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Research paper

Ultrastructure and distribution of antennal sensilla of *Bombus terrestris* (Hymenoptera: Apidae)

Xi Huang [a,1], Xi-lian Xu [a,1], Ru-xu Li [a,b], Su Wang [a], Li-xia Tian [a,*]

[a] Institute of Plant Protection, Beijing Academy of Agriculture and Forestry Sciences, Beijing, 100097, China
[b] College of Agriculture, Yangtze University, Jingzhou, 434023, China

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ABSTRACT

Bombus terrestris (Hymenoptera: Apidae) is an efficient pollinator that is widely used in agriculture. High-efficiency pollination is closely related to antennae. As sensory organs, antennae are of great significance in sensing and perceiving the external environment and information exchange between individuals. However, there remains a lack of comprehensive and systematic research on the antennae of *B. terrestris*. Therefore, we analysed the morphology and distribution of antennal sensilla (chemoreceptors) of *B. terrestris* using scanning electron microscopy (SEM). The total antennal length of *B. terrestris* was 7.0657 ± 0.0388 mm for queens, 5.9113 ± 0.0712 mm for workers, and 6.9727 ± 0.1211 mm for males. Queens and males were found to have seven different sensilla types, whereas workers had only six. Furthermore, the ultrastructure and putative functions of each sensilla type in *B. terrestris*, other bumblebees, and honeybees are described and discussed. These results provide a useful reference and guidance for the study of the pollination behaviour of *B. terrestris* and may explain the preference for some flower visits.

1. Introduction

Sensilla on the surface of insects are key structures to perceive the internal and external environment, including chemical communication, and then produce corresponding behaviours. These behaviours include a series of adaptive behavioural processes, such as searching for flowers of pollinators, host localisation, and oviposition of natural enemies (Schott et al., 2013). Receptive cells in the sensilla contain different types of membrane receptors. Interactions with different types of pheromone molecules can cause insects to undergo different reactions and perform different functions (Carde, 1990). The morphological differences between the sensilla of various insect species show significant differences in function and detected environmental signal types. Each insect has a unique receptor distribution pattern (Schneider, 1964). Therefore, insect taxonomists also regard the morphological characteristics of insect antennal receptors as an important basis for insect classification (Li and Chen, 2010).

Based on the morphological characteristics of sensilla and their distribution on insect antennae, sensilla can be classified as sensilla basiconica (Sba), sensilla chaetica (Sch), sensilla trichodea (Str), sensilla coeloconica (Sco), sensilla placodea (Spl), sensilla squamiformia (Ssq), sensilla campaniformia (Sca), and other types (Schneider, 1964; Tian et al., 2003). Based on their different physiological functions, insect sensilla can be classified as chemoreceptors, mechanoreceptors, temperature and humidity detectors, etc. The same type of sensillum can perform several physiological functions. For example, the Str of *Apis cerana cerana* workers exhibit both mechanical and chemoreceptor functions (Du, 1989).

Bombus terrestris (Hymenoptera: Apidae) is a widely used pollinator for crops, especially for tomato and other *Solanum* species that utilise an unusual pollination system called ‘buzz-pollination’ (Glover et al., 2004). Bumblebee pollination is an indispensable measure for the safe production of green food this pattern can significantly improve crop quantity and quality with a higher efficiency than artificial pollination (Velthuis and van Doorn, 2006). Studies have shown that bumblebee preference for flowers is closely related to flower colour, petal size, shape, and smell (Smith and Raine, 2014; Arroyo-correa et al., 2019; Barazani et al., 2019), but many studies have shown that olfactory signals play a more important role in the specific recognition of flowering plants by pollinators than visual signals (Rachersberger et al., 2019;

* Corresponding author.
E-mail addresses: huangxi03040923@126.com (X. Huang), 377466007@qq.com (X.-l. Xu), 1793318551@qq.com (R.-x. Li), Wangsu@ipepbaafs.cn (S. Wang), tianlixia555@126.com (L.-x. Tian).

[1] These authors contributed equally to this work.

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Raguso, 2008; Rusch et al., 2016; Wakamura et al., 2020). Therefore, For *B. terrestris*, its foraging behaviour is inseparable from the olfactory function of its antennae.

However, while the antennal sensilla of *B. hypocrita* and *B. ignitus* have been studied in detail, regarding the antennae of *B. terrestris,* the research is incomplete (Luo et al., 2011; Luan, 2009; Fonta and Masson, 1982; Spaethe et al., 2007; Fialho et al., 2014). Ågren and Hallberg (1996) observed the flagellar sensilla of bumble bee males. Furthermore, when Anfora et al. (2011) tested the hypothesis of brain and behavioural lateralisation, they measured the number of putative olfactory sensilla in the left and right antennae of *B. terrestris* using scanning electron microscopy (SEM). However, for a deeper understanding of the antennal sensilla of *B. terrestris*, we need to conduct more detailed and specific research on the types of antennal sensilla, how they are distributed, and what functions they play.

Based on the above research background, it is necessary to analyse the antennal sensilla of *B. terrestris*. To understand the types and distribution of sensilla on the antennae of *B. terrestris*, we aimed to 1) analyse the morphology and distribution of various types of sensilla on the antennae of *B. terrestris* queens, workers, and males; 2) compare the antennal sensilla of *B. terrestris* with other bees, and 3) speculate about the function of different types of sensilla. These results will provide a reference for future studies on pollination biology, behaviour, electrophysiology, and taxonomy of *B. terrestris*.

2. Materials and methods

2.1. Insects

Bombus terrestris colonies (obtained from the NongZhiYi Bees Factory, Beijing, China) were raised in an intelligent climate chamber at 28 °C and 55% relative humidity (RH) with pollen and sugar at the Institute of Plant Protection, Beijing Academy of Agriculture and Forestry Sciences, China. None of the bees had left their hives.

2.2. Scanning methods

Samples of queens, workers, and males (eight each) were collected from one colony and used for the analysis. The antennae of the three castes of bees from the antennal fossa were carefully removed using tweezers under an MZ205 stereomicroscope (Leica, Wetzlar, Germany). All specimens were dehydrated in 75% ethanol for 20 min, dehydrated step-by-step with 80%, 85%, 90%, and 95% ethanol for 20 min, and finally 100% ethanol for drying.

