

# Morphological characters of the endemic honey bee *Apis binghami binghami* across different elevations in South Sulawesi, Indonesia

JAENAR ADELIA NADI, SITTI NURAENI<sup>✉</sup>, BUDIAMAN, ANDI PRASTIYO

Department of Forestry, Faculty of Forestry, Universitas Hasanuddin. Jl. Perintis Kemerdekaan Km. 10, Makassar 90245, South Sulawesi, Indonesia.

<sup>✉</sup>email: sitti.nureny@unhas.ac.id

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**Abstract.** Nadi JA, Nuraeni S, Budiaman, Prastiyo A. 2026. Morphological characters of the endemic honey bee *Apis binghami binghami* across different elevations in South Sulawesi, Indonesia. *Biodiversitas* 27 (2): d270220. <https://doi.org/10.13057/biodiv/d270220>. *Apis binghami binghami* is an endemic honey bee of Wallacea that plays a crucial role in pollination and maintaining tropical ecosystem balance. However, information on its morphological characters along the elevational gradient in South Sulawesi remains limited. Environmental heterogeneity associated with altitude may strongly influence morphological traits related to flight performance, foraging efficiency, and physiological adaptation. This study aimed to analyze the morphological characters of *A. b. binghami* across three elevational zones lowland (0-300 masl), midland (301-700 masl), and highland (>700 masl) in South Sulawesi, Indonesia. Worker bees were collected using standardized bait traps, with 30 individuals sampled from each elevation. A total of 37 morphometric characters were measured using stereo microscopy. Data were analyzed using one-way Analysis of Variance (ANOVA), Principal Component Analysis (PCA), cluster analysis, and correlation analysis. The results revealed significant morphometric differences ( $p < 0.001$ ) among elevations, with increasing body size, wing length, abdomen, and sting dimensions at higher altitudes. PCA showed that the first principal component explained 80.22% of the total variation, primarily influenced by mesoscutum width, forewing length, including tegula, and abdominal length. Cluster analysis separated highland populations from lowland and midland groups, indicating clear morphological differentiation along the elevational gradient. These findings demonstrate pronounced morphological plasticity of *A. b. binghami* in response to altitude-related environmental conditions. The study provides the first comprehensive morphometric dataset for this endemic subspecies in South Sulawesi and offers important insights for conservation planning.

**Keywords:** Altitude gradient, body size, endemic honey bee, morphological characters, Wallacea honey bee

## INTRODUCTION

South Sulawesi forms part of the Wallacea biogeographic zone, a transitional region between Asian and Australian fauna that exhibits exceptionally high biodiversity and endemism (Rowe et al. 2019; Struebig et al. 2022). One of the most distinctive species in this region is *Apis binghami binghami*, which lives in the wild and constructs large single combs suspended from tall tree branches, rocky cliffs, or other natural structures (Nagir et al. 2016). Its solitary nesting behavior and inaccessible nest locations make it extremely difficult to domesticate, emphasizing the importance of habitat conservation to sustain its populations. Rapid deforestation, land-use conversion, and other anthropogenic pressures have severely reduced nesting sites and floral resources, threatening both bee populations and forest ecosystem stability.

Honey bees play a crucial role in maintaining ecosystem balance through their pollination activities. Their presence not only supports plant regeneration but also provides economic value through honey (Bareke and Addi 2019) and other bee products (Khalifa et al. 2021). In the context of tropical ecology in Indonesia, honey bees serve as bioindicators of environmental health because they are highly sensitive to habitat and climate changes (Quigley et al. 2019). Among Indonesia's native bee species, *A. b. binghami*, an endemic subspecies from the Wallacea

region, plays a vital ecological role in sustaining tropical forest functions across Sulawesi and surrounding islands (Budiaman et al. 2025).

Morphological analysis provides a key approach for understanding the characteristics of *A. b. binghami* across environmental gradients. This method quantitatively measures body dimensions to identify intraspecific variation and ecological. Parameters such as proboscis length, wing size, and thorax width determine flight efficiency and nectar-foraging ability (Sharaf El-Dhin et al. 2025). Investigating these traits helps reveal the relationship between morphology and ecological function, illustrating how variations in body structure reflect physiological and behavioral responses to differing habitat conditions (Peters et al. 2016).

Environmental factors such as temperature, humidity, and food resources strongly influence the morphological variation of honey bees, with altitude acting as a crucial gradient shaping these conditions (Prastiyo et al. 2024). Populations inhabiting higher elevations generally develop larger body sizes and longer wings (Lozier et al. 2021; Yang et al. 2025). Conversely, lowland bees tend to be smaller and exhibit higher metabolic activity due to warmer environments. These morphological patterns serve as valuable indicators for understanding how *A. b. binghami* responds physiologically to different environmental conditions in tropical ecosystems.

