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Research Article

Nest Structure and Pollen Analysis of Honey Bee *Apis koschevnikovi* and *Apis cerana* (Hymenoptera: Apidae) from Belitung

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ABSTRACT

Indonesia is home to several species of honey bees, two of them are *Apis koschevnikovi* the restricted distribution in Sundaland and *Apis cerana* the wide distribution in Asia region. The information on comb cell size, body size, and pollen resources used by *A. koschevnikovi* remains limited, thus we compared comb cells, worker body size, and pollen preferences between sympatric *A. koschevnikovi* and *A. cerana* in Keciput Village, Belitung, Indonesia. We measured the diameter and depth of worker and drone cells, body length, and body weight of worker bees. Pollen samples from honey and corbicula of both species were analyzed using the acetolysis method. We found that the average diameter and depth of *A. koschevnikovi* worker and drone cells were larger and deeper than *A. cerana*. The body size of *A. koschevnikovi* showed the same pattern as the cell size of both species. The pollen types in honey and corbicula collected by *A. koschevnikovi* revealed a greater variety than *A. cerana*. *Apis koschevnikovi* primarily foraged on *Acacia mangium* and *Elaeis guineensis*, while *A. cerana* collected pollen only from *A. mangium*. *Ilex cymosa* and *Syzygium urceolatum* are the local pollen species characteristic of Belitung.

1. Introduction

Honey bee nests are remarkable structures in animal architecture, that composed of combs arranged in parallel sheets of hexagonal cells (Winston 1987; Nazzi 2016). The combs consist of regions that serve as the habitat to rear the brood of honey bee worker and drone larva each in their cells (Michener 1974). Among the brood cells, the worker cells are smaller than the drone cells (Winston 1987; Yang *et al.* 2021), thus show the variation in those diameter and cell depth. Individuals reared in larger cells exhibiting greater body length and weight than those reared in smaller cells (Zhang *et al.* 2024).

The dimensions of brood cell diameter and depth vary across *Apis* species, including *Apis cerana* cerana and *Apis mellifera ligustica* (Yang *et al.* 2021). *Apis cerana cerana* constructs smaller worker cells than *A. m. ligustica*, with average diameter and depth of 4.881±0.007 mm and 9.595±0.066 mm, compared with 5.627±0.008 mm and 12.088±0.040 mm, respectively. Similarly, the diameter and depth of drone cells in *A. c. cerana* (5.706±0.015 mm and 10.533±0.144 mm) were smaller than *A. m. ligustica* (6.718±0.008 mm and 13.776±0.038 mm, respectively) (Yang *et al.* 2021). While studies on *A. c. cerana* and *A. m. ligustica* have provided insights into comb cell size variation, information on other honey bee species, such as *A. koschevnikovi*, has not yet been reported. This information is important due to the availability data can be used for species characterization among *Apis* species (Yang *et al.* 2021).

Apis koschevnikovi distribute in wet primary forests in the low to mid-elevations (Otis 1996; Hadisoesilo

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et al. 2008). Due to the conversion of primary forests into land-use, the populations of *A. koschevnikovi* are declining (Raffiudin and Shullia 2020). Recently, populations of *A. koschevnikovi* have been discovered in Keciput Village, Sijuk Sub-district, Belitung Regency, a location previously undocumented in distribution records (personal observation). *Apis koschevnikovi* was also found to be sympatric with the widely distributed *A. cerana* (Ruttner 1988).

Belitung Island lies at the eastern coast of Sumatra, Indonesia, and comprises diverse ecosystems, including heath and mangrove forests (Hamzah *et al.* 2025). These ecosystems provide abundant nectar and pollen resources, which are suitable for honey bees (Bramasta *et al.* 2023). The availability of these floral resources is essential for honey bee colonies sustainability, largely depends on surrounding food resources, particularly pollen (Di Pasquale *et al.* 2013). Pollen is a primary protein source for bees, containing lipids, minerals, and vitamins (Herbert and Shimanuki 1978), which are essential for larval growth and development (Winston 1987). Therefore, the presence of flowering plants in the surrounding environment is crucial as a continuous source of pollen (Van Drunen *et al.* 2022). Pollen mainly can be found in the hind leg of worker bees namely pollen baskets or corbicula (Hodges 1967), subsequently stored as bee bread in comb cells (Fernandes *et al.* 2024), and can be collected in honey (Layek *et al.* 2020). Melissopalynology, the study of pollen contained in honey (Louveaux *et al.* 1978), and corbicula pollen analysis are required to determine the plant origin of the pollen. This analysis provides insights into bee forage plant preferences and highlights the importance of plant diversity in maintaining the sustainability of bee populations (Mramba 2025). Identification of honey pollen (Sayusti *et al.* 2026) and corbicula pollen (Raffiudin *et al.* 2022) in *A. cerana* has been conducted. However, no studies have yet examined honey and corbicula pollen in *A. koschevnikovi*. Accordingly, considering the discovery of the *A. koschevnikovi* colony in Belitung and the abundance of bee forage plant species on the island, further research is needed to support the sustainability of the bee colony.

