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Antennal Sensilla of Queen and Worker Giant Honey Bee *Apis dorsata* and Stingless Bee *Trigona laeviceps* in Difference of Density and Ultramorphometric Analysis

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Abstract

Antennal sensilla receive many stimuli from the environment. Thus, it is crucial to study the structure of antennal sensilla, especially in the eusocial bees, such as the honey bee Apis dorsata and stingless bee Trigona laeviceps; both have females, queens and workers with different tasks in their colonies. We aimed this study to describe the types, density, distribution, and ultramorphometric measurements of antennal sensilla of queens and workers of A. dorsata and T. laeviceps. The antennae of ten workers and one queen of A. dorsata and T. laeviceps were analyses using scanning electron microscopy. This study revealed two new sensilla types, chaetica and ceoloconica of A. dorsata workers. We also describe seven new types of sensilla of T. laeviceps workers and queen: trichodea, placodea, basiconica, campaniformia, ampullacea, chaetica, and coeloconica. The current study found caste differentiation in the densities of antennal sensilla: the density of antennal sensilla in the workers is higher compared to the queen, both in A. dorsata and T. laeviceps. Age polyethism in the worker caste presumably shapes the diversity of sensilla. Further, asymmetry distribution was observed in the anterior and posterior sides of the antenna, with the anterior sensilla having nearly twice the density of sensilla compared to the posterior side, in both species of worker caste. In ultramorphometric studies we found that trichodea in A. dorsata workers is larger than that of T. laeviceps workers, while interestingly, the placodea of the giant honey bee A. dorsata is smaller than that of the smaller T. laeviceps.

Keywords: *Antennal sensilla; Apidae, Apis dorsata; Eusocial bee; Trichodea; Trigona laeviceps*

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INTRODUCTION

Insect communications mostly use chemicals such as pheromones, which are released and captured by the antenna, pass through the sensilla pore and transfer the odor molecules to the nervous system. There are several types of sensilla structures and functions such as the hair sensilla are mostly as mechanoreceptor and taste organ, the plate sensilla are as hygroreceptor and pheromone receptor, and the pits sensilla respond to temperature and humidity (Chapman, 1998).

Eusocial bees such as honey bees and stingless bees live in colonies and each colony has castes and certain task. To communicate, they have specific pheromone with different detector pheromone organ in antennal sensilla (Winston, 1987). Antennal sensilla mostly have been studied in the honey bee workers castes such as *Apis mellifera* (Esslen & Kaissling, 1976); (Yokohari et al., 1982); (Frasnelli, Vallortigara, et al., 2010), *A. florea* (Gupta, 1992), *A. andreniformis* (Suwannapong et al., 2012) and *A. cerana* (Ferawati, 2015). However, few of the antennal sensilla in honey bee queen caste have been studied.

Our study first focused on *A. dorsata,* a widely distribute giant honey bee in tropical region (Ruttner, 1988), that lack of information on the type, densities, distribution and ultramorphometric of antennal sensilla of the queen caste. However, in worker of *A. dorsata* had found five types of antennal sensilla i.e., ampullaceous, basiconica, campaniformia, placodea, trichodea and found that basiconica as well as ampullacea sensilla were not found in worker of *A. dorsata* (Suwannapong et al., 2012).

Stingless bee *Trigona laeviceps* is the second bees studied that widely distribute widely in tropical region as well (Sakagami, 1978) and both queen and worker antennal sensilla of *T. laeviceps* are unexplored as yet. Pioneered of the study of structure of antennal sensilla in workers of seven species stingless bee in Neotropical region for *Trigona frontalis*, *T. testaceicornis*, *T. pectoralis*, *T. cupira*, *T. fulviventris*, *T. silvestriana*, and *Lestrimelitta limao* and were found four sensilla types namely trichodea, basiconica, placodea, and campaniformia (Johnson & Howard, 1987).

Besides antennal sensilla structure differentiation, ultramorphometric antennal sensilla also show variations between several species of honey bee, such as *A. mellifera* worker has longer Trichodea compare to those of *A. florea* and vice versa, the worker *A. florea* has wider width area of placodea than in *A. mellifera* (Al- Ghamdi, 2006). In caste analysis, length placodea and trichodea in worker are higher than the queen caste of *Melipona quadrifasciata* (Ravaiano et al., 2014). None of ultramorphometric of antennal sensilla on queen and worker of another stingless bee has been studied. Therefore, in research, we aimed to explore (1) the differentiation of densities, distribution and ultramorphometric of antennal sensilla of worker and queen of *A. dorsata* and *T. laeviceps*; (2) the sensilla densities and distributions between anterior and posterior side of antenna in both bee species.

METHOD

Colony of *A. dorsata* and *T. laeviceps* were collected from field in Sukabumi and Bogor, West Java, respectively. The antennae of adult individual honey bees were taken using insect pins under a stereomicroscope and preserved in 70% ethanol. The antennae used were antennae from queen and worker castes. For scanning electron microscope analysis, the antenna of ten workers and one queen of *A. dorsata* and *T. laeviceps,* were processed for sample preparation using a standard protocol (Goldstein et al., 1992).

Samples were mounted in a coating of gold on stubs. Each antenna was examined by scanning electron microscope (JEOL-JSM-5310LV). The image surface of antenna per segment were recorded using a computer microscope apparatus (Zhou et al., 2013). The 1000-1500× magnifications were used to distinguish types of antennal sensilla, while 350-500× magnifications were used to analyze distributions of antennal sensilla. The number of sensilla were counted manually counted and length of antennal flagellum of queen and workers were measured by using *Image J* software (http: //www.rsbweb. nih.gov/ij).

