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Original Article

Morphometric variations of *Apis dorsata* Fabricius (Insecta: Hymnoptera: Apidae) from South Sumatra, Belitung, and West Kalimantan

Variasi morfometrik *Apis dorsata* Fabricius (Insecta: Hymnoptera: Apidae) dari Sumatera Selatan, Belitung, dan Kalimantan Barat

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ABSTRACT

Apis dorsata Fabricius is a giant forest honey bee with a wide distribution that includes Indonesia. South Sumatra, Belitung, and West Kalimantan exhibit distinct geographic and ecological characteristics that may influence the morphometric variations of this species. This study aimed to analyze the similarities and differences across various morphometric parameters of *A. dorsata* colonies from these three regions. A traditional morphometric approach was conducted to measure 23 morphometric parameters. A total of 120 individuals from 12 *A. dorsata* colonies originating from South Sumatra, Belitung, and West Kalimantan were examined. The results indicated that 12 of the 23 parameters (52.2%) differed significantly among populations. Populations from South Sumatra generally exhibited larger structural dimensions across several head, thorax, and wing parameters, whereas the Belitung populations demonstrated higher values for proboscis length and antennal socket distance. Multivariate analysis (NMDS and ANOSIM) revealed statistically significant, albeit weak, differentiation among the populations. Overall, these findings indicate the presence of localized morphometric variations across the islands, although the degree of morphological differentiation remains relatively low.

Key words: honey bees, Indonesia, island variations, morphology, traditional morphometry

ABSTRAK

Apis dorsata Fabricius merupakan lebah madu hutan raksasa yang memiliki distribusi yang luas, termasuk di Indonesia. Sumatra Selatan, Belitung, dan Kalimantan Barat memiliki karakteristik geografis dan ekologis berbeda yang berpotensi memengaruhi variasi morfometrik spesies ini. Penelitian ini bertujuan untuk menganalisis persamaan dan perbedaan setiap parameter morfometrik koloni *A. dorsata* dari ketiga wilayah tersebut. Analisis dilakukan menggunakan metode morfometrik tradisional dengan mengukur 23 parameter morfometrik. Sebanyak 120 individu yang berasal dari 12 koloni *A. dorsata* dari Sumatra Selatan, Belitung, dan Kalimantan Barat digunakan dalam penelitian ini. Hasil menunjukkan bahwa 12 dari 23 parameter morfometrik (52,2%) berbeda secara signifikan antarpopulasi. Populasi dari Sumatra Selatan umumnya memiliki dimensi struktural yang lebih besar pada beberapa parameter kepala, toraks, dan sayap, sedangkan populasi Belitung menunjukkan nilai yang lebih tinggi pada panjang probosis dan jarak soket antena. Analisis multivariat (NMDS dan ANOSIM) menunjukkan perbedaan yang signifikan secara statistik, tetapi dengan tingkat pemisahan yang lemah antarpopulasi. Secara keseluruhan, hasil ini menunjukkan adanya variasi morfometrik lokal antarpulau, tetapi tingkat diferensiasi morfologinya relatif rendah.

Kata kunci: Indonesia, lebah madu, morfologi, morfometri tradisional, variasi pulau

INTRODUCTION

Apis dorsata Fabricius is a giant forest honey bees that distribute widely across South and Southeast Asia (Ruttner 1988; Oldroyd & Wongsiri 2006). In Southeast Asia, *A. dorsata* has a distribution that covers major regions, including Thailand, Malaysia, the Philippines, and Indonesia (Ruttner 1988). Within Indonesia, *A. dorsata* occurs extensively throughout the Sundaland region—including Sumatra, Belitung, Java, and Kalimantan) (Zahara et al. 2022)—and extends into Wallacea, encompassing Sulawesi, the Lesser Sunda Islands, and the Kei Islands (Maa 1953; Ruttner 1988; Raffiudin & Shullia 2020; Lamerkabel et al. 2024).

Despite their widespread geographic distribution, honey bee populations are known to exhibit morphological variations in response to various environmental selection pressures (Cao et al. 2012; Zahara et al. 2022). Environmental factors, such as temperature, altitude (Raffiudin et al. 1999), food availability (Burkle & Irwin 2009; Nicholls et al. 2021), and geographic history, can influence the physical characteristics of these bees (Ken et al. 2003).

To investigate those variations, traditional morphometrics has been widely applied to characterize honey bees through quantitative measurements of morphological traits (Ruttner 1988; Makkar et al. 2020). In the other hand, the modern morphometrics approach, geometric morphometrics, also can detect population differentiation and evolutionary pattern using wing venation landmark-based (Bookstein 1997; Francoy et al. 2008; Zahara et al. 2022).

Traditional morphology variations effectively differentiate the *A. dorsata* and *A. laboriosa* in China using principal component, cluster, and discriminant analysis (Cao et al. 2012). However, traditional morphology of *A. dorsata* in Indonesia still limited, such as East Lombok (Herlambang et al. 2025) and Southwest Mollucas (Pattikawa et al. 2023). In contrast, the geometric morphometrics of landmark fore-wing venation differentiate the population of giant forest honey bee from Sulawesi and Sumbawa, indicating regional adaptation (Zahara et al. 2022).

As an archipelago country, Indonesia offers uniqie natural environment for studying the variation within population of widely distributed species. The Sumatra, Kalimantan, and Belitung are three different island in Sundaland region that has distinct geographic and ecological condition and making them ideal for exploring how regional isolation and environmental differences influence morphology of *A. dorsata.*

Although those islands were connected as part of the Sundaland landmass, post glacial sea-level rise led the islands separated am resulting the geographic isolations. This isolation combined with variation habitat, vegetation, and food resources availability, may have contributed to morphological differences among *A. dorsata* population (Ji et al. 2023). Therefore, the objective of this study was to analyze the similarities and differences in each morphometric parameter of *A. dorsata* colonies from South Sumatra, Belitung, and West Kalimantan.