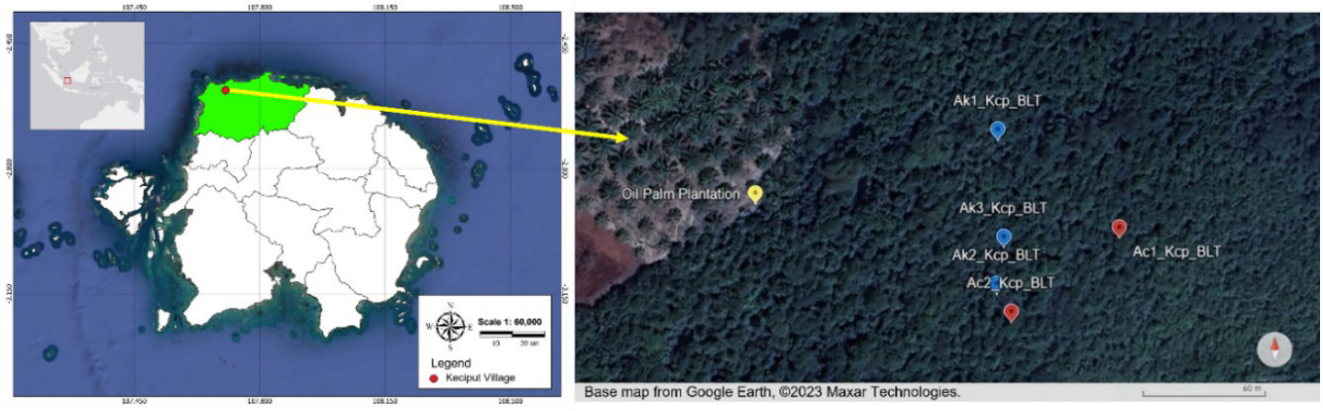
Therefore, the first part of this study aimed to analyze the worker and drone cell sizes of *A. koschevnikovi* and *A. cerana* as well as their body length and body weight in Keciput Village, Sijuk Subdistrict, Belitung Regency, Indonesia. Secondly, we conducted a survey of foraged plant preferences of both cavity-nesting honey bees by identifying the pollen found in honey and corbicula.

2. Materials and Methods

2.1. Sample Sites and Collection

We collected three and two colonies of *A. koschevnikovi* and *A. cerana*, respectively, from the beekeeping Nirun Mandiri Sejahtera at Keciput Village, Sijuk Sub-district, Belitung, Indonesia (Figure 1A, Table 1). The bee colonies are located in the heath forest, less than 150 m from an adjacent oil palm plantation (Figure 1B).

Each colony of *A. koschevnikovi* and *A. cerana* had three combs to measure the comb cell size of the workers and drone bees (Figure 2A and B), and ten worker bees were collected to measure body length and



A B

Figure 1. Sampling sites (A) Belitung Island, (B) Location of *A. koschevnikovi* (Ak) and *A. cerana* (Ac) colonies in the heath forest at Keciput, Belitung, located less than 150 m from an adjacent oil palm plantation. The number following the species abbreviation indicates the colony number. Kcp: Keciput; BLT: Belitung

weight. Honey was collected 100-250 mL per colony from the honey portion of the comb that had not been harvested within three months. The wax that capped the honey part was sliced to release the honey (Raffiudin *et al.* 2024). Pollen corbicula was collected from ten worker bees per colony for each species at 7:00 a.m. Worker bees carrying pollen in their corbiculae were carefully collected using fine forceps and placed into 1.5 mL tubes.

2.2. Measurement of Worker and Drone Cell Size, Body Length, and Body Weight

Three combs per colony were photographed using Sony A6400 Camera and the diameters of worker and drone cells were measured based on the photos of the comb by using ImageJ software (https://imagej.net/ij/). Cell depth of drone and worker in both species were measured using a digital caliper. The bees were photographed using an Olympus SZ-61 stereomicroscope equipped with an Optilab Viewer 2.2 camera and the body length were measured with Image Raster software (https://imageraster.software.informer.com/). The body weight of adult worker bees (imago) was determined using a digital scale. Each colony was measured to compare differences between species and among colonies of the same species.

Table 1. Samples of *A. koschevnikovi* and *A. cerana* from Keciput Village, Sijuk, Belitung

Colony ID	Coordinates
Ak1_Kcp_BLT	S 02°35'31.0" E107°41'54.9"
Ak2_Kcp_BLT	S 02°35'32.8" E107°41'54.9"
Ak3_Kcp_BLT	S 02°35'31.8" E107°41'54.9"
Ac1_Kcp_BLT	S 02°35'31.9" E107°41'56.3"
Ac2_Kcp_BLT	S 02°35'32.6" E107°41'55.0"

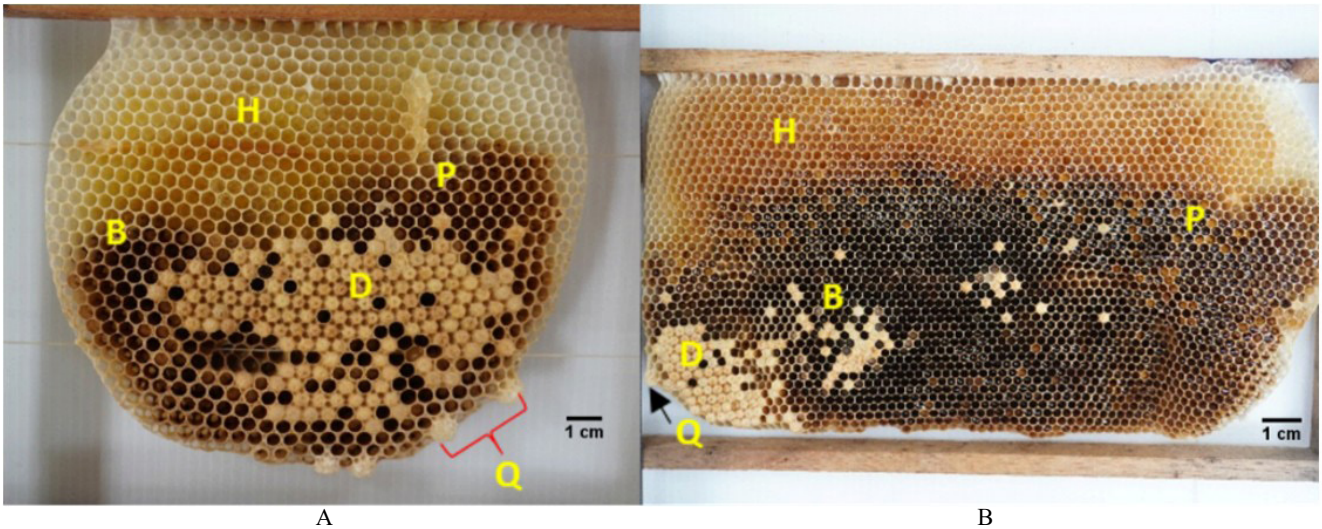
Colony ID: Ak = *Apis koschevnikovi*, Ac = *Apis cerana*, the number following the species abbreviation indicates the colony number. Kcp = Keciput, BLT = Belitung. Collectors: Rika Raffiudin, Hidayatus Sholihah Tisniasari, and Tiara Sayusti

