HAYATI
Journal of Biosciences

Vol. 33 No. 5, September 2026 1269-1279
DOI:10.4308/hjb.33.5.1269-1279
ISSN: 1978-3019
EISSN: 2086-4094

Research Article

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Variations in Wing Venation of *Apis cerana* in Kalimantan and Related Islands in Sundaland Based on Geometric Morphometrics

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ARTICLE INFO

Article history:
Received February 20, 2026
Received in revised form May 17, 2026
Accepted May 18, 2026
Available Online July 20, 2026

KEYWORDS:
Asian honey bees,
bending energy,
grid deformation,
landmark wing venation,
thin plate spline

ABSTRACT

Apis cerana has a broad distribution across mainland Asia and exhibits high variation in wing venation. However, studies on wing venation variation in the Indonesian archipelago have mainly focused on Sumatra and Java. Therefore, this study aimed to analyze wing venation variation in Kalimantan and the relationship between *A. cerana* in the Sundaland region, including Sumatra and Java. Geometric morphometric methods were applied using 19 wing venation landmarks, followed by Principal Component Analysis (PCA) and Neighbor-Joining (NJ) tree analysis. The results showed that *A. cerana* from South Kalimantan exhibited the greatest variation in wing shape, whereas samples from West Kalimantan displayed relatively conserved wing size and shape, as indicated by low variation. Landmarks 11, 16, and 17 contributed a high value of wing venation variation within *A. cerana* Kalimantan and across Sundaland. The PCA revealed that *A. cerana* from Kalimantan was generally separated from those of Sumatra and Java. This pattern was supported by the NJ tree, which showed distinct clustering between Kalimantan and the other islands, although several samples from Banten and Jambi clustered with Kalimantan. These findings highlight the biogeographic pattern of *A. cerana* across Sundaland and the potential of wing-venation geometric morphometrics for digital species identification in Indonesia.

1. Introduction

Honey bees are recognized as keystone pollinators (Oldroyd and Wongsiri 2006) with specialized morphological characters (Michener 2007). Several species of honey bees are distributed throughout Asia, and one of the most widespread species is the *Apis cerana* (Ruttner 1988). *Apis cerana*, the Asian honey bee, has a wide distribution, ranging from western Afghanistan, Pakistan, Kashmir, Korea, Japan, the Philippines, and the Indonesian archipelago (Ruttner 1988). Based on morphological traits and distribution, eight subspecies have been recognized: *A. c. cerana*, *A. c. himalaya*, *A. c. indica*, *A. c. japonica* (Ruttner 1988), *A. c. koreana* (Ilyasov *et al.* 2018), *A. c. skorikovi*, *A. c. javana*, and *A. c. johni* (Engel 1999). Morphometric studies further clustered *A. cerana* into six major groups: (I) Northern

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South and East Asia, (II) Himalayan, (III) Indian plains, (IV) Indo-Chinese, (V) Philippines, and (VI) Indo-Malayan (Radloff *et al.* 2010). The latter consists of specific regions, namely Palawan, North Borneo, Malay Peninsula, Sulawesi, Kalimantan, Sumatra, Java, Bali, and Papua (Radloff *et al.* 2010). Among these islands, Kalimantan, Sumatra, and Java are part of the Sundaland region, which formed due to sea-level fall during the glacial period (Mollengraaf 1921). Repeated landmass isolation during sea-level changes may have driven allopatric divergence in *A. cerana*, leading to morphological differences due to geographic barriers (Citeli *et al.* 2021).

Morphological variations in *A. cerana* populations have been widely documented across their distribution range (Radloff *et al.* 2010). These variations can be assessed using traditional morphometric methods (Rohlf and Marcus 1993; Adams *et al.* 2004), which have been successfully used to identify size variations in honey bees (Raffiudin *et al.* 1999; Zhu *et al.* 2017). This approach has shown that *A. cerana* in Indonesia (Raffiudin *et al.* 1999) and China (Zhu *et al.* 2017) exhibit significantly larger body sizes in highland regions compared to lowland areas. Besides honey bees, this method has also been used to identify the stingless bee *Tetrigona apicalis* in West Java, Indonesia (Miharja *et al.* 2026). These findings showed that traditional morphometrics effectively quantify size differences and patterns of variation. However, this method cannot visualize the shape (Rohlf and Marcus 1993). To address this limitation, a morphometric approach called geometric morphometrics has been introduced (Mitteroecker and Gunz 2009). Geometric morphometrics enables the quantification and analysis of biological shapes based on landmark coordinates (Rohlf and Marcus 1993). The geometric morphometric wing venation of *A. mellifera* in south-eastern Morocco differed significantly from *A. m. sahariensis* and *A. m. intermissa*; thus, this analysis can resolve to the subspecies level of honey bees (Aglagane *et al.* 2022). Similarly, this method has successfully identified the differences of *A. c. koreana* in Korea (Frunze *et al.* 2022) and distinguished *A. cerana* from the mountain highlands and lowlands populations in China (Ji *et al.* 2023).