MATERIALS AND METHODS

Study area and specimen collection

This study utilized a total of 120 individuals from 12 colonies of *A. dorsata* (10 individuals per colony). Four colonies were sampled from each of the following regions: South Sumatra, Belitung, and West Kalimantan (Table 1, Figure 1, Figure 2).

The nesting environments varied across regions. In South Sumatra, three *A. dorsata* colonies were collected from natural trees located near coffee plantations, *Calliandra* shrubs, rubber trees, and other forest vegetations, while another colony was found nesting on a cliff. In Belitung, colonies were found in Sunggau (a traditional artificial nesting structure) as well as from natural trees. In West Kalimantan, colonies were sampled from natural trees and a Tikung (artificial nesting board) located above a lake within a stable and humid tropical freshwater swamp forest ecosystem.

Preparation *A. dorsata* specimens

Each *A. dorsata* specimen used for morphometric analysis was photographed. The specimens were dissected into separate body sections: head, thorax, abdomen, fore-wing, hind-wing, and hind-leg (Ruttner 1978; Ruttner 1988; Cao et al. 2012). Dissection was performed using a scalpel and forceps. Each dissected body part was mounted on a microscope slide and was subsequently photographed to enable accurate measurement of the corresponding morphometric parameters.

Specimen imaging

Images of the dissected bee body parts were acquired using an Olympus SZ61 stereo microscope with an Optilab Viewer 2.2 digital camera system. To capture the full lateral and dorsal profiles of the bees were captured using a Sony Alpha 6400 camera fitted with a macro lens. All specimens were photographed according to standardized imaging protocols to ensure consistency across samples and minimize measurement error. A millimeter-scale calibration block was included in the frame of every image to provide an accurate reference for digital morphometric measurement.

Table 1. Collection site of *Apis dorsata* in Sundaland

No	Colony ID	Location (Subdistrict, District)	Coordinate	Elevation (m.a.sl)	Collector
Sumatra: South Sumatra					
1	Add1_Rmb_Bya	Rambutan, Banyuasin	03°07’49.3” S 104°54’57.4” E	18	FDL
2	Add2_Pnj_OKU	Penjauan, Ogan Komering Ulu	03°49’58.7” S 104°28’06.7” E	48	FDL
3	Add3_Mlu_Lht	Mulak Ulu, Lahat	04°01’51.8” S 103°29’11.4” E	524	FDL
4	Add4_Jjw_OKI	Jejawi, Ogan Komering Ilir	03°06’11.6” S 104°52’53.0” E	12	FDL
Belitung: Bangka Belitung Island					
5	Add1_Sjk_Blt	Sijuk, Belitung	02°34’32.2” S 107°42’05.4’’ E	7	RIR, NIS, DD, MRD
6	Add2_Mbl_Blt	Membalong, Belitung	03°02’56.8” S 107°40’40.1’’ E	34	RIR, NIS, DD, MRD
7	Add3_Mbl_Blt	Membalong, Belitung	03°02’56.8” S 107°40’40.1’’ E	34	RIR, NIS, DD, MRD
8	Add4_Dnd_Btm	Dendang, East Belitung	02°58’28.5” S 107°54’06.3” E	16	RIR, MS, SDH
Kalimantan: West Kalimantan					
9	Add1_Jok_Khl	Jongkong, Kapuas Hulu	00°39’59.0” N 112°28’47.4” E	19	AS, AL, HRM, SYF, JND
10	Add2_Jok_Khl	Jongkong, Kapuas Hulu	00°39’29.4” N 112°28’54.2” E	19	AS, AL, HRM, SYF, JND
11	Add3_Bhi_Khl	Bunut Hilir, Kapuas Hulu	00°45’14.5” N 112°35’55.9” E	25	AS, AL, HRM, SYF, JND, SFI
12	Add3_Bhi_Khl	Bunut Hilir, Kapuas Hulu	00°45’14.0” N 112°35’55.3” E	25	AS, AL, HRM, SYF, JND, SFI

Sample code Add1_Rmb_Bny: A.d. dorsata, 1: Colony 1, Rmb: Rambutan (refer to Subdistrict), Bya: Banyuasin (refer to Regency). Kolektor: FDL: Fadlan, RIR: Rika Raffiudin, NIS: Nurul Insani Shullia, DD: Diardi, MRD: Meggi Romadhona, MS: Muhammad Syahril, SDH: Suci Dian Hayati, MS: Muhammad Syahril, AS: Aulia Savira, AL: Astuti Latif, HRM: Hermanto, SYF: Syafril, JND: Junaidi, SFI: Syafi’i.

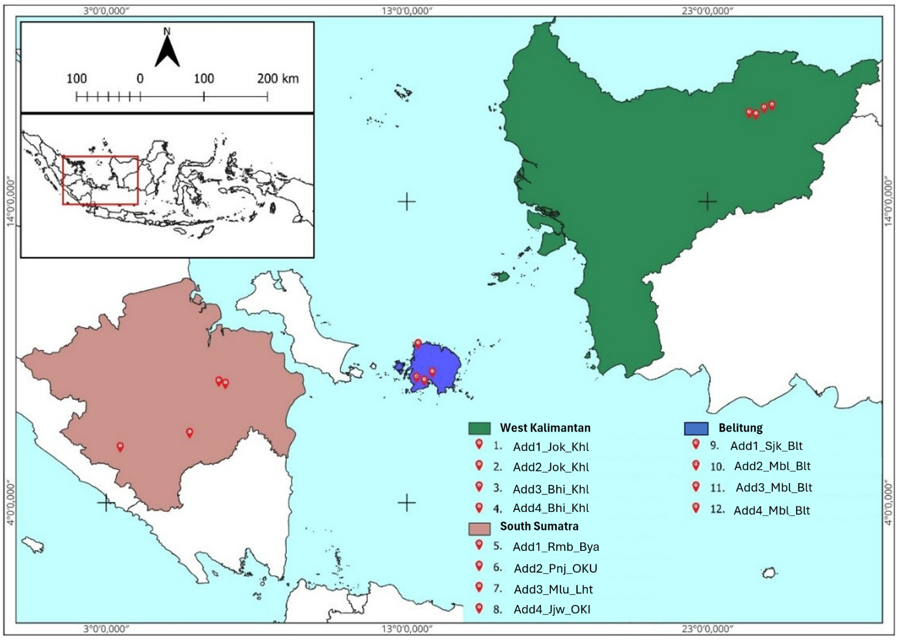


Figure 1. *Apis dorsata* sampling locations. The location code refers to Table 1.