2.3. Pollen Preparation for Identification

Melissopalynological and corbicula pollen analyses were conducted to examine pollen contained in honey and pollen collected in corbicula by both species. Pollen from honey samples was obtained by dissolving 3 mL of honey in distilled water, centrifuging, and treating the residue with glacial acetic acid to isolate pollen grains (Louveaux *et al.* 1978). Pollen from the extracted honey and corbicula pollen underwent acetolysis to reveal pollen morphological characteristics (Erdtman 1960). Acetolyzed pollen grains were transferred onto slides for microscopic observation and counted until a total of 1,200 grains per sample (Louveaux *et al.* 1978). Identification was conducted by using references (Huang 1972) and the databases: Australian Pollen and Spore Atlas (APSA) (https://apsa.anu.edu.au/), Palynological Data (https://www.paldat.org/), and the Global Pollen Project (https://globalpollenproject.org/Taxon). Observation, counting, and documentation of pollen were carried out using an Olympus CX-33 compound microscope equipped with an Optilab Viewer 2.2 camera.

2.4. Statistical Analysis

The differences in cell diameter and depth, body length, and body weight were analyzed using ANOVA followed by Tukey post hoc test in R software (R Core Team 2022).



A B

Figure 2. Honey bee comb of (A) *A. koschevnikovi*, (B) *A. cerana*. H: Honey storage cell, P: pollen cell, B: brood cell, D: drone cell, Q: queen cell

Comparisons were made both between species and among colonies within species. The frequency of each pollen type was calculated and classified into four categories: predominant pollen type (>45%), secondary pollen type (16-45%), important minor pollen type (3-15%), and minor pollen type (<3%) (Louveaux *et al.* 1978).

3. Results

3.1. Differences in Worker and Drone Cell Size, Body Length, and Body Weight

The average diameter cells of *A. koschevnikovi* (Ak) worker and drone were 5.42±0.16 and 6.64±0.12 mm, respectively, which is larger than *A. cerana* (Ac) (4.39±0.18 and 5.30±0.14 mm) (Figure 3A). The same pattern was also observed in the cell depth, which showed that Ak worker and drone had deeper cells (11.77±0.07 and 12.38±0.26 mm, respectively) than Ac (10.75±0.21 and 11.16±0.18 mm) (Figure 3B). In both species, drone cells had larger diameters and deeper depths than worker cells (Figure 3A and B).

ANOVA revealed significant differences in worker cell diameter and depth between Ak and Ac ($p<0.05$) (Figure 3A and B). Tukey test showed that the diameters and depths of worker and drone cells did not differ significantly at the intraspecies level in both species (Figure 3A and B). However, the worker cell diameters of all Ak colonies were significantly greater than Ac with $p<0.05$ (Figure 3A). Similarly, the depths of worker cells in all Ak colonies were greater than Ac (Figure 3B). Moreover, the depth of drone cells also showed significant interspecific differences, except that Ak2 and Ac2 did not show a significant difference (Figure 3B).

The average body length and body weight of Ak workers (10.25±0.16 mm and 23.18±4.60 mg, respectively) were greater than Ac (9.14±0.51 mm and 21.31±0.07 mg) (Figure 4A and B). ANOVA also indicated significant differences in both body length and body weight between the two species ($p<0.05$) (Figure 4A and B). Tukey test indicated that body length did not differ significantly at the intraspecies level in both species (Figure 4A). The differences in body length between Ak and Ac workers were also not significant. However, the body length of Ak1 was significantly greater than Ac1 and Ac2, while the colonies Ak2 and Ak3 were significantly longer than Ac2 (Figure 4A). Body weight measurements of Ak and Ac did not differ significantly at the intraspecies and interspecies level, except between Ak1-Ak2 and Ak1-Ac2 (Figure 4B).

3.2. Composition of Pollen Types in Honey and Corbicula Pollen Samples

Ten and 11 pollen types were identified from honey (Figure 5) and corbicula pollen (Figure 6) of Ak and Ac, respectively. Pollen from families Aquifoliaceae, Arecaceae, Asteraceae, Cannabaceae, Fabaceae, Fagaceae, Lamiaceae, Melastomataceae, Myrtaceae, and Pentaphylacaceae was represented by a single pollen type in the honey of both species (Figure 5). In contrast,

