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Original Scientific Article

ULTRAMORPHOLOGY OF ANTENNAL SENSILLA IN THAI SINGLE OPEN NEST HONEYBEES (HYMENOPTERA: APIDAE)

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Abstract

Relatively little known about the sensory morphology of olfactory sensilla in three species of native honeybees that play an important role as pollinators in Thailand. Here we provide a detailed description and analysis of the antennal sensilla ultramorphology of *Apis andreniformis, A. dorsata* and *A. florea* workers using scanning electron microscopy. Each antenna had one segmented scape, a pivoted pedicel and ten-segmented flagellum. There were substantial differences in the density of sensilla, with *A. andreniformis* and *A. florea* having twice the density of *A. dorsata* and nearly four times the density of *A. cerana*. There were eight types of antennal sensilla in *A. dorsata*, including sensilla ampullaceous, sensilla basiconica, sensilla campaniforme, sensilla placodea, sensilla trichodea type A, B, C and D. Only seven types of antennal sensilla were documented on *A. andreniformis* and *A. florea*, as they have no sensilla ampullaceous. The distribution pattern of antennal sensilla of *A. andreniformis* was quite similar to that of *A. florea* but differed from *A. dorsata*. This indicates that the two dwarf honeybees, which are closely related, have similar antennal morphology. *A. dorsata* showed a greater diversity of chemoreceptive antennal sensilla compared to the dwarf honeybees. Thus, *A. dorsata* may have a better ability to sense a diversity of odors than species with fewer types of antennal chemoreceptive sensilla, although this remains to be confirmed.

Keywords: antennal sensilla, flagellum, Thai open single nest honeybee, ultramorphology.

INTRODUCTION

The honeybee antenna functions as an odor receptor. Each antenna consists of one segmented scape, a pivoted pedicel, and a long slender flagellum, which is composed of 10 segments in female queen and workers, and of 11 segments in drones. Sensory organs, or sensilla, on the antennae of honeybees can be distinguished into seven different types. They are the sensilla basiconiba, campaniforme, placodea, and trichodea type A, B, C and D (Agren, 1977; Chapman, 1982). Sensilla placodea are located on the last eight segments of the antennae, register air pressure and have olfactory functions (Crane, 1990; Gupta, 1992).

Honeybees from different castes have different functions in their colony and exhibit different external and internal morphology. This is especially true for olfactory receptors (i.e., antennal sensilla). For example, honeybee queens use their antennal sensilla to perceive colony odors while workers use their antennal sensilla to detect odors such as brood pheromone, floral perfumes, and queen pheromone. Workers can distinguish the odors of plants in bloom (von Frisch, 1967). For drones, the most important use for their olfactory sensilla is to detect queen pheromone. Antennal sensilla also play an important role in detecting various odor types by *A. dorsata* foragers.

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Interestingly, this is the only honeybee species that forages during the day and after sunset (Wongsiri *et al*., 1991; Suwannapong and Wongsiri, 1999). *Apis dorsata* is closely related to two other *Apis* species, also native to Thailand: *A. andreniformis* and *A. florea.* All three species have relatively small colony sizes and construct simple open-air nests on branches of shrubs and small trees. Little is known about their comparative abilities to sense odors or their olfactory sensory physiology. We therefore performed a comparative analysis of the types of olfactory sensilla found in these three species. Such documentation could provide valuable information for future studies examining how lifestyle may influence chemosensory abilities among these three species.

MATERIALS AND METHODS

Ten foragers of *Apis andreniformis* Smith, 1858, *A. dorsata* Fabricius, 1793 and *A. florea* Fabricius, 1787 were collected from the field in Chantaburi province, Thailand. The antennae were removed from the head under a stereo microscope and fixed by Karnowsky solution at 4° C, dried by a 30-100% ethanol grade series. They were then coated with gold in an ion sputtering and examined by SEM (JSM-5410LV). The type and distribution of antennal sensilla were characterized. We present measurements as averages±1 standard deviation.

RESULTS

The antennal sensilla of *A. dorsata*

The antenna of *A. dorsata* workers contained one segment of basal scape, pivoted pedicel and a 10 segmented flagellum (Figure. 1). The total length of the flagellum was 2909.09± 11.28 μm and the first segment was the largest. Sensilla were presented on both dorsal and ventral sides of each flagellum (Tab. I,II). Furthermore, eight types of sensilla were found on the flagellum: the sensilla ampullaceous (pit organ), sensilla basiconica (peg organ), sensilla campaniforme, sensilla placodea (plate organ), sensilla trichodea type A, B, C and D. They were found on the dorsal side (82.7%) more often than on the ventral side (17.3%). The sensilla ampullaceous were found on the dorsal side of the ninth and tenth segment of the flagellum (Figure. 2C, D); however, they were lacking on the ventral side, while the sensilla basiconica occurred on the dorsal side of the fourth to the tenth segments (Figure. 3C, 2A), and on the ventral side of the eighth to the tenth segments, with their number increasing distally.

Sensilla campaniforme appeared sparsely on the dorsal side of the ninth to the tenth segments (Figure. 2C, D) and on the last segment of the ventral side. Sensilla placodea were found on the dorsal side of the third to the tenth segments (Figure. 2C, D) and on the fourth to the ninth segments of the ventral side. However, sensilla trichodea type A were found only on the dorsal end of the first to the third segments and on the first to the second segments of the ventral side (Figure. 3A, B). Sensilla trichodea type B occurred on the dorsal side of the second to the tenth and on the fourth to the tenth segments of the flagellum ventral side (Figure. 3A, C, D). This type was found on the distal ends of the flagellum more than the proximal ends, especially on the last segment (Figure. 2A). Sensilla trichodea type C were found on the dorsal side of the third to the tenth segments and on the fourth to the tenth segments of the ventral side (Figure. 3C, D). Sensilla trichodea type D appeared on the third to the tenth segments of both the dorsal and the ventral sides (Figure. 3D). Setae were also numerous on the ventral side of flagellae (Figure. 3B).