The dehydrated specimens were critical-point dried for 1.5 h in an HPC-2 oven (Hitachi, Tokyo, Japan) as described by Zhang et al. (2014). The antennae were coated with gold using an E−1010 ion sputter coater (Hitachi Ltd., Tokyo, Japan) and observed under an S–3000N scanning electron microscope (Hitachi Ltd., Tokyo, Japan). The working voltage was 20 kV. The obtained images were then used for observation and analysis.

2.3. Images analysis

The types of antennal surface sensilla were named and classified according to the morphology and reference to previous studies (Schneider, 1964; Luan, 2009; Gianfranco, 2011). The size of antennae and their sensilla were measured by ImageJ. At least 15 sensilla of the same type were measured to obtain the average value.

3. Results

3.1. Gross morphology of the antenna of B. terrestris

The antennae of *B. terrestris* are geniculate and composed of a scape, pedicel, and ten-segmented flagellum (eleven-segmented flagellum for males) (Fig. 1). The scape is long bone-shaped and connected in the antenna fossa of the head, the middle part is narrow, and the ends are thick. There were obviously few sensilla on the ventral surface of this segment ("the dorsal surface" refers to the opposite side of the two antennae in the natural pose, "the ventral surface" refers to the other side of the dorsal surface in a natural position), and most areas were smooth without sensilla (Fig. 2A, B). The pedicel was the shortest, at approximately 10% of the scape. The flagellum looks cylindrical, the first segment of the flagellum is significantly longer than other segments of the flagellum, and the end of the last segment of the flagellum resembles a dome, with a large number of different types of sensilla (Fig. 2C). The lengths of each segment of the antennae are listed in Table 1. For queens, the length of each segment is longer than that of workers and males, and the total length of males is longer than that of workers.

3.2. Characterization of sensilla

3.2.1. Types of sensilla

Through SEM of *B. terrestris* antennae, seven types of sensilla were observed, including sensilla trichodea (Str), sensilla chaetica (Sch), sensilla placodea (Spl), sensilla coeloconica (Sco), sensilla basiconica (Sba), sensilla campaniformia (Sca), and sensilla margin (Sma) and Böhm bristles. Among them, Str and Spl were the most numerous and widely distributed, and Str, Sch, Sba, and Böhm bristles were long hair structures. Sch was much longer than the other three sensilla, especially Sch B. Under a high-power electron microscope, several sensilla that are similar or have subtypes, such as Str, Sch, and Sba, can also be distinguished by observing the depression of the base, the shape of the end, and whether the surface is smooth. A comparison of sensilla of *B. terrestris* is shown in Table 2.

3.2.2. Sensilla trichodea

Sensilla trichodea (Str) was one of the most common sensilla found on the antennae of *B. terrestris*. They were found in the flagellum but not in the scape and pedicel. SEM showed that there were two types of Str distributed on the antennae of *B. terrestris*. For both subtypes, Str A was much more abundant than Str B. They were hairy, upright, or slightly curved. The end was blunt, the surface of the sensilla was grooved, the basal fossa was round at the base, and they grew at an acute angle with the antennae (Fig. 2D). In contrast, the number of Str B was small. The

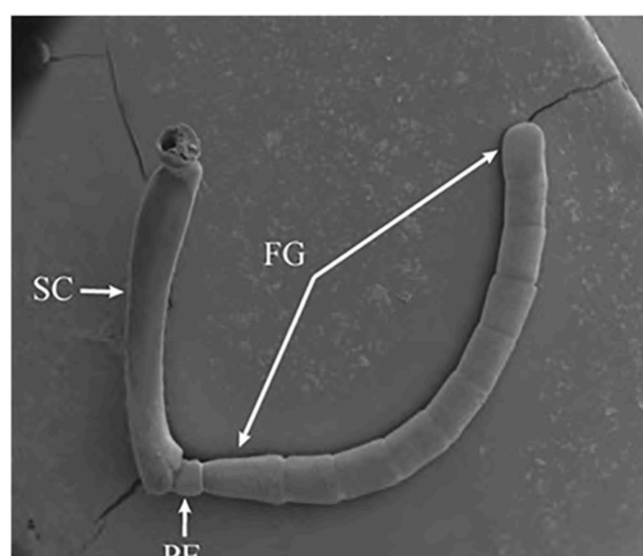

Fig. 1. Scanning electron micrographs (SEM) of the antennae of a queen of *Bombus terrestris*. Scape (SC), pedicel (PE), flagellum (FG), ten flagellar segments (F1–F10).