Our previous study in geometric morphometrics of wing venation also showed intra-species variations among *A. cerana* from the Sundaland region (Sumatra, Belitung, Java) and *A. cerana* from Bali, Sulawesi, and the Moluccas (Nisa *et al.* 2022). However, geometric morphometric analysis of *A. cerana* in Kalimantan, which is also part of the Sundaland region, remains unexplored. We hypothesized that the *A. cerana* in Kalimantan differ from those in Sumatra and Java due to geographical barriers among these islands. Therefore, using geometric morphometric analysis of wing venation landmarks, this study aimed to investigate (1) the variations in the wing venation of *A. cerana* in Kalimantan and (2) the relationship between *A. cerana* in Kalimantan and those in the Sundaland region of Sumatra and Java.

2. Materials and Methods

2.1. Sample Collections

Prior to sample collection, we collected information regarding the distribution of *A. cerana* across the five provinces in Kalimantan: West, Central, South, East, and North (Table 1). Sampling sites were selected based on the presence of active and managed *A. cerana* colonies.

Worker honey bees were used for the analysis in this study. Worker bees represent the female, non-reproductive caste in honey bee colonies and were identified based on their relatively smaller body size compared to other castes. A total of 32 colonies of *A. cerana* were collected, with each colony represented by 10 worker bees (Table 1). All samples were preserved in ethanol for further analysis. We combined the wing venation landmark datasets of *A. cerana* from Kalimantan obtained in this study with previously published datasets of *A. cerana* from Sumatra and Java (Nisa *et al.* 2022) for morphometric analysis. The database includes 18 colonies of *A. cerana* from Sumatra and 8 colonies from Java from Nisa *et al.* (2022), resulting in a total of 580 samples for Sundaland data. Samples were deposited at the National Research and Innovation Agency in Indonesia.

2.2. Dissection and Digitizing Images of The Wing Landmarks

The right forewings of 10 *A. cerana* workers per colony were dissected, and each wing was mounted on a glass slide to prepare the specimens. Specimens were photographed using an Olympus SZ61 stereomicroscope equipped with an Optilab Advance V2 camera (resolution: 4100 × 3075 pixels, 12.6 MP) and captured using Optilab Viewer Software 2.2. We digitized 19 landmarks on the forewings of *A. cerana* following Michener (2007) (Table 2, Figure 1) using tpsDig32 (Rohlf 2015) with three replications.

Table 1. Colony ID and sampling sites of *A. cerana* in five provinces of Kalimantan

Colony ID/province	Sampling sites (District, regency/city)	Coordinate
West Kalimantan		
Ac1_SnP_Mmp Ac2_ SnP_Mmp Ac3_ SnP_Mmp	Sungai Pinyuh, Mempawah	N 0°18'0.8" E 109°6'33.8"
Central Kalimantan		
Ac1_Sbg _PlR Ac2_Sbg _PlR Ac3_Sbg _PlR	Sebangau, Palangka Raya	S -2°16'30,658" E 114°1'4,558"
Ac1_Tng _PlR Ac2_Tng _PlR Ac3_Tng _PlR	Tangkiling, Palangka Raya	S -1°59'53.688" E 113°44'35.832"
South Kalimantan		
Ac1_SnL _TnB Ac2_SnL _TnB Ac3_SnL _TnB	Sungai Loban, Tanah Bumbu	S 3°39'31.4" E 115°44'44.8"
Ac1_Tks _TnL Ac2_Tks _TnL Ac3_Tks _TnL	Takisung, Tanah Laut	S 3°50'48.5" E 114°38'40.3"
Ac1_Plh _TnL Ac2_Plh _TnL Ac3_Plh _TnL	Pelaihari, Tanah Laut	S 3°48'22.8" E 114°44'10.5"
Ac1_Png _Bnj Ac2_ Png _Bnj Ac3_ Png _Bnj	Pangaron, Banjar	S 3°17'05.9" E115°04'54.8"
East Kalimantan		
Ac1_EsB _Blk Ac2_ EsB _Blk	East Balikpapan, Balikpapan	S -1°7'54.84513" E 116°59'40.29938"
Ac1_MrB _KtK Ac2_MrB _KtK Ac3_MrB _KtK	Muara Badak, Kutai Kartanegara	S -0°15'51.72281" E 117°14'53.22473"
Ac1_LKl _KtK Ac2_LKl _KtK	Loa Kulu, Kutai Kartanegara	S -0°29'39.86271" E 117°0'15.62659'
Ac1_TnS _KtK	Tenggarong Seberang, Kutai Kartanegara	S -0°14'49.23869" E 117°7'0.3317"
North Kalimantan		
Ac1_TnP _Bln Ac2_TnP _Bln Ac3_TnP _Bln	Tanjung Palas, Bulungan	N 2°49'59.72892' E 117°20'26.3403'