The antennal sensilla of *A. andreniformis*

Each antenna of *A. andreniformis* workers had one segmented scape, a pivoted pedicel and ten-segmented flagellum. There were seven types of sensilla distributed over the flagellum. The total length of the flagellum was 1545.91±5.19 μm. The sensilla were most abundant at the distal end of

flagellae. Sensilla ampullaceous were not found on the flagella segments in this species. Sensilla basiconica occurred on the third to the tenth segments of the dorsal side, and on the sixth to the tenth segments of the ventral side of flagellum. Sensilla campaniforme appeared on only the dorsal side of the flagellum except on the second, the fourth and the seventh segment, where they appeared on both dorsal and ventral sides. Sensilla placodea were found on both the dorsal and ventral sides of the third to the tenth segments. The distribution of sensilla trichodea type A was found on the first to the third segments of the dorsal side and on the first to the second segments of the ventral side. Furthermore, sensilla trichodea type B occurred on both sides of the flagella except on the first segment of ventral side. Sensilla trichodea type C was found on the first to the tenth segments on both sides. Sensilla trichodea type D appeared on the first to the tenth segments of the dorsal and the ventral sides, except on the second segment of dorsal side of the flagellae (Table III, IV).

The antennal sensilla of *A. florea*

Antennae of *A. florea* workers were similar in structure to those of *A. andreniformis* and *A. dorsata*. The total length of the *A. florea* flagellum was 1679.82±4.36 μm. There was seven types of sensilla distributed over the flagellum, just as in *A. andreniformis*. There were sensilla basiconica, sensilla campaniforme, sensilla placodea, sensilla trichodea type A, B, C and D. These sensilla were most abundant at the distal end of flagellae. Sensilla basiconica occurred on the third to the tenth segments of the dorsal side and on the seventh to the tenth segments of the ventral side of flagellum. Sensilla campaniforme appeared very rarely on the third, the fifth, the sixth, the eight and the tenth segments of the dorsal side of the flagellum. None were found on the ventral side. Sensilla placodea were found on the third to the tenth segments of the dorsal and ventral sides of the flagellum. In *A. florea*, the distribution of the four types of sensilla trichodea was similar to those of *A. andreniformis*. Sensilla trichodea type A was found on the first to the third segments of the dorsal side and on the first to the second segments of the ventral side. Sensilla trichodea type B occurred on both sides of the flagella except on the ventral side of the first segment. Sensilla trichodea type C was found on both sides of the first to the tenth segments. Sensilla trichodea type D appeared on the first to the tenth segments of both dorsal and the ventral sides, except on the dorsal side of the second segment (Table V, VI).

DISCUSSION

Antennal sensilla olfactory function of *A. mellifera* was reported by Agren (1977). The following eight types of sensilla were located on the flagellum: (1) sensilla ampullacae (a receptor for carbon dioxide); (2) basiconica (olfactory sensilla); (3) campaniforme (mechanoreceptors); (4) sensilla placodea, (odour receptors); (5) trichodea type A (olfactory sensilla); (6-7) trichodea type B and C (mechanoreceptors), and (8) trichodea type D (gustatory receptors) (Agren, 1977; Schneider and Steinbrecht, 1968). Larger numbers of sensilla occurred on the dorsal side compared to the ventral side in all three honey bee species. They were 81.8%, 59.1% and 52.9% of dorsal sides of *A. dorsata*, *A. andreniformis* and *A. florea*, respectively, while they were 18.2%, 40.9% and 47.1% on the ventral sides of *A. dorsata*, *A. andreniformis* and *A. florea*, respectively. Foragers of *A. dorsata* showed the most abundant and numerous sensilla placodea and trichodea type A as compared to *A. andreniformis* and *A. florea* (Table IX). The antennae of *A. dorsata* were larger than those of the other two species and species with smaller antennae (*A. andreniformis* and *A. florea)* actually had twice the density of sensilla found in *A. dorsata* (Table IX). However, size differences would not account for the

