous, no socket	4
Sensilla ampullaces, SAM	CN	Unknown	Socket	4
Sensilla cavitata-peg, SCP	CN	Unknown	Socket	4
Sensilla cavity, SCa	CN	Chemoreception	Aporous, socket	5
Sensilla placodea, SPl	CN	Chemoreception	Uniporous, socket	5
Sensilla ligulate, SL	CN	Unknown	Multiparous, socket	5
Sensilla uniporous peg, SU	CN	Thermo-, hygro- and co_2 reception	Uniporous, socket	5

[a]Country codes: CN = China, EG = Egypt, IN = India, and MX = Mexico.
[b]References: 1 = Gargi et al., 2022; 2 = Lei et al., 2021; 3 = Malo, Castrejón-Gómez, et al., 2004; 4 = Tian et al., 2021; 5 = Wang et al., 2023, and 6 = Zahran et al., 2023.
[c]No socket = no apparent socket visible. The term socket is used in reference to the connection site between the sensilla and the antenna (Figure 8a). However, some sensilla are connected to the antenna with no apparent socket (Figure 7d), for which we and other (Guo et al., 2022; Koh et al., 1995; Malo, Castrejón-Gómez, et al., 2004; Seada, 2015) use the term "no socket".

regions, resulting in approximately 1 million hectares of corn being damaged that same year (Wu, 2020). FAW has now become one of the most severe corn pests in China, posing a major challenge to China's corn production (Wu, 2020; Ye et al., 2022; Zhou et al., 2021).

Odor-based trapping is currently the main method used to monitor FAW in China (He et al., 2019; Qu et al., 2022; Yin et al., 2020). This method is environmentally friendly and has shown significant capture efficacy (Cruz et al., 2012; Kumar et al., 2022; Qu et al., 2022). However, current commercial attractants only capture male moths, and therefore females are left in the fields where they can continue to reproduce (Malo, Bahena, et al., 2004; Tepa-Yotto et al., 2022; Tumlinson et al., 1986). Clearly, further improvements are needed in the trapping methods used for FAW (Tabata et al., 2023).

The antennal sensilla are the fundamental sensing organs for insects, which allow them to receive and perceive external odor substances, and therefore an understanding of sensilla is important when developing odor attractants (Galizia & Rössler, 2010; Schmidt & Benton, 2020; Schneider, 1964; Zacharuk, 1980). The typical FAW antenna is filiform, consisting of three main segments: the scape, pedicel and flagellum. To date, 15 types of antennal sensilla have been recorded in FAW based on research conducted in four countries (Table 1). This number of sensilla types far exceeds what has been reported for other species of Noctuidae moths (Hu et al., 2021; Koh et al., 1995; Kristensen, 2004; Seada, 2015; Zhang et al., 2019). Studies on FAW antennal sensilla date back to 2004; when Malo, Castrejón-Gómez, et al. (2004) documented seven types of antennal sensilla in FAW, namely: trichoidea, chaetica, coeloconica, styloconica, auricillica, basiconica, and squamiformia. Later, Lei et al. (2021) recorded six types of antennal sensilla in FAW, five of which had been reported by Malo, Castrejón-Gómez, et al. (2004), but with the Böhm bristles being new. In addition, Tian et al. (2021) proposed 11 types of antennal sensilla in FAW, among which, seven matched those reported by Malo, Castrejón-Gómez, et al. (2004), seven agreed with Lei et al. (2021), and three were new: sensilla ampullaces (SAM), sensilla cavitata-peg (SCP), and sensilla gemmiformium (SG). In the report by Gargi et al. (2022), eight types of sensilla were listed, with seven matching those reported by Lei et al. (2021), and the other (sensilla auricillica) having been recorded earlier by Malo, Castrejón-Gómez, et al. (2004). More recently, Wang et al. (2023) recorded 13 types of antennal sensilla in FAW, including four new types: sensilla cavity, sensilla placodea, sensilla ligulate, and sensilla uniporous peg. In another recent report, Zahran et al. (2023) documented seven types of antennal sensilla in FAW, all of which had been previously reported.

In terms of the 15 sensor types mentioned above, six (trichoidea, chaetica, coeloconica, styloconica, squamiformia, and basiconica) have been reported in other species of Noctuidae (Kristensen, 2004). Of the remaining nine sensor types, sensilla auricillica have been reported in five FAW studies, Böhm bristles in four FAW studies, but for each of the remaining seven sensor types, they were only reported once each (Gargi et al., 2022; Lei et al., 2021; Malo, Castrejón-Gómez, et al., 2004; Tian et al., 2021; Wang et al., 2023; Zahran et al., 2023). These studies demonstrate that the antennal sensilla of FAW have received great scientific attention, reflecting the current situation where FAW has become a global pest. In the study by Zahran et al. (2023), antennal sensilla were similar between male and female FAW, except for styloconica, which were only found on males. Given such variation in terms of the number and types of sensors found in FAW, we attempted to clarify the situation by using advanced low-voltage field emission scanning electron microscopy (LVSEM) of both male and female FAW. Our main objective was to use LVSEM to confirm the presence of each sensor type, provide details on their morphology and distribution, and compare the sensilla found between male and female FAW. We hope that this research will lead to the development of improved FAW odor attractants.

2 | MATERIALS AND METHODS

2.1 | Insects

Newly emerged 1–2-day-old FAW adults were used for SEM observations. FAW adults were reared in the Insect Laboratory of Yunnan University that had been originally collected from corn fields near the Yunnan University campus in Kunming, China. The rearing conditions were set at a temperature of 26 ± 1°C, relative humidity of 65% ± 5%, and a light cycle of L12 h: D12 h. Larvae were fed with an artificial diet, which was based on the formula described by Li et al. (2023). Adult moths were provided with a diet of 5% honey water to meet their nutritional needs.

2.2 | Scanning electron microscopy

The antennae used for SEM observation were dissected from the head of male and female FAW adults under a stereomicroscope (Nikon SMZ1500, Nikon Instrument, Japan), then soaked in a 75% ethanol solution and subjected to ultrasonic cleaning for 30s to remove surface contaminants. Afterwards, the antennae were rinsed with n-hexane for cleaning, with the process being 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 onto 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× to 60,000×.

2.3 | Terminology, measurements and statistical analysis

The classification and types of sensilla identified were conducted based on the external morphology, surface features according to Schneider (1964) and Zacharuk (1980). Measurements were taken for both intact male and female antennae, including total length, basal diameter, and the number of subsegments, with 30 replicates for each sex. The measured 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 ± standard error (SE). Each type of sensilla, including Böhm's bristles, sensilla trichoidea, sensilla chaetica, sensilla coeloconica, sensilla styloconica, and sensilla squamiformia, were measured with 30 replicates for both males and females. Sensilla auricillica and sensilla basiconica, being very small and distributed beneath sensilla trichoidea, were challenging to locate, and thus sensilla auricillica were measured with four replicates and sensilla basiconica with three replicates.

Data analysis was conducted using SPSS 26.0 software (IBM). Differences in sensilla size between FAW males and females were statistically analyzed using Student's *t*-test, with an alpha level of $p < .05$. Microscopic and electron microscopic images photos of antennal sensilla were processed using Adobe Photoshop CC 2017 software (Adobe Systems).

3 | RESULTS

3.1 | The basic morphology of the antennae

The antennae of FAW were filamentous and composed of three segments: a scape, a pedicel, and a flagellum (Figure 1). The scape segment was connected to the head and was covered by scales (Figure 2b). The average length ($t = 2.43$, df = 58, $p = .018$) and diameter ($t = 2.18$, df = 58, $p = .033$) of the scape segment were significantly greater in males (length = 337.08 ± 5.35 μm; basal diameter = 282.49 ± 6.01 μm) than those in females (318.91 ± 5.22 μm; 262.94 ± 6.59 μm).

The pedicel, located between the scape and the flagellum, was densely covered with scales (Figure 2b). The average length ($t = 0.79$,

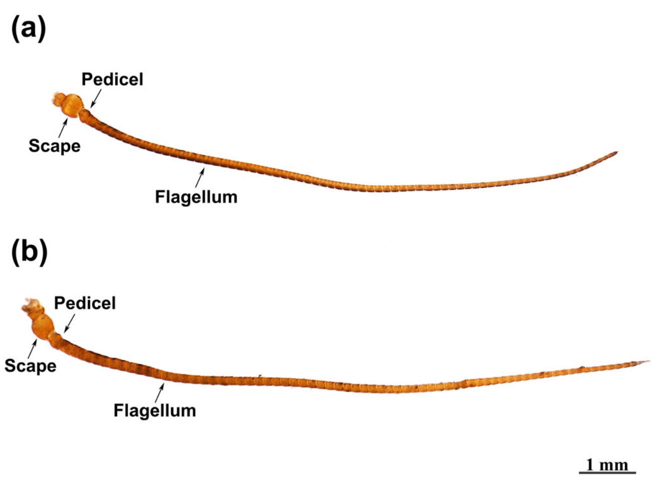

FIGURE 1 Typical appearance of the antenna from a *Spodoptera frugiperda* adult. (a) female and (b) male.