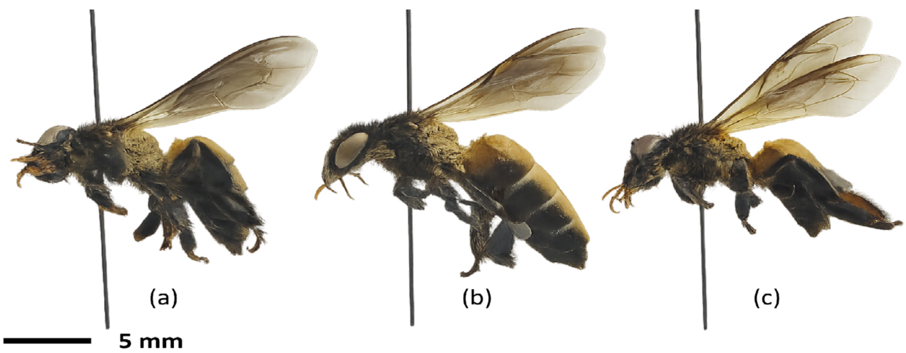


Figure 2. *Apis dorsata* from three Island. a: South Sumatra; b: Belitung; c: West Kalimantan.

Measurement of morphometric parameters

Several previous studies have examined morphometric characteristics of different body parts of the *A. dorsata*. Based on the consistency of morphometric character measurements reported in previous studies (Ruttner 1988; Cao et al. 2012; Raju & Naidu 2016; Makkar et al. 2020), a total of 23 morphometric parameters were selected to measure six parts, as shown in Table 2. The captured images of *A. dorsata* body were digitally measured using Image Raster 4.0 (https://image-raster.software.informer.com/) and Image J 1.53t.

Data analysis

Morphometric data from *A. dorsata* were processed and analyzed using the paleontological statistics (PAST) software version 4.03 (Hammer et al. 2001). Data normality was initially assessed using the Shapiro-Wilk test. Because normality assumptions were not

Table 2. Twenty three morphometric parameters used in the anatomical analysis of *Apis dorsata* based on modification from Ruttner (1988); Cao et al. (2012); Raju & Naidu (2016); Makkar et al. (2020)

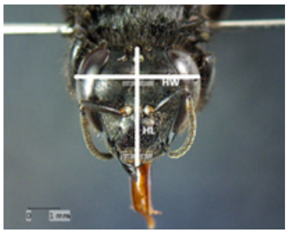
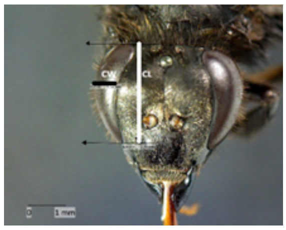
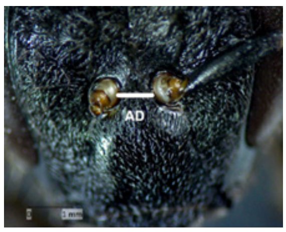
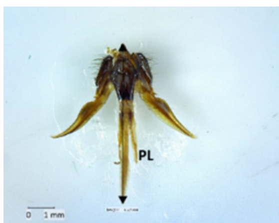
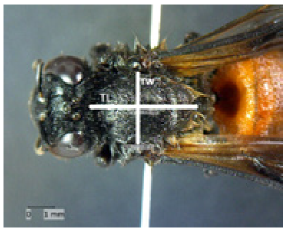
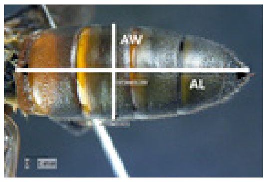
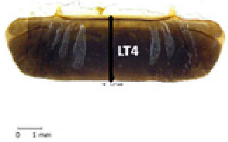
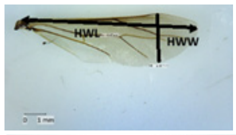
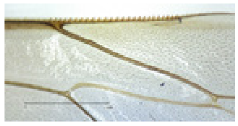
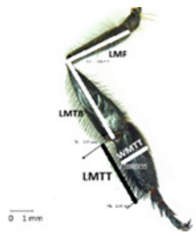
Section	Morphometric parameters	Abbreviation	Image
Body	1. Body length	BL	
Head	2. Head width	HW	
	3. Head length	HL	
	4. Compound eye width	CW	
	5. Compound eye length	CL	
	6. Distance between ocelli	DO	
	7. Antennal socket distance	AD	
	8. Proboscis length	PL	

Table 2. Twenty three morphometric parameters used in the anatomical analysis of *Apis dorsata* based on modification from Ruttner (1988); Cao et al. (2012); Raju & Naidu (2016); Makkar et al. (2020) (*Countinue...*)

Section	Morphometric parameters	Abbreviation	Image
Thorax	9. Thorax length	TL	
	10. Thorax width	TW	
Abdomen	11. Abdomen length	AL	
	12. Abdomen width	AW	
	13. Longitudinal diamater of tergite 3	LT3	
	14. Longitudinal diamater of tergite 4	LT4	
Wing	15. Forewing length 16. Forewing width	FWL FWW	
	17. Hindwing length 18. Hindwing width	HWL HWW	
	19. Number of hamuli	NH	
Leg	20. Length of metafemur	LMF	
	21. Length of metatibia	LMTB	
	22. Length of metatarsus	LMTT	
	23. Width of metatarsus	WMTT	

met, differences among the island populations were evaluated using the non-parametric Kruskal-Wallis test. When significant effects were detected, subsequent pairwise comparisons were conducted using The Mann-Whitney test.