Colony ID Ac: *Apis cerana*, SnP: Sungai Pinyuh, MmP: Mempawah, Sbg: Sebangau, PlR: Palangka Raya, Tng: Tangkiling, SnL: Sungai Loban, TnB: Tanah Bumbu, Tks: Takisung, TnL: Tanah Laut, Plh: Pelaihari, Png: Pangaron, Bnj: Banjar, EsB: East Balikpapan, Blk: Balikpapan, MrB: Muara Badak, KtK: Kutai Kartanegara, LKl: Loa Kulu, TnS: Tenggarong Seberang, TnP: Tanjung Palas, Bln: Bulungan. Collectors, West Kalimantan: Windra Priawandiputra, Edy Syaputra, Tony, Weisman Sihaloho, Siaful, Romli; Central Kalimantan: Juniarto Gautama Simanjuntak, Ahmad Muammar Kadafi, Ebryy, Adventus, Yoanes Budianya, Solichan; South Kalimantan: Astuti Latif, Nova Hariani, Syafrizal, Auliana, Andi Triawan, Ahmad Jauzan, Sugeng, Ngatimin; East Kalimantan: Fikri Irsyad Muhammad, Pamudji, Rendry, Dio, Eka Rananto, Tuniman; North Kalimantan: Fikri Irsyad Muhammad, Khairunnisa, Wulan

Table 2. Description of *A. cerana* wing landmarks based on Michener 2007

Landmark	Description
1	Rs and prestigma junctions
2	The point Rs + M
3	Point M + Cu1
4	Point M + Cu2
5	Cu-v point
6	V and Cu2 junctions
7	The vein junctions of Cu1 and Cu2
8	Point 1m-cu
9	Point 2m-cu
10	The second vein junctions of Rs + m and arbiscissa is Rs.
11	Arbiscissa junctions of r and stigma
12	The junctions of r and stigma
13	Rs and 1r-m junction
14	Rs and 2r-m junction
15	The tip point of Rs
16	2r-m point
17	End point 2m-cu
18	1r-m point
19	2m-cu and Cu1 Junction

*Rs, radial sector; prestigma, first abscissa of R1; stigma (pterostigma), the sclerotized pigmented cell on the anterior wing margin; M, media (basal vein); Cu, cubitus; Cu1, first branch of cubitus; Cu2, second branch of cubitus; v, transverse vein; 1m-cu, first recurrent (medio-cubital crossvein); 2m-cu, second recurrent (medio-cubital crossvein); r, radial crossvein; 1r-m, first radio-medial crossvein (second submarginal crossvein); 2r-m, second radio-medial crossvein (third submarginal crossvein); abscissa, a segment of a longitudinal vein; R, radius; R1, first branch of the radius (Michener 2007)

2.3. Analysis of Deformation Grid, Bending Energy, and Centroid Size of Wing Venation of *A. cerana*

We used tpsRelw (Rohlf 2015) to generate the reference landmark configuration, represented by the consensus (mean) configuration, from 320 individuals of *A. cerana* from Kalimantan and 580 individuals from Sundaland, following Procrustes superimposition. Each specimen was digitized three times (n = 3) to minimize measurement error, and the averaged coordinates were used for further analysis. The other output of TpsRelw3 was the landmark contribution value. Both the reference landmark and the landmark contribution value were used as input to TpsSplin to produce a deformation grid and bending energy, which is quantitative data on the grid deformation (Mitteroecker and Gunz 2009). Landmark configuration was also analyzed using MorphoJ (https://morphometrics.uk/MorphoJ) to compute centroid size, which was used to quantify wing size variation (Mitteroecker and Gunz 2009). Centroid size was derived from the square root of the sum of squared distances from the center of the forewing to each of the 19 landmarks (Bookstein 1997).

Differences in centroid size of wing venation of *A. cerana* across Kalimantan and Sundaland (n=580) were analyzed using the Wilcoxon test, while inter-island comparisons were conducted using the Kruskal-Wallis test. These statistical analyses were performed in

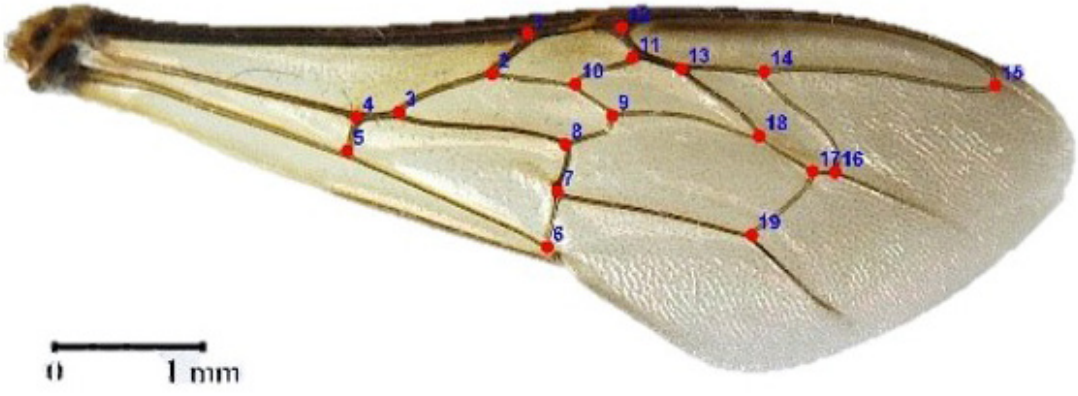

Figure 1. Nineteen landmarks of *A. cerana* wing venation from Kalimantan

RStudio (R Core Team 2023) using the ggpubr package (version 0.6.0) and ggplot2 for visualizations (http://rpkgs.datanovia.com/ggpubr/).

