Journal of Environmental Biology
p-ISSN: 0254-8704 • e-ISSN: 2394-0379 • CODEN: JEBIDP

JEB®

Original Research Paper
Volume 47 Issue 6 November 2026 pp. 1269-1275
DOI: http://doi.org/10.22438/jeb/47/6/MRN-5971

J. Environ. Biol., 2026
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Journal website : www.jeb.co.in ★ E-mail : editor@jeb.co.in

Developmental morphometrics of drone honey bees (*Apis mellifera* L.): A comparative analysis across lowland and highland agro-climatic zones

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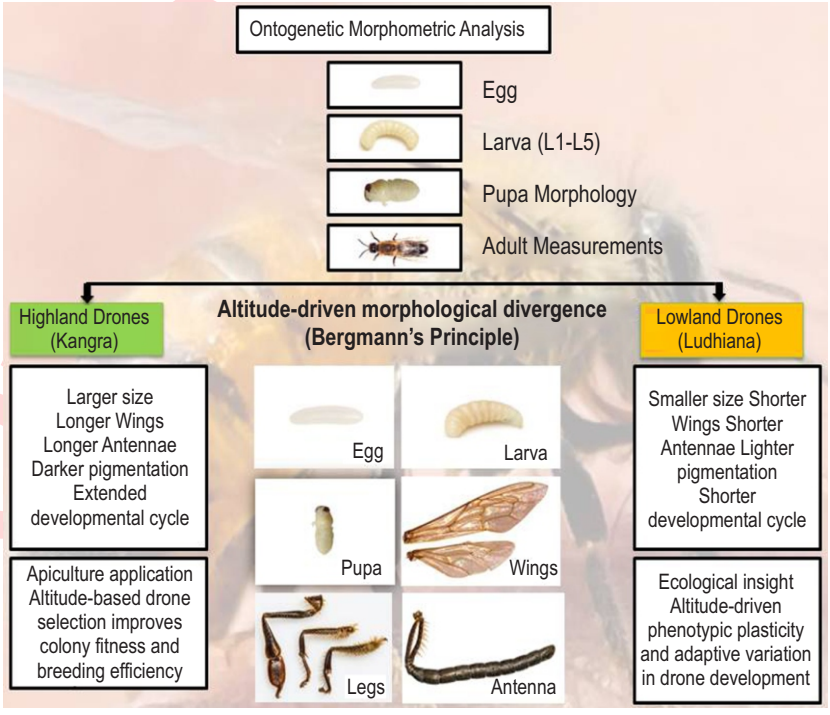
Received: 21 January 2026 **Revised:** 16 April 2026 **Accepted:** 02 September 2026

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Abstract

Aim: The present study aimed to evaluate altitude-driven ontogenetic variation in drone honey bees (*Apis mellifera* L.) by comparing morphometric traits across all developmental stages (egg, larva, pupa and adult) from two contrasting agro-climatic regions of Northern India: Kangra, Himachal Pradesh (high altitude) and Ludhiana, Punjab (low altitude).

Methodology: A total of 320 drone specimens were collected from healthy colonies maintained under standardized apicultural conditions, with equal representation from both regions. Morphometric analyses were conducted across successive developmental stages, including egg dimensions and volume, larval body length, width, weight and cephalic capsule width (L1–L5), pupal structural traits, and detailed adult anatomical measurements. Measurements were taken using calibrated stereomicroscopy, digital calipers and image analysis software, and data were expressed as mean ± SD for inter-regional comparison.



Results: Across all developmental stages, drones from high-altitude Kangra region consistently exhibited marginally larger morphometric values than those from Ludhiana. Eggs showed slightly higher volume at higher altitude. Larval growth parameters, pupal body dimensions, wing pad diameter, and adult traits including body length, compound eye size, antennal and proboscis length, leg segments, and pigmentation intensity were consistently greater in Kangra drones. These differences became more pronounced during pupal and adult stages.

Interpretation: The morphometric augmentation in high-altitude drones reflects altitude-associated developmental plasticity, likely driven by cooler temperatures, extended developmental duration and floral resource diversity, consistent with established ecological size-temperature relationships. These findings provide valuable baseline data for altitude-specific breeding, conservation, and sustainable management of *A. mellifera* drones.