Analysis Data

Sensilla type analysis

Data were analyzed for types of sensilla of *A. dorsata* were described and classified according to Jung et al., (2014), types of sensilla of *T. laeviceps*: described and classified according Stort & Barelli (1981); Ravaiano et al., (2014). We scanned all flagella segment 3 to 10 in *A. dorsata,* since there are no sensilla in 1-2 segment flagellum in Apis (Frasnelli et al., 2010), however, we scanned sensilla in flagella segment 1-10 in *T. laeviceps* (Stort & Barelli, 1981).

Density and Distribution of Antennal Sensilla

Density and distribution of antennal sensilla of *A. dorsata* and *T. laeviceps* were analyzed in anterior-posterior side of antenna both of caste distribution of sensilla along flagellum segment (Frasnelli et al., 2010; Jung et al., 2014). The values of area distribution were measured per 0.001 mm^2 (Agren & Hallberg, 1996) and the densities of sensilla is the number of sensilla divided by the total surface area of flagellum (Jung et al., 2014);

The Ultramorphometric Analysis

The ultramorphometric of length, width and area of trichodea and placodea, the two highest numbers in each segment, which have more ten number sensilla per segment (Esslen & Kaissling, 1976) were carried out using *Image J* program. The ultramorphometric data of caste and side of sensilla were analyzed with T-test using R program version 3. 1. 3 (CRAN.R–project.org).

RESULTS AND DISCUSSION

Characteristics morphology of antennal and sensilla of *A. dorsata* and *T. laeviceps.*

Antennal morphology of *A. dorsata* (Figure 1) appears longer and straight or angled than the antenna of *T. laeviceps* which appears short and slightly curved (Figure 2). Antennal morphology of *A. dorsata* and *T. laeviceps* (Figure 1 and Figure 2) from stereomicroscopic examination showed of a long basal scape (I), a rounded pedicel (II), and flagellum (III) consist of 10 flagellomeres. The area of flagellum of queen and worker *A. dorsata* were 7.96 mm^2 and 8.16 mm^2, respectively. The area in flagellum of queen and worker *T. laeviceps* were 2.29 mm^2 and 1.94 mm^2, respectively (Table 1).

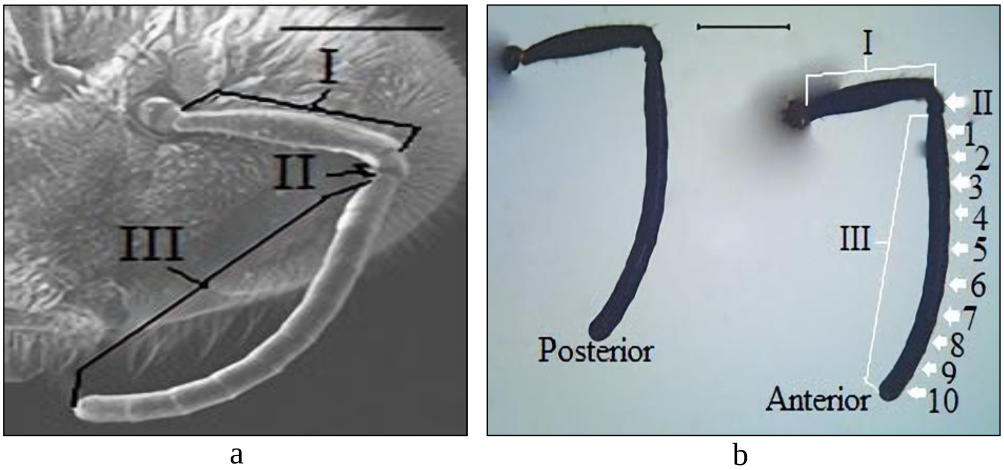

Figure 1. Antenna morphology of *Apis dorsata* worker (a) head with the antenna consists of scape (I), pedicel (II), flagellum (III); (b) anterior and posterior side. Scale Bar is 1mm

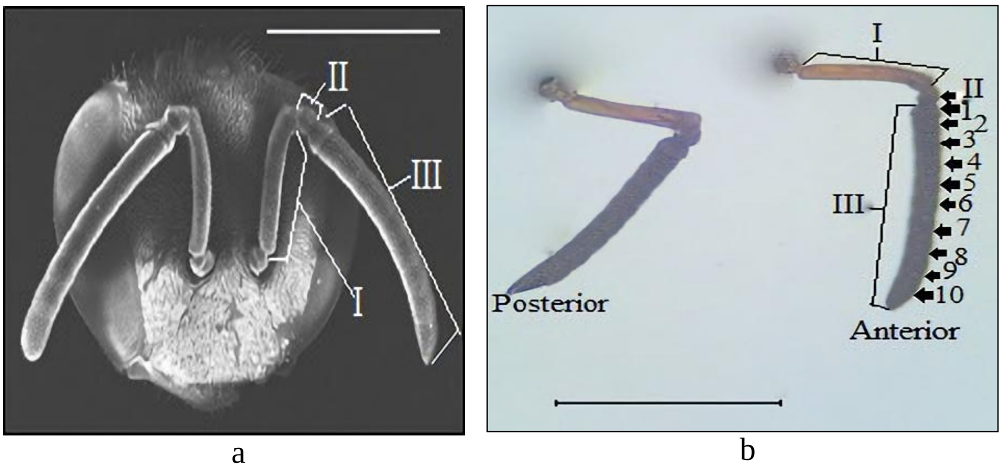

Figure 2. Antenna morphology of *Trigona laeviceps* worker (a) head with the antenna consists of scape (I), pedicel (II), flagellum (III); (b) anterior and posterior side. Scale bar is 1mm