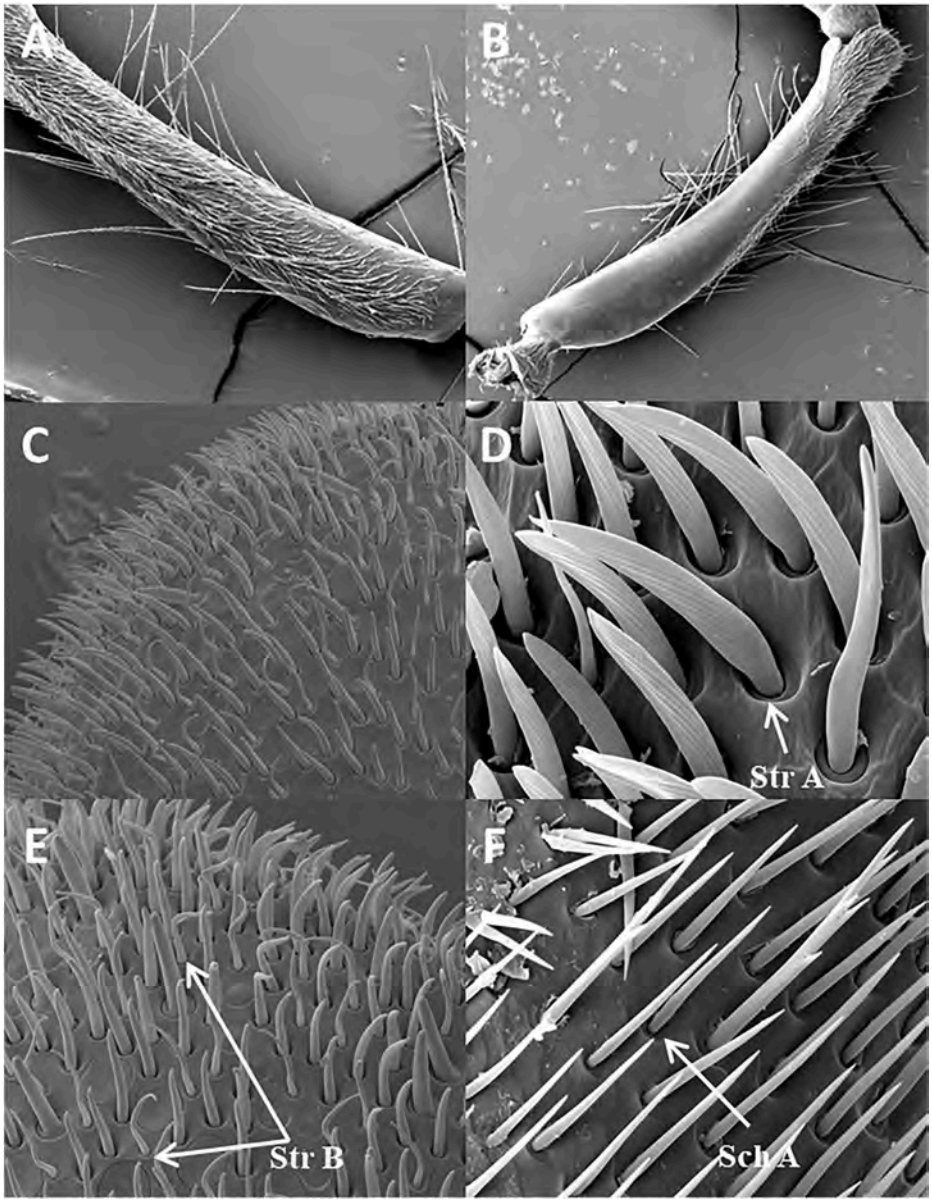

Fig. 2. Antennal sensilla of *Bombus terrestris*: (panel A) abaxial surface of scape of males; (panel B) ventral surface of scape of males; (panel C) the end of flagellum of queens; (panel D) Str A on the flagellum of workers; (panel E) Str B on the flagellum of queens; and (panel F) Sch A on the pedicel of workers.

Table 1
Length of each section of antennae of the queens, workers, and males (mm).

Antennal segments		Queens (n = 16)	Workers (n = 16)	Males (n = 16)
scape		2433.3 ± 25.3	2033.0 ± 28.3	1954.3 ± 41.1
pedicel		201.0 ± 5.7	190.0 ± 5.8	227.7 ± 18.4
flagellum	1	612.3 ± 10.1	514.0 ± 3.1	535.0 ± 13.0
	2	395.0 ± 7.8	327.7 ± 2.1	372.3 ± 4.0
	3	439.7 ± 17.4	367.0 ± 3.3	492.3 ± 8.0
	4	443.3 ± 2.2	368.0 ± 5.4	475.3 ± 5.2
	5	420.0 ± 1.4	365.0 ± 7.4	472.0 ± 4.5
	6	424.0 ± 7.3	340.7 ± 12.0	457.7 ± 14.2
	7	425.0 ± 4.2	343.3 ± 2.4	435.0 ± 14.9
	8	439.0 ± 4.1	341.3 ± 8.8	398.0 ± 12.8
	9	401.0 ± 10.6	333.7 ± 17.9	395.7 ± 13.9
	10	432.0 ± 8.3	387.7 ± 5.8	359.0 ± 12.9
	11	–	–	398.3 ± 18.0
Total length		7065.7 ± 38.8	5911.3 ± 71.2	6972.7 ± 121.1

biggest difference between Str A and Str B is that the former are slender and curved, often bent at 90° or hook shaped, and the bending direction of the end is also inconsistent. There were obvious longitudinal grooves on the surfaces. They were widely distributed in the last segment of the flagellum with shallow basal fossa and had several concentrated areas (Fig. 2E).

3.2.3. *Sensilla chaetica*

Sensilla chaetica (Sch) were distributed in the scape, pedicel, and flagellum, and could also be divided into two types as well as Str. Sch A had a needle-like shape with a thin end. Most of the growth directions were vertical to the antenna surface. They were mainly distributed in the front and end of the pedicel and at each segment of the flagellum. Their surface had obvious longitudinal grooves, but it had detailed differences from Str B because Str B does not have grooves (Fig. 2F). Most sensilla distributed on the scape and pedicel were Sch A. However, Sch B was mainly distributed in the scape and occasionally found in the pedicel but not in the flagellum. Sch B is long with several bifurcations at its thin end (Fig. 3A, B). Consequently, they are called bud-like sensilla (Sb1) or

Table 2
Comparison of antennal receptors of *Bombus terrestris* (n = 15).

Sensilla	Distribution	Length(mm)	Basal diameter(mm)	Depression diameter (mm)	Surface	Numbers
Str A	Flagellum	0.01718 ± 0.00082	0.00278 ± 0.00009	0.00518 ± 0.00020	some wrinkles	++++
Str B	Flagellum	0.01698 ± 0.00064	0.00177 ± 0.00007	0.00354 ± 0.00012	obvious longitudinal lines	++
Sch A	All	0.03742 ± 0.00115	0.00294 ± 0.00014	0.00600 ± 0.00023	obvious longitudinal lines	+++
Sch B	Scape and pedicel	0.11435 ± 0.01136	0.00493 ± 0.00023	0.00182 ± 0.00027	longitudinal lines	++
Sba A	Flagellum 2-the last	0.01181 ± 0.00106	0.00364 ± 0.00020	0.00606 ± 0.00040	longitudinal lines	++
Sba B	Queens and workers, Flagellum 2-the last	0.01568 ± 0.00086	0.00433 ± 0.00011	0.00732 ± 0.00019	Smooth without grain	++
Böhm bristles	Pedicel	0.01895 ± 0.00058	0.00338 ± 0.00015	0.00573 ± 0.00025	Smooth without grain	+
		the major axis (mm)	the minor axis (mm)			
Spl	Flagellum 2-the last	0.01392 ± 0.00022	0.00914 ± 0.00014		The wide edge look like radial groove	+++
		bulges/holes diameter (mm)	depressions diameter (mm)			
Sco	Flagellum	0.00117 ± 0.00009	0.00349 ± 0.00006		–	++
Sca	Queens and Males, flagellum	0.00147 ± 0.00004	0.00611 ± 0.00016		–	+