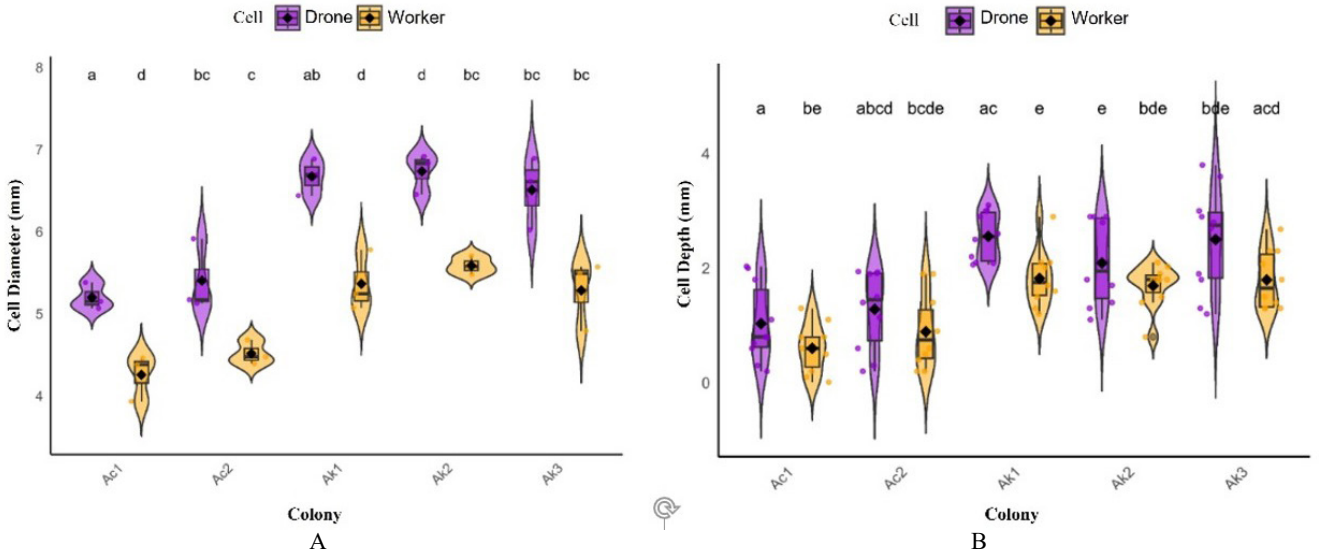


Figure 3. Worker and drone cell dimensions of *A. koschevnikovi* (Ak) and *A. cerana* (Ac). (A) Cell diameter, (B) Cell depth. The number following species abbreviations indicates the colony number. Different letters above bars denote significant differences based on Tukey test ($p<0.05$)

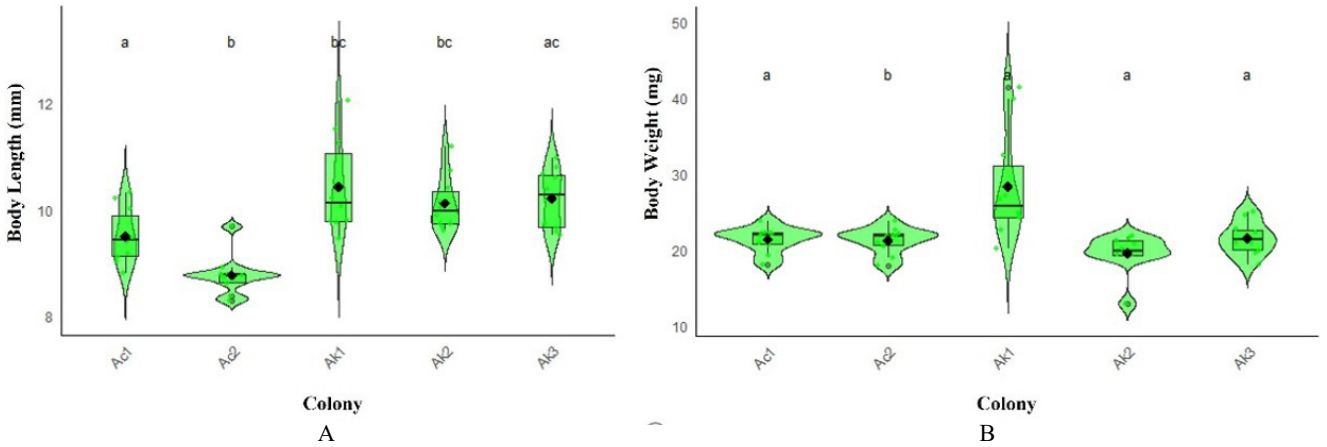


Figure 4. Size worker bees of *A. koschevnikovi* (Ak) and *A. cerana* (Ac). (A) Body length, (B) body weight. The number following species abbreviations indicates the colony number. Different letters above bars denote significant differences based on Tukey test ($p<0.05$)