Similarity patterns among the island populations were further explored using non-metric multidimensional scaling (NMDS). Overall morphological dissimilarity based on multivariate morphometric data was evaluated using an analysis of similarities (ANOSIM) with a Bray-Curtis similarity matrix. The ANOSIM *R* statistic was calculated to quantify population separation, where values approaching 1 indicate strong differentiation and values close to 0 indicate little or no separation among populations.

RESULTS

Regional differences in intra-colony morphometrics of *A. dorsata*

Morphometrics analysis of *A. dorsata* colonies from South Sumatra revealed both significant differences and similarities among colonies. Of the 23 morphometrics parameters measured, 11 parameters showed significant differences, while 12 parameters did not (Table 3). The eleven parameters exhibiting inter-colony variations were body length (BL), distance between ocelli (DO), thorax width (TW), abdomen length (AL), abdomen width (AW), forewing width (FWW), hindwing length (HWL), hindwing width (HWW), length of metafemur (LMF), length of metatibia (LMTB), and width of metatarsus (Table 3, SS1-SS4). ASS1 showed higher mean values and larger dimensions for several related parameters among South Sumatra *A. dorsata* population.

Compared to South Sumatra, giant forest honey bee from Belitung (BL1-BL4) showed a different pattern. Proboscis length (PL), compound eye length (CL), compound eye width (CW), distance between ocelli (DO), thorax length (TL), abdomen length (AL), abdomen width (AW), longitudinal diameter of tergite 3 (LT3), longitudinal diameter of tergite 4 (LT4), hindwing length (HWL), hindwing width (HWW), number of hamuli (NH), length of metafemur (LMF), and length of metatarsus (LMTT) showes the significantly variation among *A. dorsata* colonies from Belitung (Table 3, BL1-BL4). Colony BL1 have larger morphometric proportion for several parameters among other Belitung populations, especially related to proboscis and abdominal size.

West Kalimantan *A. dorsata* colonies have the fewest parameters (10) and differ significantly from those in South Sumatra and West Kalimantan. The 10 parameters are head length (HL), head width (HW), distance between ocelli (DO), antennal socket distance (AD), abdomen length (AL), abdomen width (AW), longitudinal diameter of tergite 3 (LT3), longitudinal diameter of tergite 4 (LT4), hind-wing length (HWL), and number of hamuli (NH) (Table 3, WK1-WK4). Colony WK2 commonly exhibits the highest mean values for several parameters, suggesting larger morphological features in several body parts.

Morphometric analyses of *A. dorsata* from South Sumatra, Belitung, and West Kalimantan revealed location-specific patterns of intra-colony variations. Giant forest honey bees from South Sumatra, the parameters of slightly more than half did not differ significantly. The exhibited significant variations among colonies. In Belitung populations, the significant parameters are more frequently observed in head-related, abdominal, and hindwing measurements. In contrast, significant differentiation in the parameters of colonies from West Kalimantan was restricted mainly to head dimensions, abdominal traits, tergite lengths, hindwing length, and the number of hamuli. Overall, while all locations exhibited a combination of shared and variable morphometric traits among colonies, the number and distribution of significantly different parameters varied across regions, indicating differences in the degree and pattern of intra-population morphometric variations. These results provide a baseline for subsequent comparisons of morphometric variations among the broader regional locations.

Morphometrics variations of *A. dorsata* among locations

Comparative morphometrics analysis of *A. dorsata* from three locations revealed both shared and significantly different traits among the populations (Table 4). Eleven morphometric characters: body length (BL), head width (HW), compound eye width (CW), abdomen length (AL), abdomen width (AW), forewing width (FWW), hindwing width (HWW), number of hamuli (NH), length of metafemur (LMF), length of metatibia (LMTB), and width of metatarsus (WMTT) did not differ significantly among the three locations. These results indicate a relatively conserved pattern for these traits across populations. The significant average size of these morphometric parameters suggests that the body size of South Sumatra population is larger than in Belitung and West Kalimantan (Table 4).

In contrast, twelve morphometric parameters have significantly different variations, namely proboscis length (PL), head length (HL), compound eye length (CL), distance between ocelli (DO), antennal socket distance (AD), thorax length (TL), thorax width (TW), longitudinal diameter of tergite 3 (LT3), longitudinal diameter of tergite 4 (LT4), forewing length (FL), hindwing length (HWL), and the length of the metatarsus (LMTT) (Table 4). These findings indicate the presence of distinct morphometric differentiation among populations across sampling locations.

The Belitung giant forest honey bee populations exhibited the highest mean values for proboscis length (5.81±0.53 mm) and antennal socket distance (0.79±0.08 mm), which were significantly greater than those observed in the other locations ($P<0.05$). Meanwhile, the South Sumatra *A. dorsata* populations showed the highest mean values for ten morphometric including head length (3.56±0.52 mm), compound eye length (2.76±0.24 mm), distance between ocelli

Table 3. Morphometric measurement and standard deviation among *Apis dorsata* colonies from South Sumatra, Belitung, and West Kalimantan