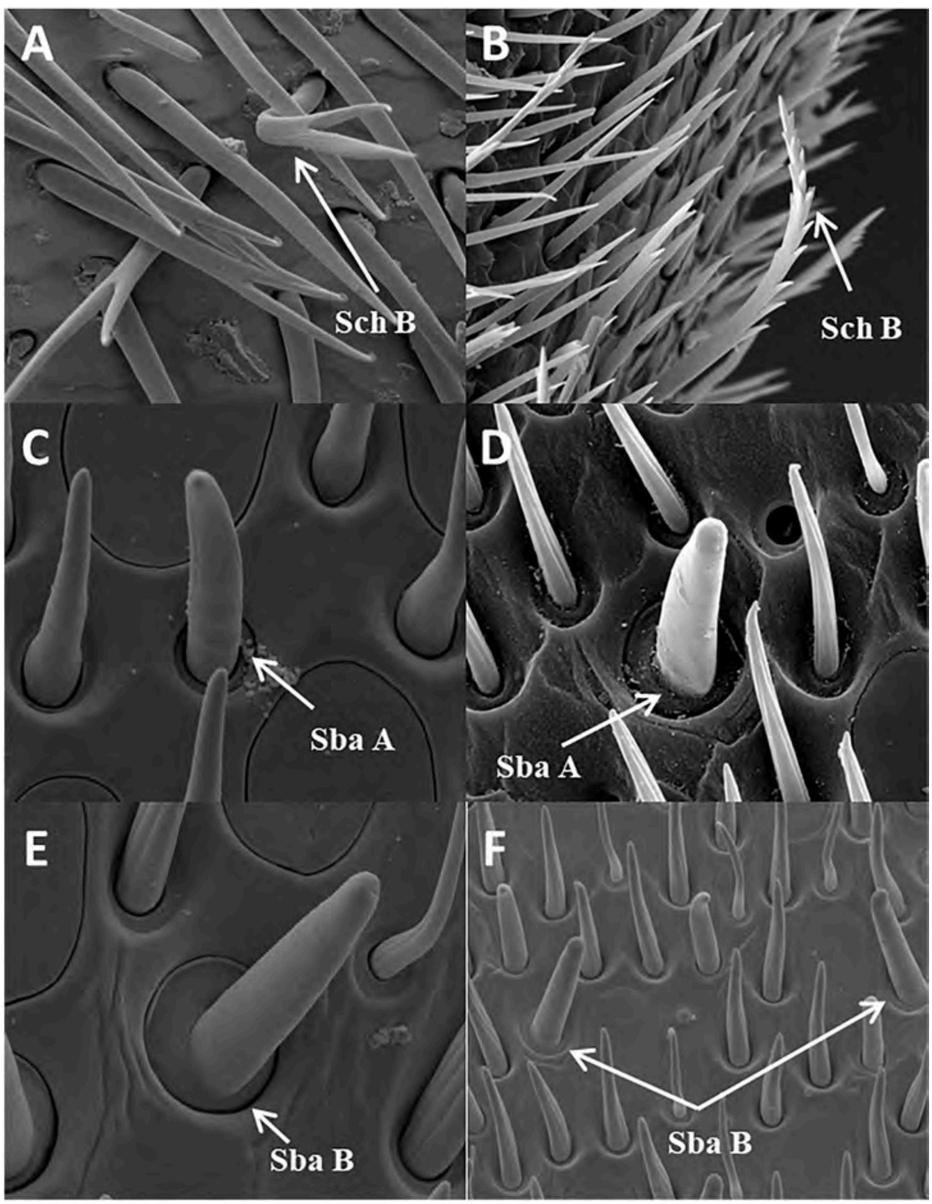

Fig. 3. Antennal sensilla of *Bombus terrestris:* (panel A) Sch B on the scape of queens; (panel B) Sch B on the pedicel of workers; (panel C) Sba A on the flagellum of queens; (panel D) Sba A on the flagellum of workers; (panel E) Sba B on the flagellum of queens; and (panel F) Sba B on the flagellum of queens.

finger-like sensilla (Sfl) (Luo et al., 2011).

3.2.4. Sensilla basiconica

Sensilla basiconica (Sba) was found in the flagellum of *B. terrestris* antennae and was distributed in all flagellomeres. In contrast to the distribution of Str and Sch, Sba is separated by a slight distance. There was no basal fossa at the base, but there was an obvious root circumference, which was thicker than the Str. Sba A was uniformly thinner from the base to the apex and suddenly sharper to the apex of the sensilla in a sharp cone shape. They always grew upright or naturally curved toward the end of the antenna (Fig. 3C, D). Sba A was found in queens, workers, and males, whereas Sba B was found only on the antennae of workers and queens but not on the antennae of males. Unlike Sba A, Sba B is thick and upright, with an expanded base. They had a smooth surface and a blunt end (Fig. 3E, F).

3.2.5. Sensilla placodea

Sensilla placodea (Spl) was distributed in the flagellum of *B. terrestris* but not in the scape, pedicel, or first segment of the flagellum. They were distributed from the second to the last segment, and a large number of them were distributed from the 4th to the last segment of the flagellum (Fig. 4A, B). The Spl has an oval disc-shaped structure with a wide edge and radial grooves on its edge. In the rich area of Spl, many Str, Sch A, Sba, and Sco were also distributed between their rows and in the gaps between sensilla. Spls were evenly arranged on the dorsal surface of *B. terrestris* antennae, with almost no distribution on the ventral surface.