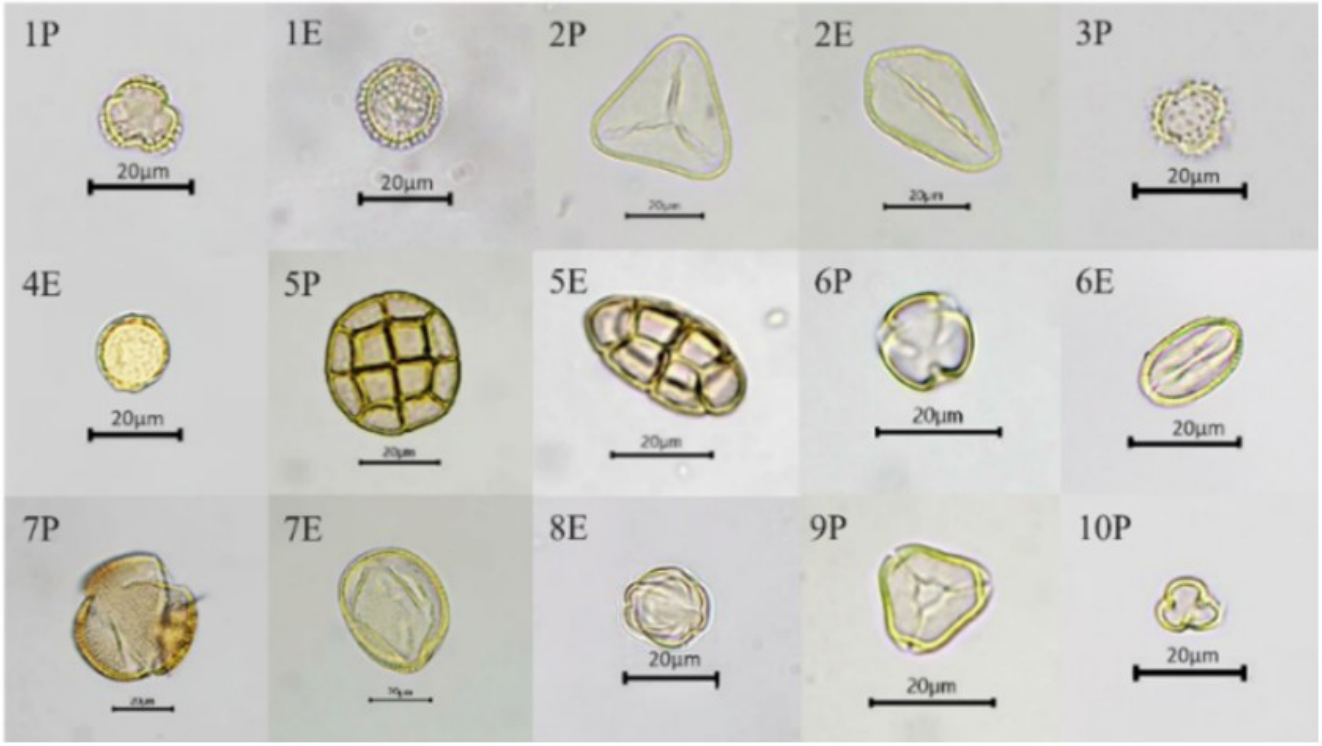


Figure 5. Pollen types in the honey of *A. koschevnikovi* and *A. cerana*. Aquifoliaceae: (1) *Ilex cymosa*; Arecaceae: (2) *Elaeis guineensis*; Asteraceae: (3) *Ageratum conyzoides*; Cannabaceae: (4) *Trema orientale*; Fabaceae: (5) *Acacia mangium*; Fagaceae: (6) *Lithocarpus* sp.; Lamiaceae: (7) *Vitex pinnata*; Melastomataceae: (8) *Melastoma malabathricum*; Myrtaceae: (9) *Syzygium urceolatum*; Pentaphylacaceae: (10) *Eurya* sp. P: polar view, E: equatorial view

corbicula pollen contained one family, Arecaceae, that was represented by two pollen types, while the other families, i.e., Asteraceae, Cyperaceae, Fabaceae, Fagaceae, Melastomataceae, Pentaphylacaceae, and Pinaceae, were each represented by only one pollen type (Figure 6).

Further comparison of pollen types between the two species revealed differences in the number and shared pollen types in honey and corbicula pollen (Figure 7A-E). We found that the honey of Ak contained a higher number of ten pollen types compared to six pollen types of Ac. All pollen types found in Ac honey, i.e.,

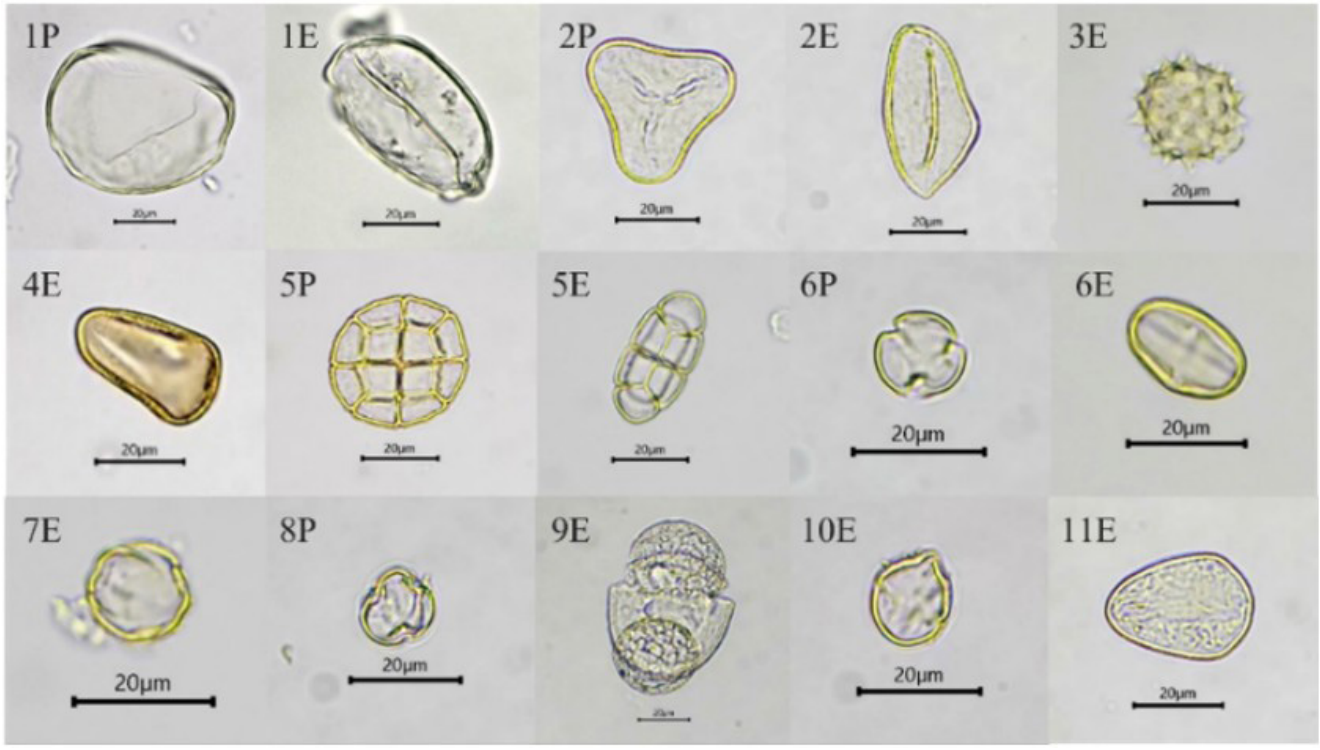


Figure 6. Pollen types in the corbicula of *A. koschevnikovi* and *A. cerana*. Arecaceae: (1) *Cocos nucifera*, (2) *Elaeis guineensis*; Asteraceae: (3) *Bidens* sp.; Cyperaceae: (4) *Cyperus* sp.; Fabaceae: (5) *Acacia mangium*; Fagaceae: (6) *Lithocarpus* sp.; Melastomataceae: (7) *Melastoma malabathricum*; Pentaphylacaceae: (8) *Eurya* sp.; Pinaceae: (9) *Pinus* sp.; Unidentified: (10) Sp1, (11) Sp2. P: polar view, E: equatorial view