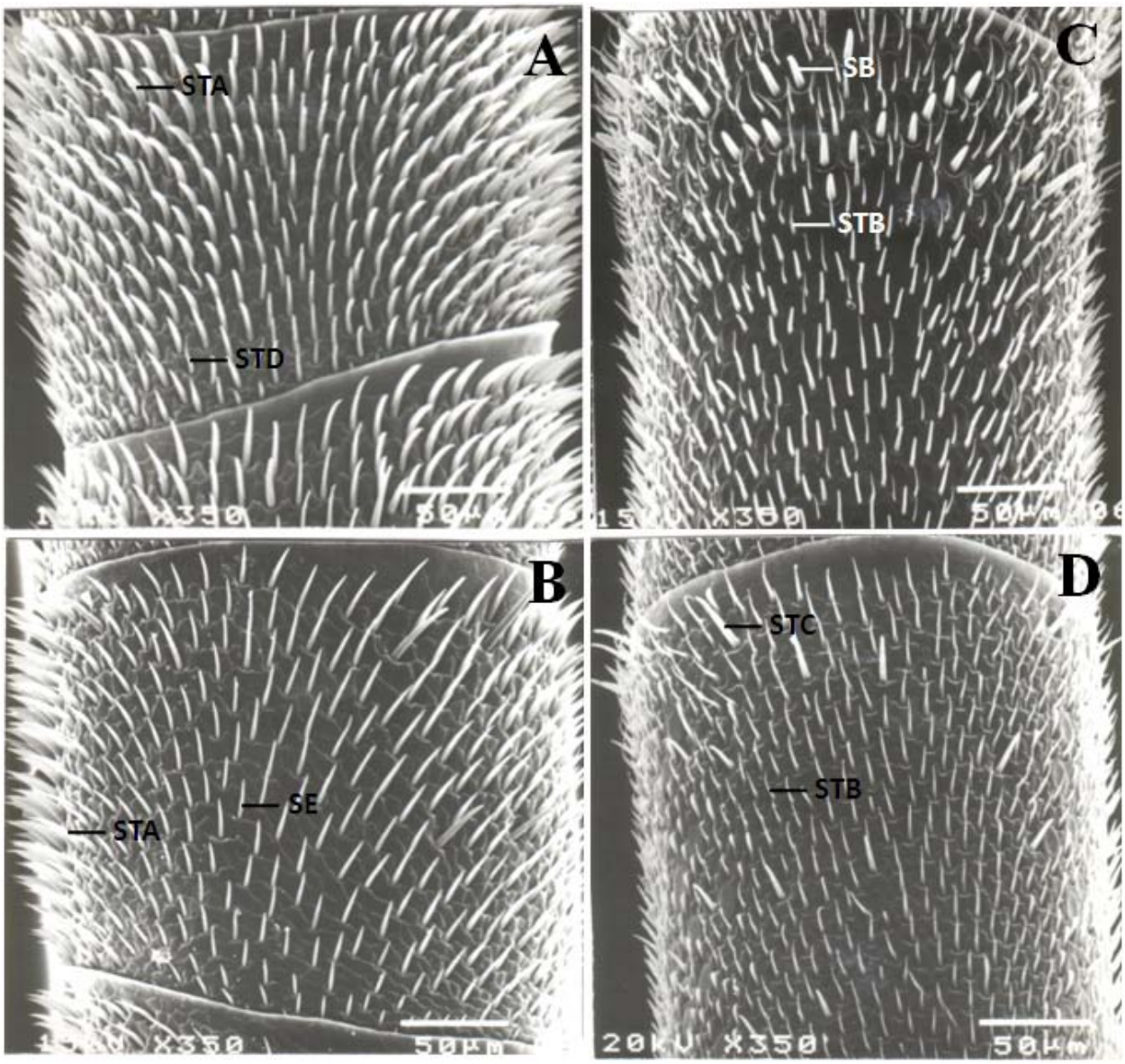

Figure 1. Scanning electron micrographs of the distribution of numerous types of antennal sensilla of *A. dorsata*. **A**. Dorsal side of the second flagellar segment showing sensilla trichodea type A and D. **B.** Ventral side of the second flagellar segment showing abundant setae, few sensilla trichodea type A are present and occur on the segment. **C**. Dorsal side of the seventh flagellar segment, the sensilla trichodea type B distribute at the distal end of the segment and few of sensilla basiconica. **D**. The ventral side of the seventh flagellar segment. (SB: sensilla basiconica, SE: setae; STA: sensilla trichodea type A; STB: sensilla trichodea type B; STC: sensilla trichodea type C; STD: sensilla trichodea type D).

