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MORPHOMETRIC TEMPLATES OF DRONE WINGS AS A TOOL FOR SUBSPECIES AND POPULATION IDENTIFICATION IN *APIS MELLIFERA* COLONIES OF THE LVIV REGION, UKRAINE

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To develop morphometric templates (reference standards) of drone wings as a tool for determining the subspecies and population affiliation of honey bee colonies representing local populations.

A total of 3,206 drone wings from 31 colonies maintained at six apiaries in the Lviv region, Ukraine, were analyzed. Wing morphology was characterized within the framework of classical morphometry using a set of index-based traits, including established indices (Ci, Dbi, Pci, Disc. sh., and Ri) and additional indices proposed by the authors (Ci.1.1, Ci.2.1, Ci.2.2, and Ci.3). Cluster assignment of wing samples from the studied colonies was performed using Mahalanobis distances between the centroids of the reference templates and empirical clusters.

Both regional and local morphometric templates of drone wings were identified and associated with the Troiseck, Peschetz, and Sklenar breeding lines of A. m. carnica. In addition, local templates were identified for the apiary located in Grebeniv and designated as "Peschetz(G)" (A. m. carnica), "UkrBee1(G)" (presumably A. m. caucasica), and "UkrBee2(G)", for which subspecies affiliation remains unresolved. These templates enabled the identification of 51 (85.0%) of the examined wing clusters and the assessment of the degree of morphological similarity (DS) for 30 (88.2%) clusters within individual apiaries, thereby providing evidence of admixture between lines or populations.

The analysis revealed the presence of multiple honey bee populations in the Lviv region, attributable to the subspecies Apis mellifera carnica and Apis mellifera caucasica. The assignment of drone wing phenotypes to subspecies and populations using classical morphometry demonstrated the utility of the proposed approach. The methodology may provide a preliminary means of assessing the probable composition of haploid genomes in drones and, indirectly, in queens, particularly with respect to genomic components associated with wing morphology.

Keywords: Apis mellifera carnica, Apis mellifera caucasica, Carpathian bees, Ukrainian Steppe bees, drones, wing morphology, classical morphometry, discriminant analysis, wing venation, Mahalanobis distance, Western Ukraine

Introduction. The Western honey bee (*Apis mellifera* L.) plays a critical role in both natural ecosystems and agricultural systems, as reflected in the inclusion of apiculture-related objectives within international development frameworks, including the United Nations Sustainable Development Goals (SDGs; Goals 2 and 15). Ukraine is among the countries of the Eurasian region with a high density of honey bee colonies, and its honey bee populations have been the subject of sustained biological and ecological research (Volkov, 2024). Understanding the diversity and structure of honey bee populations is essential for elucidating evolutionary processes associated with anthropogenic influences and for conserving natural genetic resources. At the same time, local populations are often genetically heterogeneous and may be characterized by hybrid origin. Their genetic structure is investigated using SNP diagnostics (Donthu et al., 2024), molecular markers (Knoll et al., 2025), including inter-simple sequence repeats (ISSR) markers (Adss et al., 2025), mtDNA analysis (Szalanski et al., 2025), as well as Illumina SNP chips (Lukic et al., 2024).

Morphological traits remain an important tool in animal taxonomy, including entomology. The classical framework for morphometric analysis of *Apis mellifera* established by Ruttner (1988) remains widely used. However, relatively few studies have applied this comprehensive approach to subspecies identification, largely because of the considerable labor and resources required to measure a large number of morphological characters (e.g., 41 traits) (Özdil et al., 2022). In this context, wing morphology provides a substantial set of taxonomically informative characters (Krtinic et al., 2016; Kekecoglu et al., 2023), enabling the assessment of subspecies affiliation at both individual and colony levels. Compared with the classical Ruttner approach, wing-based morphometry offers advantages in terms of analytical efficiency and

practical applicability. Studies of other insect taxa have demonstrated that wing morphology can reflect adaptive changes occurring over multiple generations under controlled conditions (Soto et al., 2008). In honey bees, however, the seasonal nature of colony development and the life cycle of individual castes limits the direct extrapolation of morphometric patterns to broader aspects of colony biology.