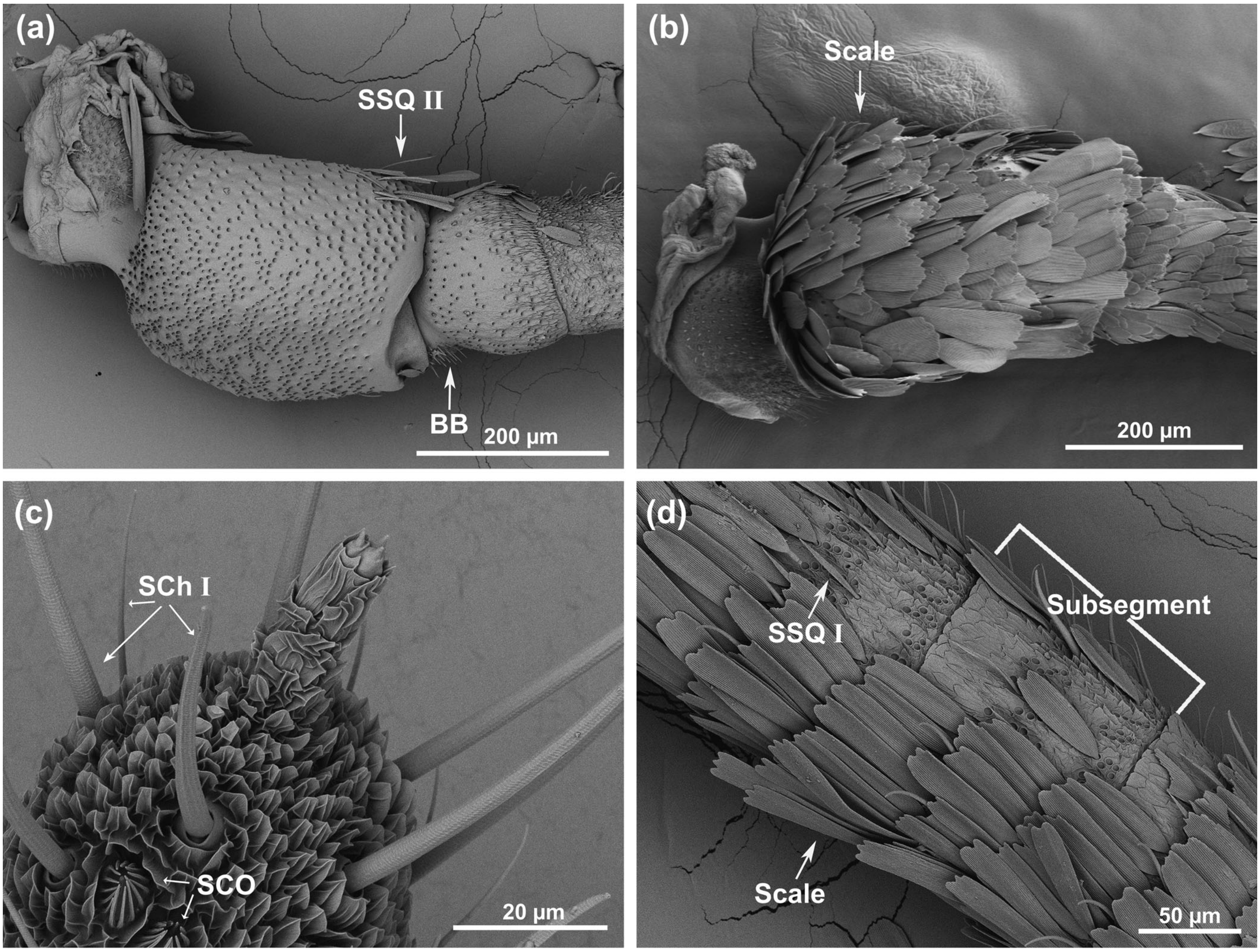

FIGURE 2 Scanning electron micrographs of the antennal pedicel, scape and flagellum of *Spodoptera frugiperda*. (a) The scape and pedicel after removing scales, (b) the scape and scape with scales present, (c) the tip of the flagellum, and (d) scale arrangement on flagellum subsegments. BB, Böhm bris-tles; SCh I, Sensilla chaetica I; SCO, Sensilla coeloconica; SSQ I, Sensilla squamiformia I; SSQ II: Sensilla squamiformia II.

df = 58, p = .430) and basal diameter (t = 0.27, df = 58, p = .786) of the pedicel segment were not significantly different between males (length = 143.02 ± 3.39 μm, basal diameter = 184.31 ± 5.20 μm) and females (length = 139.14 ± 3.50 μm, basal diameter = 182.42 ± 4.59 μm).

The flagellum was composed of several subsegments, with a variable number of subsegments. In females, the flagellum consisted of 68.90 ± 1.01 subsegments (n = 20) on average, while in males, it was composed of 72.35 ± 0.66 subsegments (n = 20). At the end of the flagellum, there was a conical structure covered by petal-like folds, and the tip was adorned with two or three small cones (Figure 2c). The average length of the flagellum was 8.56 ± 0.21 mm in females and 9.07 ± 0.09 mm in males, with a significant difference between the two sexes (t = 2.23, df = 38, p = .035).

Scales were the most prominent structures covering the surface of the flagellum and were distributed along the dorsal side, 60% of the total antennal surface area, based on visual approximation (Figure 2d). Each subsegment had two rows of scales with an overlapping tile arrangement, where the scales of the preceding subsegment covered the base of the next subsegment. The shape of the scales is depicted in Figure 2b,d, showing parallel vertical ridges on their surface. The average length of scales did not vary between the sexes (t = 0.84, df = 58, p = 0.407), being 65.90 ± 1.47 μm in females and 68.07 ± 2.16 μm in males. However, this difference was not statistically significant.

3.2 | Types of antennal sensilla

Our study identified eight types of antennal sensilla and two subtypes, namely: Böhm bristles, sensilla trichoidea, sensilla chaetica I and II (SCh I and SCh II), sensilla coeloconica (SCO), sensilla styloconica (SS), sensilla squamiformia I and II (SSQ I and SSQ II), sensilla auricillica (SAU), and sensilla basiconica (SB).

3.2.1 | Böhm bristles

Böhm bristles (BB) were exclusively present on the scape and pedicel (Figure 3a). BB were densely and uniformly distributed on the surface

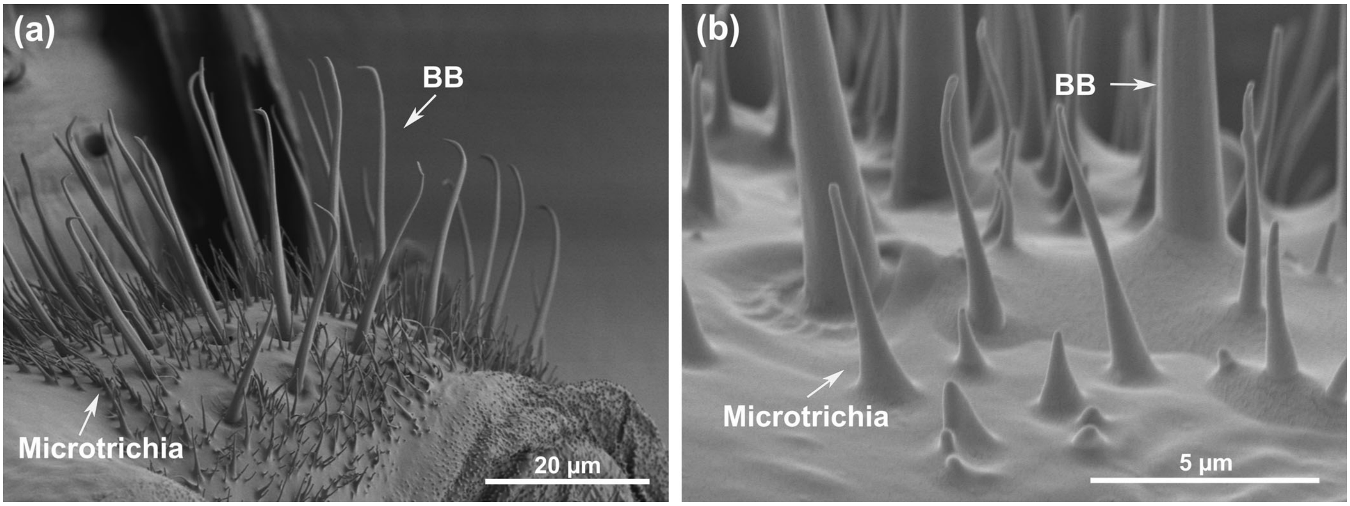

FIGURE 3 Morphological characteristics and distribution of Böhm bristles of *Spodoptera frugiperda*. (a) BB, Böhm bristles, and microtrichia (b) the details about BB and microtrichia.

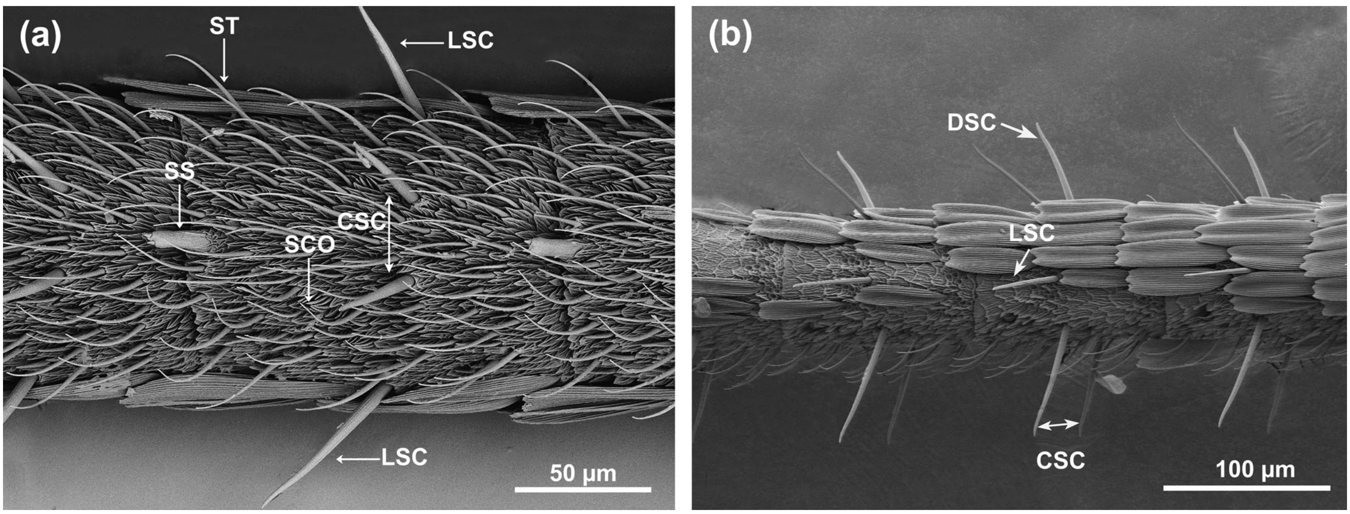

FIGURE 4 Morphological characteristics and distribution of various sensilla of the flagellum of *Spodoptera frugiperda*. (a) On the ventral side, (b) on the lateral side. CSC, central sensilla chaetica; DSC, dorsal sensilla chaetica; LSC, lateral sensilla chaetica; SCO, Sensilla coeloconica; SS, Sensilla styloconica; ST, Sensilla trichoidea.

of the scape and form a ring-like arrangement at the distal end of the pedicel (Figure 3b). BB arise from a socket-like depression, with an average basal diameter of 1.81 ± 0.05 μm in females and 1.85 ± 0.07 μm in males ($t = 0.52$, df = 58, $p = .604$). BB gradually taper from the base to the tip, ending in a sharp and curved point, with a smooth surface. The average length of BB was significantly different between females and males, measuring 15.66 ± 0.37 μm and 18.78 ± 0.61 μm, respectively ($t = 4.38$, df = 58, $p < .001$).