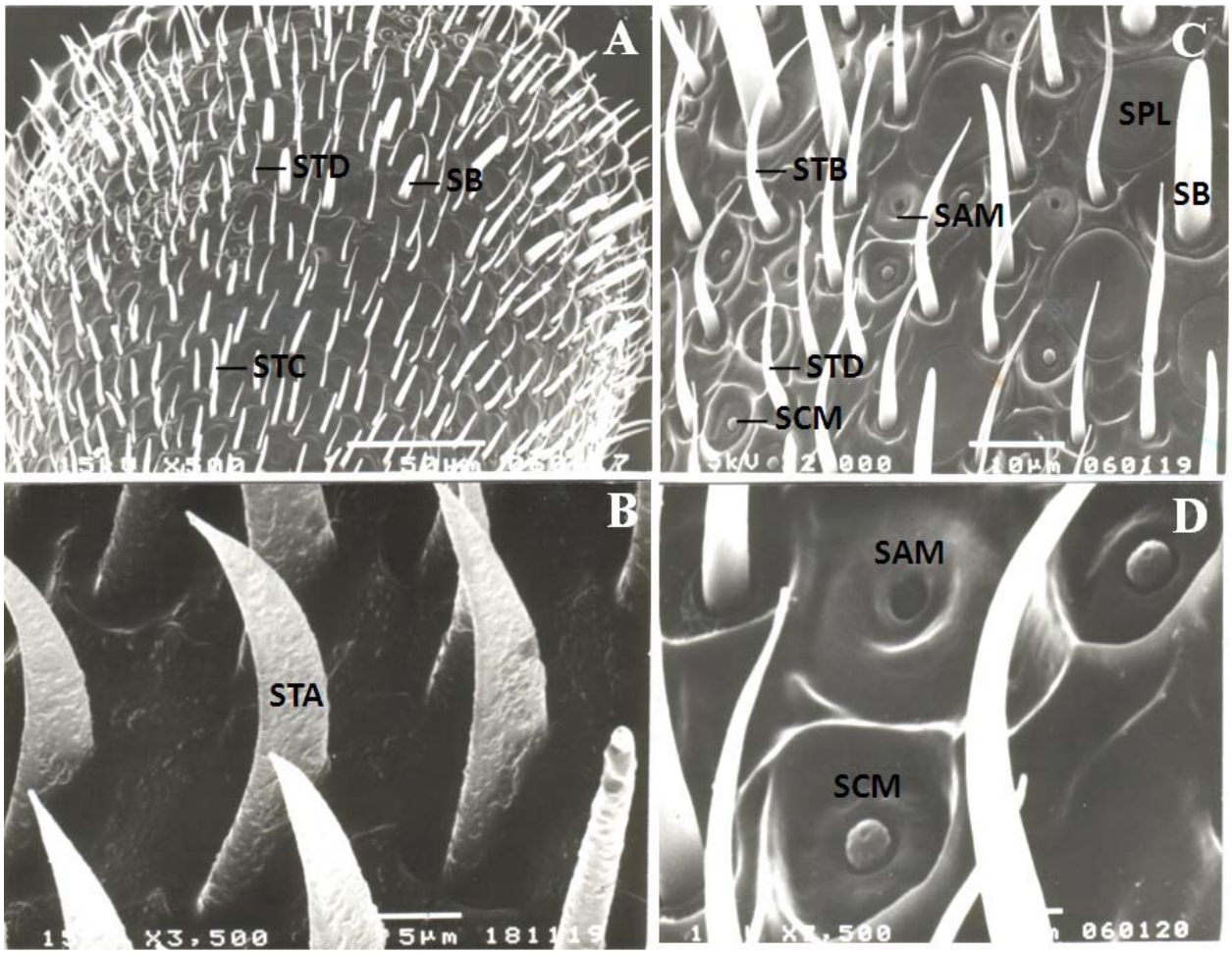

Figure 2. A. The scanning eclectron micrograph of the distribution of numerous types of antennal sensilla on the dorsal side of the tenth flagellar segment of *A. dorsata* worker. **B**. Closed up of antennal sensilla distributed on the dorsal side of the tenth flagellar segment. **C.** The numerous type of antennal sensilla distributed on the dorsal side of the tenth flagellar segment **D.** The dorsal side of the tenth of the flagellar segment show sensilla ampullaceous, sensilla campaniforme (SAM: sensilla ampullaceous; SB: sensilla basiconica; SCM: sensilla campaniforme; SPL: sensilla placodea; STA: sensilla trichodea type A; STB: sensilla trichodea type B; STC: sensilla trichodea type C; STD: sensilla trichodea type D).