Geometric morphometrics is currently the predominant approach for analyzing wing venation in worker bees (Klingenberg, 2011; Tatsuta et al., 2018), with increasing emphasis on automated image analysis and large-scale data processing (Rodrigues et al., 2022; Oleksa et al., 2023). By contrast, studies specifically addressing drone wing morphology remain relatively scarce (Čápek et al., 2018; Groeneveld et al., 2020; Henriques et al., 2020; Tofilski et al., 2024). Because drones are haploid, their genotype–phenotype relationship is more direct than that of diploid worker bees and is less affected by the genetic contribution of a second parental genome. Consequently, the analysis of drone wing morphology may provide a particularly informative approach for investigating population structure and assessing subspecies affiliation (Yarovets et al., 2023a).

The mountainous part of the Lviv region borders the Zakarpattia and Ivano-Frankivsk regions and forms part of the historical distribution range of Carpathian honey bees belonging to the subspecies *Apis mellifera carnica*. During the 20th century, state-supported breeding and zoning programs promoted the propagation of these bees (Law of Ukraine "On Beekeeping", 2000). Queen stock for apiaries was primarily supplied by breeding centers located in the Zakarpattia and Lviv regions. During this period, morphometric studies of worker bee wings were conducted to assess colony lineage and, in some cases, to establish reference standards (Petko et al., 2022). To the best of our knowledge, however, drone wing morphology has not been systematically investigated in this region. A recent study conducted in 2022 across seven apiaries in the Skole territorial community (Stryi district) revealed the coexistence of colonies attributed to *A. m. carnica* and a local micropopulation designated "Localbees", whose subspecies affiliation remained unresolved (Yarovets et al., 2023b). A substantial proportion of drone wing phenotypes attributed to *A. m. carnica* were associated with established European breeding lines as well as with the Carpathian ecotype. These findings require further verification within a robust taxonomic framework and underscore the need for expanded research to clarify the genetic and phenotypic structure of honey bee populations in the Lviv region.

The aim of this study was to establish reliable morphometric templates of drone wings for populations of *A. m. carnica* and other honey bee subspecies occurring in western Ukraine. The resulting local and regional templates for Lviv Oblast enabled the assignment of 51 (85.0%) of the examined wing clusters and provided a basis for assessing the morphological similarity and probable population affiliation of the remaining clusters.

Materials and methods. A total of 3,206 drone wings from six apiaries located in the settlements of Tukhlya (5 colonies), Skole (3), Dashava (2), Malechkovychi (1), Basivka (2), and Grebeniv (18) in Lviv Oblast, Ukraine, were examined. For each colony, 100 or more drones were sampled. The drone-management protocol provided sufficient isolation to minimize inter-colony migration. In addition, the authors' archival experimental data were used to establish reference standards: (1) DE-6-115-2019 (Germany), instrumental insemination (II), line CP (Peschetz), originating from queen 17-2-112/17 (island-mated) × drones 11-208-79/2015K, line C-07, breeder S. Rausch; (2) queen 11-70-1008-2015 (2a) × drones 99-120-71369-2015 (4a), line Perner, originating from II in Ukraine (2017), line Sklenar, breeder V. Lipatov; (3) 6-115-2018 (Germany), island-mated, line CT-1075 (Troiseck), originating from queen 17-257/16 × drones 6-42-19/2015K, line C/Peschetz, breeder S. Rausch; and (4) experimental data comprising 150 drone wings from queen DE-11-70, UA-1-6-4-2022 4a, line Sklenar, breeder B. Bolyubash (BeeBreed.eu). In total, 545 reference wings were included in the analysis.

The right forewings were mounted on a microscope slide parallel to the longitudinal coordinate axis using glycerin. High-resolution images were captured using a 50 MP digital camera mounted on a stereomicroscope (MST 131, PZO Warszawa) at 25× magnification and stored in a digital database. Landmark placement and coordinate acquisition were performed according to Fig. 1 using the tpsDig2 software.