Research on *A. b. binghami* in South Sulawesi remains scarce, particularly concerning altitudinal variation and its influence on morphological traits. Previous studies have primarily focused on general ecology and pollination behavior, with limited attention to interpopulation morphological differences along elevation gradients. However, no study has specifically clarified how elevation-driven morphological shifts shape the ecological performance, foraging capability, and long-term viability of this endemic subspecies, despite its crucial role in maintaining forests. This creates a clear research gap because understanding morphological characters across elevations is essential for identifying which populations possess unique traits that may be at greater risk under ongoing habitat loss and climate warming. Understanding these variations is crucial for identifying local patterns that contribute to population resilience under climate change and habitat degradation.

This study aims to analyze the morphological characters of *A. b. binghami* across different altitudinal zones in South Sulawesi to elucidate its ecological responses to differing environmental conditions. Morphological traits of *A. b. binghami* vary systematically along the elevational gradient in South Sulawesi, with higher elevations associated with larger body size and enhanced wing and thoracic dimensions as adaptive responses. The novelty of this study lies in the detailed quantitative assessment of morphometric characters such as sting length, abdominal length, thoracic, and wing dimensions across distinct elevations, representing the first comprehensive dataset for *A. b. binghami* in the Wallacea region. By integrating ecological and morphological perspectives, this study contributes to both the advancement of tropical insect biology and the long-term sustainability of Indonesia's forest ecosystems.

## MATERIALS AND METHODS

### Sampling sites

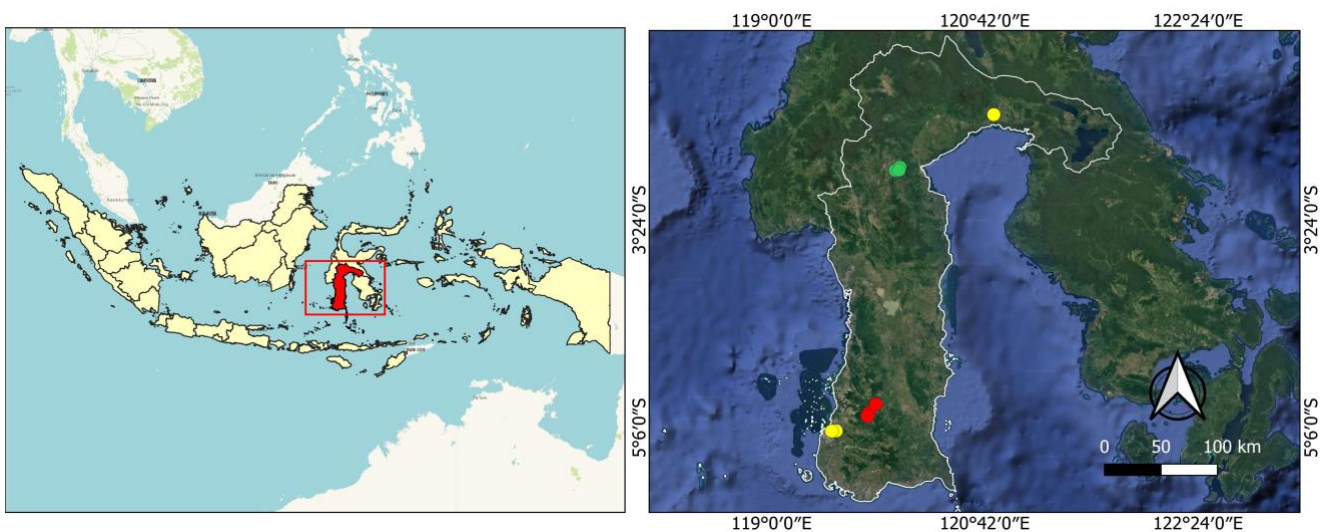
This study was conducted from February to June 2025, with bee sampling carried out at three locations in South Sulawesi, namely lowland (0-300 masl), midland (301-700 masl), and highland (>700 masl) (Prastiyo et al. 2024). The dominant vegetation in the lowland, midland, and highland areas was represented by *Mangifera indica*, *Melastoma malabathricum*, and *Coffea arabica*, respectively. The sampling sites were selected using a purposive sampling method, focusing on differences in altitude (Figure 1).