Key words: Apiculture biodiversity, *Apis mellifera*, Drone development, Morphometry, Ontogeny, Regional adaptation

How to cite: Sharma A. and L. Marwaha: Developmental morphometrics of drone honey bees (*Apis mellifera* L.): A comparative analysis across lowland and highland agro-climatic zones. *J. Environ. Biol.*, **47,** 1269-1275 (2026).

Introduction

The Western honey bee (*Apis mellifera* L.) is a keystone pollinator of immense ecological and agricultural value (Michener, 2007; Thoker *et al.,* 2025). Within its eusocial hierarchy, drones the haploid males fulfill a singular reproductive role, ensuring genetic diversity and colony fitness through mating with multiple queens (Gençer and Kahya, 2020; Marwaha, 2023). Detailed knowledge of drone reproductive development also underpins applied reproductive technologies such as instrumental insemination in managed honey bee breeding programmes (Moškrič *et al.*, 2020). Although drones neither forage nor contribute to colony labor, their morphometry provides valuable insight into genotypic traits and developmental responses to environmental conditions (Yarovets *et al.,* 2024). Beyond their reproductive function, drones also exhibit distinct in-nest behavioural patterns, including synchronized hyperactivity, that may be shaped by developmental and colony-environmental factors (Neubauer *et al.*, 2023). In honey bees and other insects, ontogenetic morphometric analysis is an effective approach for investigating population differentiation and adaptive phenotypic plasticity (Pathania *et al.,* 2022; Sharma *et al.,* 2025). Previous morphometric studies have focused mainly on workers and queens due to their direct functional significance, leaving drone morphology comparatively underexplored, particularly across ecological and altitudinal gradients.

This gap is consequential, as drones, being purely reproductive, mirror colony-level fitness and environmental sensitivity. Exploring their morphometric variation across habitats can thus illuminate adaptive processes linked to climatic and resource heterogeneity. India's diverse biogeographic zones offer an ideal setting for such comparative analyses. Regional differences in temperature, floral diversity and seasonal dynamics create a sharp ecological contrast between the fertile lowlands of Punjab and the high-altitude temperate zones of Himachal Pradesh (Guthula *et al.,* 2022). These environmental contrasts are hypothesized to shape drone development through region-specific influences on larval growth, pupal morphogenesis, and adult structural traits. However, prior studies have rarely incorporated a stage-by-stage ontogenetic framework or examined the cumulative developmental trajectories underlying morphological outcomes. This study bridges that gap by conducting a comparative ontogenetic morphometric analysis of *A. mellifera* drones from two distinct ecological zones Ludhiana (Punjab, low altitude) and Kangra (Himachal Pradesh, high altitude). By quantifying morphometric traits across eggs, larvae, pupae and adults, we aim to elucidate how regional environmental parameters especially altitude, temperature and nectar diversity influence drone morphogenesis.

A developmental-stage approach enables identification of subtle ontogenetic shifts often masked in adult-only analyses (Arora and Marwaha, 2022; Bawa and Marwaha, 2026). Beyond its academic relevance, this investigation carries applied significance for apicultural management. Understanding regional differentiation in drone morphology can inform selective breeding programs, improve colony fertility, and enhance resilience to climatic stressors. In the broader context of pollinator decline, such fine-scale morphometric insights into drone biology advance both evolutionary understanding and sustainable apicultural practices ((Kapahi *et al.,* 2023; Saini *et al.,* 2025) Building on this rationale, the present study aimed to systematically characterize ontogenetic morphometric variation across all developmental stages, egg, larva, pupa and adult of *A. mellifera* drones between the lowland (Ludhiana) and highland (Kangra) agro-climatic zones of Northern India. While an earlier study from this research group documented adult-stage regional differentiation in drone morphometry (Sharma *et al.,* 2025), the novelty of the present work lies in its comprehensive, stage-by-stage ontogenetic framework, which has not been previously applied to drone morphometry across an altitudinal gradient, thereby offering a more mechanistic understanding of when and how altitude-driven phenotypic plasticity manifests during drone development.