3.2.6. Sensilla coeloconica

Sensilla coeloconica (Sco) was mainly distributed from the 7th to the last segment of the flagellum, occasionally from the first segment, but not in the scape and pedicel. Sco appeared as small holes, and the holes were hollow structures that were mostly distributed near the end of the flagellum. From the antennal plane, the entire cavity of Sco was concave. The middle cavity of the Sco was very different. On the queens and workers, Sco had an almost round, hole shape (Fig. 4C, F), but in the males, there was a bulge around the round hole first and then a depression (Fig. 5A, B), while on the workers, there was a direct depression around the round hole, like the basal fossa of Str and Sch. For

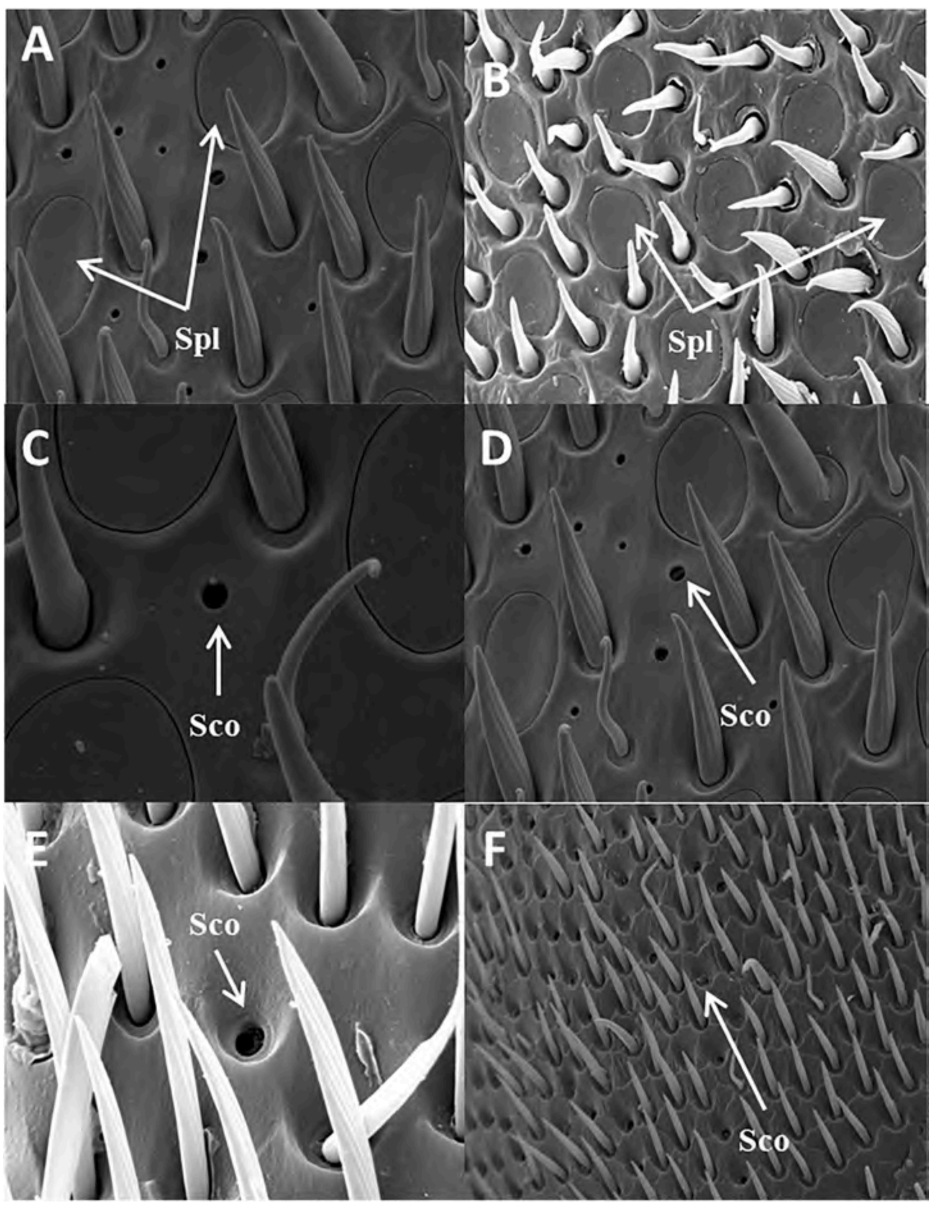

Fig. 4. Antennal sensilla of ***Bombus terrestris***: (panel A) Spl on the flagellum of queens; (panel B) Spl on the flagellum of workers; (panel C and D) Sco on the flagellum of queens; (panel E and F) Sco on the flagellum of workers.