Table 1. Density comparison of number sensilla per mm^2 of flagellum in queen and worker of *A. dorsata* and *T. laeviceps* on anterior and posterior side

	Queen		**Worker**	
	Anterior	**Posterior**	**Anterior**	**Posterior**
A. dorsata				
Number of sensilla	2039	919	5823	3551
Flagellum Area (mm^2)	7.48	8.42	8.21	8.12
Density of sensilla/mm^2	306.02	117.96	694.76	442.99
Percentages of densities sensilla	71.99	28.01	61.06	38.94

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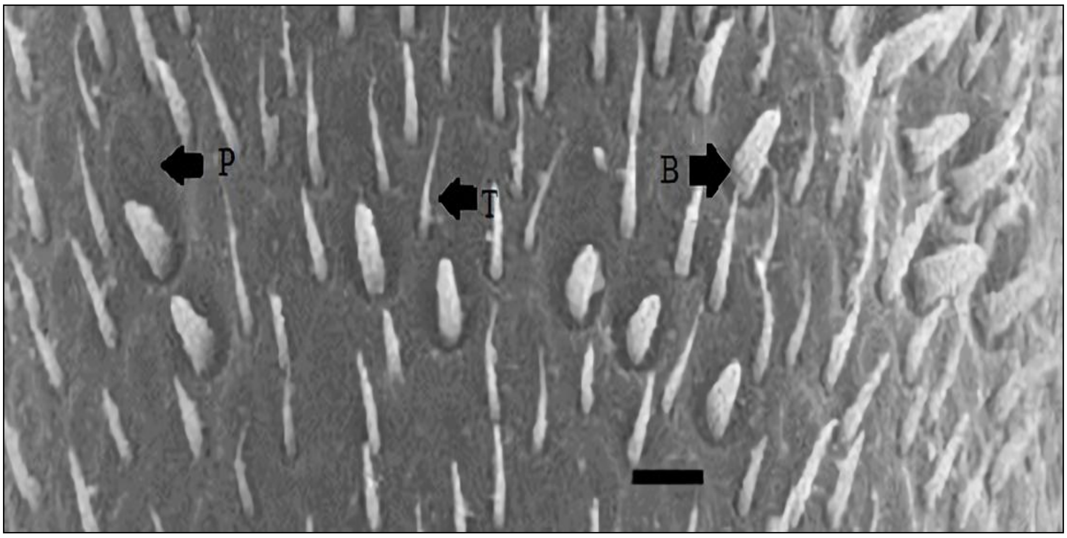
	Queen		Worker	
	Anterior	**Posterior**	**Anterior**	**Posterior**
T. laeviceps				
Number of sensilla	1516	1079	2736	1333
Flagellum Area (mm^2)	2.41	2.17	1.98	1.91
Density of sensilla/mm^2	594.34	477.64	1312.96	657.66
Percentages of densities sensilla	55.44	44.56	66.59	33.41



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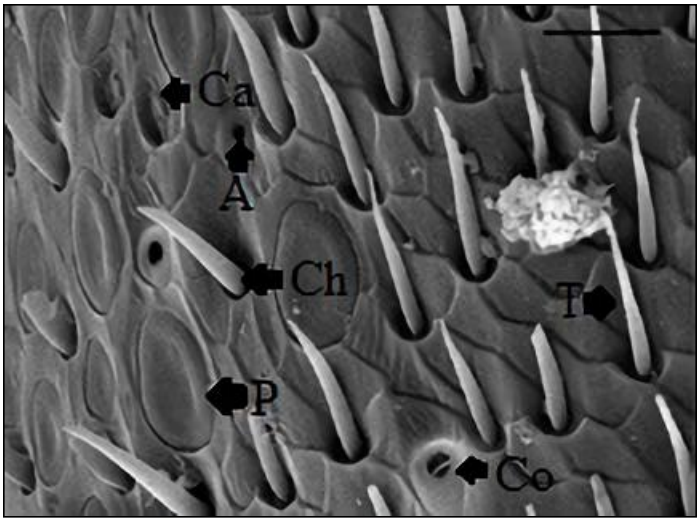

b

Figure 3. SEM of *A. dorsata* sensilla (a) Fl^6 in worker (b); Fl^4 in queen (T= trichodea; B= basiconica; P= placodea; Ch= chaetica; Ca= campaniform; A= ampullacea; Co= coeloconica). Scale bar is 15µm

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Type of sensilla on the surface of flagellum indicated with uses of electron microscope (Figure 3 and Figure 4). We recognize seven types of sensilla in both species: Trichodea, Placodea, Chaetica, Basiconica, Campaniformia, Coeloconica, dan Ampullacea. Trichodea or hair sensory is thick, straight, shorter, thin, longer and narrow to the tip (Figure 3 and Figure 4). These sensilla are the most abundant and present on antenna flagellum in both of species.

Placodea or plates sensory are elliptical or elongated plates on the surface of the cuticle (Figure 3 and Figure 4). Chaetica is a stout sensillum with circular membrane at base and there an apical pore (Figure 3b and Figure 4b). Basiconica is a sensillum with pegs or cones with thick hair and rounded tips (Figure 3a and Figure 4b). Campaniformia showed a circular disc and had a knob-shaped in the center (Figure 3b and Figure 4a). Coeloconica and ampullacea were the pitted organs on the surface of the cuticle. Coeloconica showed a protrude hair sensillum in the center of the pore (Figure 3b and Figure 4a). Ampullacea was an open pore on the cuticle surface of antenna (Figure 3b and Figure 4a).