Materials and Methods

Sample collection: The study was conducted across two ecologically distinct regions of Northern India; Ludhiana, Punjab and Kangra, Himachal Pradesh (Khan, 2024a,b). Ludhiana represents the subtropical, semi-arid plains dominated by agricultural flora, whereas Kangra lies within the temperate, high-altitude Himalayan foothills characterized by cooler temperatures, high humidity and diverse floral resources. These contrasting agro-climatic zones provided an ideal framework for examining the influence of regional and environmental variation on the ontogenetic morphometry of *Apis mellifera* drones (Table 1). Colonies were maintained under standard apicultural management and no pesticide exposure was recorded during the study period. Sample collection and field observations were carried out over one complete colony season, from March 2024 to March 2025, and followed the standard morphometric sampling protocol established for *Apis mellifera* (Ruttner, 1988), from which the morphometric characters measured in this study were adapted.

Sample size and design: A total of 320 biological specimens of *A. mellifera* drones were analyzed, equally distributed between Ludhiana and Kangra (160 per site). Each region contributed 20 samples per developmental stage eggs, five larval instars (L1–L5), pupae, and adults to ensure comprehensive ontogenetic representation. All specimens were collected from ten healthy, disease-free colonies per location under similar apicultural conditions. Adult drones were sampled immediately after eclosion from capped drone cells to prevent environmental wear. This stratified and balanced design enabled accurate inter-regional comparison of developmental morphometric variation.

Sample preparation and measurement protocol: Freshly laid drone eggs (0–24 hr) were collected using sterilized forceps, placed on moist filter paper, and measured for longitudinal and transverse axes; egg volume was calculated using the standard

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Table 1: Geographical coordinates of sampling collection

Species Name	Ecotype (Race)	Sampling site		Geographical distribution		
		Place	State	Longitude	Latitude	Altitude
Apis mellifera Station (Kangra)	Hill Pradesh	Bee research	Himachal	32.1107°N	76.5364°E	1,220m
Apis mellifera Farm (Ludhiana)	Plain	Tiwana Bee	Punjab	30.9009°N	75.8573°E	244m

ellipsoid formula. Larvae were identified by instar stage (L1–L5) using head capsule width, rinsed with 1× PBS and measured for body length, width, and cephalic capsule width under a calibrated stereomicroscope before preservation in 70% ethanol. Pupae, ranging from white-eyed to dark-eyed stages, were removed from sealed brood cells, straightened and measured for body length, thorax width, abdomen length, head width, eye diameter and wing pad diameter using digital calipers. Adult drones, anesthetized with CO_2, were dissected immediately and measured for thoracic, abdominal and appendicular characters using MICAPS MICROVIEW software integrated with a stereo zoom microscope (Radical). All samples were preserved in 70% ethanol for long-term morphological validation, ensuring consistent, high-resolution data acquisition across developmental stages (Joshi and Mall, 2025).

Morphometric characters of *Apis mellifera* drones: A comprehensive suite of morphometric parameters was assessed across all developmental stages to quantify structural and functional differentiation in *A. mellifera* drones. For eggs, length, width and calculated volume served as indicators of maternal investment and early developmental potential. Larval morphometry included total body length, body width, wet weight and cephalic capsule width across five instars to capture growth dynamics. Pupal traits body length, thorax width, abdomen length, head width, eye diameter, and wing pad diameter were selected for their correlation with adult morphology. Adult morphometric analysis encompassed 24 anatomical traits associated with reproductive and sensory functions, including body length, antenna and proboscis lengths, compound eye dimensions, inter-ocellar distance, abdominal tergite and sternite measurements, pigmentation grading, and detailed fore- and mid-leg segmentation (coxa, trochanter, femur, tibia, and metatarsus). Collectively, these measurements provide a developmental morphometric atlas enabling precise evaluation of ontogenetic variation and ecological adaptation between lowland and highland *A. mellifera* populations .

Statistical analysis: All morphometric data were first tested for normality using the Shapiro-Wilk test. Data were expressed as mean ± standard deviation (SD) for each developmental stage and trait. Inter-regional comparisons between Kangra and Ludhiana were performed using an independent-samples Student's t-test for normally distributed variables, with the Mann-Whitney U test applied to non-normally distributed traits. A probability value of $p < 0.05$ was considered statistically significant. All statistical analyses were performed using SPSS statistical software.