Numerous microtrichia were observed around BB (Figure 3a,b) and were exclusively located on the scape and pedicel. These microtrichia appeared to lack a socket-like depression, and they were rather short and slender with a relatively rounded and blunt tip. The average basal diameter was 0.91 ± 0.03 μm in females and 0.95 ± 0.04 μm in males ($t = 0.91$, df = 58, $p = .366$), while their length measured on average 6.37 ± 0.25 μm in females and 7.01 ± 0.21 μm in males ($t = 1.97$, df = 58, $p = .055$).

3.2.2 | Sensilla trichoidea

Sensilla trichoidea were the most abundant sensory structures on the antennae of FAW, comprising approximately 89% of the total sensilla count. They were primarily located on the ventral side of the flagellum (Figures 4a, 5a). The average basal diameter of sensilla trichoidea was 2.54 ± 0.06 μm in females and 2.64 ± 0.05 μm in males ($t = 1.33$, df = 58, p =0 .188). These sensilla gradually tapered from the base to the tip, with a rounded and blunt apex. The surface of sensilla trichoidea exhibited two types of ridges: longitudinal ridges at the base and helical ridges that spiral upwards to cover about one-third of the flagellum length towards the tip (Figure 5a). The average length of sensilla trichoidea was 32.78 ± 0.27 μm in females and 33.12 ± 0.34 μm in males, with no significant difference between the sexes ($t = 0.79$, df = 58, $p = 0.434$).

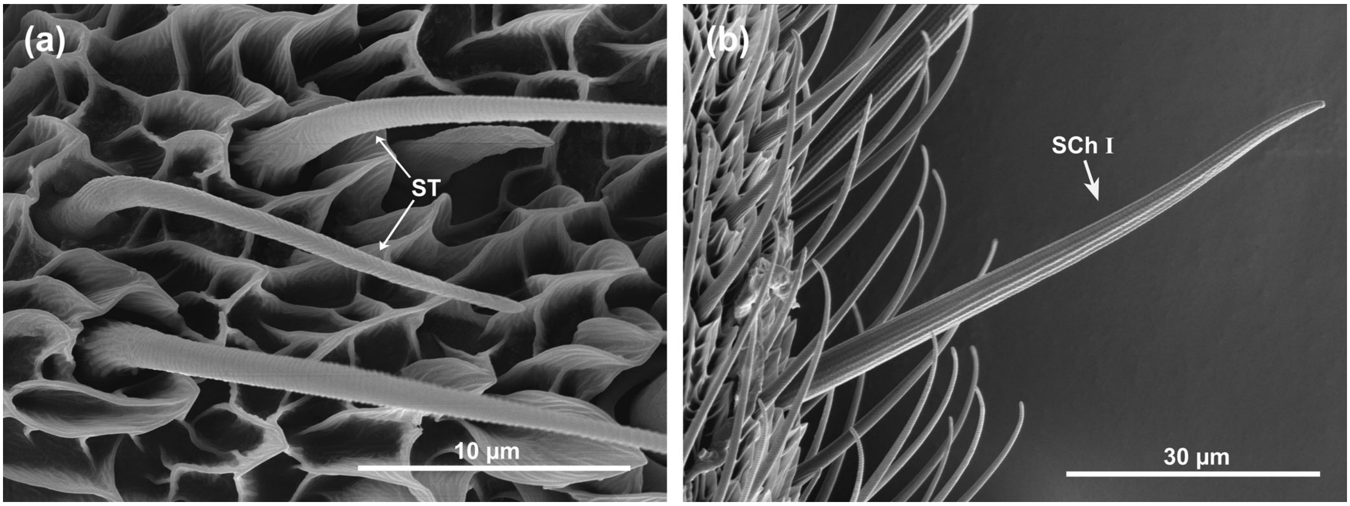

FIGURE 5 Morphological characteristics of two sensilla of *Spodoptera frugiperda*. (a) Overall appearance and basal structure of sensilla trichoidea, (b) the morphological characteristics of sensilla chaetica I. SCh I, Sensilla chaetica I; ST, Sensilla trichoidea.

3.2.3 | Sensilla chaetica I

Sensilla chaetica type I (SCh I) was a subtype of sensilla chaetica and was distributed around the subsegments of the flagellum, with five or six sensilla per subsegment (Figure 4, 5b). SCh I resembled an upright spine, with its base arising from a ridge-like elevation on the edge of a socket-like depression, tapering slightly towards the tip, which was blunt and rounded (Figure 5b). Based on their location on each subsegment, SCh I can be classified into lateral sensilla chaetica (LSC), central sensilla chaetica (CSC), and dorsal sensilla chaetica (DSC) (Figure 4a,b). These three types varied slightly in size. The average length of lateral sensilla chaetica was 65.17 ± 1.00 μm in females and 72.60 ± 0.82 μm in males, with a basal diameter of 4.46 ± 0.07 μm in females and 4.62 ± 0.08 μm in males. The average length of central sensilla chaetica was 57.71 ± 1.55 μm in females and 60.05 ± 1.04 μm in males, with a basal diameter of 4.28 ± 0.08 μm and 4.74 ± 0.10 μm. For dorsal sensilla chaetica, the average length was 64.32 ± 0.63 μm in females and 66.02 ± 0.68 μm in males, with a basal diameter of 4.06 ± 0.07 μm and 4.41 ± 0.11 μm. The average length of lateral sensilla chaetica was significantly greater in males than in females ($t = 5.73$, df $= 58$, $p < .001$), while the lengths of central ($t = 1.25$, df $= 58$, $p = .216$) and dorsal sensilla chaetica ($t = 1.84$, df $= 58$, $p = .072$) showed no significant differences.

3.2.4 | Sensilla chaetica II

This newly discovered sensillum was distributed on the dorsal side of the flagellum (Figure 6a), adjacent to sensilla chaetica and sensilla squamiformia, and emerged from beneath the scales. Approximately half of the sensilla was covered by scales, while its tip extended beyond the scales. The sensillum's appearance was reminiscent of sensilla chaetica, tapering from a socket-like depression at the base to a narrower tip, featuring parallel ring-like ridges along the outer surface (Figure 6b,c). The tip was blunt with five small pores present at the apex (Figure 6d). Sensilla chaetica II were observed on three females and two males. For one of the males the sensilla measured approximately 40.06 μm in length and had a basal diameter of 3.18 μm, after scale removal. We classified this sensillum as sensilla chaetica based on its distinct characteristics and anatomical features.

3.2.5 | Sensilla coeloconica

Sensilla coeloconica (SCO) were scattered on the ventral side of the flagellum (Figure 7a,b), with two to six sensilla per subsegment. These sensilla resemble chrysanthemum flowers and were composed of three layers. The outermost layer consisted of two folded petal-like structures, forming a cavity-like body. The second layer was composed of approximately 12–15 fringe hairs with longitudinal ridges on their surface. These fringe hairs curved inwards from the base, converging towards the center in a dome-like fashion. The central layer featured a hollow, conical structure with longitudinal ridges and (Figure 7a,b). The average basal diameter of these sensilla was 9.75 ± 0.11 μm in females ($n = 30$) and 10.29 ± 0.15 μm in males ($n = 30$), with the SCO sensilla in males being significantly larger than females ($t = 2.76$, df $= 58$, $p = .008$).

3.2.6 | Sensilla styloconica

Sensilla styloconica (SS) were present at the top of each subsegment of the flagellum (Figure 7c,d), with one sensillum per subsegment. These sensilla had a cylindrical shape and no apparent socket, with the base featuring larger folds, the central portion with smaller folds, and the tip having a smooth surface. The tip of the sensillum had either one or two pointed protrusions. Each subsegment of the flagellum had one sensillum styloconica. The average basal diameter of