Types of sensilla in queen and worker of *A. dorsata* were almost different, which the worker have seven types of antennal sensilla; trichodea, placodea, chaetica, coeloconica, campaniformia, ampullacea, and basiconica (Figure 3). The six of type sensilla in worker are also found in queen of *A. dorsata*. Thus, basiconica was absent in *A. dorsata* queen. However, sensilla type in queen and worker of *T. laeviceps* were similar. There were seven types of antennal sensilla where similar results were found only in worker of *A. dorsata* (Figure 4).

Density and distribution of sensilla of *A. dorsata* and *T. laeviceps* in anterior and posterior sides of antenna

Overall, the densities of antennal sensilla in *T. laeviceps* were twice higher than those of *A. dorsata* (Figure 5a) and between castes, the densities of sensilla in workers were higher than in queen in both species (Figure 5b-c). However, the density of coeloconica for queen was higher than worker in both of species (Figure 6e and Figure 7e). Densities of antennal sensilla in anterior were higher than posterior side of antenna in both species and castes (Table 1). Further, in queen of *T. laeviceps* show less percentage different between densities of sensilla in the both sides of antenna compare to densities sensilla in worker of *A. dorsata* (Table 1).

Several differences of the distributions of each sensilla type per antenna segment in *A. dorsata* and *T. laeviceps* were observed. Trichodea was distributed in the Fl^3 of *A. dorsata* flagellum. However, trichodea, chaetica and placodea were found distributed in both sides and in both caste in Fl^2 of *T. laeviceps*. Furthermore, campaniformia, ampullacea and coeloconica do not show any distribution pattern in both species (Figure 6 and Figure 7).

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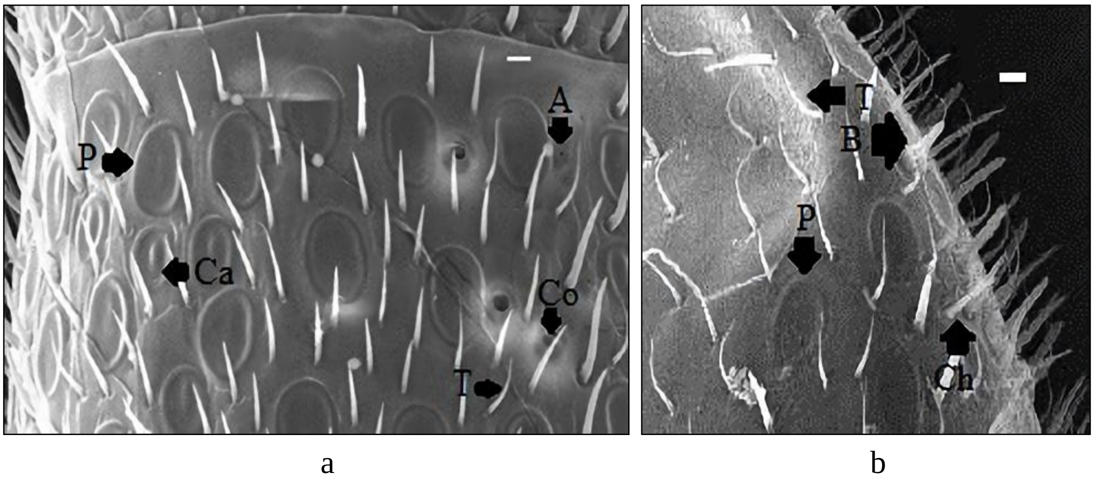

Figure 4. SEM of *T. laeviceps* sensilla (a) Fl^6 in worker (b); Fl^{10} in worker (T: trichodea; B: basiconica; P: placodea; Ch: chaetica; Ca: campaniform; A: ampullacea; Co: coeloconica). Scale bar is 5µm