### Data collection

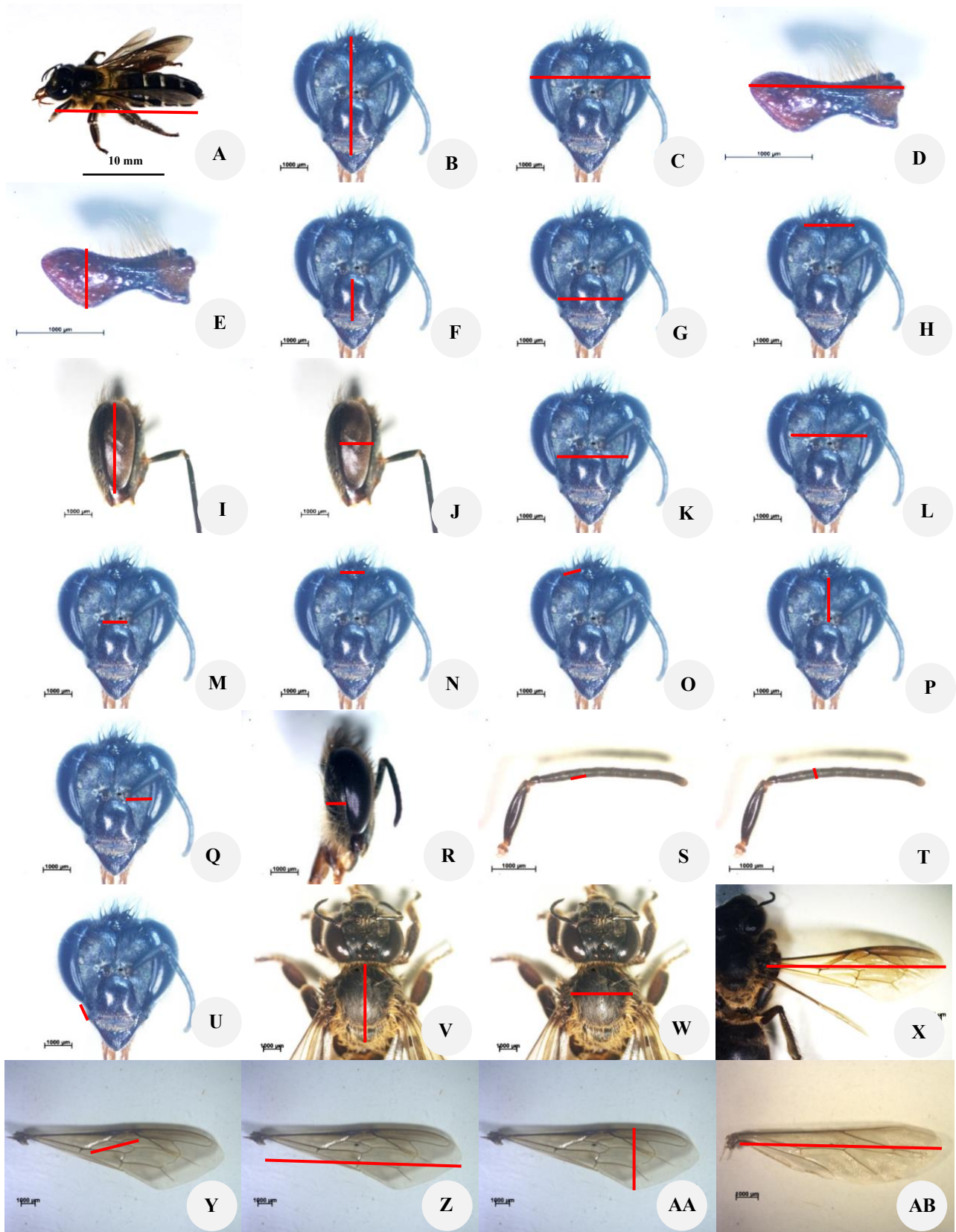
Sampling in this study was conducted using worker bees of *A. b. binghami*. We sampled worker bees attracted to traps baited with honey and sugar. The sampling points were taken using a pseudo-random sampling method, where the location points were based on altitude, and bee samples were taken without special selection at the three elevation locations. Traps were standardized using a sugar solution dissolved in water at a 1:1 ratio, then placed in a sterile sponge placed on a tray. The traps were set 1 m above ground level. Three identified colonies were set at each altitude. The distance between the traps and the colonies was estimated at 50-100 m. Traps were set in the morning (8:00-10:00) and afternoon (15:00-17:00). Bees that landed on the bait traps were collected using microtubes, preserved, and conveyed to the laboratory for morphological measurements.