2.4. Principal Component Analysis (PCA) and Neighbor-Joining Tree Construction

Principal Component Analysis (PCA) of 580 individuals *A. cerana* from Kalimantan and Sundaland was conducted using the two highest relative warps (RW) scores in Paleontological Statistics (PAST) (Hammer *et al.* 2001). A neighbor-joining tree of *A. cerana* from 14 provinces in the Sundaland region was constructed from TPSrelw32 results using the 'ape' package. 5.7-1 (Paradis and Schliep 2019) in R Studio (R Core Team 2023).

3. Results

3.1. Wing Variation of *A. cerana* Kalimantan and Sundaland Based on Deformation Grid, Bending Energy, and Centroid size

The wing shape variations among *A. cerana* in Kalimantan (Figure 2A-E) and Sundaland (Figure 3A-C) were visualized using deformation grids, which were compared with the reference landmarks (Figure 2F). The displacement of wing landmarks in *A. cerana* relative to the reference landmark (mean of landmark configuration), with smaller displacements representing lower variation. This was shown in the deformation grid of *A. cerana* in all Kalimantan provinces (Figure 2A, B, D, E), except for *A. cerana* wing shape variations from South, which showed high shape variations (Figure 2C). Within Sundaland, deformation grids of *A. cerana* from Sumatra (Figure 3B) and Java (Figure 3C) revealed away landmark displacements from the reference landmarks (Figure 3D), indicating high wing shape variation.

The complexity of shape differences observed in the deformation grids was quantified using bending energy values (Figure 4A and B). We found that *A. cerana* from South Kalimantan has the highest bending energy among all provinces in Kalimantan (Figure 4A), consistent with the deformation grids (Figure 2C). In contrast, the lowest bending energy was recorded in West Kalimantan (Figure 4A). Among the Sundaland, *A. cerana* from Sumatra and Java (Figure 4B) showed a higher bending energy than *A. cerana* from Kalimantan, supported by the high displacement in deformation grids (Figure 3B and C).

The wing venation landmark displacement of *A. cerana* in the deformation grid was influenced by landmark contribution values. Landmarks 11, 16, and 17 showed the highest contributions to shape variation

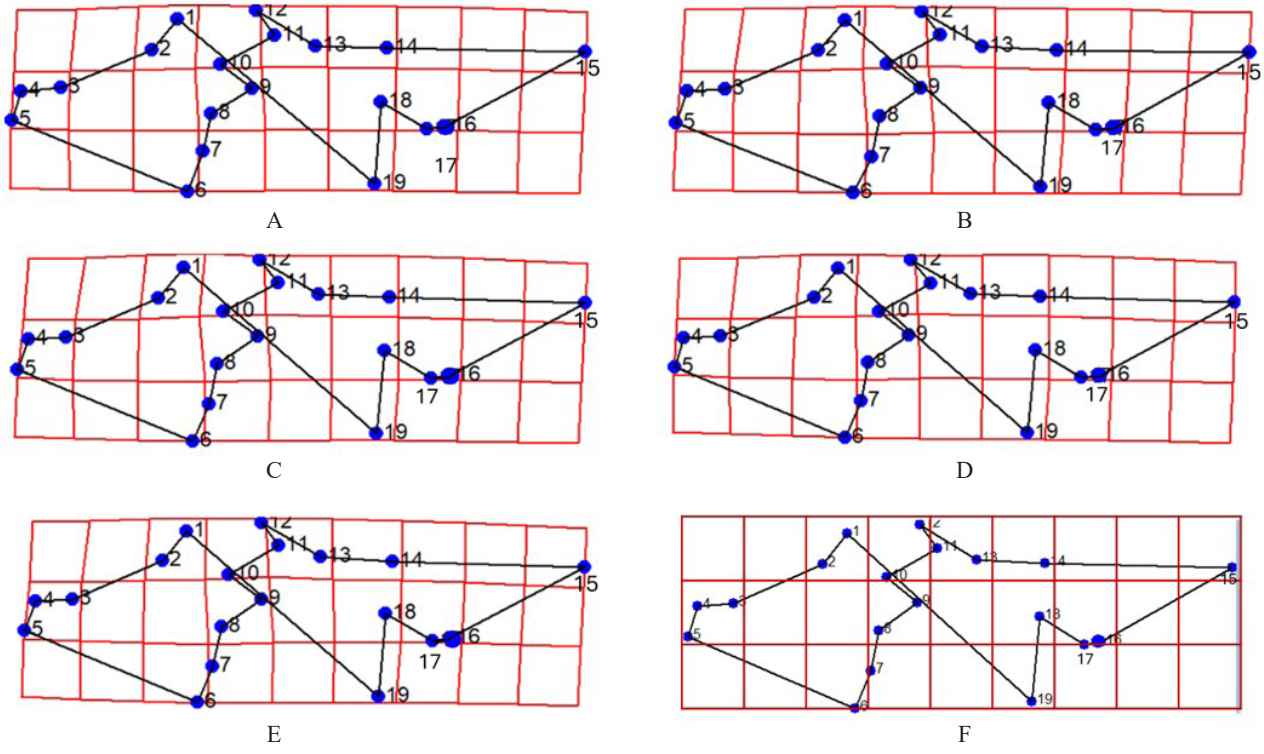

Figure 2. Grid deformation of *A. cerana* wing venations in five provinces of Kalimantan: A. West, B. Central, C. South, D. East, E. North, F. Reference landmark (mean) landmark configuration 320 Individuals *A. cerana* Kalimantan