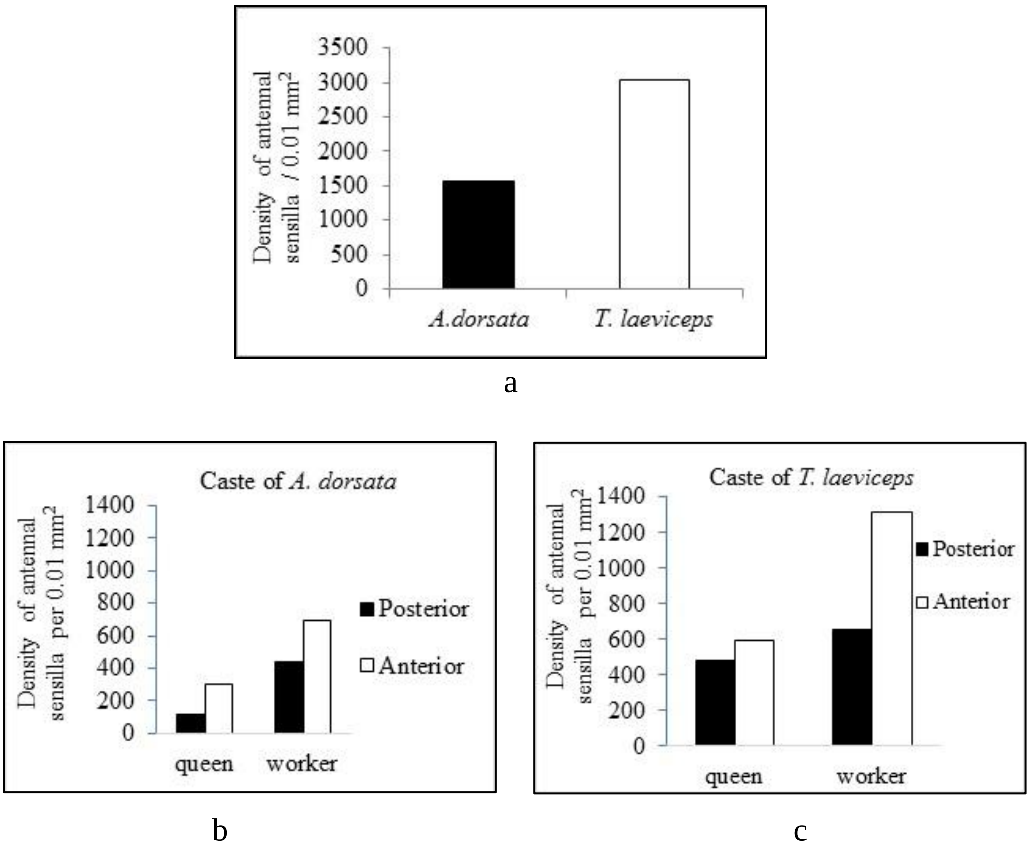

Figure 5. Antennal sensilla density (a) *A. dorsata* and *T. laeviceps*; (b) in antenna side and castes of *A. dorsata*; (c) in antenna side and castes of *T. laeviceps*.

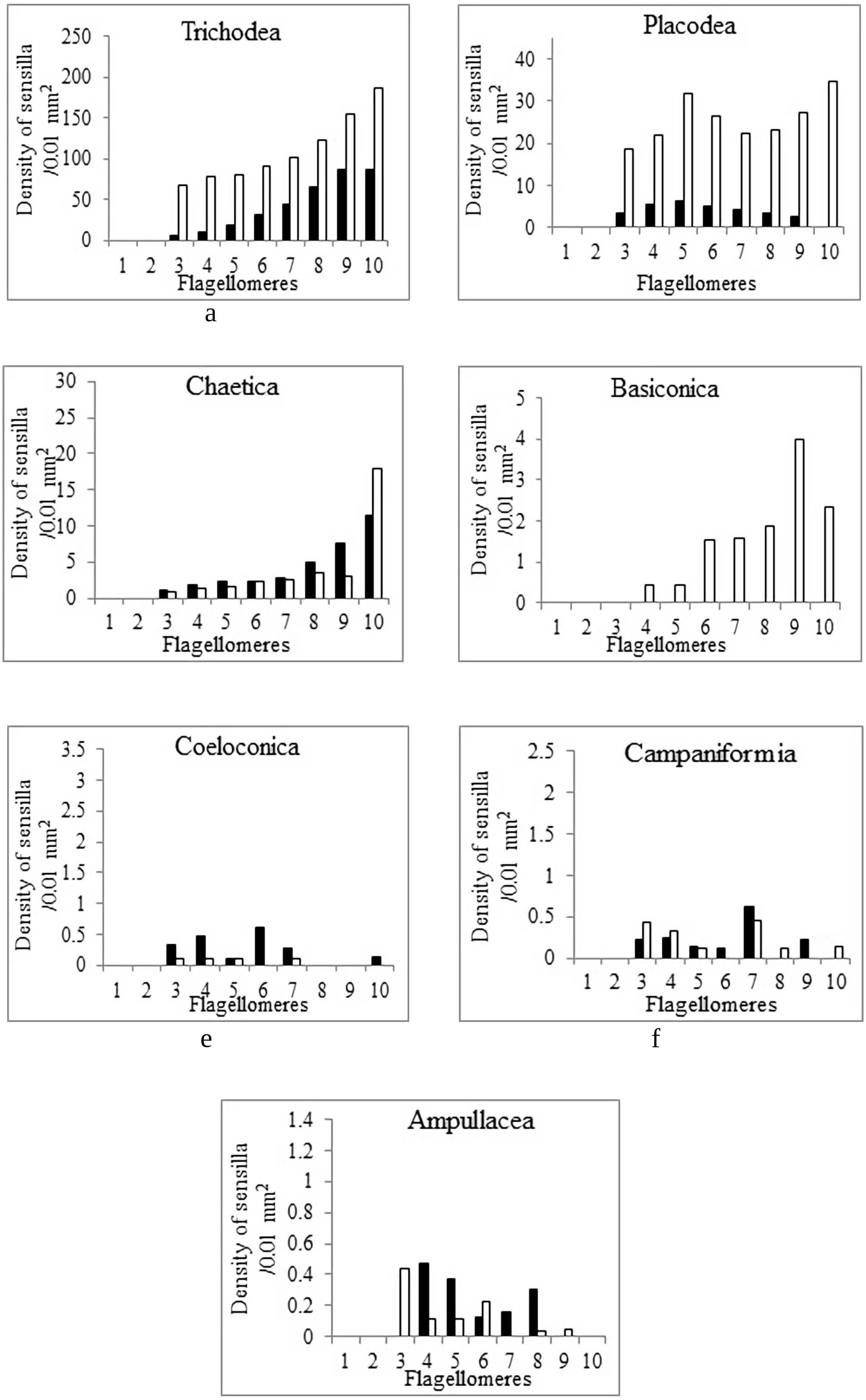

Figure 6. The mean of sensilla density per segment in queen (▪) and worker (▫) of *A. dorsata.* a. Trichodea; b. Placodea; c. Chaetica; d. Basiconica; e. Coeloconica; f. Campaniformia; g. Ampullacea.