Results and Discussion

The comparative morphometric assessment of Apis mellifera drones from Kangra (Himachal Pradesh) and Ludhiana (Punjab) revealed consistent developmental trends with region-specific variations across all life stages. Comprehensive measurements are summarized graphically in Fig. 1, encompassing egg, larval, pupal, and adult morphometric traits.

Egg stage: Drone eggs from both regions exhibited a high degree of morphological uniformity, with only marginal variations in size. Egg samples collected from Kangra measured 1.544 ± 0.203 mm in length, 0.362 ± 0.019 mm in width and 0.103 ± 0.005 mm^3 in volume, while those from Ludhiana were slightly smaller measuring 1.523 ± 0.179 mm, 0.348 ± 0.014 mm and 0.102 ± 0.004 mm^3, respectively (Fig. 1A). Although differences were not statistically significant, the trend of larger egg dimensions in Kangra may reflect subtle environmental effects such as temperature or resource variability associated with higher altitudes.

Larval stage: Morphometric analysis across five larval instars (L1–L5) demonstrated a consistent growth pattern in both populations, with Kangra larvae exhibiting slightly higher values for all measured parameters (Fig. 1B-F). At L1, larvae measured 1.472 ± 0.074 mm in length and 0.364 ± 0.018 mm in width, while Ludhiana larvae recorded 1.428 ± 0.072 mm and 0.343 ± 0.017 mm, respectively. This trend persisted through successive instars, culminating at L5 with Kangra larvae reaching 9.878 ± 0.49 mm in length, 2.881 ± 0.144 mm in width, and 3.46 ± 0.346 mg in weight, compared to Ludhiana's 9.837 ± 0.49 mm, 2.843 ± 0.142 mm, and 3.44 ± 0.344 mg. Cephalic capsule width also remained marginally greater in Kangra larvae throughout, indicating slightly enhanced larval growth under high-altitude climatic conditions.

Pupal stage: During pupal phase, drones from Kangra consistently showed higher morphometric values than those from Ludhiana (Fig. 1G). The mean pupal length of drones from Kangra was 15.238 ± 0.246 mm versus 14.933 ± 0.153 mm in Ludhiana, while thorax width measured 5.283 ± 0.070 mm and 5.104 ± 0.068 mm, respectively. Abdomen length remained nearly similar between populations (8.409 ± 0.083 mm in Kangra;