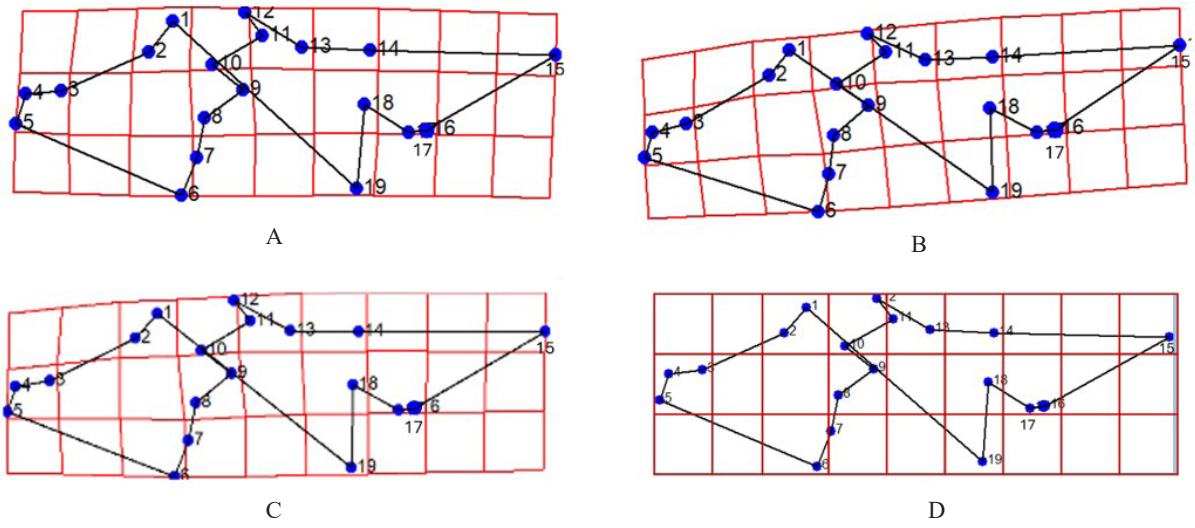

Figure 3. Grid deformation of *A. cerana* wing venations in Sundaland: A. Kalimantan, B. Sumatra, C. Java, D. Reference landmark (mean) landmark configuration 580 Individuals *A. cerana* Sundaland

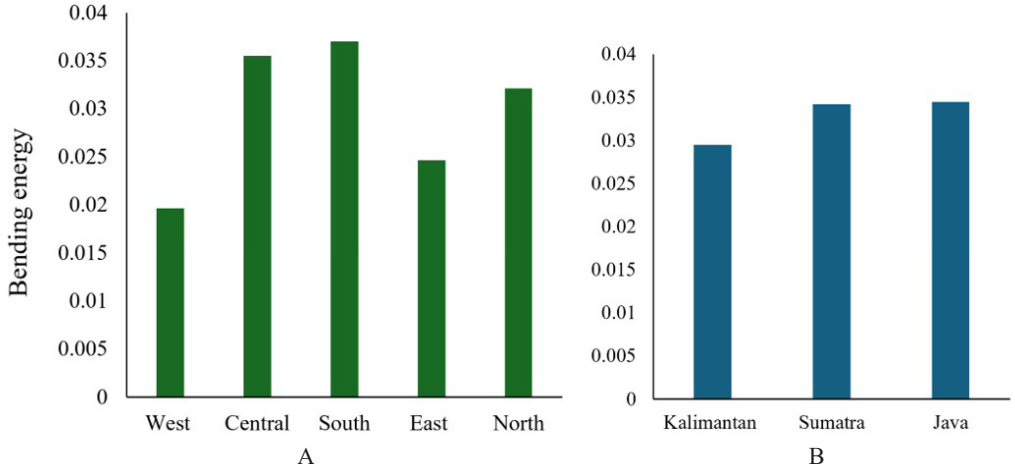

Figure 4. Bending energy of *A. cerana* wing venations: A. Five provinces in Kalimantan, B. Sundaland: Kalimantan, Sumatra, and Java

across Kalimantan, Sumatra, and Java (Table 3). These results indicate that the three landmarks contributed the highest displacements among the 19 landmarks.

Based on centroid size measurement, wing size variations of *A. cerana* from Kalimantan (Figure 5A) and Sundaland (Figure 5B) were varied. The smallest mean size was recorded in West Kalimantan, whereas the largest was found in South Kalimantan (Figure 5A). Furthermore, *A. cerana* from Java showed the largest mean centroid size across Sundaland (Figure 5B). However, statistical analysis revealed that the differences in average centroid size among all Kalimantan provinces and across Sundaland were not significant ($p = 0.797$) and ($p = 0.5103$), respectively.

3.2. The relationship of *A. cerana* Kalimantan, Sumatra, and Java (Sundaland) based on Principal Component Analysis (PCA)

The Principal component analysis (PCA) of 320 *A. cerana* individuals from Kalimantan revealed that the first two relative warps (RW1 and RW2) explained 24.8% of the total shape variation in the ordination plot (Figure 6a). *Apis cerana* from Central, South, East, and North Kalimantan were broadly distributed and overlapped across all quadrants (Figure 6A). In contrast, *A. cerana* from West Kalimantan was grouped in quadrants 1 and 2 (Figure 6A).