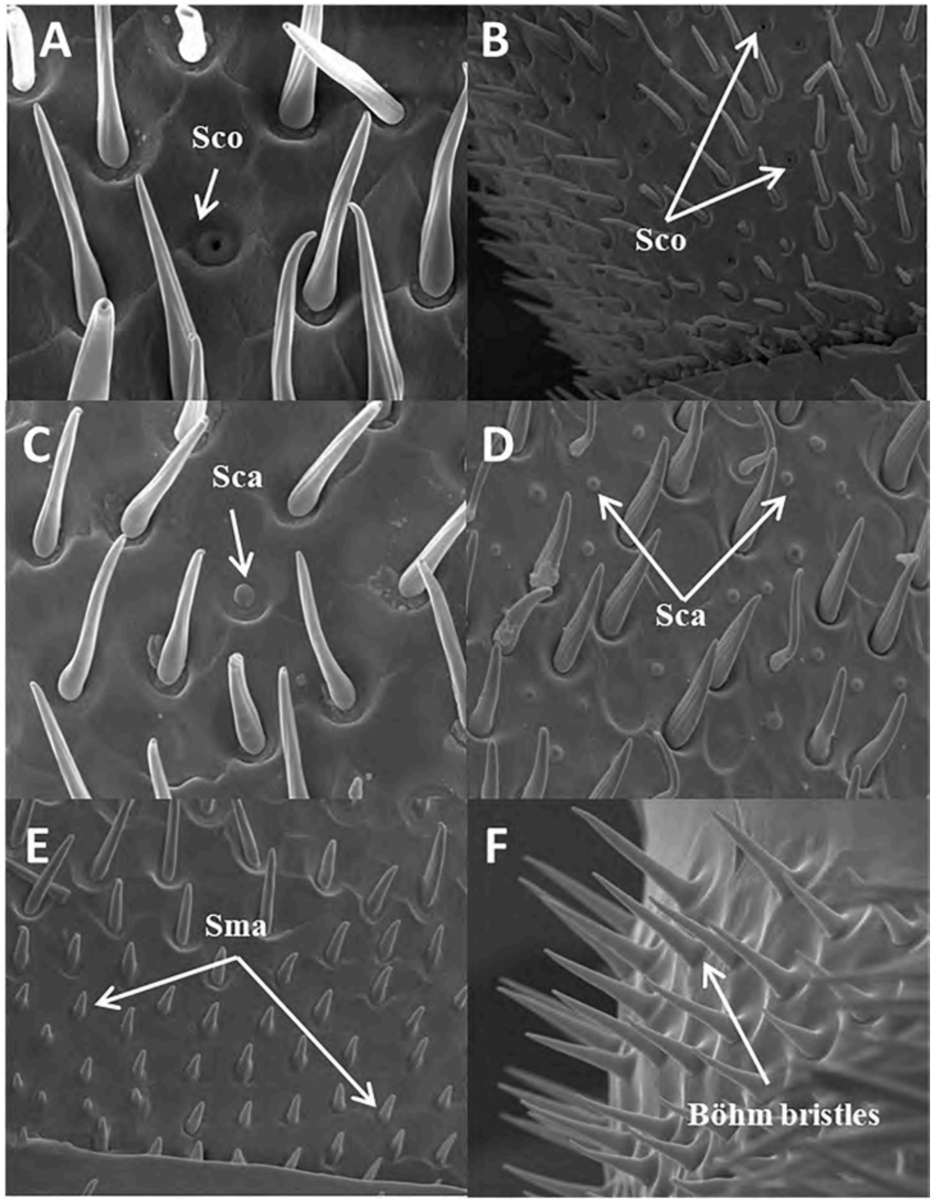

Fig. 5. Antennal sensilla of ***Bombus terrestris***: (panel A and B) Sco on the flagellum of males; (panel C) Sca on the flagellum of males; (panel D) Sca on the flagellum of queens; (panel E) Sma on the flagellum of queens; and (panel F) Böhm bristles on the pedicel of queens.

the Sco of males, there was a circle of thicker protrusions around the round hole, which looked like a ring, making the round hole smaller.

3.2.7. *Sensilla campaniformia*

Sensilla campaniformia (Sca) was mainly distributed in the flagellum of queens and males, especially from the 7th to the last segment, but was not found in workers. Sca is like a button and bulges on the surface of the antennae; however, there is a small circle of depression around some Sca, which is similar to the plane depression of Spl (Fig. 5C, D).

3.2.8. *Sensilla margin*

Sensilla margin (Sma) were distributed in the connecting part between the segments of the flagellum in the antennae of three castes of *B. terrestris*, which were similar to the scaled-down Str or Sba. The end was thin, and there was no obvious groove. The length of the Sma was significantly short, and occasionally only small protrusions were observed (Fig. 5E).

3.2.9. *Böhm bristles*

Böhm bristles were found at the base of the pedicel with a small quantity but not on the scape and flagellum. Their distribution was not as dense as Str and Sch. Böhm bristles were similar to Sch but were shorter and sharper than Sch. They had a uniform thickness and no basal fossa. They were mostly perpendicular to the surface of the pedicel, and the surface of the sensilla was smooth without any grains (Fig. 5F).

4. Discussion

Insects sense the information transmitted by the external environment through various receptors in the epidermis, which leads to foraging behaviour and oviposition sites. Antennae are not only important sensory appendages of insects but are also the main organs to sense or perceive. Sensilla on antennae are the key structures to complete the specific process of feeling and regulate the corresponding behaviour, such as bees' flower visits and feeding. Some studies have focused on worker bees (Du, 1989; Gupta, 1992; Nie et al., 2018). In nature and application, workers usually undertake the function of getting out to collect pollen and nectar. Males mainly mate with queens to reproduce. We examined the antennae of *B. terrestris* queens, workers, and males in our current study.

Insect sensilla consist of formative, sensory nerve, and auxiliary cells that evolved from a mother cell through different cell divisions (Schneider, 1964; Ma and Du, 2000). This homology of sensilla cells indicates that the morphology of some sensilla is too similar to distinguish. In addition, there is no uniform standard for the nomenclature of insect antennal sensilla at home and abroad, resulting in the phenomenon of different names of receptors with similar morphology. For example, through the comparison of electron microscope images, we believe that Sbl and Sfl mentioned in Luo's study (2011) are the same as Sch B in Luan's results (2009), and this kind of sensilla was also named Sch B here.

Str are the most common and numerous sensilla on the antennae of insects. Str is considered an olfactory sensilla in many insects because there are usually many holes on the surface of the sensilla. Electrophysiology examination has shown that chemosensory cells located in the sensillae below these holes receive and detect these odour molecules (Clyne et al., 1997). However, there are also Str without micropores on the surface, which are generally considered to be a kind of mechanical receptor (Baaren et al., 1996; Dweck, 2009). In this study, no pore was found in Str; this may be due to the insufficient magnification of SEM used in this study. In addition, some studies have indicated that Str can sense informational compounds such as sex pheromones and terpenes (Almaas and Mustaparta, 1991; Wu, 1993; Du and Tang, 1995; Jin et al., 2004). Later molecular biology studies found that there are odorant-binding proteins in the Str (Carolina et al., 2018), which can promote the insect to produce olfactory responses to feel the external chemical information (Sachse and Krieger, 2011). This makes it more clear that the Str has chemical sensing function. Str can be divided into various subtypes according to its length, thickness, bending degree, the presence or absence of holes, and the location, and Str A is considered to be a mechanical sensilla (Schneider, 1964; Gren, 1977). These four subtypes can be observed on the antennal flagellum of *A. cerana cerana* and workers of *B. hypocrita* (Zhao et al., 2019; Luo et al., 2011), but only Str A and B were found in *B. terrestris*. Therefore, determining whether olfactory and mechanoreceptor functions are involved will require further study.

Sch is longer than Str and Sba. It has been speculated that it has a mechanoreceptor (Jin et al., 2004). In *B. hypocrita*, it was found that the wall of the Sch was very thick, but there were no pores on the surface. Therefore, we speculated that it was not a chemoreceptor. The single sensilla test also proved that Sch had no response to sex pheromone stimulation but responded to mechanical vibration (Du and Tang, 1995). Cônsoli et al. (2015) speculated that Sch also has the function of localising wasps, which helps with finding the host. In addition, Zhao et al. (2019) did not report the presence of Sch on honeybee antennae. Therefore, Sch may play an important role in sensing the mechanical stimulation of *B. terrestris* and honeybees.