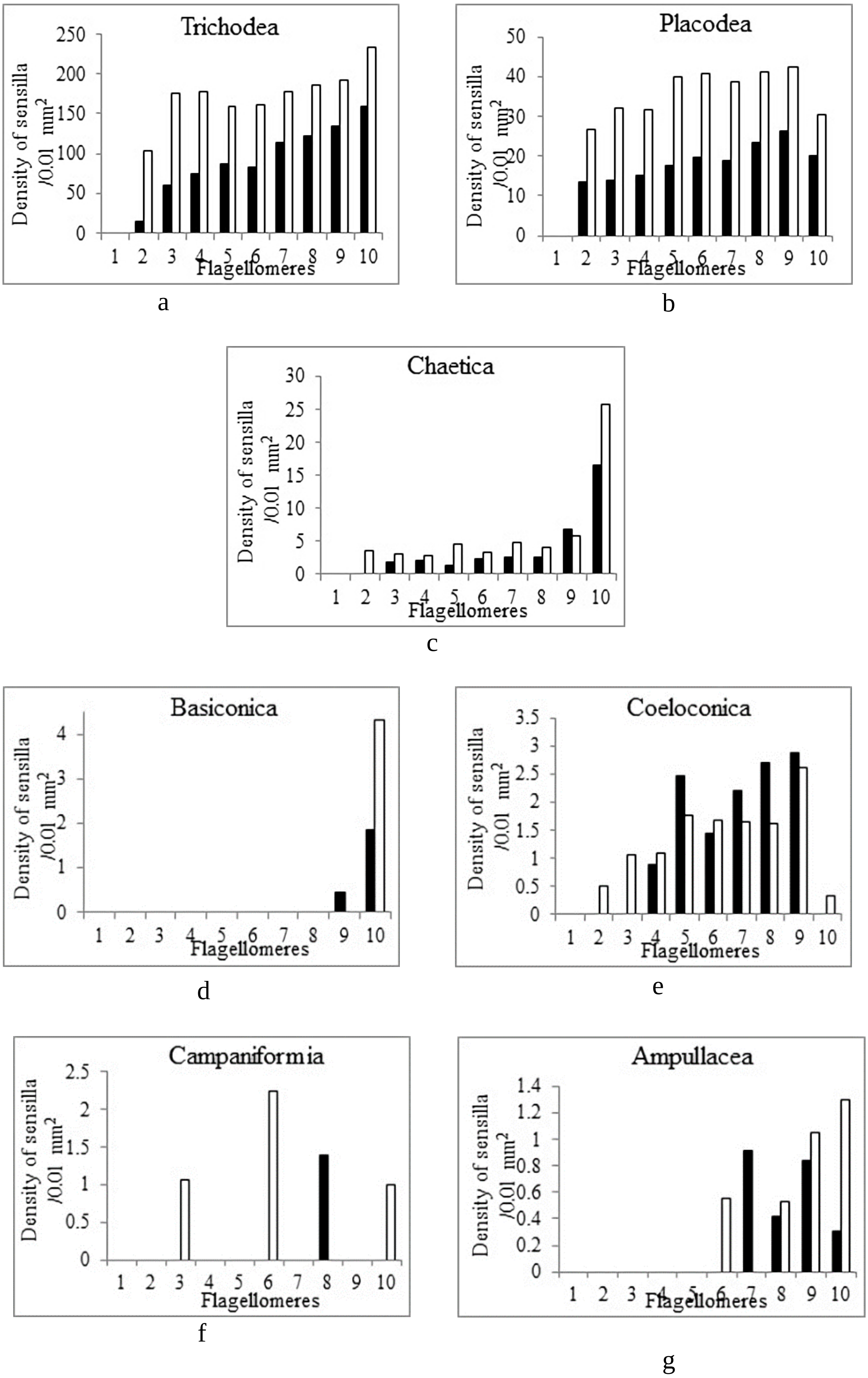

Figure 7. The mean of sensilla density per segment in queen (▪) and worker (▫) of *T. laeviceps*. a. Trichodea; b. Chaetica; c. Basiconica; d. Placodea; e. Campaniformia; f. Ampullacea; g. Coeloconica.

Ultramorphometric variation of trichodea and placodea between queen and worker of *A. dorsata* and *T. laeviceps* at two sides of antenna

The measurement of trichodea and placodea, which are the most abundant sensilla on the antennae of *A. dorsata* and *T. laeviceps*. Both species show the same pattern in length of trichodea with the queen longer compare to the worker (Table 2). Ultramorphometric of measurement trichodea area in queen and worker of *A. dorsata* castes are significantly different ($p<0.05$). However, length and width of trichodea are not significantly different in queen and worker castes. Further, all the three measurements are not significantly in queen and worker of *T. laeviceps* (Table 2).

Both species show the different pattern in area of placodea. In *A. dorsata*, the worker has longer compared to the queen. However, in *T. laeviceps*, the queen was longer than the worker (Table 2). In the queen and worker both of species show the measurement width and area of placodea were significantly different ($p<0.05$). However, the queen and workers castes both of species show the measurement of length not significantly different ($p>0.05$) (Table 2).