In the combined analysis of all *A. cerana* from Sundaland ($n = 580$), the first two relative warps (RW1

Table 3. Variation of landmarks contribution values of *A. cerana* wing venation in Sundaland

Landmark	Contribution value		
	Kalimantan	Sumatra	Java
1	0.02362	0.03310	0.02976
2	0.02422	0.03227	0.02873
3	0.01884	0.02078	0.01922
4	0.03573	0.05243	0.04904
5	0.01215	0.01943	0.01881
6	0.01217	0.01265	0.01223
7	0.05505	0.05774	0.05771
8	0.05668	0.05843	0.05674
9	0.03407	0.03475	0.03335
10	0.03809	0.03673	0.03448
11	0.11837*	0.13445*	0.11353*
12	0.04881	0.05949	0.04792
13	0.03316	0.03075	0.02783
14	0.00799	0.00721	0.00657
15	0.00039	0.00033	0.00033
16	0.18067*	0.15267*	0.17658*
17	0.27288*	0.23214*	0.26331*
18	0.02507	0.02279	0.02207
19	0.00205	0.00187	0.00180

*High value

and RW2) explained 36.43% of the total shape variation (Figure 6B), representing the largest proportion of variation among the 34 relative warps. The PCA plot revealed a partial separation of *A. cerana* from Kalimantan from those of Sumatra, occupying quadrants 1 and 4 (Figure 6B). By contrast, *A. cerana* from Sumatra and Java were spread across all quadrants, with a dominant grouping in quadrants 2 and 3 (Figure 6B).

The clustering pattern of *A. cerana* in Sundaland in the PCA plot (Figure 6B) was generally supported by a Neighbor-Joining analysis, which revealed three major clusters (Figure 7). *Apis cerana* from the five provinces of Kalimantan were grouped in cluster 2, with *A. cerana* from Jambi (Sumatra) and *A. cerana* from Banten (Java) (Figure 7). In contrast, *A. cerana* from Sumatra was distributed across all three clusters, grouping with Java and Kalimantan in clusters 1 and 2, respectively (Figure 7). Moreover, *A. cerana* from three provinces of Sumatra, i.e., Aceh, West Sumatra, and North Sumatra, formed a distinct group in cluster 3 (Figure 7).

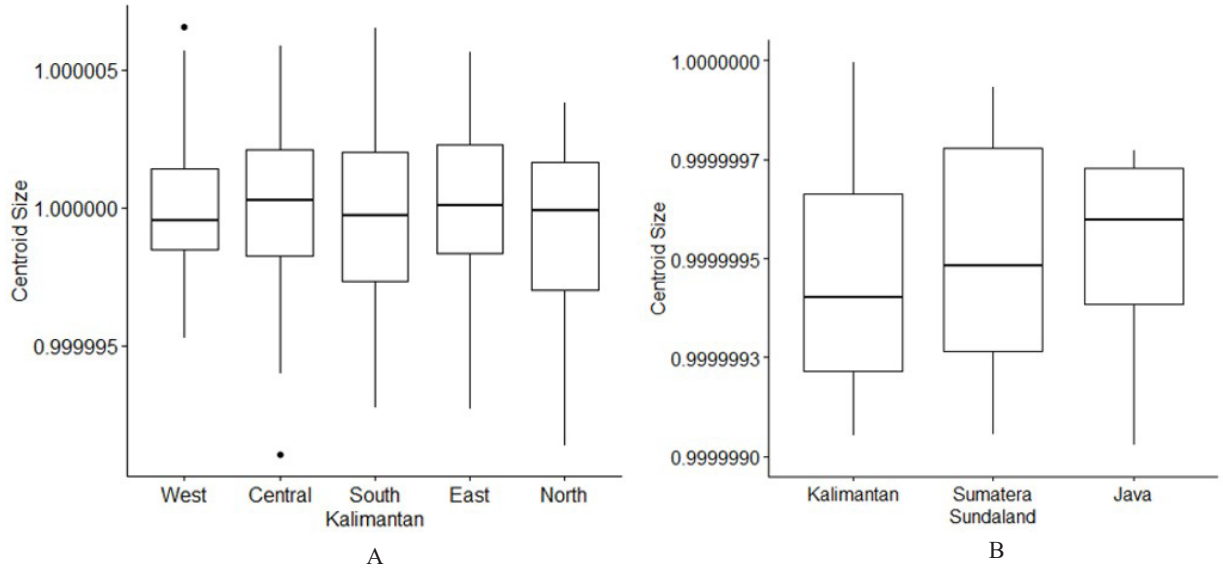

Figure 5. Centroid size of *A. cerana* wing venations from: A. Five provinces in Kalimantan, B. Sundaland: Kalimantan, Sumatra, and Java