Section	Morphometric parameters	Location											
		SS1	SS2	SS3	SS4	BL1	BL2	BL3	BL4	WK1	WK2	WK3	WK4
Body	BL	16.69±1.17[b]	16.96±1.34[b]	17.26±1.50[a]	18.38±0.85[a]	18.24±1.00[a]	18.15±1.96[a]	17.82±1.58[a]	17.97±1.69[a]	17.88±1.59[a]	17.44±1.16[a]	17.23±1.32[a]	18.48±1.02[a]
Head	PL	5.11±0.50[a]	5.35±0.75[a]	5.14±0.63[a]	5.59±1.41[a]	6.08±0.44[a]	5.39±0.65[b]	6.01±0.14[a]	5.74±0.50[b]	5.42±0.60[a]	5.66±0.62[a]	5.85±0.46[a]	5.34±0.68[a]
	HL	3.65±0.37[a]	3.69±0.53[a]	3.43±0.83[a]	3.49±0.09[a]	3.48±0.24[a]	3.48±0.06[a]	3.48±0.11[a]	3.54±0.08[a]	3.45±0.07[a]	3.49±0.08[a]	3.35±0.10[b]	3.54±0.10[b]
	HW	4.33±0.34[a]	4.35±0.64[a]	3.95±0.98[a]	4.09±0.10[a]	4.04±0.28[a]	4.11±0.07[a]	4.12±0.08[a]	4.17±0.09[a]	4.10±0.06[b]	4.18±0.06[a]	4.07±0.08[b]	4.18±0.07[a]
	CL	2.84±0.28[a]	2.74±0.07[a]	2.74±0.40[a]	2.73±0.07[a]	2.80±0.07[a]	2.72±0.08[a]	2.68±0.08[b]	2.74±0.07[a]	2.65±0.08[a]	2.83±0.56[a]	2.59±0.14[a]	2.73±0.11[a]
	CW	0.71±0.09[a]	0.70±0.10[a]	0.66±0.09[a]	0.75±0.08[a]	0.63±0.04[b]	0.67±0.05[a]	0.66±0.04[a]	0.69±0.07[a]	0.66±0.04[a]	0.71±0.11[a]	0.67±0.67[a]	0.68±0.03[a]
	DO	0.91±0.24[a]	0.77±0.14[b]	0.75±0.17[b]	0.70±0.26[ab]	0.84±0.16[a]	0.64±0.23[b]	0.53±0.21[b]	0.45±0.03[b]	0.40±0.02[b]	0.70±0.21[a]	0.43±0.04[a]	0.46±0.04[a]
	AD	0.72±0.12[a]	0.72±0.11[a]	0.74±0.13[a]	0.67±0.16[a]	0.82±0.03[a]	0.77±0.14[a]	0.79±0.05[a]	0.78±0.03[a]	0.71±0.05[b]	0.79±0.02[a]	0.75±0.05[a]	0.76±0.09[a]
Thorax	TL	4.10±0.55[a]	4.28±0.53[a]	4.33±0.36[a]	4.01±0.24[a]	4.05±0.14[ab]	3.80±0.28[b]	4.02±0.19[b]	4.31±0.29[b]	4.00±0.16[a]	4.12±0.22[a]	3.93±0.15[a]	3.96±0.25[a]
	TW	3.71±0.51[a]	3.84±0.40[a]	3.81±0.42[a]	2.92±0.47[ab]	2.78±0.17[a]	2.72±0.45[a]	2.77±0.20[a]	2.85±0.21[a]	2.75±0.26[a]	2.88±0.21[a]	2.64±0.20[a]	2.71±0.16[a]
Abdomen	AL	8.84±0.59[b]	9.24±0.85[b]	8.21±1.76[b]	10.88±1.12[a]	10.77±0.96[a]	9.06±0.86[b]	7.96±0.42[c]	7.91±1.67[c]	8.91±0.98[a]	8.51±0.43[a]	8.18±0.80[a]	10.59±1.34[b]
	AW	4.72±0.16[a]	4.49±0.14[b]	4.30±0.78[b]	4.71±0.32[ab]	4.84±0.24[a]	4.59±0.18[b]	4.44±0.12[c]	4.28±0.72[b]	4.56±0.18[b]	4.51±0.09[b]	4.49±0.24[b]	4.70±0.14[a]
Abdomen	LT3	2.83±0.04[a]	2.80±0.08[a]	2.75±0.09[a]	2.88±0.21[a]	2.75±0.05[a]	2.62±0.07[b]	2.66±0.10[b]	2.71±0.06[a]	2.62±0.06[b]	2.76±0.03[a]	2.69±0.07[b]	2.76±0.05[a]
	LT4	2.76±0.03[a]	2.73±0.11[a]	2.70±0.07[a]	2.78±0.20[a]	2.68±0.03[a]	2.55±0.08[b]	2.58±0.10[b]	2.67±0.06[a]	2.56±0.05[b]	2.69±0.03[a]	2.60±0.09[b]	2.67±0.06[a]
Wing	FWL	12.90±0.71[a]	12.88±0.78[a]	12.56±0.71[a]	12.93±0.25[a]	12.75±0.16[a]	12.60±0.26[a]	12.80±0.25[a]	12.81±0.15[a]	12.68±0.22[a]	12.79±0.13[a]	12.72±0.19[a]	12.67±0.22[a]
	FWW	4.29±0.20[a]	4.24±0.26[a]	4.10±0.23[b]	4.24±0.09[a]	4.22±0.07[a]	4.20±0.07[a]	4.27±0.08[a]	4.26±0.09[a]	4.28±0.09[a]	4.25±0.05[a]	4.26±0.10[a]	4.21±0.06[a]
	HWL	8.69±0.39[a]	8.88±0.19[a]	8.56±0.19[b]	8.72±0.22[a]	8.54±0.16[b]	8.38±0.32[b]	8.50±0.21[b]	8.82±0.43[a]	8.57±0.15[b]	8.83±0.10[a]	8.55±0.21[b]	8.59±0.19[b]
	HWW	2.37±0.11[a]	2.46±0.17[a]	2.32±0.06[b]	2.33±0.06[b]	2.36±0.06[a]	2.31±0.05[b]	2.33±0.06[b]	2.42±0.13[a]	2.35±0.05[a]	2.38±0.06[a]	2.32±0.08[a]	2.31±0.05[a]
	NH	25.10±1.91[a]	26.70±1.70[a]	26.10±1.45[a]	25.60±1.96[a]	25.40±2.37[b]	25.10±2.13[b]	26.20±2.04[a]	24.20±1.03[b]	24.50±1.72[b]	27.20±1.32[a]	24.90±1.91[b]	25.80±2.10[b]
Leg	LMF	3.17±0.23[b]	3.03±0.19[b]	2.81±0.40[a]	3.09±0.07[b]	3.06±0.06[b]	3.66±0.32[a]	3.07±0.32[b]	3.07±0.06[b]	3.03±0.15[a]	3.08±0.03[a]	3.09±0.06[a]	3.11±0.05[a]
	LMTB	4.10±0.32[a]	3.90±0.22[ab]	3.68±0.41[b]	3.95±0.07[a]	3.89±0.08[a]	3.74±0.16[a]	3.76±0.40[a]	3.88±0.04[a]	3.85±0.21[a]	3.89±0.10[a]	3.89±0.11[a]	3.96±0.07[a]
	LMTT	2.97±0.25[a]	2.84±0.21[a]	2.71±0.26[a]	2.88±0.11[a]	2.89±0.07[a]	2.73±0.07[b]	2.72±0.15[b]	2.80±0.08[b]	2.76±0.17[a]	2.86±0.05[a]	2.78±0.09[a]	2.85±0.12[a]
	WMTT	1.32±0.11[a]	1.31±0.11[a]	1.19±0.12[b]	1.29±0.07[a]	1.25±0.04[a]	1.26±0.04[a]	1.24±0.06[a]	1.27±0.05[a]	1.25±0.03[a]	1.27±0.04[a]	1.27±0.03[a]	1.31±0.06[a]