According to Ågren (1978), there was no Sba on the antennae of males of *A. mellifera*, whereas Zhao found Sba on *A. cerana cerana*. Some studies have made ultrathin sections of insect antennae and found that Sba has many small holes. It has been suggested that this type of sensilla is an olfactory sensilla that has the ability to recognise odours (Ochieng et al., 2000; Bleeker et al., 2004; Jin et al., 2004). Slifer and Sekhon (1961) proposed that Sba of *A. mellifera* workers also has olfactory function, and studies have shown that Sba can sense the stimulation of plant odour (Ochieng et al., 2000; Jin et al., 2004; Bleeker et al., 2004). In this study, pores were also found at the top of the Sba of *B. terrestris*, suggesting that they may play an important role in olfactory recognition.

Spl is the most common sensilla on the antennae of Hymenoptera Apoidea (Luo et al., 2011). However, previous research and the results of this study show that Spl does not exist on the ventral surface of the antennae. Some studies have speculated that an area without Spl on the ventral surface may be related to the olfactory sensitivity of bees. For example, the area without Spl on the ventral surface of the antennae of *A. mellifera* is larger than that of *A. cerana cerana*. Therefore, it is considered that this is the main reason *A. cerana cerana* is more sensitive to honey and powder sources than *A. mellifera* (Yang, 2004). The number of sensilla was not compared in this study. Therefore, elucidating whether the area of non-Spl of *B. terrestris* is related to olfactory sensitivity requires further research. In addition, Lacher and Schneider (1963) and Kaissling and Renner (1968) reported that Spl has olfactory function and is sensitive to queens and pheromones secreted from the Nasanov glands; males were more receptive than workers.

Few related studies have been conducted on Sco, Sca, and Böhm bristles. It has been reported that Sco can respond to water and temperature, and the number of sensilla on the antennae of males is higher than that of workers. Yokohari (1983) thought that the Sca of *A. mellifera* could sense temperature and humidity, while Ågren (1978) thought that this type of sensilla might be mechanical and not innervated. In *B. terrestris*, Sca was only found on the antennae of queens and males but not in workers. Therefore, it is possible that Sca is not very helpful to the foraging function of workers but may play an important role in the mating process between queens and males and the oviposition of queens. However, this requires further investigation. Böhm bristles are mechanical sensors that sense gravity (Schneider, 1964); when encountering mechanical stimulation, they can buffer the force of gravity to control the falling speed of the antenna. It is worth mentioning that almost all studies of antennal sensilla have reported that Böhm bristles have no basal fossa. Our study showed that the basal fossa of Böhm bristles was not obvious, but the existence of the basal fossa can be clearly seen in *A. cerana cerana* (Zhao et al., 2019).

Compared with the antennal sensilla of other *Bombus,* they are different in type and distribution. In *B. terrestris*, 7 kinds of antennal sensilla were found, including Str, Sch, Sba, Spl, Sco, Sca, and Sma, and Böhm bristles. Among these sensilla, Str and Spl were the most numerous and widely distributed. In *B. ignitus*, there are 4 main sensilla on the antennae of workers that constitute its olfactory organs, mainly Spl and Sch, and Str and Sco (Wang et al., 2019). In Luo et al. (2011) study on the antennal sensilla of *B. hypocrita*, it was found that 11 types of sensilla were widely distributed on the antennae. In addition to the seven types found in *B. terrestris*, sensillum ampullaceum (Sam), bud-like sensilla (Sbl), and finger-like sensilla (and setae) were also found. In addition, four subtypes of Str were also reported, but only two subtypes of Str were found in our study.

By comparing with the other four bumblebee species (Table 3), we found that there was no significant difference in the length of each segment of antennae between the different castes of *B. terrestris* and these four bumblebees. The antennae of workers were the shortest, and those of queens were the longest and thickest. However, there was little difference between males and workers. In terms of the types of sensilla, previous research results showed that other kinds of bumblebees also have sensilla cylindric (Scy) in addition to Str, Sch, Sco, Spl, and Sba, but they were not found in *B. terrestris* (Luo et al., 2011; Luan, 2009). However, Sca and Sma were also found in *B. terrestris*, which were also found in *B. hypocrita* (Luo et al., 2011), but they had not been reported in Luan's study (2009).

Compared to the antennal sensilla of honeybees, there are more types of sensilla in *A. cerana cerana* than in *B. terrestris*, and there are more subtypes of specific sensilla. Du (1989) found that there were seven types of sensilla on the antennae of *A. cerana cerana*, including Spl, Sco, Sam, Sco, Sba, Str (four subtypes), and Sma, and various types of setae. Zhao et al. (2019) found eight sensilla types. However, the antennal sensilla of *A. cerana cerana* did not exhibit Sch. In addition, they found Sst, which only exists in the flagellum of the antennae of males. Sam is similar to Sco in form. They were adjacent to the antennae of workers; however, the number of Sams was small, and they were only found on the antennae of workers. Such sensilla formed a bean-shaped protrusion in the centre with a small area. Sst was thumb-shaped, short, and thick at the bottom. They were inserted into the mortar fossa and had shallow

Table 3
Antenna length of several bumblebees and two honeybees.