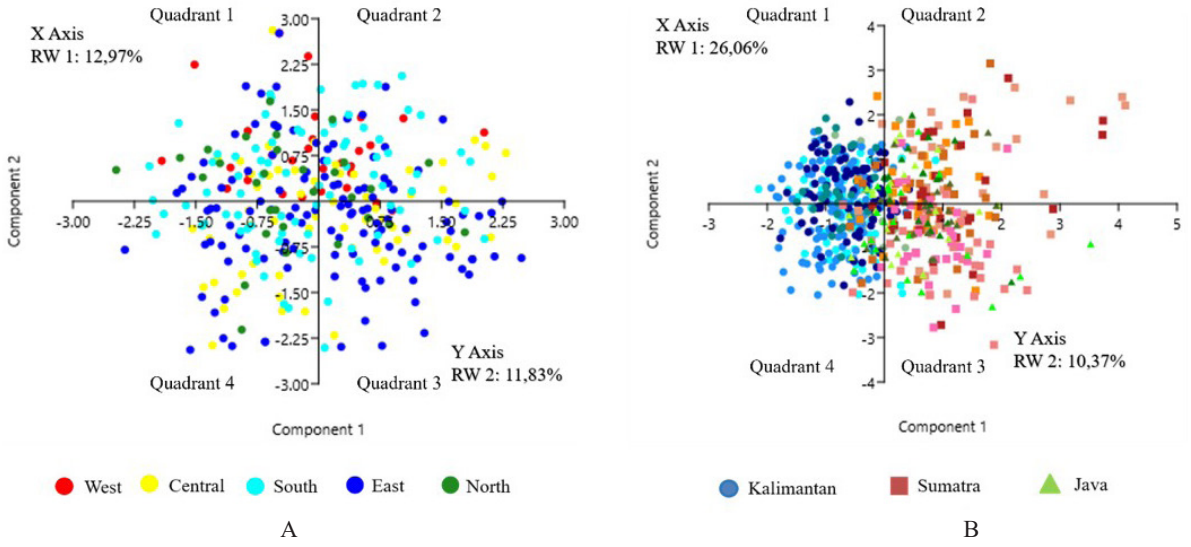

Figure 6. Principal Component Analysis (PCA) of *A. cerana* wing venations based on landmark variations in: A. Five provinces in Kalimantan, B. Sundaland: Kalimantan, Sumatra, and Java

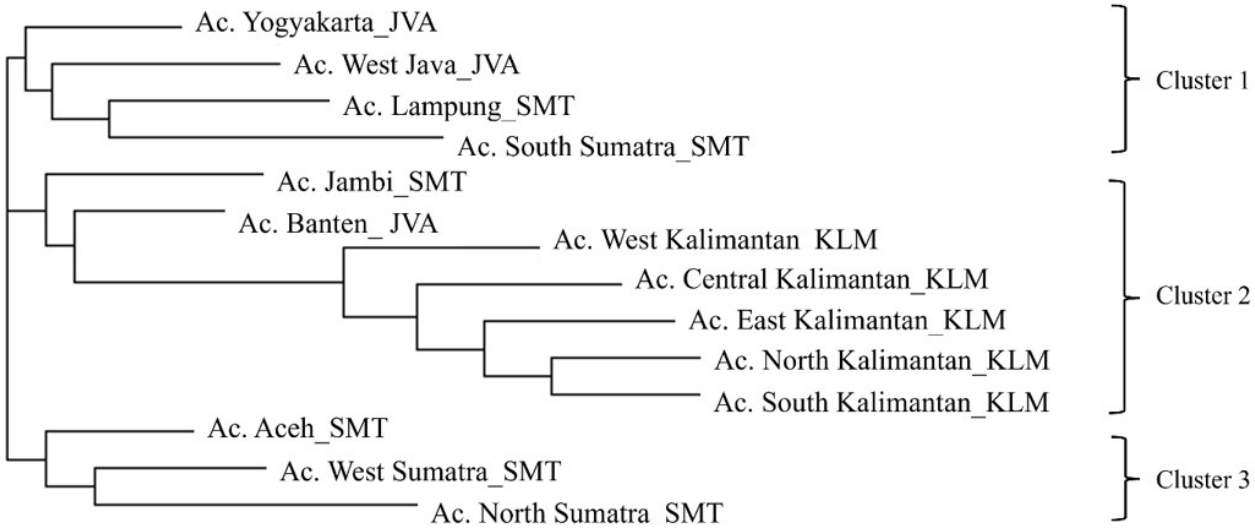

Figure 7. The rooted phylogenetic tree shows three clusters of *A. cerana* in Sundaland based on landmark variations of wing venation. Ac: *A. cerana*, KLM: Kalimantan, SMT: Sumatra, JVA: Java

4. Discussion

Our study reveals new insights into the wing venation of *A. cerana* in Kalimantan. The key finding is that *A. cerana* from South Kalimantan shows the highest variation, as indicated by the deformation grid (Figure 2), bending energy values (Figure 4A), and centroid size (Figure 5A). This morphological variation is consistent with genetic evidence from mitochondrial DNA of cytochrome c oxidase 1 (COI), cytochrome c oxidase 2 (COII), and the intergenic spacer (igs) (Muhammad *et al.* 2026). Genetic analysis has shown that *A. cerana* from South Kalimantan exhibits multiple haplotypes, including the Javanese haplotype (Muhammad *et al.* 2026).