SS: South Sumatra; BL: Belitung; KB: West Kalimantan.

Different letters in the same row indicate significant differences (Mann-Whitney test).

BL: body length; HW: head width; HL: head length; CW: compound eye width; CL: compound eye length; DO: distance between ocelli; AD: antennal socket distance; PL: proboscis length; TL: thorax length; TW: thorax width; AL: abdomen length; AW: abdomen width; LT3: longitudinal diamater of tergite 3; LT4: longitudinal diamater of tergite 4; FWL: forewing length; FWW: forewing width; HWL: hindwing length; HWW: hindwing width; NH: number of hamuli; LMF: length of metafemur; LMTB: length of metatibia; LMTT: length of metatarsus; WMTT: width of metatarsus.

(0.78±0.21 mm), thorax length (4.18±0.44 mm), thorax width (3.57±0.58 mm), longitudinal diameter of tergite 3 (2.81±0.12 mm), longitudinal diameter of tergite 4 (2.74±0.12 mm), forewing length (12.82±0.64 mm), hindwing length (8.71±0.27 mm), and metatarsus length (2.85±0.23 mm). Overall, the results demonstrate that while several morphometric traits are conserved across *A. dorsata* populations from different locations, a specific subset of characters exhibits significant geographic variations.

Morphometric variation as a reflection of local adaptation

The NMDS ordination showed a substantial overlap among individual *A. dorsata* from South Sumatra, Belitung, and West Kalimantan (Figure 3). Despite this visual overlap. The ANOSIM detected a statistically significant difference among the populations (R = 0.06233, p = 0.0006) (Figure 3). However, the low R-value suggests that interpopulation differentiation is weak relative to within-population variation.

DISCUSSION

Morphometric variations of *A. dorsata* within and among locations

The results show that morphometric variation within *A. dorsata* colonies differs among South Sumatra, Belitung, and West Kalimantan, with some parameters showing stronger statistical differences than others (Table 3). Overall, this pattern suggests a moderate level of

Table 4. Mean and standard deviation of each morphometric parameter among *Apis dorsata* from South Sumatra, Belitung, and West Kalimantan

Section	Morphometric parameters	Locations		
		SS	BL	WK
Body	BL	17.32±1.35[a]	18.04±1.54[a]	17.76±1.3[a]
Head	PL*	5.30±0.88[b]	5.81±0.53[a]	5.57±0.60[a]
	HL*	3.56±0.52[a]	3.49±0.14[ab]	3.46±0.11[b]
	HW	4.18±0.61[a]	4.11±0.16[a]	4.13±0.08[a]
	CL*	2.76±0.24[a]	2.74±0.09[a]	2.70±0.30[b]
	CW	0.71±0.09[a]	0.66±0.06[a]	0.68±0.07[a]
	DO*	0.78±0.21[a]	0.62±0.22[b]	0.50±0.16[c]
	AD*	0.71±0.13[b]	0.79±0.08[a]	0.75±0.06[b]
Thorax	TL*	4.18±0.44[a]	4.04±0.29[ab]	4.01±0.20[b]
	TW*	3.57±0.58[a]	2.78±0.27[b]	2.74±0.22[b]
Abdomen	AL	9.29±1.50[a]	8.89±1.57[a]	9.04±1.31[a]
	AW	4.56±0.45[a]	4.54±0.43[a]	4.56±0.19[a]
	LT3*	2.81±0.12[a]	2.69±0.09[b]	2.71±0.08[b]
	LT4*	2.74±0.12[a]	2.62±0.09[b]	2.63±0.08[b]
Wing	FWL*	12.82±0.64[a]	12.74±0.22[b]	12.71±0.19[b]
	FWW	4.22±0.21[a]	4.24±0.08[a]	4.25±0.08[a]
	HWL*	8.71±0.27[a]	8.56±0.33[b]	8.63±0.20[ab]
	HWW	2.37±0.12[a]	2.35±0.09[a]	2.34±0.07[a]
	NH	25.88±1.80[a]	25.23±2.02[a]	25.60±2.01[a]
Leg	LMF	3.02±0.28[a]	3.22±0.34[a]	3.08±0.09[a]
	LMTB	3.91±0.31[a]	3.82±0.22[a]	3.90±0.14[a]
	LMTT*	2.85±0.23[a]	2.78±0.12[b]	2.81±0.12[ab]
	WMTT	1.28±0.11[a]	1.25±0.05[a]	1.28±0.05[a]

Different letters in the same row indicate significant differences (Mann-Whitney test). *Significant differences.