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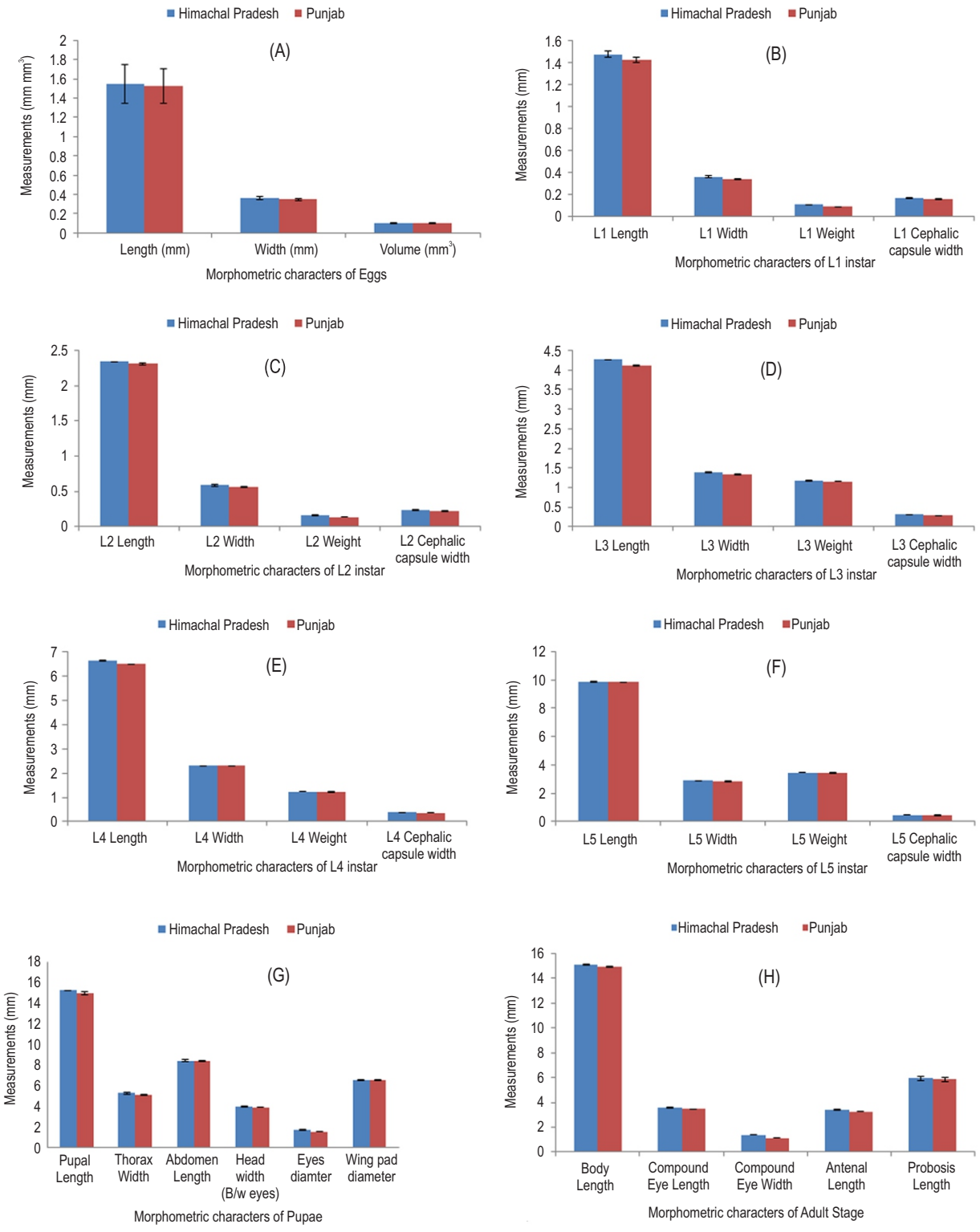


Fig. 1: Comparative ontogenetic morphometric profiles of *Apis mellifera* drones across developmental stages from two agro-climatic regions Kangra (Himachal Pradesh, high altitude) and Ludhiana (Punjab, low altitude). Graphs (A-K) depict mean (±SD) values for measured morphometric traits at different stages of drone development. (A) Egg morphometric parameters; (B–F) larval morphometric traits across instars (L1–L5) including body length, body width, wet weight, and cephalic capsule width; (G) pupal morphometric characters such as body length and thorax width; (H–K) adult morphometric traits including body length, antennal and proboscis lengths, compound eye dimensions, leg measurements, and pigmentation parameters.