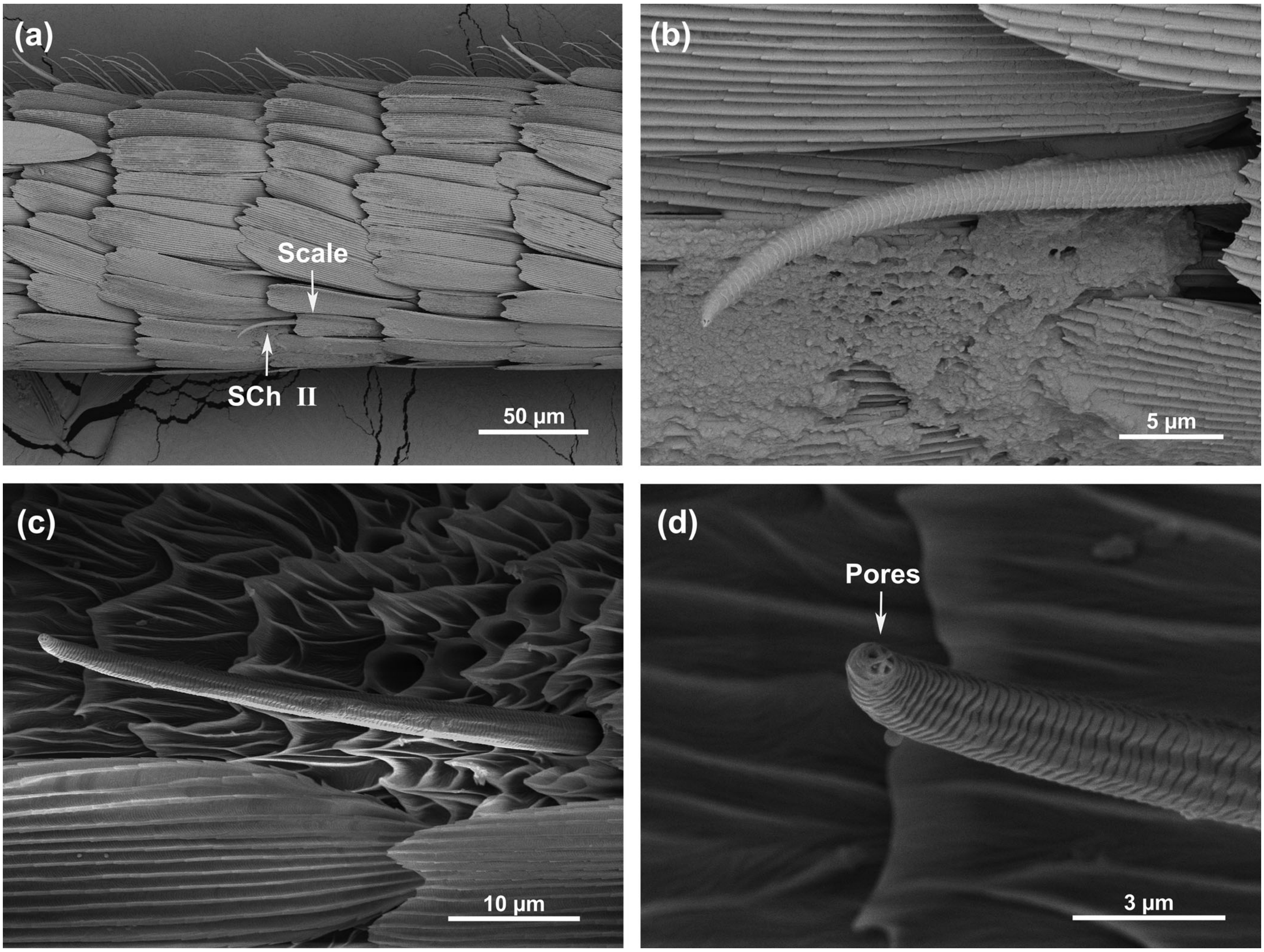

FIGURE 6 Morphological characteristics of sensilla chaetica II of *Spodoptera frugiperda*. (a) the sensilla chaetica II emerging from beneath the scales, (b) the surface structure of sensilla chaetica II, (c) the basal structure of sensilla chaetica II, and (d) the tip of sensilla chaetica II showing five small pores. Scheme II: Sensilla chaetica II.

sensilla styloconica was 6.41 ± 0.20 μm in females, and 6.59 ± 0.15 μm in males. Their average length was 25.41 ± 0.36 μm in females and 26.36 ± 0.38 μm in males. There was no significant difference between the sexes in SS length ($t = 1.82$, df $= 58$, $p = .073$) or the basal diameter ($t = 0.70$, df $= 58$, $p = .488$).

3.2.7 | Sensilla squamiformia I

Sensilla squamiformia I (SSQ I) were sparsely scattered on the dorsal side of the flagellum, with their base covered by scales but with the tip exposed. These sensilla had a sword-like shape, with a wider base that gradually narrowed towards the tip. The surface of SSQ I sensilla had several longitudinal grooves with edges having upward-pointing serrations (Figure 8a). The average basal diameter of sensilla squamiformia was 1.86 ± 0.04 μm in females and 1.80 ± 0.05 μm in males ($t = 1.04$, df $= 58$, $p = .301$). The average length measured 37.92 ± 0.64 μm in females and 38.72 ± 0.79 μm in males, with no significant difference between the sexes ($t = 0.79$, df $= 58$, $p = .433$).

3.2.8 | Sensilla squamiformia II

Sensilla squamiformia II (SSQ II) represent another subtype of sensilla squamiformia (Figure 8b) and were found sparsely distributed on the scape and pedicel. These sensilla had an elongate spindle-shaped structure with vertical stripes on their surface, with an extremely slender and slightly curved tip. The average basal diameter was 2.24 ± 0.05 μm in females and 2.44 ± 0.06 μm in males, with males significantly larger than females ($t = 2.61$, df $= 58$, $p = .012$). The average SSQ II length in females and males was 61.01 ± 1.35 μm and 64.61 ± 1.71 μm, respectively, with no significant difference between the two sexes ($t = 1.66$, df $= 58$, $p = .103$).

3.2.9 | Sensilla auricillica

Sensilla auricillica (SAU) were scattered on the ventral side of the flagellum (Figure 8c). These sensilla arose from socket-like depressions, with their base curving inwards on both sides, a wider central portion,

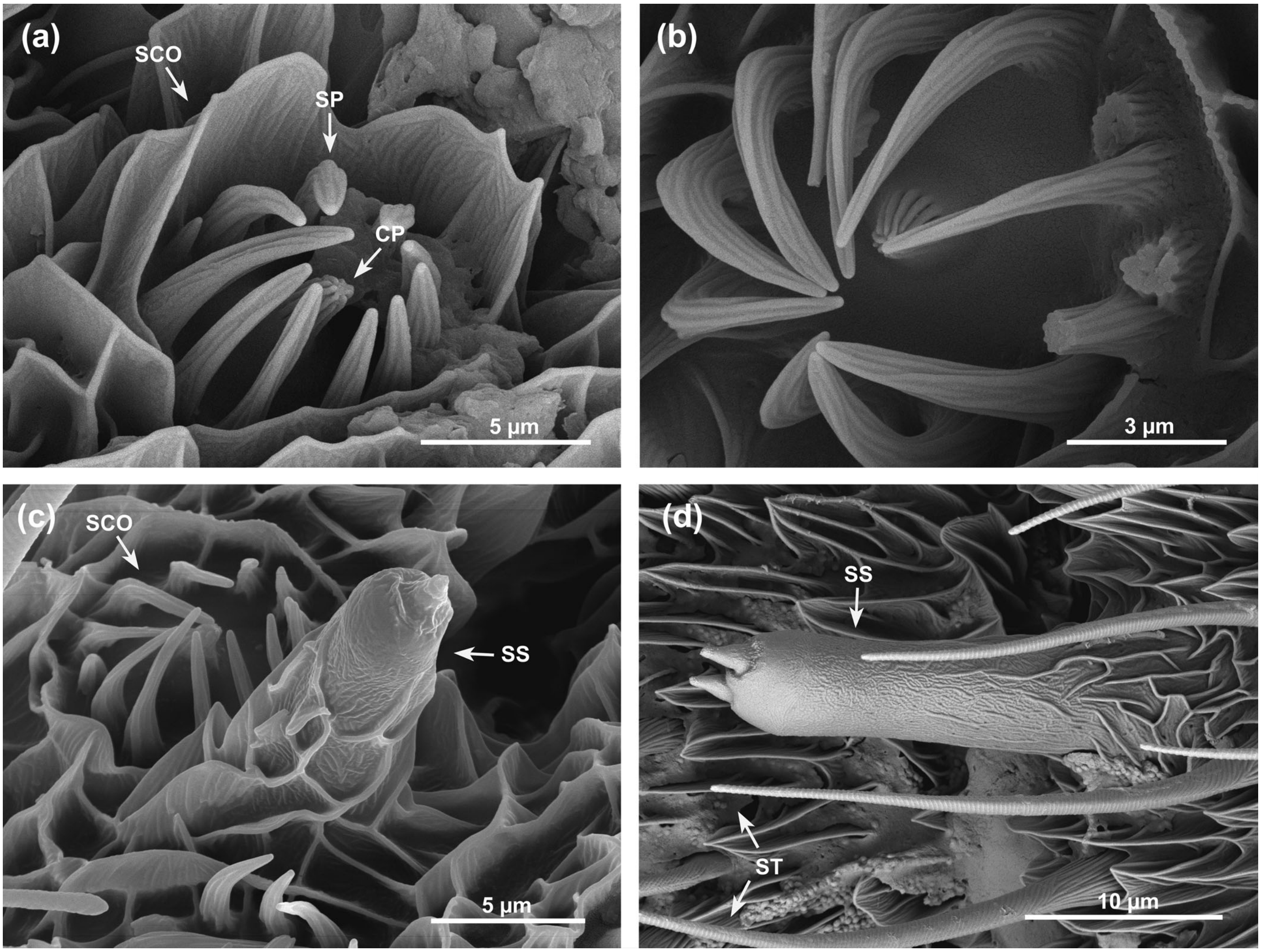

FIGURE 7 Morphological characteristics of two sensilla of *Spodoptera frugiperda*. (a) the overall appearance of sensilla coeloconica, (b) detailed structural characteristics of sensilla coeloconica, (c) sensilla styloconica with one pointed cone, and (d) sensilla styloconica with two pointed cones. SCO: Sensilla coeloconica, SP: Spine, CP: Central peg, SS: Sensilla styloconica, and ST: Sensilla trichoidea.

and a narrower tip that was blunt and flat. The overall shape resembled that of rabbit ears, giving them their name. The surface of sensilla auricillica featured longitudinal ridges along the central axis. Near the tip, about 1/5 to 1/2 of the way down, there were oblique ridges that slope inward from both sides and converged with the central longitudinal ridges. SAU were very small and scattered among the sensilla trichoidea, making them difficult to detect. The average length of sensilla auricillica was 22.28 ± 4.10 μm in females ($n = 4$) and 26.30 ± 2.68 μm in males ($n = 4$).