SS: South Sumatra; BL: Belitung; KB: West Kalimantan.

BL: body length; HW: head width; HL: head length; CW: compound eye width; CL: compound eye length; DO: distance between ocelli; AD: antennal socket distance; PL: proboscis length; TL: thorax length; TW: thorax width; AL: abdomen length; AW: abdomen width; LT3: longitudinal diamater of tergite 3; LT4: longitudinal diamater of tergite 4; FWL: forewing length; FWW: forewing width; HWL: hindwing length; HWW: hindwing width; NH: number of hamuli; LMF: length of metafemur; LMTB: length of metatibia; LMTT: length of metatarsus; WMTT: width of metatarsus.

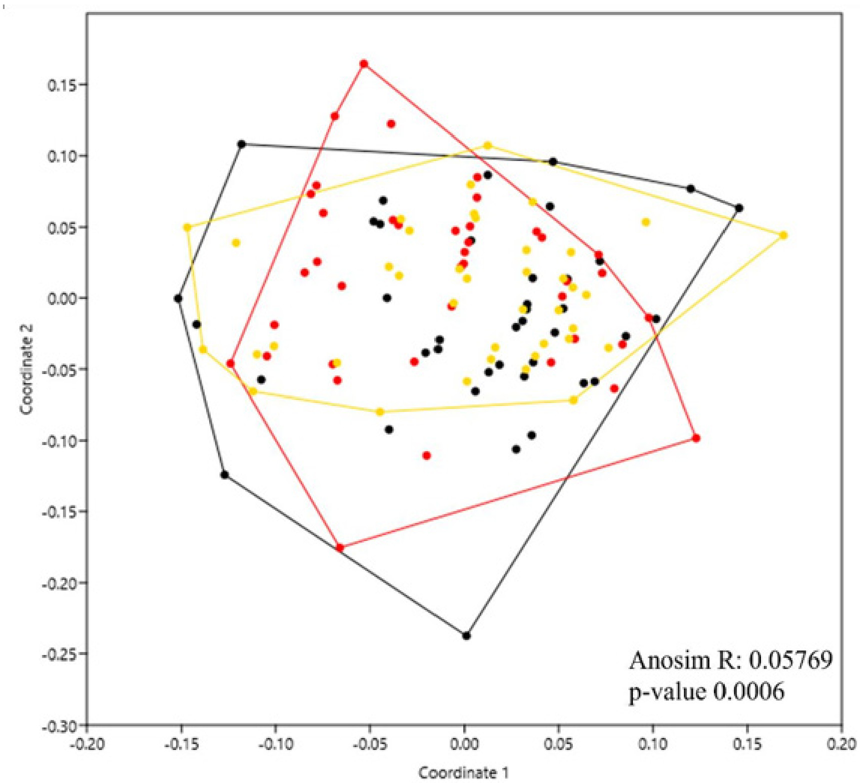


Figure 3. Non-metric multidimensional scaling (NMDS) ordination plot of *Apis dorsata* populations based on 23 morphometric parameters. Colors indicate sampling locations: South Sumatra (black), Belitung (red), and West Kalimantan (gold). Polygons enclose all individual data points for each region, illustrating the substantial morphometric overlap among the three populations. The NMDS stress value was 0.20.

geographic structuring of morphometric variations without clear morphological discontinuities among the populations.

Apis dorsata from South Sumatra did not differ significantly nearly half of the measued paramters among *A. dorsata* colonies, suggesting moderated intra-population homogeneity. The significant variations detected primarily involved overall core body dimensions, wing dimensions, and hind-leg structures. These traits are closely related to flight performance, dispersal capacity, and resource transport. Colony SS1 of this giant forest honey bee consistently exhibited higher mean values (Table 3), suggesting localized influences on structural development. Similarly, morphometric variability of *A. dorsata* in India showed limited differences within the same geographic (Uniyal et al. 2019; Rajak & Basavarajappa 2016). Environmental factors such as resource availability, microclimate, and colony nutritional status are important factors in size variations (Hepburn & Rafloff 2004; Hoiss et al. 2012). Variations in body parts of the bees associated with feeding proboscis, compound eyes ocelli, and abdominal characteristics may reflect differences in ecological conditions across the island. Larger body size is generally associated with longer flight distances and greater resistance to habitat fragmentation (Greenleaf et al. 2007; Cariveau et al. 2016), which could be an advantage in areas with dispersed floral food sources. Furthermore, larger wing size can influence flight efficiency and foraging range, two characteristics often related to environmental conditions and resource distribution (Hoiss et al. 2012). Tropical rainforests in South Sumatra likely provide abundant and diverse food sources. This is reinforced by the positive relationship between vegetation diversity and the variation in pollen collected by bees, supporting the hypothesis that resource-rich environments promote the development of more optimal morphology (Raffiudin et al. 2024).

Apis dorsata from West Kalimantan showed a similar degree of morphological uniformity, with only 10 parameters differing significantly, mainly in head dimensions, abdominal measurements, tergite lengths, hind-wing length, and the number of hamuli (Table 3). The relatively high proportion of non-significant parameters suggests greater local homogeneity, possibly facilitated by more continuous forest habitats.