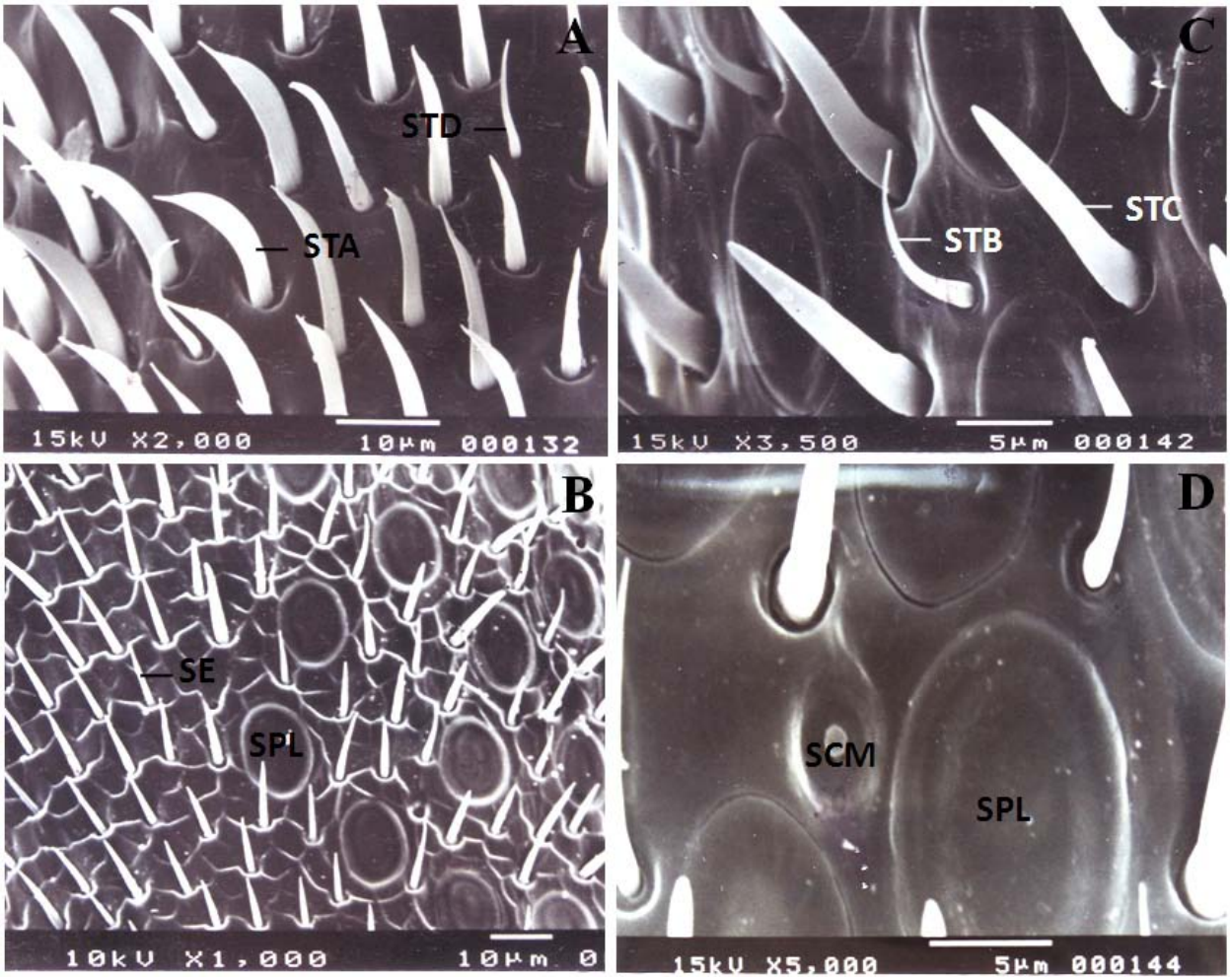

Figure 3. A. The scanning eclectron micrograph of the distribution of numerous types of antennal sensilla on the dorsal side of the second flagellar segment of *A. andreniformis* worker. **B**. Closed up of antennal sensilla distributed on the dorsal side of the eighth flagellar segment of *A. andreniformis* worker comprising of sensilla trichodea type B and type D and sensilla placodea. **C.** The numerous type of antennal sensilla distributed on the ventral side of the seventh flagellar segment **D.** The dorsal side of the ninth segment shows sensilla campaniforme. (SB: sensilla basiconica, SE: setae; STA: sensilla trichodea type A; STB: sensilla trichodea type B; STC: sensilla trichodea type C; STD: sensilla trichodea type D)**.**

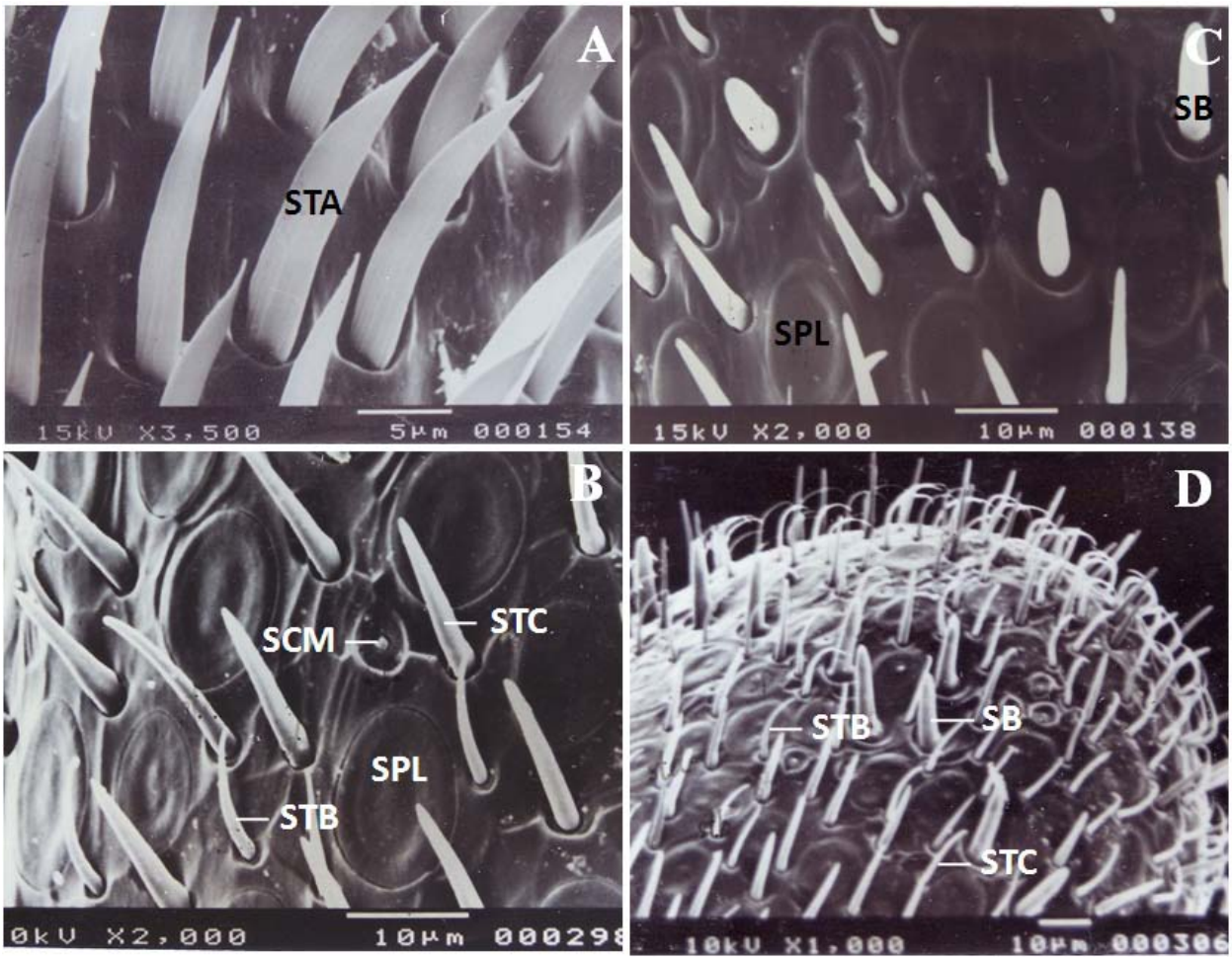

Figure 4. A. Scanning eclectron micrograph of the sensilla trichodea type A distributed on the dorsal side of the second flagellar segment of *A. florea* worker. **B**. The distribution of numerous types of antennal sensilla on the dorsal side of the sixth segment of *A. andreniformis* worker. **C.** The dorsal side of the eighth flagellar segment shows sensilla campaniforme. **D** Dorsal side of the tenth flagellar segment showing numerous types of sensilla. (SB: sensilla basiconica, SE: setae; STA: sensilla trichodea type A; STB: sensilla trichodea type B; STC: sensilla trichodea type C; STD: sensilla trichodea type D).