Table 2. Ultramorphometric comparison of trichodea and placodea sensilla of the queen and worker castes of *A. dorsata* and *T. laeviceps*

Measurement	*Apis dorsata*			*Trigona laeviceps*		
	Queen	**Worker**	***p* value**	**Queen**	**Worker**	***p* value**
Trichodea						
Length (µm)	21.6 ±3.2	19.8±1.6	p= 0.05	15.4±2.4	14.7±1.7	p= 0.36
Width (µm)	2.0±0.2	2.1±0.5	p= 0.39	1.6±0.2	1.6±0.2	p= 0.47
Area (µm^2)	45.3±6.8	41.0±2.9	p= 0.02	32.6±4.8	31.4±3.5	p= 0.41
Placodea						
Length (µm)	15.3±2.4	16.6±1.0	p= 0.19	18.0±1.4	17.5±2.9	p= 0.17
Width (µm)	6.5±1.2	8.1±0.9	p=0.003	11.6±0.8	10.6±2.9	p= 0.01
Area (µm^2)	36.5±6.3	41.9±3.9	p= 0.04	45.9±2.4	43.6±2.4	p= 0.02

Ultramorphometric in both caste of *A. dorsata* show different pattern in measurement of trichodea both side of antenna. In queen of *A. dorsata*, the measurement length and area of trichodea are significantly different ($p<0.05$) in anterior and posterior side of antenna. However, in worker of *A. dorsata* the measurement length and area of trichodea in anterior and posterior side are not significantly different ($p>0.05$). In contrast with the queen of *A. dorsata*, the worker of *A. dorsata* has significantly different in anterior and posterior side with the measurement width of trichodea, as well in measurement length and area of trichodea. Subsequently, ultramorphometric in *T. laeviceps* show similar pattern in both side and both castes. The measurement of length and area are significantly different ($p<0.05$) and for measurement of width are not significantly different ($p>0.05$) (Table 3).

The difference characteristics of sensilla in queen and workers of *A. dorsata* and *T. laeviceps*

The present study was aimed to examine the types, densities and distribution of antennal sensilla in queen and worker bees of *A. dorsata* and *T. laeviceps* by scanning the surface antenna using electron microscope for the bases of bee's electrophysiology studies (Agren, 1977). Queens and worker in social insect are developed from fertilized eggs; however, they will differentiate their phenotypes depending on the environments and nutrition obtained during larva. Thus, the queen and worker show differences in morphology, physiology, and behavior. One morphological difference between the two castes is the antennal sensilla type, which has been reported in the queen of Asian honey bee *A. cerana* (Ferawati et al., 2015) for the absent of coeloconica. Here, we detected the absent of basiconica in the queen of *A. dorsata*, might possible due to the function of basiconica is needed to recognize odors released by plants (Lopes et al., 2002).

The two castes of giant honey bee also show difference in the most abundant type of sensilla; only two types of sensilla (trichodea and placodea) occurred in the queen, while four sensilla types were observed in the workers (trichodea, placodea, basiconica and coeloconica). In the contrary of *A. dorsata*, we found similar seven types of sensilla in stingless bee *T. laeviceps* queen and workers, namely trichodea, placodea, basiconica, campaniformia, ampullacea, chaetica, and coeloconica, which is a new report for tropical stingless bee. The same type of sensilla between queen and workers were also detected in other Apidae, i.e., stingless bee *M. quadrifasciata* (Ravaiano et al., 2014) and bumble bee *Bombus patagiatus* (Shang et al., 2010). These phenomena also showed in other social insects such as hornet *Vespa orientalis* (Khodairy & Awad, 2013) and carpenter ant *Camponotus japonicas* (Nakanishi et al., 2009).

In terms of sensilla densities, we observed that the density of antennal sensilla in worker is higher than that of queen caste both in our studies of *A. dorsata* and *T. laeviceps*. In agreement with that, the total densities of antennal sensilla in *A. andreniformis* and *A. cerana* workers were higher than that of queen caste (Ferawati et al., 2015) and in the weaver ant *Oecophylla smaragdina* (Babu et al., 2011). This different in densities of antennal sensilla were show different sensory ability in the queen and worker caste. This might be due to the workers perform multi age polyethism inside and outside the colony compare to indoor task of queen that serve to mate, egg produce, and pheromone controller (Winston, 1987).

Our study also elucidates new data for the two sensilla type of *A. dorsata* worker, those are chaetica and coeloconica. Besides them, we observed other five types antennal sensilla of this giant honey bee worker, i.e., trichodea, placodea, basiconica, campaniformia, ampullacea, which have been reported by Suwannapong et al., (2012) as well. The research based on the observation on Fl^1, Fl^2, Fl^3 and Fl^{10} in *A. dorsata* worker, found three of sensilla types namely trichodea, campaniformia and placodea (Kumar et al., 2014).

Table 3. Ultramorphometric comparison of trichodea and placodea sensilla on anterior and posterior sides of the queen and worker castes of *A. dorsata* and *T. laeviceps*