In contrast, Belitung showed slightly greater intracolony differentiation, especially in proboscis length, compound eye length, ocellar distance, thorax, abdomen, and wings (Table 3). Variations was concentrated in feeding-related (proboscis length) and sensory (compound eye length, ocellar distance). The significant differences in feeding and sensory structures may reflect ecological heterogeneity across the island landscape. Belitung is characterized by fragmented heath forests, grasslands, mangroves, and coastal vegetation mosaics on acidic sandy soils (Mannion 2011; Oktavia et al. 2024). Habitat heterogeneity initiates microenvironmental variations that can influences developmental, such habitat heterogeneity can generate microenvironmental variation that influences developmental pathways and enhances phenotypic plasticity in social bees (Hepburn & Radloff 2004; Carré et al. 2009). This ecology is consistent with the history of Belitung as part of the Sundaland savanna corridor during the Quaternary period (Bird et al. 2005; Sarr et al. 2019), which may have contributed to long-term ecological differentiation relative to the main Sundaland regions. Belitung populations exhibited significantly greater proboscis length and antennal socket distance than *A. dorsata* in South Sumatra and West Kalimantan. Proboscis length is closely linked to nectar foraging efficiency and floral specialization (Hepburn & Radloff 2004), suggesting potential ecological adaptation and local floral resources composition. The similar pattern of environmental-morphometric variations has been documented in *A. dorsata* populations in Karnataka (Dhananjaya et al. 2021) and Lombok (Herlambang et al. 2025), as well as differences in landmark fore-wing venation of *A. dorsata* across Indonesian islands (Zahara et al. 2022).

A comparison of average morphometric values across *A. dorsata* populations from South Sumatra, Belitung, and West Kalimantan shows that some traits remain consistent, while others vary depending on geographic location. Eleven characters, including body length, head width, compound eye width, abdominal dimensions, wing width, number of hamuli, and hind-leg measurements (Table 4), did not differ significantly among locations. These results suggest that several structural traits remain relatively conserved across regional populations.

Conversely, twelve parameters–including proboscis length, head length, compound eye length, ocellar distance, antennal socket distance, thorax dimensions, tergite lengths, forewing length, hindwing length, and metatarsus length–exhibited significant geographic variations. These differences indicate measurable morphometric differentiation among populations from the three islands/regions.

Across the three regions, ocellar distance, abdominal dimensions, tergite length, and hindwing length repeatedly showed significant variations, indicating that these traits may be particularly responsive to environmental or developmental factors. Colonies of *A. dorsata* from India in different ecological conditions showed differences in thoracic and abdominal characteristics (Rajak & Basavarajappa 2016). A range of environmental factors, including altitude (Redhead et al. 2016), habitat type, and the availability of resources (Hoiss et al. 2012), are known to influence morphometric traits in bees. Moreover, variations in habitat structure and landscape features can also contribute to differences in insect morphology (Hepburn & Radloff 2004; Carré et al. 2009). Overall, these results suggest that morphological variation in *A. dorsata* is not consistent across all traits, but is mainly associated with certain characteristics that are sensitive to environmental conditions and differ across regions.

Morphometric variations of *A. dorsata* in Belitung as a reflection of local environmental conditions

Although overall body size was consistent, *A. dorsata* populations from Belitung exhibited significantly longer proboscises and wider distances between the antennal sockets than those from two other regions. This extended proboscis length may enhance nectar extraction efficiency (Waddington & Herbast 1987), particularly in habitats with diverse or morphologically restrictive floral resources. The extended proboscis length may further enhance nectar extraction efficiency, particularly in habitats with diverse or structurally complex of flowers.

The distinct morphometric characteristics of the Belitung populations may also be influenced by the island's geological and ecological history. Belitung formed part of the Sundaland savanna corridor during the late Quaternary and became isolated following the Holocene sea-level rise (Bird et al. 2005; Sarr et al. 2019; Meltzner et al. 2017). Present-day Belitung is dominated by heath forests on acidic sandy soils, interspersed with savanna and mangrove habitats (Mannion 2011; Oktavia et al. 2024). Soil properties and plant community composition in such savanna-like ecosystems are known to influence insect community structure, including morphological traits in bees (Haddad et al. 2009; Rodrigues et al. 2018).

Proboscis lenght is an important factor in bees utilize of floral resources, as it influences theis ability to reach nectar in flowers with different corolla depths (Inouye 1980; Nicolson 2011). Bees with longer proboscides are often able to exploit a wider range of flowers and esctract netar more efficiently (Harder 1985; Cariveau et al. 2016). Palynological data further suggest that *A. dorsata* in Belitung collects resources from diverse plant species across varied habitats (Bramasta et al. 2023), suggesting that variations in proboscis length represents a functional to local floral resource composition and spatial distribution, likely driven by selective pressures in this environment.

However, multivariate analysis using NMDS ordination revealed considerable overlap among *A. dorsata* individuals from Belitung, South Sumatra, and West Kalimantan (Figure 3), indicating overall morphometric separation among populations is limited. Although ANOSIM showed statistically significant differences ($R = 0.06233$, $p < 0.0005$), the low R-value indicates weak differentiation between *A. dorsata* populations relative to within-population variations. Thus, while *A. dorsata* Belitung populations exhibit distinct feeding-adaptation, such as a longer proboscis, these may correlate broadly with a conserved morphological framework rather than forming discrete another morphology.

The extended proboscis observed in Belitung populations represents population-level morphological variation associated with local environmental conditions, habitat heterogeneity, and historical island isolation. The NMDS results also support the interpretation that the variations is subtle and quantitative, reflecting geograhical and ecological adaptation or phenotypic plasticity rather than discrete taxonomic divergence.

CONCLUSION

Populations of *A. dorsata* from South Sumatra, Belitung, and West Kalimantan obtained both stable and variable morphometric traits. Although most measurements do not differ significantly among locations, several characters vary noticeably, suggesting a degree of morphological differentiation measurable but limited. This variations not uniform across all morphological characters but is driven by specific, environmentally responsive characters, particularly those related to head, abdominal, and wing morphology. Despite thesse differences, multivariate analyses show considerable overlap amogn *A. dorsata* from the three populations, indicating weak overall morphological structuring. This suggests that *A. dorsata* retains generally similar morphology across Sundaland, with only slight quatitative differences that are likely influenced by local environmental conditions rather than clear population divergence.

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