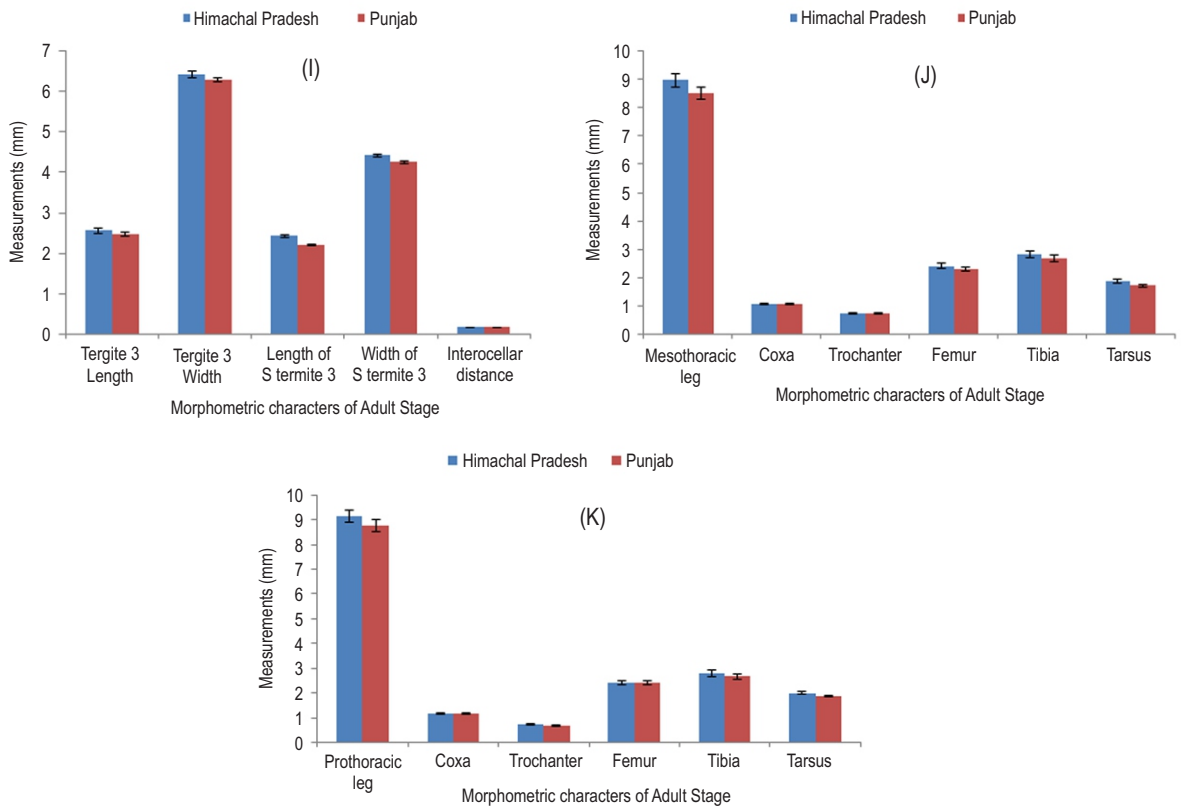


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8.369 ± 0.061 mm in Ludhiana). Head width and eye diameter were also marginally greater in Kangra samples (3.928 ± 0.034 mm and 1.686 ± 0.023 mm) than those collected from Ludhiana (3.904 ± 0.029 mm and 1.530 ± 0.018 mm), as was wing pad diameter (6.526 ± 0.029 mm vs 6.512 ± 0.025 mm). These subtle but consistent differences suggest an altitudinal influence favoring slightly larger pupal morphogenesis in the highland population.

Adult stage: Adult morphometric traits followed similar pattern of regional differentiation (Fig. 1 H-K). Kangra drones exhibited greater mean body length (15.099 ± 0.03 mm), compound eye length (3.565 ± 0.022 mm), eye width (1.393 ± 0.017 mm), antennal length (3.419 ± 0.022 mm), and proboscis length (5.939 ± 0.198 mm) than Ludhiana drones, which measured 14.900 ± 0.02 mm, 3.459 ± 0.013 mm, 1.140 ± 0.007 mm, 3.270 ± 0.013 mm and 5.852 ± 0.198 mm, respectively. Abdominal traits such as Tergite 3 length (2.561 ± 0.073 mm) and width (6.426 ± 0.081 mm) were slightly higher in Kangra than in Ludhiana (2.487 ± 0.047 mm, 6.275 ± 0.053 mm). Pigmentation intensity also varied, with Kangra drones exhibiting medium pigmentation, while Ludhiana drones showed lighter tones. Sternite 3 dimensions, interocellar distance and leg morphometry followed similar pattern: all segmental measurements (foreleg 9.136 ± 0.239 mm; midleg 8.969 ± 0.235 mm) were slightly greater in Kangra than in Ludhiana drone sample (8.768 ± 0.229 mm and 8.511 ± 0.223 mm, respectively).