3.2.10 | Sensilla basiconica

Sensilla basiconica (SB) were located on the ventral side of the flagellum, being relatively short and cone-shaped. These sensilla lacked socket-like depressions at their base, and they had a blunt tip. The surface was characterized by longitudinal ridges with numerous pores between the ridges (Figure 8d). SB were very small in size, relatively scarce in number, and difficult to locate. The average length of sensilla basiconica was 13.90 ± 3.00 μm in females ($n = 3$) and 15.71 ± 2.84 μm in males ($n = 3$).

4 | DISCUSSION

Antennal sensilla are the basic units by which insects receive and perceive external information (Chapman, 1982; Nation, 2001). With such information, insects are able to engage in various life activities, such as finding host plants, avoiding predators, and selecting mates (Schneider, 1964). Because antennae are important sensory organs that allow insects to perceive their environment, they provide researchers the opportunity to explore insect perception mechanisms as well as develop novel odor attractants.

The identification of antennal sensilla types provides a foundation for conducting research on antennal sensilla functionality (Steinbrecht, 1997). Currently, the identification and nomenclature

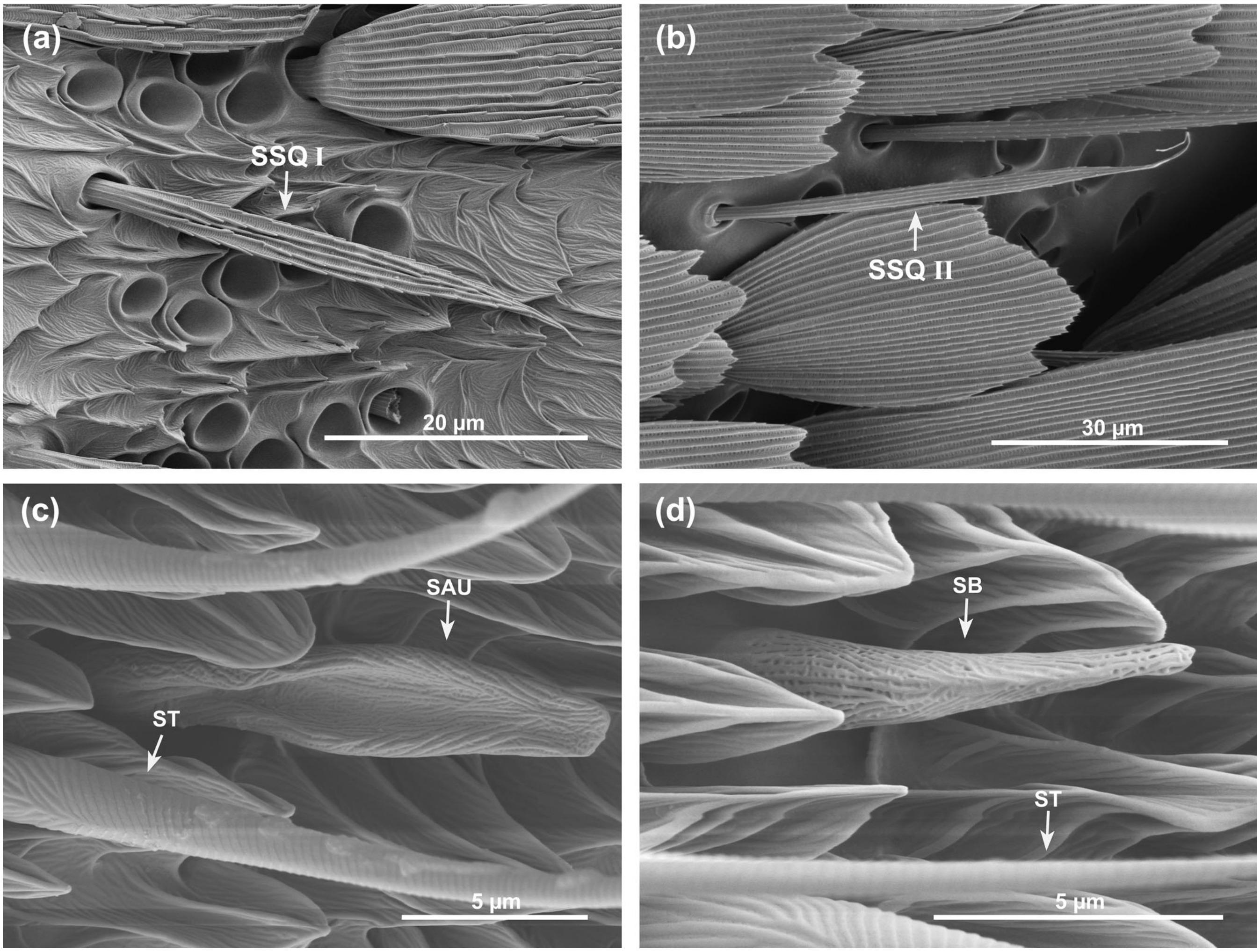

FIGURE 8 Morphological characteristics of four sensilla of *Spodoptera frugiperda*: (a) overall appearance and morphological characteristics of sensilla squamiformia I, (b) overall appearance and morphological characteristics of sensilla squamiformia II, (c) morphological characteristics of sensilla auricillica, and (d) detailed surface structure of sensilla basiconica. SSQ I: Sensilla squamiformia I, SSQ II: Sensilla squamiformia II, SAU: Sensilla auricillica, ST: Sensilla trichodea, and SB: Sensilla basiconica.

used for most insect antennal sensilla are determined through sensilla morphology (Kristensen, 2004; Nation, 2001). However, sensilla identification is often difficult because the surface structure of antennae is very complex and differences in sensilla characteristics can be exceedingly subtle. Additionally, variations in equipment quality and observation perspectives can also affect sensilla identification. Currently, the primary approach to address these issues involves multidimensional verification of sensilla, especially those that are newly discovered, which includes methods such as comparative morphology, tissue anatomy, and electrophysiological functional testing. Morphological testing often involves, comparative analysis with antennal sensilla of insects of the same genus or family, or the same type of sensilla in different insect groups (Galizia & Rössler, 2010; Zacharuk, 1980).

The types, functions, quantities, and distribution of antennal sensilla are relatively stable within the same insect taxonomic groups (Kristensen, 2004; Schneider, 1964; Zacharuk, 1980). For instance, in Lepidoptera, antennae commonly possess the following eight sensilla types: sensilla trichoidea, sensilla chaetica, sensilla coeloconica, sensilla squamiformia, sensilla basiconica, sensilla styloconica, sensilla auricillica, and Böhm bristles (Chang et al., 2015; Hu et al., 2021; Koh et al., 1995; Rani, Pathour, et al., 2021; Roh et al., 2016; Yang et al., 2017; Zhang et al., 2019). In the Noctuidae, which includes FAW, these same eight sensilla types are common. However, the types, functions, quantities, and distribution of antennal sensilla do vary among different noctuid species, reflecting the unique characteristics of each species. For instance, within the Noctuidae, different species exhibit varying numbers of antennal sensilla types, e.g. five types have been reported in *Spodoptera litura* (Aruna et al., 2019), six types in *Spodoptera exigua* (Xu et al., 2008), seven types in *Helicoverpa assulta* (Koh et al., 1995), seven types in *Mythimna separata* (Chang et al., 2015), and eight types in both *Athetis lepigone* (Hu et al., 2021), and *Helicoverpa armigera* (Rani, Pathour, et al., 2021).

In the current study, eight types and two subtypes of antennal sensilla were identified and recorded in FAW. Among the eight sensilla types, six of them, including sensilla trichoidea, sensilla chaetica, sensilla coeloconica, sensilla styloconica, sensilla basiconica, and sensilla squamiformia, have been documented in all six previous studies. Böhm bristles have been documented by four research papers but were not recorded by both Malo, Castrejón-Gómez, et al. (2004) and Zahran et al. (2023). Sensilla auricillica has been reported in five articles, but not recorded by Lei et al. (2021). Sensilla gemmiformium, sensilla ampullaces, and sensilla cavitata-peg were only described by Tian et al. (2021), but were not mentioned in the other four earlier studies nor in the present study. Sensilla cavity, sensilla placodea, sensilla ligulate, and sensilla uniporous peg were only reported in the recent study by Wang et al. (2023) but not recorded by either Zahran et al. (2023) nor in the present study. Perhaps sensilla uniporous pegs are relatively rare and difficult to detect as reported by Faucheux (1993, 1997). For all details regarding the documentation of each sensilla type, refer to Table 1. The present study documented two sensilla subtypes for the first time (sensilla chaetica II, and sensilla squamiformia II), which are distinct from any previously reported sensilla types. To facilitate future verification and research on FAW sensilla, we provided detailed descriptions and photos of each sensillum type (Figures 3–8). It is unclear why there has been so much variation in the types of sensilla reported for FAW, but it may reflect differences in equipment and sample preparation, or possibly even differences in FAW populations in different parts of their worldwide range. Similar cases where differences in the sensilla observed by different researchers have been reported for the oriental fruit fly (*Bactrocera dorsalis*) (Diptera) and the noctuid *Spodoptera litura*. For example, sensilla clavate were reported by Lee et al. (1994) for *B. dorsalis*, but not by Liu et al. (2021). Likewise, sensilla basiconica were reported for *S. litura* by Liu et al. (2009) but not by Aruna et al. (2019).

The types of FAW antennal sensilla found in the present study encompassed mechanical sensilla, chemical sensilla, temperature and humidity sensilla, taste sensilla, and more (Gargi et al., 2022; Lei et al., 2021; Malo, Castrejón-Gómez, et al., 2004; Tian et al., 2021; Wang et al., 2023; Zahran et al., 2023). There were two types of antennal mechanical sensilla, including Böhm bristles and sensilla squamiformia, which receive mechanical stimuli from the external environment (Kristensen, 2004; Schneider, 1964). Böhm bristles were one of the earliest types of antennal sensilla studied in insects (Schneider, 1964). Böhm bristles commonly were found on the pedicel and flagellum segments of filiform antennae, as well as on the intersegmental membranes between these segments. It is thought that Böhm bristles can detect the position and movement of the antennae, thus providing information that allow adjusting the orientation of antennae (Castrejón-Gómez et al., 2003; Koh et al., 1995). The morphological characteristics and distribution of the Böhm bristles in FAW are consistent with those reported in the noctuids *Helicoverpa assulta* (Koh et al., 1995) and *Athetis lepigone* (Hu et al., 2021).