Based on the resulting landmark coordinates, nine morphometric indices were calculated: the Cubital index (Ci), Dumb-bell index (Dbi), Discoidal shift (Disc. sh.), Precubital index (Pci), and Radial index (Ri), following the standard definitions described by Bouga et al. (2011), together with four additional indices proposed by the authors (Ci.1.1, Ci.2.1, Ci.2.2, and Ci.3). The four additional indices characterize three central cubital cells of the wing (cubital cells, CC), following the nomenclature of Meixner et al. (2013). The indices were calculated as ratios of Euclidean distances between wing landmarks: Ci.1.1 = $d(6,1)/d(5,4)$, Ci.2.1 = $d(10,4)/d(5,6)$, Ci.2.2 = $d(10,4)/d(8,6)$, Ci.3 =

$d(9,17)/d(9,8)$, where $d(m,n)$ denotes the Euclidean distance between landmarks *m* and *n* (Fig. 1). Inclusion of these additional classification variables provides a more comprehensive description of wing shape and improves the discriminatory capacity of the model: the variables make a statistically significant contribution to classification, accompanied by a reduction in Wilks' Lambda and an increase in classification correctness (Yarovets et al., 2022; Cherevatov et al., 2023). All nine indices were used as input variables for discriminant analysis implemented in the STATISTICA software package.

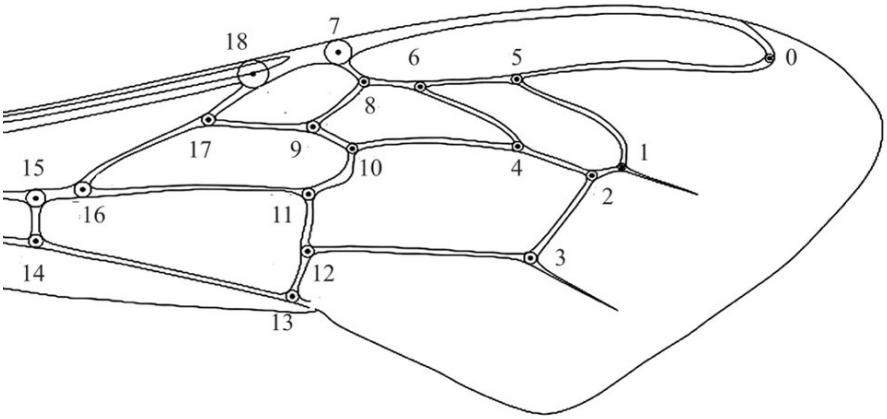


Fig.1. Scheme of numbering and order of applying reference points on the wing

Based on the results of discriminant analysis, drone wings from each individual colony were assigned to two phenotypic clusters. These clusters were interpreted as representing the two alternative haploid paternal-genome backgrounds potentially transmitted by the diploid queen to her drone offspring. Eight morphometric datasets, designated "Sklenar1", "Sklenar2", "Peschetz1", "Peschetz2", "Troiseck1", "Troiseck2", "65(1)", and "65(2)", were used as primary linear reference templates. These templates served as baseline markers for specific breeding lines, with subspecies affiliation defined *a priori* from documented queen pedigrees. The templates were subsequently used for cluster identification in 18 colonies from Grebeniv and 13 colonies from other apiaries in the Lviv region. In addition, the dataset comprising 545 drone wings from the four reference queens was classified into three clusters, which were treated as local reference templates and designated "Troiseck(L)", "Peschetz(L)", and "Sklenar(L)". Furthermore, 1,780 drone wings from the Grebeniv apiary were independently classified into three clusters. These clusters were subsequently used as additional local reference templates for the Grebeniv apiary and neighboring apiaries.