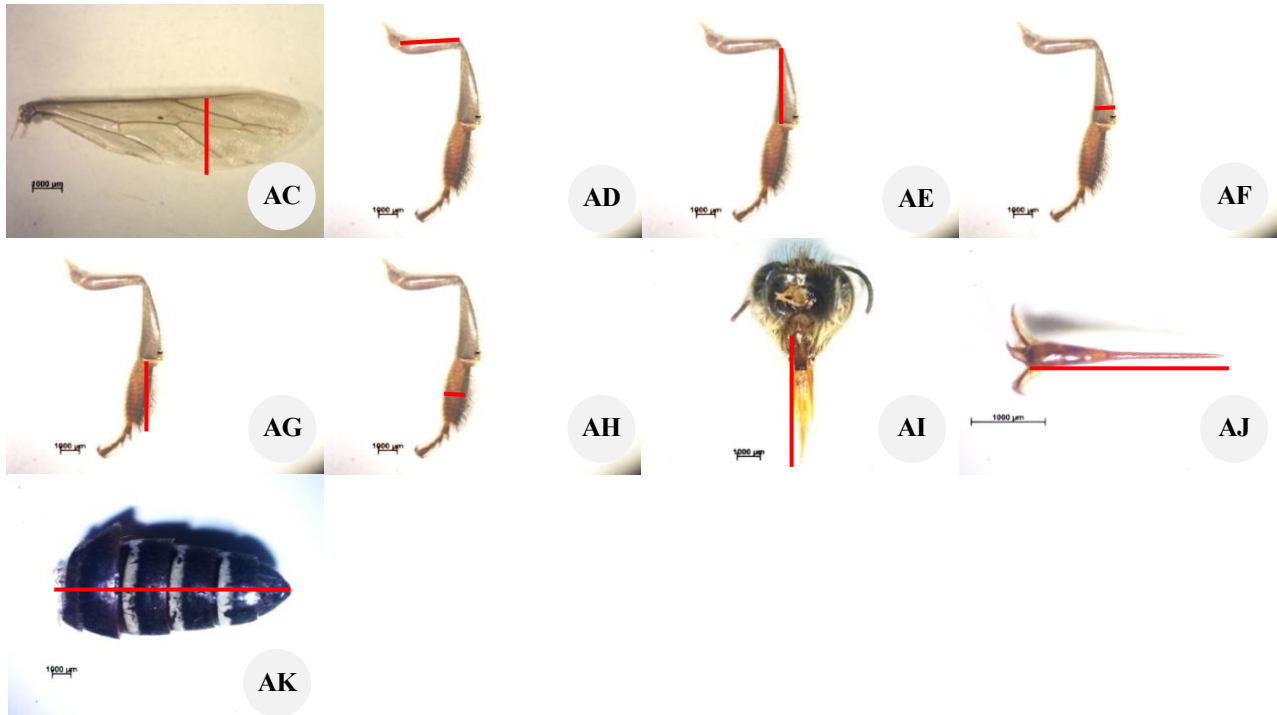
### Morphological measurements

Morphological measurements of *A. b. binghami* were carried out using a stereo microscope (STEM 2000 with an ERC 5S photo tube camera). A total of 30 worker bee individuals per location were measured. 37 morphological characters (Figure 2) of the bee body were examined.



**Figure 1.** Map of sampling locations of *Apis binghami binghami* bees at different altitudes in South Sulawesi, Indonesia. Yellow: Lowland, Red: Midland, Green: Highland





**Figure 2.** Morphological characters of *Apis binghami binghami* measured in this study include: A. body length, B. head length, C. head width, D. mandible length, E. mandible width, F. clypeus length, G. lower interocular distance, H. upper interocular distance, I. eye length, J. eye width, K. lower interorbital distance, L. maximum interorbital distance, M. interantennal distance, N. interocellar distance, O. ocellocular distance, P. antennocellar distance, Q. antennocular distance, R. gena width, S. length of flagellomere IV, T. width of flagellomere IV, U. malar length, V. mesoscutum length, W. mesoscutum width, X. length of forewing including tegula, Y. distance between m-cu bifurcation, Z. forewing length, AA. forewing width, AB. hind wing length, AC. hind wing width, AD. hind femur length, AE. hind tibia length, AF. hind tibia width, AG. hind basitarsus length, AH. hind basitarsus width, AI. proboscis length, AJ. sting length, and AK. abdominal length