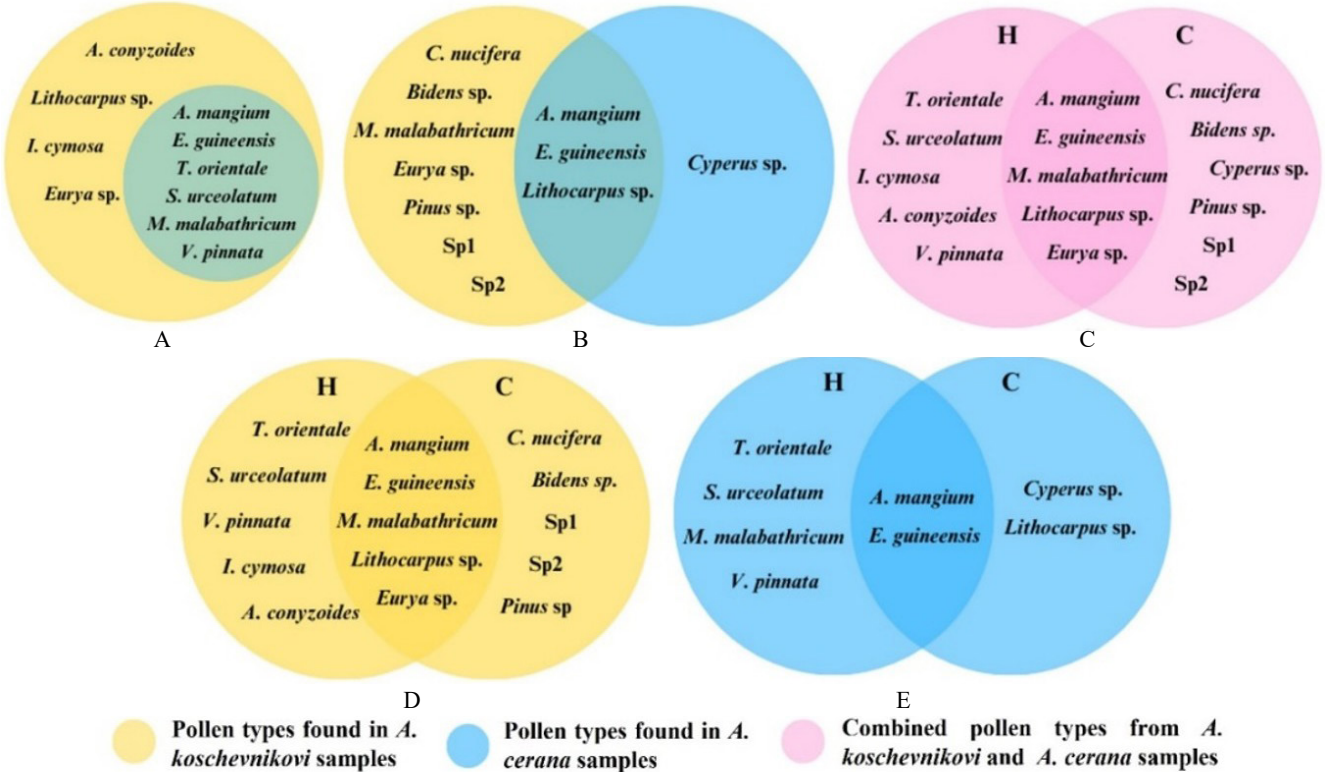


Figure 7. Composition of pollen types. (A) Honey, (B) corbicula pollen, (C) combined data from *A. koschevnikovi* and *A. cerana*, (D) honey and corbicula pollen of *A. koschevnikovi*, (E) honey and corbicula pollen of *A. cerana*. H: Honey, C: corbicula pollen

Acacia mangium, Elaeis guineensis, Trema orientale, Syzygium urceolatum, Melastoma malabathricum, and *Vitex pinnata* were also present in Ak honey (Figure 7A). Moreover, four pollen types of *Ageratum conyzoides, Lithocarpus* sp., *Ilex cymosa*, and *Eurya* sp., were only found in Ak honey (Figure 7A). Similarly, Ak collected a higher number of pollen types in corbicula pollen, i.e., ten types compared to four types in Ac (Figure 7B). Seven pollen types of *Cocos nucifera, Bidens* sp., *M. malabathricum, Eurya* sp., *Pinus* sp., Sp1, and Sp2 were only found in corbicula pollen of Ak, while *Cyperus* sp. was only found in Ac (Figure 7B). However, both species shared three pollen types of *A. mangium, E. guineensis,* and *Lithocarpus* sp. (Figure 7B).

Based on the combined pollen type of Ak and Ac samples, ten and 11 pollen types were found in the honey and corbicula pollen, respectively (Figure 7C). Pollen types of *A. mangium, E. guineensis, M. malabathricum, Lithocarpus* sp., and *Eurya* sp. were also found both in honey and corbicula pollen (Figure 7C). The total of 15 pollen types from 11 families was collected by Ak, with five pollen types were identified in honey and corbicula (Figure 7D). Meanwhile, Ac collected a total of eight pollen types from eight families, with two pollen types identified in honey and corbicula (Figure 7E). These results indicate that Ak collected a greater variety of pollen types than Ac.

3.3. Bee Forage Plant Preference Based on Honey and Corbicula Pollen Samples

Acacia mangium was the predominant pollen type in Ak1 honey (77%), whereas *E. guineensis* dominated in Ak2 (70.89%) and Ak3 (65.11%) honey (Figure 8). Similarly, Ac1 and Ac2 honey contained pollen sources, with A. mangium as the predominant pollen type, i.e., 95.44% and 67.44%, respectively (Figure 8). This result indicates that Ak1, Ac1, and Ac2 had the same foraged plant preferences of *A. mangium*, while *E. guineensis* was preferred by Ak2 and Ak3. In addition, *A. mangium* was also identified as a secondary pollen type in Ak2 and Ak3 honey, while *E. guineensis* was a secondary pollen type in Ac1 and Ac2 honey (Figure 8). The honey of Ak contained a greater variety of important minor and minor pollen types than Ac. Furthermore, *V. pinnata, M. malabathricum,* and *S. urceolatum* were recorded as minor pollen types in the honey of both species (Figure 8).