Bees	Caste	Scape length (mm)	Pedicel length (mm)	Flagellum length (mm)	Total length (mm)	Antenna diameter (mm)
B.terrestris (Luan, 2009)	Queens	2.4333 ± 0.0253	0.000201 ± 0.0057	4.4313 ± 0.0172	7.0657 ± 0.0388	0.3426 ± 0.0054
	Workers	2.0330 ± 0.0283	0.000190 ± 0.0057	3.6883 ± 0.0508	5.9113 ± 0.0712	0.2830 ± 0.0036
	Males	1.9543 ± 0.0411	0.000228 ± 0.0184	4.7907 ± 0.0791	6.9727 ± 0.0121	0.2776 ± 0.0038
B. ignitus (Luan, 2009)	Queens	1.9369 ± 0.0218	0.000284 ± 0.0156	3.9384 ± 0.0467	6.2045 ± 0.0120	0.3390 ± 0.0007
	Workers	1.3573 ± 0.0372	0.000231 ± 0.0126	2.9155 ± 0.0901	4.5033 ± 0.01262	0.2750 ± 0.0076
	Males	1.5827 ± 0.0166	0.000231 ± 0.0101	3.9020 ± 0.0477	5.7152 ± 0.0686	0.2759 ± 0.0071
B. patagiatus (Luan, 2009)	Queens	2.5234 ± 0.1175	0.000180 ± 0.0087	3.4730 ± 0.0497	6.1763 ± 0.01514	0.3162 ± 0.0054
	Workers	1.4078 ± 0.0112	0.000126 ± 0.0047	2.5266 ± 0.1294	4.0755 ± 0.01424	0.2407 ± 0.0202
	Males	1.8976 ± 0.0286	0.000173 ± 0.0038	3.6639 ± 0.1309	5.7347 ± 0.01508	0.2786 ± 0.0194
B. hypocrita (Luan, 2009)	Queens	1.7241 ± 0.0310	0.000226 ± 0.0161	3.6888 ± 0.1298	5.6391 ± 0.01766	0.3116 ± 0.0243
	Workers	1.5762 ± 0.0307	0.000203 ± 0.0116	2.9158 ± 0.1251	4.6949 ± 0.01123	0.2576 ± 0.0041
	Males	1.3956 ± 0.0362	0.000220 ± 0.0118	4.0085 ± 0.0912	5.6238 ± 0.01108	0.2893 ± 0.0020
B. lucorum (Luan, 2009)	Queens	2.0410 ± 0.0833	0.000208 ± 0.0125	3.4897 ± 0.0959	5.7388 ± 0.0764	0.2926 ± 0.0020
	Workers	1.7428 ± 0.0361	0.000224 ± 0.0092	3.2650 ± 0.1243	5.2322 ± 0.01351	0.2892 ± 0.0165
	Males	1.5774 ± 0.0365	0.000192 ± 0.0211	4.1903 ± 0.0055	5.9593 ± 0.0523	0.2888 ± 0.0136
A.cerana (Zhao et al., 2019)	Queens	–	–	–	–	–
	Workers	1.2400	0.1500	2.5600	3.9500	0.1900
	Males	0.8000	0.1500	2.8000	3.7500	0.2400

longitudinal lines on their surface (Zhao et al., 2019). This may reflect differences in the flower-visiting strategies used by these species and the role that sensilla play in pollination behaviour. Of *A. cerana cerana*'s two unique sensilla, Sam has been reported to respond to CO_2 using electrophysiological methods (Lacher and Schneider, 1963). Sst has not been reported in Hymenoptera insects. Ultrastructural studies have shown that there are abundant nerve cells in Sst that can sense changes in temperature and humidity (Hallberg et al., 1994), taste, and smell (Feng, 1992). This may indicate that bees are more sensitive to the external environment than bumblebees. However, more research is needed for validation.

Comparing the parasitoid and *B. terrestris*, we found that they also have several identical sensilla. The main types of antennae sensilla of parasitoid include Str, Sch, Böhm bristles, Sba, Sco, and Spl (Zhu et al., 2021). These results are consistent with the antennal sensilla of *B. terrestris*. For example, in Zhang et al. (2014) research on antennal sensilla of the autoparasitoid *Encarsia sophia*, Str, Sch, and Sco were also found, such as in *B. terrestris*. It is possible that they have a common mechanism for sensing temperature and humidity and some changes in the external environment. However, they were significantly different. Zhang et al. (2014) reported several special types of sensilla, including basiconic capitate peg sensilla (BCPS), multiporous, grooved-surface placoid sensilla (MG-PS), uniporous rod-like sensilla (PO-UP), and nonporous finger-like sensilla (FL-NP). These sensilla have also been reported in studies of antennal sensilla of *E. guadeloupae* (Zhou et al., 2013) and *E. amicula* (Wang and Huang, 2007) but not in pollinating bees. For parasitoids, their sensilla should mainly help locate their host and oviposition. Whether they can find and identify the host and parasitise directly determines the survival and reproduction of future generations (Lou and Cheng, 2000). The role of *B. terrestris* sensilla is mainly in the foraging and feeling environment. For example, MG-PS in parasitic wasps has been suggested to play an important role in host location and detection of host-related semiochemicals (Bleeker et al., 2004; Dweck, 2009; Zhou et al., 2013). In addition, *E. sophia* is a parasitoid used for the biological control of *Bemisia tabaci*, which often damages tomatoes. *B. terrestris* is commonly used to pollinate tomatoes. In our unpublished experimental data, *B. terrestris* showed a preference for tomato plants damaged by *B. tabaci*. Therefore, it is also possible that *E. sophia* and *B. terrestris* have similarities in the sensory recognition of tomato volatiles related to *B. tabaci*.

The distribution of the same type of sensilla on the antennae of the different species was slightly different. In terms of the distribution and number of sensilla, *B. terrestris* and the parasitic wasp *E. sophia* have similarities and differences. Specifically, Sch was distributed in the scape, pedicel, and flagellum of *B. terrestris* but was found on the radicula and pedicel only in *E. sophia*. Str were inserted in the flagellum only in *B. terrestris* but were abundant on all of the antennal segments except for the radicula in *E. sophia*. Similarly, Str have a large number in both species. For Sco, they were only distributed on the flagellum of the antennae, but there was only one Sco per antenna in *E. sophia*, while they had a certain amount in *B. terrestris*. Moreover, the morphology of Sco in male and female *B. terrestris* was different. Apart from the obvious differences in lifestyles, phylogenetic differences need to be considered.

5. Conclusion

Together with the nervous system, sensilla regulate and control insect behaviour. They are the structural basis for the insect body to perceive the environment and the information-receiving device for chemical communication. The sensilla on the antennae of *B. terrestris* were studied by SEM. Investigation of the morphology of antennal sensilla of *B. terrestris* showed that, with the exception that Sca only existed in the queen and males, there was no difference in the types and distribution of other antennal sensilla among queens, workers, and males. They were composed of scape, pedicel, and flagellum, and the antennae of the queen were slightly longer than those of the other two. The difference in the lengths of the antennae may be due to the size of the individual species. These results provide a reference and guidance for the study of the pollination behaviour of *B. terrestris* to better provide pollination for crops. In addition, the antennal sensilla of *B. terrestris* were similar to those of other bumblebees but different from those of honeybees and parasitic wasps. The functions of various sensilla were speculated based on previous studies; however, further studies are needed.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data that has been used is confidential.

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