### Data analysis

The morphometric data of *A. b. binghami* were analyzed using a one-way Analysis of Variance (ANOVA) with IBM SPSS version 25.0. A normality test was conducted to ensure that the data met the assumptions required for ANOVA. Data normality testing was performed using the Shapiro-Wilk test with a significance level of  $p > 0.05$  before further statistical analysis. The ANOVA test was used to determine whether there were significant differences ( $p < 0.05$ ) in the morphological traits of *A. b. binghami*. The ANOVA results showed significant differences, and the post hoc Duncan Multiple Range Test (DMRT) was applied to identify differences between altitude groups. Subsequently, Principal Component Analysis (PCA) was performed using XLSTAT software. PCA was applied to identify and interpret the variables that explained most of the variability by simplifying the dataset into principal components. Additional analysis was conducted using Agglomerative Hierarchical Clustering (AHC) to classify the data based on the similarity level of morphometric traits among *A. b. binghami* samples. The analysis was performed using Ward's merging method with Euclidean distance to group the samples. This method was employed to identify patterns of relatedness and relationships among bee populations from different study locations based on their morphological dimensions. The results of AHC were visualized in a dendrogram illustrating the degree of

similarity among individuals or groups. These analyses were conducted to provide a comprehensive understanding of the morphological variation of *A. b. binghami* across altitudinal gradients in South Sulawesi.

## RESULTS AND DISCUSSION

### Morphological variation at different elevations

The results of the one-way ANOVA analysis revealed significant ( $p < 0.001$ ) morphological variation of *A. b. binghami* among the three elevation zones (lowland, midland, and highland) in South Sulawesi (Table 1). Most morphological traits showed a consistent increase in size with increasing elevation. The body length of *A. b. binghami* significantly differed among the three altitudes, with the smallest individuals found in the lowland ( $20.63 \pm 0.49$  mm) and the largest in the highland ( $22.37 \pm 0.49$  mm). Similarly, head length and head width gradually increased from  $4.15 \pm 0.03$  mm and  $4.53 \pm 0.02$  mm in the lowland to  $4.19 \pm 0.03$  mm and  $4.59 \pm 0.02$  mm in the highland, respectively. Morphological dimensions associated with sensory and feeding structures, such as mandible width, clypeus length, and eye parameters (eye length, eye width, and interocellar distance), also exhibited significant differentiation related to elevation. The thoracic traits, including mesoscutum width and length of forewing with

tegula, increased significantly from lowland ( $2.73\pm 0.04$  and  $14.55\pm 0.16$  mm) to highland ( $3.01\pm 0.01$  and  $14.75\pm 0.01$  mm). Furthermore, leg dimensions such as hind femur, tibia, and basitarsus lengths were significantly larger in highland populations ( $3.35\pm 0.06$ ,  $1.28\pm 0.01$ , and  $3.63\pm 0.02$  mm, respectively) compared to lowland bees

( $3.32\pm 0.02$ ,  $1.22\pm 0.01$ , and  $3.48\pm 0.01$  mm). The length of the sting, proboscis, and abdomen also exhibited significant differences with altitude. These results collectively indicate that *A. b. binghami* exhibits marked morphological plasticity along the elevational gradient in South Sulawesi.