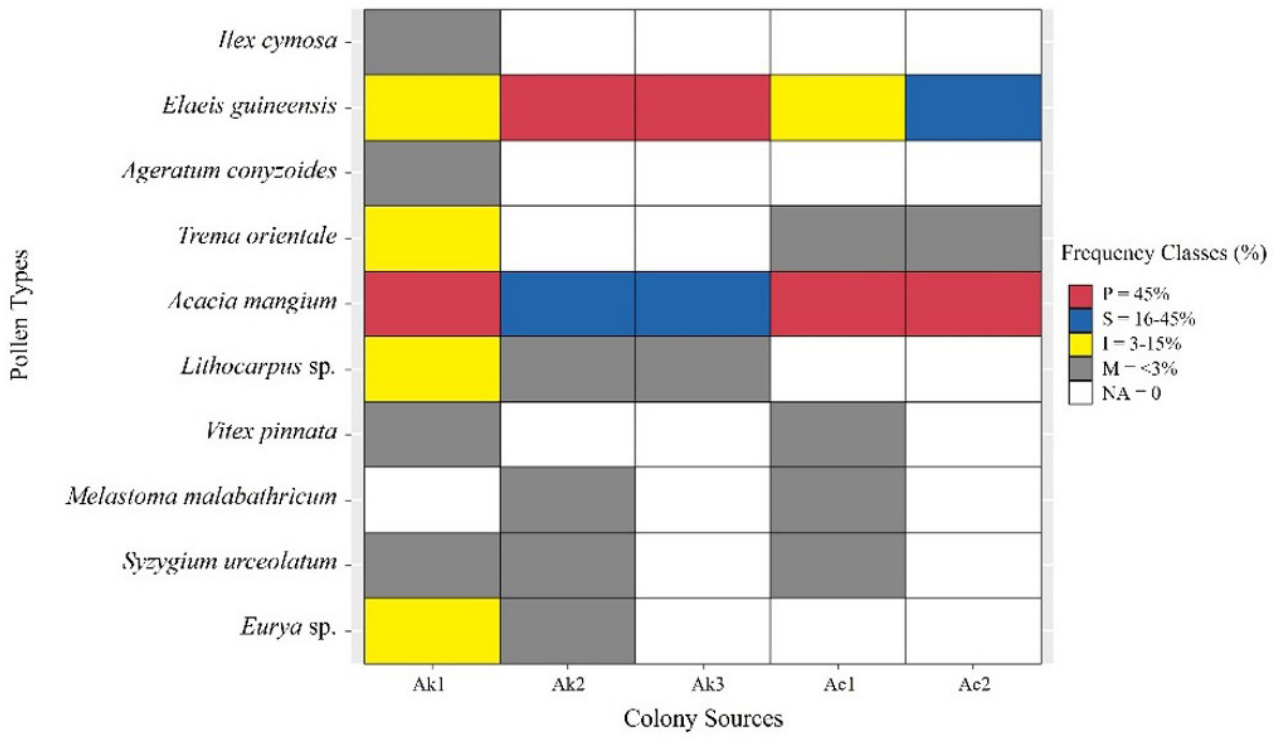


Figure 8. Frequency of pollen types in honey of *A. koschevnikovi* (Ak) and *A. cerana* (Ac). The number following species abbreviations indicates the colony number. Frequency Classes of pollen types = P: Predominant pollen, S: secondary pollen, I: Important minor pollen, M: Minor pollen, NA: Not available

Identification of corbicula pollen revealed that Ak colonies have different preferences for pollen resources, i.e., *A. mangium, E. guineensis,* and *Lithocarpus* sp., respectively for Ak1, Ak2, and Ak3 (Figure 9). Meanwhile, Ac1 and Ac2 preferred *A. mangium* as their pollen resource (Figure 9). Consistent with honey samples, Ak collected a greater variety of corbicula pollen than Ac.

4. Discussion

The structural organization of honey bee comb reflects collective building behavior and provides adaptive functional advantages (Smith *et al.* 2024). The comb consists of honey, pollen, and brood cells of worker and drone, located in the upper, middle, and lower sections, respectively (Seeley and Morse 1976). In this study, we compared the worker and drone cell sizes of honey bees *A. koschevnikovi* and *A. cerana* as well as their body length and body weight. Our results exhibited that *A. koshevnikovi* has larger worker and drone cell dimensions than *A. cerana* (Figure 3A and B). The larger cell dimensions in *A. koschevnikovi* were consistent with the larger body length and body weight compared to *A. cerana* (Figure 4A and B). The average body length of *A. koschevnikovi* workers was 12.14% larger than *A. cerana* (Figure 4A). This pattern aligns with morphometric findings showing that *A. koschevnikovi* has a body size 10-15% larger than *A. cerana* in several traits, including wings, legs, and sclerites (Rinderer *et al.* 1989). The results were also supported by the report that the body length of *A. koschevnikovi* was approximately 10-11 mm (Maa 1953), while *A. cerana* was 9-10 mm (Erwan *et al.* 2025). The observed size differences between *A. koschevnikovi* and *A. cerana* may indicate divergence within a shared cavity-nesting lineage, despite their close phylogenetic relationship as sister taxa within the *A. cerana, A. nigrocincta,* and *A. nuluensis* cluster (Raffiudin and Crozier 2007). The larger cell dimensions in *A. koschevnikovi* presumably provide more space for larval growth, thereby supporting the development of larger individuals compared to *A. cerana* (Zhang *et al.* 2024).

A positive relationship between comb cell size and body size has also been reported in experiments on *A. mellifera*, showing that bees reared in larger cells tend to exhibit greater body size than those reared in smaller cells (Zhang *et al.* 2024). Differences in comb cell size are also associated with the sex-determination mechanism