Sensilla squamiformia is the relatively dominant sensillum type found on filiform antennae in insects (Schneider, 1964). These sensilla do not have pores, suggesting that they lack a major role in chemical sensing (Steinbrecht, 1997). Sensilla squamiformia are considered a type of mechanoreceptor that are likely involved in perceiving mechanical movements or related to factors such as airflow pressure and velocity (Rani, Pathour, et al., 2021). Bawin et al. (2017) proposed that sensilla squamiformia are involved in perceiving air vibrations in *Tuta absoluta* (Lepidoptera: Gelechiidae). Sensilla squamiformia are located beneath the antennal scales and can sense air vibrations while avoiding mechanical damage. Although sensilla squamiformia I and sensilla squamiformia II showed significant differences in length and width, they were similar in morphology. Therefore, we have classified sensilla squamiformia II as a subtype of squamous sensilla.

Sensilla styloconica, which are common among Lepidoptera, are often categorized as humidity and temperature sensing sensilla. Sensilla styloconica have been reported by some researchers as not having pores and thus not having odor perception functionality (Rani, Pathour, et al., 2021; Roh et al., 2016; Steinbrecht, 1997). In the present study, however, pores were found at the tips of sensilla styloconica but we did not confirm whether these pores allow these sensilla to perceive chemical substances. In the study by Chang et al. (2015) on *Mythimna separata* (Lepidoptera: Noctuidae), sensilla styloconica were reported as having pores. They provided tissue-section photographs and suggested that these sensilla were capable of perceiving chemical stimuli and odors. It is possible that there are multiple types of sensilla styloconica, and that some can perceive more than humidity and temperature. The peg-like structures at the tip of sensilla styloconica have often been used as the basis for subtype classification (Chang et al., 2015). Within the Noctuidae, sensilla styloconica with 2–3 conical structures is common (Zheng et al., 2014).

The antennal chemosensory sensilla found in FAW included sensilla coeloconica, sensilla trichoidea, sensilla chaetica, sensilla auricillica and sensilla basiconica. Among these, sensilla coeloconica were the most complex sensilla found on FAW antennae. Sensilla coeloconica have also been reported in *Bombyx mori* (Lepidoptera: Bombycidae), in which the conical structures at the center of the sensillum had pores distributed in a dot-like pattern, suggesting they serve as the information-receiving units (Hunger & Steinbrecht, 1998). The cavity-like structure and spines of the sensilla coeloconica can serve to protect the central cone from mechanical damage (Rani, Pathour, et al., 2021; Yang et al., 2009). Some authors have also suggested that the cavity-like structure can maintain a certain level of humidity, which may enhance the efficiency of capturing chemical odorants (Rani, Pathour, et al., 2021). The distribution of these sensilla on noctuid antennae have not shown a distinct pattern (Chang et al., 2015; Rani, Pathour, et al., 2021; Seada, 2015). It appears that sensilla coeloconica are multifunctional sensilla, capable of perceiving not only temperature, humidity, and water vapor, but also perceiving sex pheromones and plant odors (Rani, Pathour, et al., 2021; Rani, Shashank, et al., 2021; Seada, 2015; Yang et al., 2017; Zhang et al., 2019).

Sensilla trichoidea was the most abundant type of sensillum found on the antennae of FAW. They were distributed on several subsegments of the flagellum, which is consistent with many other lepidopterans (Malo, Castrejón-Gómez, et al., 2004; Rani, Shashank, et al., 2021; Roh et al., 2016; Seada, 2015; Yang et al., 2017; Zhang et al., 2019). For example, *Mythimna separata* has three subtypes of sensilla trichoidea (Chang et al., 2015). However, we noted only one subtype of sensilla trichoidea in FAW, which aligns with the findings of Malo, Castrejón-Gómez, et al. (2004) and Gargi et al. (2022), but not Lei et al. (2021) who reported that FAW had two subtypes of sensilla trichoidea. Some researchers also suggested that these sensilla trichoidea can perceive sex pheromones and plant odors (Rani, Shashank, et al., 2021; Roh et al., 2016; Seada, 2015; Yang et al., 2017; Zhang et al., 2019). Observations based on transmission electron microscopy (TEM) on *Diaphania angustalis* (Lepidoptera: Crambidae) indicated numerous pores on the walls of sensilla trichoidea, suggesting that these sensilla should possess olfactory functionality (Zhang et al., 2019). For example, in *Spodoptera littoralis*, sensilla trichoidea on male antennae respond to female sex pheromones (Ljungberg et al., 1993). Perhaps sensilla trichoidea in FAW are also involved in perceiving sex pheromones, as well as other odorants in the environment (Tian et al., 2021). Malo, Castrejón-Gómez, et al. (2004) found that the abundance of sensilla trichoidea in females of FAW contributes to their significant EAG (electroantennographic) response to chemical substances.

Sensilla chaetica, the spine-like sensilla, are common in Noctuidae, such as *Helicoverpa assulta* (Koh et al., 1995), *Helicoverpa armigera* (Diongue et al., 2013; Rani, Shashank, et al., 2021), *Athetis lepigone* (Hu et al., 2021), *Mythimna separata* (Chang et al., 2015; Yuan et al., 2017), *Mamestra configurata* (Liu & Liu, 1984), and *Spodoptera littoralis* (Seada, 2015). The external features and distribution of sensilla chaetica observed in our study were generally consistent with previous reports (Gargi et al., 2022; Lei et al., 2021; Malo, Castrejón-Gómez, et al., 2004; Tian et al., 2021; Wang et al., 2023). The presence of a single pore at the tip of the sensillum aligned with Zacharuk's (1980) description of contact/chemoreceptors, suggesting a potential function for chemical communication with the external environment. In Seada's (2015) study on *Spodoptera littoralis*, it was suggested that sensilla chaetica had a taste function, and may play a crucial role in oviposition site selection by female moths (Bawin et al., 2017; Jiang et al., 2015). Zhang et al. (2019) discovered that *Diaphania angustalis* females are capable of landing on odor sources and touching them with the tips of their antennae, suggesting a mechanoreceptive function in sensilla chaetica. The notably longer and wider features of these sensilla, compared to the other types, suggest that besides potentially serving as mechanoreceptors or contact/chemical receptors, they might also serve to protect other types of sensilla (Chang et al., 2015; Rani, Shashank, et al., 2021).

Sensilla chaetica type II was documented for the first time in the present study. They were so named because of their resemblance to sensilla chaetica and having consistent characteristics with the sensilla chaetica found in other Noctuidae. These sensilla had five pores at their tip, resembling the features of previously reported sensilla chaetica, with similar pore features, differing only in quantity (Faucheux, 1991). In the noctuid *Noctua pronuba* all sensilla chaetica are uniporous (Faucheux, 1990). By contrast, in the noctuid *Mormo maura* the ventral sensilla chaetica are aporous (as Ch I of *Spodoptera*), whereas the dorsal sensilla chaetica, which are among scales, are uniporous (as Ch II of *Spodoptera*) (Faucheux, 1997). Therefore, we classified this sensillum as a subtype of sensilla chaetica. Given the presence of several small pores at the tip of this sensillum, it may perceive odorants, suggesting an olfactory perception function. Further clarification of the type and function of this sensillum requires TEM and electrophysiological studies.

Sensilla auricillica, also known as ear-like sensilla due to their rabbit ear or tongue-like shape, share a surface structure similar to cone-shaped sensilla (sensilla auricillica) found in many Lepidoptera. Sensilla auricillica possess numerous small pores on their walls. TEM studies have indicated that the internal structure of sensilla auricillica was simpler compared to sensilla trichoidea and sensilla chaetica, featuring a thin cuticular wall with pores (Zhang et al., 2019). This porous structure is thought to be a characteristic of its olfactory chemoreceptive function. Sensilla auricillica in *Cydia pomonella* (Lepidoptera: Tortricidae) have been shown to exhibit electrochemical responses to plant chemicals and sex pheromones (Ansebo et al., 2005). Seada (2015) discovered that the distribution of sensilla auricillica do not differ in quantity between the proximal and distal ends of the antenna in female *Spodoptera littoralis*, suggesting that these sensilla play a significant role in the selection of host plants for oviposition.

Sensilla basiconica, usually positioned between sensilla trichoidea, were relatively short in length with thin surfaces (Schneider, 1964). These sensilla were small and were found in very low numbers in FAW antennae (Malo, Castrejón-Gómez, et al., 2004). Two subtypes of sensilla basiconica were identified in *Mamestra configurata* (Liu & Liu, 1984) and *Lophocorona pediasia* (Lepidoptera: Lophocoronidae) (Faucheux, 2006). In our study, we found only one subtype of sensilla basiconica in FAW, which was consistent with previous research (Gargi et al., 2022; Malo, Castrejón-Gómez, et al., 2004; Wang et al., 2023). However, there were differences in length and thickness of this sensilla type between males and females (Malo, Castrejón-Gómez, et al., 2004). Many studies have suggested that the grooves and stripes on the outer surface of sensilla basiconica, that are perforated by numerous small pores, indicate their olfactory chemoreceptive function, likely aiding in detection of pheromones and plant odors (Chang et al., 2015; Liu & Liu, 1984; Rani, Shashank, et al., 2021; Zhang et al., 2019).