**Table 1.** Morphological characters of *A. b. binghami*

Characters	Morphological (mm)						P-value
	Lowland		Midland		Highland		
	Min-Max	Mean±SD	Min-Max	Mean±SD	Min-Max	Mean±SD	
Body length (A)***	20.00-21.00	20.63±0.49a	21.00-22.00	21.43±0.50b	22.00-23.00	22.37±0.49c	0.001
Head length (B)***	4.09-4.20	4.15±0.03a	4.15-4.21	4.18±0.02b	4.12-4.24	4.19±0.03c	0.001
Head width (C)***	4.50-4.58	4.53±0.02a	4.52-4.59	4.55±0.02b	4.56-4.63	4.59±0.02c	0.001
Mandible length (D)***	1.57-1.59	1.58±0.01a	1.59-1.62	1.60±0.01b	1.62-1.64	1.63±0.01c	0.001
Mandible width (E)***	0.61-0.63	0.62±0.01a	0.62-0.64	0.63±0.01b	0.65-0.67	0.66±0.01c	0.001
Clypeus length (F)***	0.50-0.53	1.52±0.01a	1.51-1.54	1.52±0.01a	1.52-1.57	1.55±0.02b	0.001
Lower interocular distance (G)***	2.35-2.38	2.37±0.01a	2.37-2.39	2.38±0.01b	2.41-2.42	2.41±0.01c	0.001
Upper interocular distance (H)***	1.78-1.80	1.79±0.01a	1.80-1.82	1.81±0.01b	1.84-1.85	1.84±0.00c	0.001
Eye length (I)***	3.21-3.23	3.22±0.01a	3.22-3.24	3.23±0.01b	3.27-3.29	3.28±0.01c	0.001
Eye width (J)***	1.32-1.34	1.33±0.01a	1.34-1.35	1.34±0.00b	1.36-1.37	1.37±0.00c	0.001
Lower interorbital distance (K)***	2.80-2.82	2.81±0.01a	2.80-2.82	2.81±0.01a	2.82-2.83	2.83±0.00b	0.001
Maximum interorbital distance (L)***	2.60-2.62	2.61±0.01a	2.62-2.64	2.63±0.01b	2.63-2.65	2.64±0.01c	0.001
Interantennal distance (M)***	0.36-0.37	0.36±0.00b	0.35-0.36	0.36±0.00a	0.37-0.39	0.38±0.01c	0.001
Interocellar distance (N)***	0.40-0.42	0.41±0.01a	0.41-0.43	0.42±0.01b	0.42-0.47	0.43±0.01c	0.001
Ocellocular distance (O)***	0.33-0.35	0.34±0.01a	0.34-0.36	0.35±0.01b	0.36-0.37	0.36±0.01c	0.001
Antennocellar distance (P)***	1.60-1.61	1.60±0.00a	1.61-1.63	1.62±0.01b	1.64-1.65	1.64±0.00c	0.001
Antennocular distance (Q)***	0.78-0.79	0.79±0.00a	0.81-0.82	0.81±0.00b	0.84-0.85	0.85±0.00c	0.001
Gena width (R)***	0.68-0.69	0.69±0.00a	0.68-0.69	0.69±0.00a	0.71-0.73	0.72±0.01b	0.001
Length of flagellomere IV (S)***	0.33-0.35	0.34±0.01a	0.36-0.38	0.37±0.01b	0.36-0.39	0.37±0.01c	0.001
Width of flagellomere IV (T)***	0.21-0.23	0.22±0.01a	0.22-0.23	0.23±0.01b	0.24-0.25	0.24±0.00c	0.001
Malar length (U)***	0.44-0.46	0.45±0.01a	0.47-0.48	0.48±0.01b	0.48-0.49	0.49±0.00c	0.001
Mesoscutum length (V)***	4.23-4.25	4.24±0.01a	4.24-4.26	4.25±0.01b	4.29-4.30	4.29±0.00c	0.001
Mesoscutum width (W)***	2.72-2.74	2.73±0.01a	2.81-2.83	2.82±0.01b	3.00-3.02	3.01±0.01c	0.001
Length of forewing including tegula (X)***	14.50-14.56	14.55±0.01a	14.61-14.62	14.61±0.01b	14.74-14.76	14.75±0.01c	0.001
Distance between m-cu bifurcation (Y)***	3.40-3.42	3.41±0.01a	3.41-3.42	3.42±0.01b	3.47-3.48	3.48±0.01c	0.001
Fore wing length (Z)***	13.46-13.47	13.46±0.01a	13.51-13.53	13.52±0.01b	13.59-13.62	13.61±0.01c	0.001
Fore wing width (AA)***	4.22-4.28	4.26±0.02a	4.31-4.33	4.32±0.01b	3.34-3.36	4.35±0.01c	0.001
Hind wing length (AB)***	9.04-9.06	9.05±0.01a	9.10-9.12	9.11±0.01b	9.19-9.21	9.20±0.01c	0.001
Hind wing width (AC)***	2.38-2.39	2.38±0.01a	2.40-2.41	2.40±0.01b	2.54-2.58	2.57±0.01c	0.001
Hind femur length (AD)***	3.31-3.32	3.32±0.00a	3.31-3.34	3.33±0.01b	3.33-3.35	3.35±0.01c	0.001
Hind tibia length (AE)***	3.96-3.97	3.96±0.00a	4.11-4.13	4.12±0.01b	4.13-4.15	4.14±0.01c	0.001
Hind tibia width (AF)***	1.21-1.23	1.22±0.01a	1.22-1.24	1.23±0.01b	1.27-1.29	1.28±0.01c	0.001
Hind basitarsus length (AG)***	3.47-3.49	3.48±0.01a	3.54-3.56	3.55±0.01b	3.54-3.64	3.63±0.02c	0.001
Hind basitarsus width (AH)***	1.11-1.15	1.12±0.01a	1.14-1.16	1.15±0.01b	1.21-1.23	1.22±0.01c	0.001
Proboscis length (AI)***	5.86-5.89	5.87±0.01a	5.94-5.96	5.95±0.01b	6.24-6.26	6.26±0.01c	0.001
Sting length (AJ)***	2.58-2.59	2.59±0.00a	2.64-2.65	2.65±0.01b	2.69-2.70	2.70±0.00c	0.001
Abdominal length (AK)***	11.87-11.89	11.88±0.01a	12.48-12.49	12.48±0.00b	13.28-13.29	13.28±0.01c	0.001