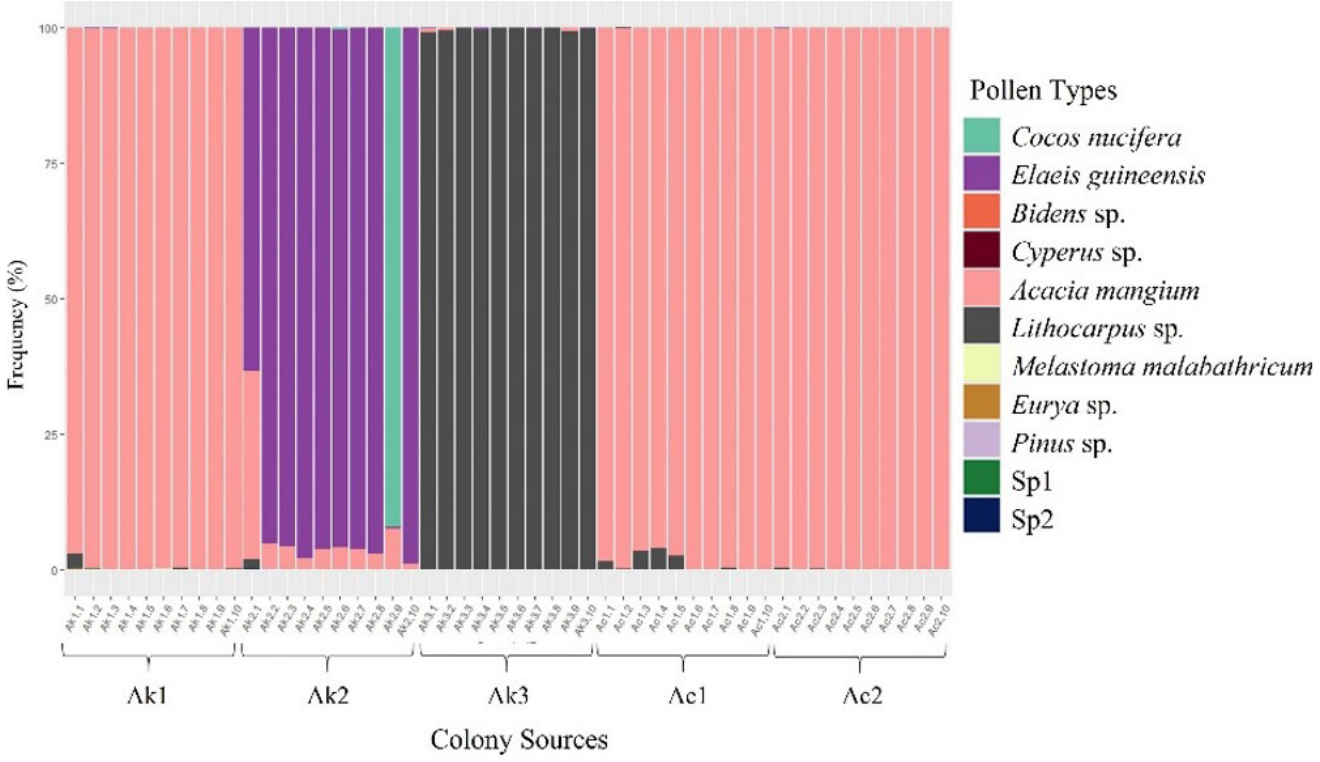


Figure 9. Frequency of pollen types in corbicula of *A. koschevnikovi* (Ak) and *A. cerana* (Ac). The number following species abbreviation indicates the colony and individual

of the queen (Winston 1987). The queen selects haploid (drone) or diploid (worker) eggs to be laid based on the cell diameter, which is measured using her front legs (Winston 1987). Therefore, these findings highlight that comb architecture plays a key role in shaping morphological differentiation (Zhang *et al.* 2024), which in turn affects foraging ability. Consequently, differences in body size of *A. koschevnikovi* and *A. cerana* can influence their foraging pattern, including pollen collection and preferences for pollen sources.

Our results revealed distinct differences in pollen composition and preference of *A. koschevnikovi* and *A. cerana*, which showed that *A. koschevnikovi* contained a higher number of pollen types than *A. cerana* (Figure 7A-E). In contrast, research in Central Sulawesi showed that *A. cerana*, a more widely distributed species, collected more pollen types than the native *A. nigrocinta* (Raffiudin *et al.* 2022). These contrasting patterns indicate that the way each species utilizes floral resources does not necessarily align with geographical range; thus, the broad or restricted distribution of honey bee does not determine the variety of pollen sources collected by the bee species. Furthermore, *A. koschevnikovi* collected a greater variety of pollen than *A. cerana*, presumably due to the larger body size than *A. cerana*, which allows longer foraging distances and access to a wider range of floral resources (Kendall *et al.* 2022).

Based on pollen in honey, we found that *A. koschevnikovi* has two foraged plant preferences, i.e., *A. mangium* and *E. guineensis*, while *A. cerana* only preferred *A. mangium* (Figure 9). This pattern was consistent with the corbicula pollen result, which showed that *A. koschevnikovi* colonies have three foraged plant preferences, i.e., *A. mangium, E. guineensis,* and *Lithocarpus* sp., while *A. cerana* only preferred a single species of *A. mangium* (Figure 9). This variation of pollen preferences of *A. koschevnikovi* suggests that worker bees communicated these different floral resources through the waggle dance among colonies. *Acacia mangium* and *E. guineensis* were located relatively close to the colonies, at 100-500 m to the north and less than 150 m to the west, respectively (Figure 1B). These distances were within the foraging range of *A. cerana* (650 m; Dhaliwal and Sharma 1974). Furthermore, pollen from these species has also been identified in the honey of stingless bees *Heterotrigona itama* and *Tetragonula laeviceps* in the same location of Keciput Village, Sijuk Sub-district, Belitung (Priambudi *et al.* 2021). In addition, 11 of the 16 total pollen types found in the honey and corbicula pollen of *A. koschevnikovi* and *A. cerana* were also identified in the melissopalynological analysis of *H. itama* in Belitung (Hamzah *et al.* 2025). Among these pollen types, *I. cymosa* and *S. urceolatum* are shown to be local pollen species characteristic of Belitung. Thus, the result highlights the important role of these species as forage sources for various bee species in Belitung.

In conclusion, *A. koschevnikovi* exhibited larger worker and drone cells, greater body length and body weight, and exhibited a wider variety of pollen types than *A. cerana*. This study provides practical insights for designing comb foundations tailored to species-specific requirements and reveals forage plant preferences of these two sympatric species. These findings are valuable for improving beekeeping practices and supporting the conservation of *A. koschevnikovi*, a species with a restricted geographic distribution. Further studies on nest structure and pollen analysis in other bee species are needed to understand the ecological differences that support conservation and beekeeping.

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