The criterion used to determine the probable subspecies and population affiliation of wing clusters was the Mahalanobis distance (MD) between the centroids of the reference templates and those of the studied clusters. An empirical similarity scale, established on the basis of previous (Yarovets et al., 2024) and present analyses, was applied as follows: MD values of 0–2.0 indicated high similarity, values of >2.0–2.6 indicated moderate similarity, values of >2.6–3.5 indicated low similarity, and values >3.5 indicated no similarity.

Results and discussion. At the first stage of the study, drone wings from each of four colonies whose queens were considered reference queens for the subspecies *A. m. carnica* were classified into two morphometric clusters (Table 1). Each of the eight resulting datasets of trait-index values was defined as a separate initial linear template.

At the second stage, a global classification of 545 drone wings from the four colonies was performed, resulting in three morphometric clusters. Pairwise correlations among most indices within the clusters ranged from 0 to 0.27, with some correlations ranging from 0.35 to 0.41 ($p < 10^{-7}$), indicating predominantly weak and, in some cases, moderate relationships among the indices. These results supported the inclusion of all nine indices in the classification model. The contribution of individual indices to classification performance was assessed using the Partial Lambda criterion. In ascending order of discriminatory importance, the indices were ranked as follows: Ci.2.2, Ri, Ci.2.1, Ci, Ci.1.1, Ci.3, Disc. sh., Dbi, and Pci. Thus, Ci.2.2 and Ri showed the lowest discriminatory contribution, whereas Dbi and Pci contributed most strongly to the separation of the clusters. Overall classification correctness reached 96.8% (Table 2).

Table 1.

Mean values of classification features for 8 clusters of drone wings (n=545) producing four queens, taken as reference

Indexes	"Peschetz1"* means ± SE	"Peschetz2"* means ± SE	"Sclenar1"* means ± SE	"Sclenar2"* means ± SE	"Troiseck1"* means ± SE	"Troiseck2"* means ± SE	"65(1)"** means ± SE	"65(2)"** means ± SE
Ci	1.973 ± 0.034	2.097 ± 0.037	1.901 ± 0.043	2.232 ± 0.0530	2.190 ± 0.050	2.292 ±0. 039	2.196 ± 0.038	2.138 ± 0.033
Dbi	0.955 ± 0.007	0.869 ± 0.007	1.011 ± 0.008	0.953 ± 0.010	0.855 ± 0.007	0.923 ± 0.006	0.961 ± 0.006	1.056 ± 0.008
Pci	2.988 ± 0.014	3.051 ± 0.013	3.098 ± 0.016	2.933 ± 0.016	2.910 ± 0.020	2.921 ± 0.010	2.824 ± 0.014	2.76 ± 0.016
Disc. sh.	2.296 ± 0.244	-0.025 ± 0.282	3.055 ± 0.212	1.519 ± 0.200	-0.480 ± 0.198	1.636 ± 0.152	-0.235 ± 0.146	2.112 ± 0.168
Ri	1.548 ± 0.010	1.427 ± 0.011	1.565 ± 0.008	1.471 ± 0.007	1.368 ± 0.008	1.450±0.006	1.434 ± 0.007	1.572 ± 0.008
Ci.3	1.598 ± 0.018	1.542 ± 0.016	1.796 ± 0.020	1.731 ± 0.017	1.896 ± 0.017	1.903±0.013	1.608 ± 0.013	1.539 ± 0.015
Ci.2.1	1.796 ± 0.009	1.607 ± 0.009	1.879 ± 0.012	1.699 ± 0.011	1.518 ± 0.009	1.645±0.009	1.667 ± 0.009	1.785 ± 0.012
C.2.2	4.073 ± 0.052	4.404 ± 0.071	3.558 ± 0.041	3.868 ± 0.056	4.010 ± 0.075	3.649±0.044	3.744 ± 0.038	3.805 ± 0.052
Ci.1.1	3.297 ± 0.018	3.484 ± 0.018	3.125 ± 0.018	3.334 ± 0.025	3.730 ± 0.026	3.508 ± 0.020	3.41 ± 0.015	3.281 ± 0.014
Number of wings	64	60	80	70	42	79	85	65

*Note: * – experimental data for individual colonies were used according to the work: (Babenko et al., 2024), the numbers after the dot indicate the cluster numbers; ** – experimental material for queen DE-11-70, UA-1-6-4-2022 4a, race/line Sclenar.*

Table 2.