Table I. Average numbers of antennal sensilla on the dorsal side of flagella of *A. dorsata*

Types of sensilla	Numbers of sensilla on each flagella segment (mean±SE)									
	I	II	III	IV	V	VI	VII	VIII	IX	X
Ampullacae	-	-	-	-	-	-	-	-	1.4±0.5	7.0±0.7
Basiconica	-	-	-	4.0±1.0	4.0±1.0	11.7±1.5	12.7±0.6	18.3±1.50	23.7±0.6	21.4±2.1
Campaniforme	-	-	-	-	-	-	-	-	4.5±0.5	6.3±3.1
Placodea	-	-	351.0±0.30	367.0±34.8	376.3±10.8	315.0±12.1	378.6±22.8	388.6±16.7	378.0±10.1	383.4±6.4
Trichodea type A	313.6±0.6	373.0±4.4	38.0±7.4	-	-	-	-	-	-	-
Trichodea type B	-	12.6± 0.5	17.6±0.6	35.6±2.5	47.3±4.1	114.6±2.5	156.0±14.8	181.6±2.6	197.3±12.8	154.9±7.8
Trichodea type C	-	22.0±12.5	3.3±0.5	4.6±0.7	1.8±0.8	2.50±0.7	9.3±2.5	12.6±1.30	12.3±2.1	25.2±7.3
Trichodea type D	-	-	289.0±3.1	293.0±4.8	351.3±8.5	281.6±8.2	357.0±7.0	369.3±11.3	371.0±46.2	384.6±51.2

Table II. Average numbers of antennal sensilla on the ventral side of flagella of *A. dorsata*

Types of sensilla	Numbers of sensilla on each flagella segment (mean±SE)									
	I	II	III	IV	V	VI	VII	VIII	IX	X
Ampullacae	-	-	-	-	-	-	-	-	-	-
Basiconica	-	-	-	-	-	-	-	10.5±0.5	15.5±0.5	17.6±1.5
Campaniforme	-	-	-	-	-	-	-	-	-	6.3±3.1
Placodea	-	-	-	92.0±9.8	105.3±6.8	115.6±24.5	97.00±6.	84.3±7.4	84.6±9.7	56.4±6.6
Trichodea type A	74.7±2.6	82.7±8.3	-	-	-	-	-	-	-	-
Trichodea type B	-	-	12.3±2.1	17.5±2.8	28.4±4.1	32.3±5.1	25.6±4.2	49.7±2.6	34.3±2.8	43.0±9.8
Trichodea type C	-	-	-	15.7±1.6	7.6±1.1	5.3±0.7	3.0±1.0	2.3±0.7	4.7±0.7	19.6±1.5
Trichodea type D	-	-	17.5±0.6	81.0±4.4	41.7±6.1	57.0±2.6	47.4±3.6	51.7±4.3	36.1±4.5	21.0±6.0

Table III. Average numbers of antennal sensilla on the dorsal side of flagella of *A. andreniformis*

Types of sensilla	Numbers of sensilla on each flagella segment (mean±SE)									
	I	II	III	IV	V	VI	VII	VIII	IX	X
Ampullacae	-	-	-	-	-	-	-	-	-	-
Basiconica	-	-	0.3±0.6	2.7±1.5	2.7±0.6	5.3±1.5	6.3±2.1	8.3±0.6	18.7±1.5	13.7±1.5
Campaniforme	1.7±1.5	-	0.3±0.6	-	0.7±0.6	1.0±1.0	-	1.3±0.6	1.0±1.0	6.3±0.6
Placodea	-	-	81.3±4.9	87.3±5.5	87.7±3.2	96.3±1.5	96.3±2.1	10.3±3.8	88.3±1.5	92.0±4.0
Trichodea type A	53.3±2.1	156.7±6.8	4.3±1.2	-	-	-	-	-	-	-
Trichodea type B	1.7±0.6	7.3±0.6	34.0±4.0	35.3±2.5	37.7±2.5	49.7±2.1	62.3±6.4	86.3±6.0	123.3±5.5	215.3±5.5
Trichodea type C	7.7±1.5	13.3±0.1	5.4±0.6	6.7±0.6	6.3±0.6	7.3±1.5	8.0±1.7	10.3±0.6	19.0±1.0	51.3±4.2
Trichodea type D	25.7±2.5	-	134.7±6.8	136.0±10.6	131.7±2.5	134.3±9.3	125.0±6.6	136.3±15.8	128.7±3.2	111.7±3.5

Table IV. Average numbers of antennal sensilla on the ventral side of flagella of *A. andreniformis*