The high variation in wing venation in *A. cerana* from South Kalimantan is presumably due to anthropogenic factors. This region has the highest Human Development Index (HDI) in Kalimantan (National Development Planning Agency 2024), is easily accessible, and may therefore have experienced the introduction of honeybees from Java for agricultural purposes. This phenomenon also occurs in *A. mellifera*, which has five morphotype groups based on wing venation following beekeeper

introductions in Thailand (Buala and Sopaladawan 2022).

Our second finding was low variation in *A. cerana* from West Kalimantan, which contrasted with the high variation in *A. cerana* from South Kalimantan. This morphological pattern is also consistent with the genetic variation of *A. cerana* in this region, which revealed low haplotype diversity and contained only the native Borneo haplotype (Muhammad *et al.* 2026). We propose that the relatively low diversity is presumably influenced by geographical isolation. Natural barriers, such as the Kapuas River and Baturaya Mountain in West Kalimantan (Regional Development Planning Agency 2024), may limit dispersal and gene flow. These findings align with the understanding that geographical isolation is a primary driver of population differentiation in *A. mellifera* in the southwest Indian Ocean (Techer 2017).

Landmarks 11, 16, and 17 showed the highest contribution to variation in Kalimantan and Sundaland. The highest contribution value of these three landmarks was similar to that of *A. cerana* from Sumatra, *A. nigrocincta* (Nisa *et al.* 2022), and *A. dorsata* from Sulawesi (Zahara *et al.* 2022) in Indonesia. Interestingly, landmarks 2, 3, and 15 were also identified as the most significant in *A. cerana* from China (Zhou *et al.* 2016), corresponding to the same positions as landmarks 11, 16, and 17 in the present study (i.e., landmark 2=11, 3=16, and 15=17), despite differences in landmark numbering schemes. In *A. mellifera*, the most important features for subspecies classification were landmarks 15 and 17, which can differentiate *A. m. carnica*, *A. m. caucasia*, *A. m. iberiensis*, *A. m. ligustica*, and *A. m. mellifera* (Rodrigues *et al.* 2022). Landmarks 16 and 17, which showed the highest variation (Table 3), correspond to a traditional morphometric character, namely the cubital index (CI) (Ruttner 1988). This finding indicates that geometric morphometric analysis reveals variation patterns consistent with those obtained using traditional morphometric approaches. Moreover, traditional morphometrics has been shown to effectively detect morphological differences in *A. cerana* from lowland and highland areas in West Java (Raffiudin *et al.* 1999) as well as in Sumatra (Raffiudin, personal observation). Similarly, *A. cerana* indica in India also showed morphological differences between *A. c. indica* from plain (lowland) and hill (highland) based on 29 characters and cubital index value (Lalremliana *et al.*2024).

Comparative analysis across the Sundaland regions showed that *A. cerana* from Kalimantan was separated from *A. cerana* from Yogyakarta and West Java based on variations in the 19 wing venation landmarks (Figure 7). However, *A. cerana* from Kalimantan clustered closely with several *A. cerana* samples from Banten. This morphological similarity between the *A. cerana* from Kalimantan and Java was also supported by molecular analysis of COI, COII, and igs (Muhammad *et al.* 2026), suggesting that 19 landmarks can detect local Javanese variation in Kalimantan. The local variation based on 19 landmarks of wing venation was also detected in *A. mellifera pomonella* (local bees) from southern Kazakhstan, which is more similar to *A. mellifera carnica* than *A. m. mellifera* (Temirbayeva *et al.* 2023). These findings demonstrate that geometric morphometric analysis of wing venation is effective in differentiating honey bees at the subspecies level. Based on wing shape and size, this approach has successfully distinguished *A. m. mellifera* and *A. m. carnica* in northern Poland (Oleksa and Tofilski 2015) and *A. m. intermissa* and *A. m. sahariensis* in Morocco (Aglagane *et al.* 2022).

In conclusion, the present study revealed considerable variation in the wing venation morphology of *A. cerana* in Kalimantan. *Apis cerana* from South Kalimantan exhibited the highest variation in wing shape, whereas samples from West Kalimantan showed relatively conserved wing size and shape, indicated by lower levels of variation. Comparative analyses across the Sundaland region revealed that *A. cerana* Kalimantan was predominantly separated from *A. cerana* Sumatra and Java in both the PCA and NJ tree analyses. Nevertheless, several samples from Banten and Jambi clustered with *A. cerana* from Kalimantan, suggesting similarities in wing-venation morphology among certain regional groups. Overall, these findings showed the effectiveness of wing venation geometric morphometrics in detecting morphological variation and assessing relationships among *A. cerana* across Sundaland, with potential applications for the development of digital identification systems for Apis species in Indonesia.

Acknowledgements

We thank the Ministry of Research and Technology - National Research and Innovation Agency (Indonesia) for funding this research under the scheme Penelitian Dasar Kompetensi Nasional (PDKN) on behalf of the corresponding author, entitled "Evolution of honeybee *Apis cerana* in Indonesia: Morphology and Molecular Approach" (Contract number: 001/E5/PG.02.00PL/2023). The first author was supported by

the East Kalimantan provincial government for a Master Degree Scholarship (Kaltim Tuntas). We also thank all the bee farmers who provide *A. cerana* samples. We appreciate all assistants who supported the *A. cerana* Kalimantan sample collection.

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