Antennal scales are commonly found in Lepidoptera (Kristensen, 2004). In FAW, the scape and pedicel segments were entirely covered by scales (Figure 2), while only about 60% of the surface area of the flagellum segment was covered by scales (Figure 2d). These scales were densely arranged, overlapping like roof tiles, and likely provide mechanical protection to the antenna and aiding in waterproofing and drainage (Koh et al., 1995). It has also been proposed that antennal scales could aid in capturing and accumulating compounds, thus helping to determine the direction of stimulus sources (Castrejón-Gómez et al., 2003). Pores penetrated the scales have been reported in *Tirathaba rufivena* (Lepidoptera: Pyralidae) (Guo et al., 2022), but we did not find any pores in FAW.

The number, distribution, and types of antennal sensilla in insects often vary by sex. Regarding the sensilla uniporous peg, they were only found in FAW females, potentially playing a role in detecting temperature and humidity changes within the host habitat (Wang et al., 2023). The length and basal diameter of the scape, pedicel and flagellum in FAW males were larger than those in females (Gargi et al., 2022). We also found that the length and basal diameter of the scape and flagellum in FAW males were greater than in females. The number of sensilla trichoidea in FAW males was greater than in females (Malo, Castrejón-Gómez, et al., 2004). Furthermore, the size of sensilla trichoidea, sensilla chaetica and sensilla squamiformia were larger in FAW males than in females (Gargi et al., 2022; Wang et al., 2023). Differences in sensilla size between the sexes may be due to sex-specific requirements to detect particular stimuli, such as sex pheromones and cues for oviposition-site selection (Malo, Castrejón-Gómez, et al., 2004; Nakano et al., 2023; Roh et al., 2016).

5 | CONCLUSIONS

Our study demonstrated that FAW possesses eight types and two subtypes of sensilla, Böhm's bristles, sensilla trichoidea, sensilla chaetica (I and II), sensilla coeloconica, sensilla styloconica, sensilla squamiformia (I and II), sensilla auricillica, and sensilla basiconica. These findings provide a morphological basis to better understand FAW antennal sensilla. Further studies using electrophysiological recordings and behavioral assays may help to identify the precise functions of each sensilla type in FAW.

AUTHOR CONTRIBUTIONS

Yong-Ping Li: Conceptualization; methodology; writing – review and editing; writing – original draft; data curation. **Hai-Yan Zhou:** Methodology; investigation; data curation; writing – original draft. **Yang Yang:** Methodology; investigation. **Hui Ye:** Conceptualization; writing – review and editing; funding acquisition; writing – original draft. **Robert A. Haack:** Writing – review and editing; writing – original draft. **Jun Cao:** Conceptualization; funding acquisition; supervision; investigation; project administration.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

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REFERENCES

Ansebo, L., Ignell, R., Löfqvist, J., & Hansson, B. S. (2005). Responses to sex pheromone and plant odours by olfactory receptor neurons housed in sensilla auricillica of the codling moth, *Cydia pomonella* (Lepidoptera: Tortricidae). *Journal of Insect Physiology*, *51*, 1066–1074.

Aruna, R., Jeyarani, S., Mohankumar, S., & Durairaj, C. (2019). Documentation and validation of chemosensory structures in antennae of *Spodoptera litura* (Fabricius) through scanning electron microscope (SEM). *Indian Journal of Agricultural Research*, *53*, 554–559.

Bawin, T., Collard, F., De Backer, L. B., Yarou, B., Compère, P., Francis, F., & Verheggen, F. J. (2017). Structure and distribution of the sensilla on the antennae of *Tuta absoluta* (Lepidoptera: Gelechiidae). *Micron*, *96*, 16–28.

Castrejón-Gómez, V. R., Nieto, G., Valdes, J., Castrejón, F., & Rojas, J. C. (2003). The antennal sensilla of *Zamagiria dixolophella* Dyar (Lepidoptera: Pyralidae). *Annals of the Entomological Society of America*, *96*, 672–678.

Chang, X. Q., Zhang, S., Lv, L., & Wang, M. Q. (2015). Insight into the ultrastructure of antennal sensilla of *Mythimna separata* (Lepidoptera: Noctuidae). *Journal of Insect Science*, *15*, 124.

Chapman, R. (1982). Chemoreception: The significance of receptor numbers. *Advances in Insect Physiology*, *16*, 247–356.

Cruz, I., de Lourdes, M., Figueiredo, C. R., da Silva, R. B., da Silva, I. F., Paula, C. D., & Foster, J. E. (2012). Using sex pheromone traps in the decision-making process for pesticide application against fall armyworm (*Spodoptera frugiperda* [smith] [Lepidoptera: Noctuidae]) larvae in maize. *International Journal of Pest Management*, *58*, 83–90.

Diongue, A., Yang, J. T., & Lai, P. Y. (2013). Biomorphometric characteristics of different types of sensilla detected on the antenna of *Helicoverpa armigera* by scanning electron microscopy. *Journal of Asia-Pacific Entomology*, *16*, 23–28.

FAO. (2018). *Integrated management of the fall armyworm on maize: A guide for farmer field schools in Africa* (p. 130). Food and Agriculture Organization of the United Nations.

FAO. (2020). Forecasting threats to the food chain affecting food security in countries and regions. In *Food chain crisis early warning bulletin* (Vol. 36). Food and Agriculture Organization of the United Nations.

Faucheux, M. J. (1990). External structure of sensilla on the male and female flagellum of *Noctua pronuba* L. (Lepidoptera: Noctuidae). *Annales de la Société Entomologique de France*, *26*, 173–184.

Faucheux, M. J. (1991). Morphology and distribution of sensilla on the cephalic appendages, tarsi and ovipositor of the European sunflower moth, *Homoeosoma nebulella* Den. & Schiff. (Lepidoptera: Pyralidae). *International Journal of Insect Morphology and Embryology*, *20*, 291–307.

Faucheux, M. J. (1993). Uniporous pegs associated with sensilla auricillica on the antennae of Noctuidae (Lepidoptera). *Nota Lepidopterologica*, *16*, 13–17.

Faucheux, M. J. (1997). L'Ethnobotanique au carrefour des sciences naturelles et des sciences humaines. *Bulletin de la Société Des Sciences Naturelles de l'Ouest de la France*, *19*, 29–39.

Faucheux, M. J. (2006). Antennal sensilla of male *Lophocorona pediasia* common 1973 and their phylogenetic implications (Lepidoptera: Lophocoronidae). *Annales de la Societe Entomologique de France*, *42*, 113–118.

Galizia, C. G., & Rössler, W. (2010). Parallel olfactory systems in insects: Anatomy and function. *Annual Review of Entomology*, *55*, 399–420.

Gargi, C., Kennedy, J. S., & Jayaba, T. D. (2022). Morphometrics and distribution of antennal sensillae of both sexes of *Spodoptera frugiperda* (smith) (Lepidoptera: Noctuidae). *Journal of Applied and Natural Science*, *14*, 41–48.

Goergen, G., Kumar, P. L., Sankung, S. B., Togola, A., & Tamò, M. (2016). First report of outbreaks of the fall armyworm *Spodoptera frugiperda* (JE smith) (Lepidoptera, Noctuidae), a new alien invasive pest in west and Central Africa. *PLoS One*, *11*, e0165632.

Guo, J., Du, Z., Cui, G., Wang, Z., Wang, J., & Zhou, X. (2022). Ultrastructure characteristics and sexual dimorphism of antennal sensilla in *Tirathaba rufivena* (Lepidoptera: Pyralidae). *Insects*, *13*, 73.

He, W., Zhao, S., Ge, S., Jiang, Y. Y., Zhao, X., & Wu, K. M. (2019). Population prediction method using sexual trapping for *Spodoptera frugiperda*. *Plant Protection*, *45*, 48–53.

Hu, G. L., Zhang, C. M., Wang, Z. Q., Chen, Q. X., & Lu, J. Q. (2021). Sensilla of the antenna and proboscis of *Athetis lepigone* (Möschler) (Lepidoptera: Noctuidae). *Journal of Morphology*, *282*, 733–745.

Hunger, T., & Steinbrecht, R. A. (1998). Functional morphology of a double-walled multiporous olfactory sensillum: The sensillum coeloconicum of *Bombyx mori* (Insecta, Lepidoptera). *Tissue and Cell*, *30*, 14–29.

Jiang, X. J., Ning, C., Guo, H., Jia, Y. Y., Huang, L. Q., Qu, M. J., & Wang, C. Z. (2015). A gustatory receptor tuned to D-fructose in antennal sensilla chaetica of *Helicoverpa armigera*. *Insect Biochemistry and Molecular Biology*, *60*, 39–46.

Koh, Y. H., Park, K. C., & Boo, K. S. (1995). Antennal sensilla in adult *Helicoverpa assulta* (Lepidoptera: Noctuidae): Morphology, distribution, and ultrastructure. *Annals of the Entomological Society of America*, *88*, 519–530.

Kristensen, N. (2004). *Handbook of zoology, Volume IV Arthropoda: Insecta, part 36 Lepidoptera, moths and butterflies, Volume 2: Morphology, physiology, and development*. de Gruyter.

Kumar, R. M., Gadratagi, B. G., Paramesh, V., Kumar, P., Madivalar, Y., Narayanappa, N., & Ullah, F. (2022). Sustainable management of invasive fall armyworm, *Spodoptera frugiperda*. *Agronomy*, *12*, 2150.

Lee, W., Chang, J. C., Hwang, Y., & Lin, T. L. (1994). Morphology of the antennal sensilla of the oriental fruit fly, *Dacus dorsalis* Hendel (Diptera: Tephrltidae). *Zoological Studies*, *33*, 65–71.

Lei, T., Guo, F., Chen, S., Li, M., & Yan, N. (2021). Ultrastructure of antennae sensilla of *Spodoptera frugiperda*. *Journal of Biosafety*, *30*, 183–188.

Li, Y. P., Yao, S. Y., Feng, D., Haack, R. A., Yang, Y., Hou, J. L., & Ye, H. (2023). Dispersal behavior characters of *Spodoptera frugiperda* larvae. *Insects*, *14*, 488.