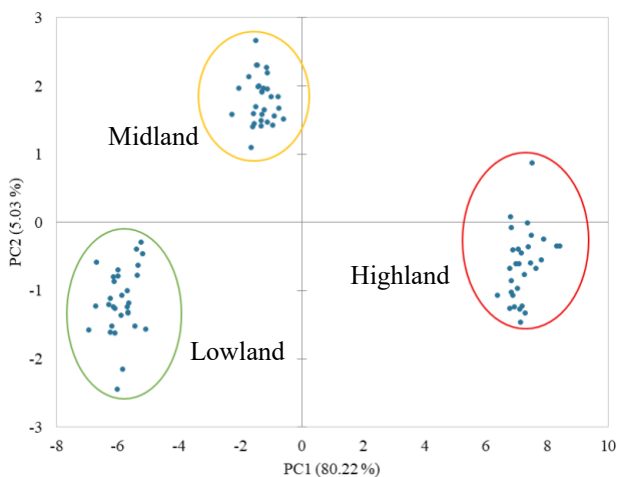
Note: The (\*\*\*) indicates a significant influence with a  $p < 0.001$ . Values are presented as mean ± standard deviation (Mean±SD) and minimum-maximum range (Min-Max) for each bee morphometric character. All measurements are expressed in millimeters (mm)

### Principal component analysis (PCA)

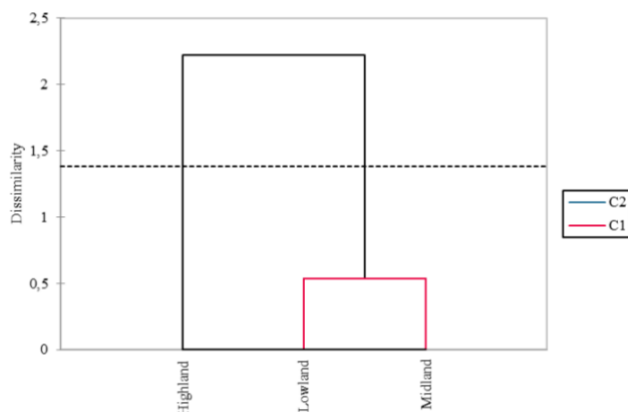
Principal component analysis of the morphological characters of *A. b. binghami* showed that the first principal component (PC1) explained 80.22% of the total variation, while the second component (PC2) accounted for only 5.03%. Figure 3 shows a clear presentation among the groups of *A. b. binghami* bees with morphological characters at different altitudes. The morphological characters that contribute most to PC1 and PC2 are the width of the mesoscutum, the length of the forewing to the tegula, and the length of the abdomen.

### Cluster analysis

Cluster analysis of the morphological characteristics of *A. b. binghami* based on location revealed two main groups (C1 and C2), reflecting the level of similarity among populations (Figure 4). Populations from the lowland and midland formed one cluster (C1) with a low dissimilarity value. In contrast, the highland population formed a separate cluster (C2) with a higher dissimilarity value.



**Figure 3.** PCA plot of morphological variations of *A. b. binghami* from locations with different altitudes in South Sulawesi



**Figure 4.** Morphological clustering of *A. b. binghami* populations from different locations

### Discussion

Morphological clustering analysis revealed that the variation of *A. b. binghami* among study sites is a result of the ecological and altitudinal gradient. According to Kitnya et al. 2024, the *A. b. binghami* bee is genetically distinct from other giant bee species, such as *Apis dorsata*. Similar phenomena have been reported in *Apis florea* from Thailand and *Apis andreniformis* from India populations, which exhibited differences in body and wing size associated with elevation (Soipijit et al. 2024; Taye et al. 2025). Such morphological variation along an altitudinal gradient function as a strategy to ensure foraging success and colony stability under challenging ecological conditions. Increased morphological size in high-altitude populations may serve as a mechanism to maintain lift and heat production (Siraj et al. 2022).

The strong ecological correlation among zones indicates that morphological variation occurs along a continuous environmental gradient rather than as spatial isolation. This gradient produces gradual transitions in environmental factors such as temperature, humidity, and floral resource availability, all of which influence bee growth and development. Bakhchou et al. (2025) explained that microclimatic variability directly influences body size, wing length, and several morphological traits of honey bees. The higher the elevation, the greater the need for morphological adjustment to maintain metabolic efficiency and flight performance. Yancan et al. (2019) and Zapata-Hernandez et al. (2024) also demonstrated that honey bees exhibit consistent morphological changes in response to climatic fluctuations. These findings are also consistent with the thermal-size regulation model, which suggests that insects developing in cold conditions tend to grow larger (Szentgyorgyi et al. 2018). This mechanism may explain why high-altitude colonies exhibit larger morphological dimensions.