Types of sensilla	Numbers of sensilla on each flagella segment (mean±SE)									
	I	II	III	IV	V	VI	VII	VIII	IX	X
Ampullacae	-	-	-	-	-	-	-	-	-	-
Basiconica	-	-	-	-	-	0.7±1.2	2.3±0.6	1.3±1.2	0.7±1.2	4.3±0.6
Campaniforme	-	-	-	-	-	-	-	-	-	-
Placodea	-	-	24.3±3.1	31.7±1.6	30.7±2.1	29.3±2.5	30.0±1.0	31.7±2.5	28.3±2.1	22.3±2.5
Trichodea type A	47.0±1.5	66.7±9.6	-	-	-	-	-	-	-	-
Trichodea type B	-	5.3±0.6	19.7±1.5	17.3±1.5	24.3±3.2	37.0±1.0	48.7±3.1	98.3±3.2	145.0±6.58	206.3±4.7
Trichodea type C	5.3±0.6	3.7±0.58	7.0±1.0	5.3±0.6	7.3±0.6	9.3±2.1	10.0±1.0	12.7±0.6	13.3±0.6	43.7±3.5
Trichodea type D	12.3±2.6	73.0±3.6	112.6±13.6	150.7±5.9	168.3±6.0	164.3±2.1	165.3±1.5	123.3±10.9	59.3±2.5	62.3±4.04

Table V. Average numbers of antennal sensilla on the dorsal side of flagella of *A. florea*

Types of sensilla	Numbers of sensilla on each flagella segment (mean±SE)									
	I	II	III	IV	V	VI	VII	VIII	IX	X
Ampullacae	-	-	-	-	-	-	-	-	-	-
Basiconica	-	-	0.3±0.6	1.0±1.0	3.3±0.6	4.3±0.6	7.7±1.5	10.7±2.1	17.7±1.5	15.7±1.5
Campaniforme	-	-	1.0±1.0	-	1.3±0.6	1.0±0.0	-	1.3±0.6	-	6.3±0.6
Placodea	-	-	101.7±4.0	104.7±2.1	95.7±2.1	109.7±5.8	96.3±2.5	108.3±10.2	102.3±2.9	96.0±3.0
Trichodea type A	82.7±2.5	266.0±7.0	18.7±1.5	-	-	-	-	-	-	-
Trichodea type B	1.0±1.0	12.7±1.5	34.0±3.0	41.0±3.0	36.3±1.5	42.7±2.5	59.9±3.1	74.0±2.6	11.3±7.5	323.7±6.03
Trichodea type C	7.7±1.2	7.0±1.0	4.3±0.6	6.0±1.0	10.67±1.5	10.7±0.6	10.0±1.0	12.3±0.6	15.0±1.0	53.3±3.1
Trichodea type D	4.0±1.0	-	161.0±4.6	137.3±6.7	160.33±4.1	163.0±2.6	155.3±4.0	107.7±4.5	176.0±3.0	155.3±4.04

Table VI. Average numbers of antennal sensilla on the ventral side of flagella of *A. florea*

Types of sensilla	Numbers of sensilla on each flagella segment (mean±SE)									
	I	II	III	IV	V	VI	VII	VIII	IX	X
Ampullacae	-	-	-	-	-	-	-	-	-	-
Basiconica	-	-	-	-	-	-	2.0±1.0	2.0±1.0	1.0±1.0	3.0±1.0
Campaniforme	-	-	-	-	-	-	-	-	-	-
Placodea	-	-	30.7±1.2	33.7±1.5	30.3±2.1	43.0±5.6	43.7±1.5	46.7±1.5	44.7±1.5	47.0±2.7
Trichodea type A	22.7±2.1	73.0±4.6	-	-	-	-	-	-	-	-
Trichodea type B	-	1.0±1.7	13.0±1.0	10.7±1.5	25.3±5.1	34.3±2.1	48.7±2.1	55.0±2.7	144.0±3.6	314.0±4.6
Trichodea type C	3.7±0.7	3.7±0.6	7.3±0.6	8.0±1.0	5.3±1.5	8.0±1.0	11.3±1.5	8.7±2.1	15.7±1.5	56.7±2.1
Trichodea type D	23.3±2.5	82.0±2.0	193.0±6.0	223.0±7.0	224.3±5.5	200.0±2.7	206.0±7.9	204.3±5.1	141.7±2.5	63.3±4.0

Table VII Percentages of antennal sensilla found on dorsal and ventral sides

Types of sensilla	Percentages (%) of antennal sensilla found on dorsal and ventral sides								
	A. andreniformis			*A. florea*			*A. dorsata*		
	Dorsal(d)	Ventral(v)	Total (d+v)	Dorsal(d)	Ventral(v)	Total (d+v)	Dorsal(d)	Ventral(v)	Total(d+v)
Ampullacae	0.00	0.00	0.00	0.00	0.00	0.00	0.14	0.00	0.07
Basiconica	1.53	0.47	1.00	1.42	0.00	0.71	1.13	3.17	2.15
Campaniforme	0.21	0.00	0.11	0.15	0.00	0.08	0.17	0.46	0.32
Placodea	22.06	10.19	16.12	22.44	10.23	16.33	47.39	46.11	46.75
Trichodea TypeA	7.42	3.33	5.37	8.96	2.58	5.77	5.55	11.43	8.49
Trichodea TypeB	27.28	25.63	26.46	24.34	27.40	25.87	13.40	14.53	13.96
Trichodea TypeC	4.68	5.88	5.28	4.31	4.54	4.42	0.90	2.80	1.85
Trichodea TypeD	36.82	54.51	45.66	38.39	55.24	46.82	31.31	21.51	26.41
			100.0			100.00			100.00

Table VIII Comparison of mean ±SE number of antennal sensilla among native honeybee species of Thailand