Liu, H., & Liu, T. (1984). Sensilla on the antennal flagellum of the bertha armyworm moth, *Mamestra configurata* Walker (Lepidoptera: Noctuidae): A scanning electron microscope study. *Annals of the Entomological Society of America*, *77*, 236–245.

Liu, J. X., Zhong, G. H., Chen, X. F., Hu, L. M., & Hu, M. Y. (2009). Ultrastructures of the sensilla of *Spodoptera litura*. *Journal of Southwest University (Natural Science Edition)*, *6*, 35–40.

Liu, Z., Hu, T., Guo, H.-W., Liang, X.-F., & Cheng, Y.-Q. (2021). Ultrastructure of the olfactory sensilla across the antennae and maxillary palps of *Bactrocera dorsalis* (Diptera: Tephritidae). *Insects*, *12*, 289. https://doi.org/10.3390/insects12040289

Ljungberg, H., Anderson, P., & Hansson, B. (1993). Physiology and morphology of pheromone-specific sensilla on the antennae of male and female *Spodoptera littoralis* (Lepidoptera: Noctuidae). *Journal of Insect Physiology*, *39*, 253–260.

Malo, E. A., Bahena, F., Miranda, M. A., & Valle-Mora, J. (2004). Factors affecting the trapping of males of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) with pheromones in Mexico. *Florida Entomologist*, *87*, 288–293.

Malo, E. A., Castrejón-Gómez, V. R., Cruz-López, L., & Rojas, J. C. (2004). Antennal sensilla and electrophysiological response of male and female *Spodoptera frugiperda* (Lepidoptera: Noctuidae) to conspecific sex pheromone and plant odors. *Annals of the Entomological Society of America*, *97*, 1273–1284.

Nation, J. L. (2001). *Insect physiology and biochemistry*. CRC Press.

Nakano, M., Morgan-Richards, M., Clavijo-McCormick, A., & Trewick, S. (2023). Abundance and distribution of antennal sensilla on males and females of three sympatric species of alpine grasshopper (Orthoptera: Acrididae: Catantopinae) in Aotearoa New Zealand. Zoomorphology, 142, 51–62.

Overton, K., Maino, J. L., Day, R., Umina, P. A., Bett, B., Carnovale, D., Ekesi, S., Meagher, R., & Reynolds, O. L. (2021). Global crop impacts, yield losses and action thresholds for fall armyworm (*Spodoptera frugiperda*): A review. *Crop Protection*, *145*, 105641.

Qu, C., Li, B., Wang, R., Li, F., Li, Q., Xu, M., Zhao, H., & Luo, C. (2022). Formulation screening and field application evaluation of sex pheromones for *Spodoptera frugiperda*. *China Plant Protection*, *42*, 73–76.

Rani, A. T., Pathour, S., Meshram, N., Kammar, V., Majumder, S., Srivastava, C., Pandey, K., & Singh, J. (2021). Morphological characterization and distribution of antennal sensilla of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) using scanning electron microscopy. *Microscopy Research and Technique*, *85*, 1371–1391.

Rani, A. T., Shashank, P. R., Meshram, N. M., Sagar, D., Srivastava, C., Pandey, K. K., & Singh, J. (2021). Morphological characterization of antennal sensilla of *Earias vittella* (Fabricius) (Lepidoptera: Nolidae). *Micron*, *140*, 102957.

Roh, H. S., Park, K. C., Oh, H. W., & Park, C. G. (2016). Morphology and distribution of antennal sensilla of two tortricid moths, *Cydia pomonella* and *C. Succedana* (Lepidoptera). *Microscopy Research and Technique*, *79*, 1069–1081.

Schmidt, H. R., & Benton, R. (2020). Molecular mechanisms of olfactory detection in insects: Beyond receptors. *Open Biology*, *10*, 200252.

Schneider, D. (1964). Insect antennae. *Annual Review of Entomology*, *9*, 103–122.

Seada, M. A. (2015). Antennal morphology and sensillum distribution of female cotton leaf worm *Spodoptera littoralis* (Lepidoptera: Noctuidae). *The Journal of Basic & Applied Zoology*, *68*, 10–18.

Sharanabasappa, K., Asokan, R., Swamy, H. M., Maruthi, M., Pavithra, H., Hegbe, K., Navi, S., Prabhu, S., & Goergen, G. E. (2018). First report of the fall armyworm, *Spodoptera frugiperda* (JE smith) (Lepidoptera: Noctuidae), an alien invasive pest on maize in India. *Pest Management Horticulture Ecosystem*, *24*, 23–29.

Steinbrecht, R. A. (1997). Pore structures in insect olfactory sensilla: A review of data and concepts. *International Journal of Insect Morphology and Embryology*, *26*, 229–245.

Sun, X. X., Hu, C. X., Jia, H. R., Wu, Q. L., Shen, X. J., Zhao, S. Y., Jiang, Y. Y., & Wu, K. M. (2021). Case study on the first immigration of fall armyworm, *Spodoptera frugiperda* invading into China. *Journal of Integrative Agriculture*, *20*, 664–672.

Tabata, J., Nakano, R., Yasui, H., Nakamura, K., Takehara, K., Matsuda, H., Ikenoue, Y., Kusuhata, Y., Kinjo, K., & Nakama, K. (2023). Sex pheromone of the fall armyworm, *Spodoptera frugiperda*: Identification of a trace component that enhances attractiveness and specificity. *Entomologia Experimentalis et Applicata*, *171*, 535–541.

Tepa-Yotto, G. T., Meagher, R. L., Winsou, J. K., Dahoueto, B. T., Tamò, M., Sæthre, M. G., & Nagoshi, R. N. (2022). Monitoring *Spodoptera frugiperda* in Benin: Assessing the influence of trap type, pheromone blends, and habitat on pheromone trapping. *Florida Entomologist*, *105*, 71–78.

Tian, C., Jianrong, H., Yanna, W., Shengnan, Z., Shengnan, L., & Hongqiang, F. (2021). Ultrastructure and morphology of antennal sensilla of the adult *Spodoptera frugiperda* (J. E. Smith). *Plant Protection*, *47*, 216–221.

Tumlinson, J., Mitchell, E., Teal, P., Heath, R., & Mengelkoch, L. (1986). Sex pheromone of fall armyworm, *Spodoptera frugiperda* (J. E. Smith) identification of components critical to attraction in the field. *Journal of Chemical Ecology*, *12*, 1909–1926.

Wang, W. W., He, P. Y., Liu, T. X., Jing, X. F., & Zhang, S. Z. (2023). Morphology and distribution of antennal sensilla on *Spodoptera frugiperda* (Lepidoptera: Noctuidae) larvae and adults. *Diversity*, *15*, 992.

Wu, K. M. (2020). Management strategies of fall armyworm (*Spodoptera frugiperda*) in China. *Plant Protection*, *46*, 1–5.

Wu, Q. L., Jiang, Y. Y., Liu, J., Hu, G., & Wu, K. M. (2021). Trajectory modeling revealed a southwest-northeast migration corridor for fall armyworm *Spodoptera frugiperda* (Lepidoptera: Noctuidae) emerging from the North China plain. *Insect Science*, *28*, 649–661.

Xu, J., Li, Y. P., Cheng, W. N., Song, Y. Q., Wu, J. X., Sun, H. Z., & Jia, H. (2008). Morphological studies on the types and distribution of antennal sensilla in *Spodotera exgua* (Hubner). *Journal of Northwest Agriculture & Forest University*, *36*, 189–193.

Yang, H., Yan, S. C., & Liu, D. (2009). Ultrastructural observations on antennal sensilla of *Coleophora obducta* (Meyrick) (Lepidoptera: Coleophoridae). *Micron*, *40*, 231–238.

Yang, S., Liu, H., Zhang, J., Liu, J., Zheng, H., & Ren, Y. (2017). Scanning electron microscopy study of the antennal sensilla of *Monema flavescens* Walker (Lepidoptera: Limacodidae). *Neotropical Entomology*, *46*, 175–181.

Ye, H., Li, Y. P., Feng, D., & Li, C. L. (2022). Construction of prevention and control barriers for *Spodoptera frugiperda* in the border areas of Yunnan Province. *Journal of Yunnan University (Natural Science Edition)*, *44*, 1054–1061.

Yin, Y. Q., Li, X. Y., Zhao, X. Q., Wang, M., Liu, Y., Zhang, H. M., Liu, H. A., Qiu, Y., & Chen, A. D. (2020). Activities characteristics of adult of *Spodoptera frugiperda* in autumn and winter season using sexual trapping in Yunnan. *Journal of Environmental Entomology*, *42*, 1338–1343.

Yuan, H., Zhao, X., Ge, S., Huang, X., Liu, J., & Wang, Y. (2017). A new type of *Mythimna separata* (Lepidoptera: Noctuidae) antennal sensilla. *Entomological News*, *127*, 11–20.

Zacharuk, R. Y. (1980). Ultrastructure and function of insect chemosensilla. *Annual Review of Entomology*, *25*, 27–47.

Zahran, N., Hamza, A., & Kandil, M. (2023). Comparative study of antennal sensilla in irradiated male and female fall armyworm, *Spodoptera frugiperda* with gamma radiation. https://www.researchsquare.com/article/rs-2654827/v1

Zhang, Y. J., Chen, D. Y., Chao, X. T., Dong, Z. S., Huang, Z. Y., Zheng, X. L., & Lu, W. (2019). Morphological characterization and distribution of antennal sensilla of *Diaphania angustalis* Snellen (Lepidoptera: Crambidae). *Microscopy Research and Technique*, *82*, 1632–1641.

Zheng, H., Liu, H., Guo, S., Yan, Y., Zong, S., & Zhang, J. (2014). Scanning electron microscopy study of the antennal sensilla of *Catocala remissa*. *Bulletin of Insectology*, *67*, 63–71.

Zhou, Y., Wu, Q. L., Zhang, H. W., & Wu, K. M. (2021). Spread of invasive migratory pest *Spodoptera frugiperda* and management practices throughout China. *Journal of Integrative Agriculture*, *20*, 637–645.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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