Higher altitudes are generally characterized by relatively larger wing and thorax dimensions to compensate for lower air density. This agrees with Hailu et al. (2020), where bees inhabiting higher elevations tend to develop longer wings that generate greater lift. Such morphological shifts reflect not only genetic variation but also phenotypic plasticity in response to environmental stressors. Studies on *Apis cerana* in China (Zhang et al. 2025) and *Apis mellifera* in India (Siraj et al. 2022) reported proportional changes in body and wing size along altitudinal gradients. Similarly, Mistick et al. (2016) found that bees from colder regions possess longer wings that enable them to maintain aerodynamic efficiency and flight stability under reduced temperatures. However, distinguishing between genetic divergence and environmental plasticity is essential for interpreting these patterns. Recent genomic studies on bee populations suggest that wing and body size variation often arises from combined influences of plastic responses and localized allelic selection on flight-related genes (Parejo et al. 2023).

In addition to temperature, the availability of floral resources plays a key role in driving morphological differentiation. Brasil et al. (2023) reported the effects of seasons and urbanization on body size, wild bee abundance,

and foraging effort. This is further supported by Ogilvie and Forrest (2017), who observed that tropical bees experiencing fluctuating floral resources undergo morphological adjustments to optimize nectar exploitation efficiency. Baguette et al. (2020) and Lopez-Urbe et al. (2025) noted that long-term habitat differences can lead to ecological speciation. This finding aligns with Tej et al. (2017) and Efin et al. (2019), who emphasized that morphological analysis serves as an effective tool for understanding the relationship between body structure and ecological dynamics in bees.

Specific morphological traits, such as a tendency for larger body size at high altitudes or more robust wing structures in resource-poor environments, have direct conservation implications. Populations exhibiting unique morphological traits should be prioritized for habitat protection. Therefore, these findings highlight the need for conservation strategies that protect diverse microhabitats across elevational gradients, maintain ecological connectivity to prevent genetic erosion, and incorporate morphological markers as criteria for identifying evolutionary significant units (ESUs) within this endemic subspecies. Establishing habitat corridors, protecting floral resource continuity, and preventing forest fragmentation will be essential to sustain population resilience.

The morphological variation of *A. b. binghami* along the altitudinal gradient plays a crucial role in reflecting its morphological characteristics. These findings confirm that the higher the altitude, the larger the body characteristics of several *A. b. binghami* bees. Therefore, this study highlights the morphological characteristics of the body size of *A. b. binghami* bees at different altitudes in South Sulawesi. Future monitoring should be replicated at several locations and genetic identification in Sulawesi to provide a deeper understanding of the adaptation of this species.

Despite these insights, the study has limitations. Sampling was restricted to three sites and a single season, which may not capture temporal variability. The analysis relied on worker bees only, and morphological variation could not be disentangled from potential genetic differentiation or phenotypic plasticity. Environmental covariates (temperature, humidity, and floral resource availability) were not measured directly. Future research should incorporate longitudinal and seasonal sampling, expand geographic replication across Sulawesi, and integrate genetic or genomic analyses to distinguish plastic from heritable variation. Coupling morphometrics with microclimatic and floral resource data would further clarify adaptive mechanisms and inform conservation strategies for this Wallacean endemic under ongoing habitat change and climate warming.

In conclusion, this study demonstrates clear elevational differentiation in the morphology of the endemic honey bee *Apis binghami binghami* across South Sulawesi. Analyses showed significant differences ( $p < 0.05$ ) in most of the 37 measured morphometric traits among elevation zones, with consistent increases in body size. Mean body length increased from  $20.63 \pm 0.49$  mm in the lowland to  $22.37 \pm 0.49$  mm in the highland, accompanied by larger mesoscutum width (from  $2.73 \pm 0.01$  to  $3.01 \pm 0.01$  mm),

forewing length including tegula (from  $14.55 \pm 0.01$  to  $14.75 \pm 0.01$  mm), and abdominal length (from  $11.88 \pm 0.01$  to  $13.28 \pm 0.01$  mm). Multivariate analyses corroborated these patterns: PCA explained 80.22% of total variation on PC1, driven primarily by thoracic, wing, and abdominal traits, while cluster analysis separated highland populations from lowland-midland groups, indicating structured morphological divergence along the elevational gradient. Collectively, these results support the conclusion that higher elevations are associated with larger morphological dimensions in *A. b. binghami*.

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