This study provides the first comprehensive ontogenetic morphometric comparison of *Apis mellifera* drones across two contrasting agro-climatic regions of Northern India Kangra (Himachal Pradesh, high altitude) and Ludhiana (Punjab, low altitude) revealing consistent altitude-associated variation throughout development. The findings demonstrate that environmental gradients, particularly temperature, humidity and floral resource diversity, exert measurable influence on drone morphogenesis, supporting the hypothesis that altitude modulates developmental plasticity and anatomical differentiation in honey bees. These results are consistent with previous reports of regional morphometric differentiation among adult *A. mellifera* drones from Punjab and Himachal Pradesh (Sharma *et al.,* 2025) and extend recent evidence of agroclimatic-

zone-associated morphometric variation in Apis mellifera populations of the Kumaun Himalaya (Joshi and Mall, 2025), while reinforcing the broader recognition that climatic periodicity shapes reproductive and developmental outcomes in *A. mellifera* colonies (Bawa and Marwaha, 2026). The observed increase in morphometric dimensions in drones from higher-altitude Kangra region suggests a compensatory developmental strategy in response to cooler microclimatic conditions. Larger eggs, as recorded in this study, may represent enhanced maternal investment through increased yolk provisioning an adaptive mechanism facilitating embryonic resilience under low-temperature stress (Blanckenhorn, 2000; Fischer *et al.,* 2014). This trend extends through larval and pupal phases, where prolonged developmental durations and slower metabolic rates typical of highland environments (Niehaus and Ellers, 2008) likely allow for extended tissue differentiation and larger final body size (Atkinson, 1994; Hodkinson, 2005).

The incremental increase in larval cephalic capsule width and pupal thoracic dimensions further reflects the influence of environmental modulation on caste-specific growth trajectories, consistent with temperature-size relationships described in other insect taxa (Angilletta *et al.,* 2004; Colinet *et al.,* 2015). At adult stage, the larger body size, extended antennal and proboscis lengths, and expanded compound eyes observed in Kangra drones have significant functional implications. These morphological enhancements may optimize flight stability, improve mate detection efficiency, and enhance mating success within heterogeneous mountain landscapes where visual and olfactory cues are more spatially complex (Kapustjanskij *et al.,* 2007; Waddington *et al.,* 2010). The observed increase in pigmentation intensity among high-altitude drones may further indicate an adaptive photoprotective response to elevated ultraviolet exposure, a phenomenon commonly reported in alpine insect populations. Ecologically, these findings underscore the importance of altitudinal adaptation and morphological plasticity as mechanisms of resilience in *A. mellifera*.

The consistent morphometric augmentation across all developmental stages illustrate how environmental selection pressures shape drone phenotypes to maintain reproductive competence under variable climatic regimes. From an applied perspective, recognizing such regional differentiation is vital for the development of altitude-specific breeding programs and selection of locally adapted genetic lines capable of sustaining pollination efficiency under changing environmental conditions. Morphometric data combined with genetic characterization have similarly guided *A. mellifera* stock-selection decisions in regions of natural hybridization elsewhere (Litvinoff *et al*., 2023), underscoring the applied value of the developmental dataset generated here. In conclusion, this study establishes a clear link between altitude-driven ecological variation and the ontogenetic modulation of drone morphology in *Apis mellifera.* By integrating stage-specific morphometric data, it provides a robust framework for understanding how environmental gradients influence the insect developmental biology. The ecological and apicultural implications of these findings highlight the necessity of incorporating altitude and regional adaptation parameters into honey bee management, breeding, and conservation strategies to enhance colony productivity and climate resilience.

Acknowledgments

The authors sincerely acknowledge the provision of laboratory and field resources by the Department of Zoology, Lovely Professional University, Phagwara, Punjab, India. We also thank the technical staff for their invaluable assistance in data collection and processing.

Authors' contribution: A. Sharma: Initiated and designed the study, conducted the primary data collection, performed analysis, and drafted the initial manuscript; **L. Marwaha:** Served as the corresponding author, providing critical guidance throughout the research process, supervising experimental design, validating results, and revising the manuscript for intellectual content and coherence.

Funding: This research did not receive any specific grant from funding agencies.

Research content: The research content of manuscript is original and has not been published elsewhere.

Ethical approval: Not applicable.

Conflict of interest: The authors declare that there is no conflict of interest.

Data availability: Not applicable.

Consent to publish: Both the authors agree to publish the paper in *Journal of Environmental Biology.*

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