Types of sensilla	Number of sensilla on the antennae of native honeybee species of Thailand			
	A. andreniformis	*A. florea*	*A. cerana**	*A. dorsata*
Ampullacae	-	-	45.0±0.33	8.4±0.67
Basiconica	53.7±4.0	45.0±3.8	48.0±12.5	113.9±0.7
Campaniforme	6.0±1.5	4.7±2.1	16.0±2.7	17.1±0.3
Placodea	841.6±22.6	1002.0±49.6	1316.0±22.6	3537.1±76.1
Trichodea TypeA	281.0±4.1	357.7±5.6	70.67±4.04	501.2±51.1
Trichodea TypeB	1301.7±30.1	1547.9±20.1	1385.1±58.9	1031.1±12.9
Trichodea TypeC	253.1±4.0	265.4±10.2	122.3±17.6	94.7±3.1
Trichodea TypeD	2155.6±78.3	2780.9±41.9	73.4±3.7	2237.5±88.4
Total number of sensilla	*4892.64*	*6003.60*	*3076.47*	*7577.02*

Note: *data of *A. cerana* from Naik *et al*, 1995

Table IX Comparison of density of number of sensilla per square millimeter of flagellum among native honeybee species of Thailand

Species	Radius of antenna(μm)	length(μm)	Flagellum surface area (μm^2)	Density of sensilla/mm^2
A. dorsata	125.0±5.32	2909.09±11.28	2,285,714.29	3,314.95
A. andreniformis	68.8±3.05	1545.91±5.19	668,053.96	7,323.72
A. florea	75.0±4.55	1679.82±6.36	791,915.14	7,581.12
A. cerana	123.33±2.03	1982.96±9.73	1,536,850.66	2,001.80

observation that *A. dorsata* has sensillae ampullacae, known to be sensitive to carbon dioxide, that were not found in the other two species. The other two species likely have other receptors for sensing carbon dioxide.

Although the functional significance of sensillae abundance is unclear, it is possible that the chemoreceptivity of *A. dorsata* foragers is equal, if not greater than, that of the other two species. After collecting nectar and pollen, foragers are assisted in returning to their hive or colony by using sensilla to perceive colony odors. The other role of foragers is to collect honey for their cells, then use their invertase enzyme to convert nectar and pollen to honey in their honey crops and finally use their mechanoreceptor to locate an empty cell for storage of honey. This function coincides with the location of sensilla trichodea type B and C at the end of the flagellum.

Sensilla basiconica, described as peg organs, were found only at the dorsal side of the fourth to the tenth segments of the flagellum. Agren (1977) suggested that this type cannot bend at the socket joint, indicating that it is improbable that this sensilla is a mechanoreceptor. It was also classified to be olfactory sensilla which is connected to a receptor neurons and auxiliary cells (Schneider and Steinbrecht, 1968). The sensilla campaniforme is usually near the sensilla ampullaceous on the distal part of the last two segments. This differs from the dorsal side of the third to the tenth segments of *A. florea* workers, and the first to the tenth segments in *A. andreniformis* workers. On the dorsal side of flagella segments of *A. dorsata* there are 47.39% of sensilla placodea which is considered to be sense of smell or odor receptor, 8.96% in *A. florea* and 7.42% in *A. andreniformis*. The data suggest that *A. dorsata* foragers might have more efficient odor receptors than either *A. florea* or *A. andreniformis*. It is possible that *A. dorsata* workers can detect odor from flowers at longer distances compared to *A. florea* and *A. andreniformis*. In addition it is related to their foraging behavior that their foraging occurs during the day time and continue after sunset (Suwannapong and Wongsiri, 1999).

We compared our data on number of sensilla of *A. andreniformis, A. florea* and *A. dorsata,* which have open air nests, to *A. cerana*, which nests inside closed cavities. *Apis adreniformis* showed higher number of sensilla trichodea type D, a gustatory receptor as compared to *A. cerana* (Table VII). The highest number of sensilla campaniforme, a thermo- and hygroreceptor, was found in *A. cerana,* while the lowest number was found in *A. dorsata*. These differences might be related to their nesting behavior, or perhaps to their evolutionary history or ecological niches. Interestingly, *Apis cerana* show the highest number of sensilla ampullacae, a receptor for carbon dioxide (Naik *et al*., 1995). *Apis dorsata* had a relatively smaller number of the ampullacae than *A. cerana*. Neither of the two dwarf honeybees had these ampullacae. Thus, there is no clear association between nesting (in the open or in cavities) and the ampullacae. We speculate that *A. dorsata* may have an increased sensitivity to carbon dioxide, such as is produced by the breath of predators that reflects a selective pressure that did not occur in the evolution of *A. florea* or *A. andreniformis*. Future investigations may therefore focus on how *A. dorsata* uses, and why it needs, these ampullacae.

campaniforme, sensilla placodea, sensilla trichodea type A, B, C and D. Only seven types of antennal sensilla were documented on *A. andreniformis* and *A. florea*, as they have no sensilla ampullaceous. The distribution pattern of antennal sensilla of *A. andreniformis* was quite similar to that of *A. florea* but differed from *A. dorsata*. This indicates that the two dwarf honeybees, which are closely related, have similar antennal morphology. *A. dorsata* showed a greater diversity of chemoreceptive antennal sensilla compared to the dwarf honeybees. Thus, *A. dorsata* may have a better ability to sense a diversity of odors than species with fewer types of

antennal chemoreceptive sensilla, although this remains to be confirmed.

CONCLUSION

There were substantial differences in the density of sensilla, with *A. andreniformis* and *A. florea* having twice the density of *A. dorsata* and nearly four times the density of *A. cerana*. There were eight types of antennal sensilla in *A. dorsata*, including sensilla ampullaceous, sensilla basiconica, sensilla

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