	Apis dorsata					
Measurement	**Queen**			**Worker**		
	Anterior	**Posterior**	**p value**	**Anterior**	**Posterior**	**p value**
Trichodea						
Length (μm)	19.3±2.8	23.9±1.63	0.00	19.5±0.6	20.1±2.1	0.42
Width (μm)	1.9±0.1	2.061±0.2	0.33	2.4±0.3	1.8±0.2	0.00
Area (μm^2)	40.2±5.1	50.3±3.6	0.00	40.8±1.6	41.2±3.9	0.82
Placodea						
Length (μm)	14.3±2.9	16.3±1.6	0.29	16.1±1.0	17.1±0.8	0.04
Width (μm)	6.6±1.4	6.3±0.9	0.68	8.1±0.6	8.2±1.3	0.92
Area (μm^2)	34.9±8.0	38.1±4.3	0.51	39.5±3.1	44.4±3.3	0.02
	Trigona laeviceps					
Measurement	**Queen**			**Worker**		
	Anterior	**Posterior**	**p value**	**Anterior**	**Posterior**	**p value**
Trichodea						
Length (μm)	16.8±2.1	13.9±1.9	0.01	13.5±1.6	15.8±0.8	0.002
Width (μm)	1.6±0.2	1.6±0.1	0.73	0.6±0.2	1.7±0.1	0.59
Area (μm^2)	35.3±4.2	29.9±3.9	0.01	29.1±3.3	33.7±1.9	0.003
Placodea						
Length (μm)	18.5±0.9	17.6±1.7	0.18	17.4±4.1	17.5±1.0	0.94
Width (μm)	11.6±0.9	11.7±0.7^{ns}	0.65	9.7±1.5	11.4±0.9	0.01
Area (μm^2)	45.6±1.8	46.2±3.1	0.63	42.4±2.6	44.8±1.6	0.07

Does antennal sensilla influence by the environment?

Social insect builds a remarkable adaptation in sensing the environments, facilitate by the chemosensory structure like sensilla. Sensilla such as trichodea involve as mechanosensory in honey bee *A. mellifera* (Dostal, 1958) and gustatory receptor in bumble bees (Agren & Hallberg, 1996). Further, placodea is the main olfactory sensilla (Esslen & Kaissling, 1976), coeloconica is important to detect humidity, temperature or other environment parameters for honey bee (Streinzer et al., 2013), and basiconica able to recognize odors released by plants (Lopes et al., 2002).

Regarding their huge size differentiation between the small stingless bee *T. laeviceps* and giant honey bee *A. dorsata,* our result shows that the densities of antennal sensilla are higher in *T. laeviceps* than in the *A. dorsata*. We also suggest that due to *T. laeviceps* lives in a dark cavity nest, they might need more sensory receptors compare to open nesting *A. dorsata*. In agreement with our results, the sensilla density of the cavity nesting honey bee *A. mellifera* is higher compare to the open nesting *A. florea* (Brockmann & Bruckner, 2001). This presumably also because the giant honey bee *A. dorsata* is more adapted in visual and acoustic signal of their nocturnal activity (Kirchner & Dreller, 1993; Somanathan et al., 2009).

Another interesting phenomenon that we observed are the sensilla density of the worker *A. dorsata* and *T. laeviceps* is higher on anterior compare to the posterior side in both species. Similar results the antennal sensilla in anterior side of *A. cerana* and *A. mellifera* were significantly higher ($p<0.05$) than the posterior side (Jung et al., 2014), as well as the anterior sensilla of *A. andreniformis* and *A. cerana* worker were twice higher than that of posterior side (Ferawati et al., 2015). We predict this difference occur due to the anterior antenna are exposed more to the odors release from the environment. In accordance to our result, Frasnelli et al., (2010) revealed that the odor accessed is mainly via the anterior side of left antenna of *A. mellifera,* subsequently will serve as the long-term memory of the bee.

Current study also found the morphometric measurements of placodea of *A. dorsata* is smaller compare to that of *T. laeviceps* which in parallel with that of the same sensilla in the worker of *A. mellifera* and *A. florea* (Al- Ghamdi, 2006). However, the trichodea in *A. dorsata* worker is larger than *T. laeviceps*, which agrees with length measurement in trichodea is higher in *A. mellifera* than *A. florea* (Brockmann & Bruckner, 2001).

The last interesting phenomena we observed in our study are in the first and second antennal segment of stingless bee *T. laeviceps*. We detected placodea, trichodea and chaetica which support by the other stingless bee *Scaptotrigona postica* workers (Stort & Barelli, 1981), although minute number of placodea occurred. Stort & Barelli (1981) proposed that the occurrence of sensilla in the first two segments of antenna presumably related to the trail pheromone communication to reach the food source. In other social insect such as carpenter ant *C. japonicas,* trichodea, basiconica, coeloconica, ampullacea and campaniformia also distribute at first segment (Nakanishi et al., 2009). Thus, he stated that the pattern of sensilla distribution in the first and second segment probably related to the habitats of the social insect species. However, there is disagree and stated that no relationship between the trail pheromone use in communication food to number or density of olfactory sensilla (Johnson & Howard, 1987). Therefore, in the next research, it is tempting to explore further by using electrophysiology and behavioral experiments (Jung et al., 2014), to understand the functional of sensilla arrangement in the first two segments of stingless bee.

CONCLUSION

The type of antennal sensilla found were different between queen and workers *A. dorsata*. A new type of sensila in the worker caste of *A. dorsata* is chaetica dan ceoloconica. Basiconica was not found in the flagellum of queen *A. dorsata*. Queen and workers from *T. laeviceps* have the same type of sensilla. *T. laeviceps* has a higher sensilla density than *A. dorsata*. On caste analysis, workers have higher sensilla density than queens in both species. Distribution Antenna sensilla found more on the anterior side than on the posterior side both of species. Ultramorphometrics of Trichodea show different patterns in both castes and both sides of *A. dorsata* and *T. laeviceps*. Ultramorphometric placodea show the same pattern in both castes and species. Length size trichodea in *A. dorsata* was larger *than T. laeviceps*, whereas in the size of the placodea area in *A. dorsata* was smaller than in *T. laeviceps.*

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