Mean values of indices for three clusters of drone wings (n=545)

Indexes	Cluster 1 means ± SE	Cluster 2 means ± SE	Cluster 3 means ± SE
Ci	2.301 ± 0.023	1.958 ± 0.025	2.154 ± 0.021
Dbi	1.018 ± 0.004	0.976 ± 0.005	0.888 ± 0.003
Pci	2.796 ± 0.007	3.05 ± 0.010	2.935 ± 0.008
Disc. sh.	1.824 ± 0.104	3.081 ± 0.144	0.013 ± 0.110
Ri	1.506 ± 0.005	1.558 ± 0.006	1.406 ± 0.004
Ci.3	1.607 ± 0.01	1.731 ± 0.014	1.707 ± 0.012
Ci.2.1	1.720 ± 0.006	1.830 ± 0.008	1.607 ± 0.005
C.2.2	3.812 ± 0.028	3.802 ± 0.036	3.969 ± 0.032
Ci.1.1	3.384 ± 0.011	3.190 ± 0.012	3.477 ± 0.013
Number of wings	262	143	140

The three resulting datasets of morphometric indices were subsequently used as local reference templates associated with the Troiseck, Peschetz, and Sklenar breeding lines. These templates were designated "Troiseck(L)", "Peschetz(L)", and "Sklenar(L)" and were used to assess the affiliation of wing-phenotype clusters from the studied colonies with the subspecies *Apis mellifera carnica*.

To expand the empirical basis for *A. m. carnica*, additional samples were included from 13 colonies whose queens originated from breeders in Austria and Germany, or from their first-generation descendants (F1), although formal pedigree documentation was not available. Wing samples from each colony were classified into two clusters and identified using the local templates (Table 3).

The 19 reliably identified clusters were added to the dataset comprising 545 wings. As a result, 1,546 wings were classified into three clusters (Table 4). The classification correctness was 96.9%.

Table 3.

Result of identification of wing phenotypes of clusters of 13 colonies for five apiaries in Lviv region. MD – Mahalanobis distance between centroids of templates and clusters of drone wings. Number of wings examined: n=1426

Colonia*	MD	Templates**	Colonia	MD	Templates**
M 1(1)	1.94	"Troiseck(L)"	T 21(1)	>2.60	No indific
M_1(2)	2.30	"Peschetz(L)"	T_21(2)	1.61	"Troiseck(L)"
B 2(1)	1.51	"Peschetz(L)"	T 9(1)	2.01	"Troiseck(L)"
B_2(2)	>2.60	No indific	T_9(2)	2.18	"Peschetz(L)"
B 3(1)	>2.60	No indific	T 7(1)	>2.60	No indific
B_3(2)	2.03	"Peschetz(L)"	T_7(2)	2.14	"Peschetz(L)"
D_1(1)	2.04	"Sklenar(L)"	T_13(1)	2.23	"UkrBee(G)"
D_1(2)	>2.60	No indific	T_13(2)	2.02	"Sklenar(L)"
D_10(1)	>2.60	No indific	T_15(1)	2.03	"Troiseck(L)"
D 10(2)	2.29	"Peschetz(L)"	T 15(2)	1.55	"Sklenar(L)"
S_10(1)	1.98	"Troiseck(L)"	S_1X(1)	1.59	"Peschetz(L)"
S_10(2)	1.81	"Troiseck(L)"	S_1X(2)	1.79	"Troiseck(L)"
S_12(1)	1.66	"Troiseck(L)"	S_12(2)	>2.60	No indific

*Note: * – symbols: M, B, T, D, S indicate the location of the apiary, namely the villages: Malechkovychi, Basivka, Tukhlya, Dashava, Skole, respectively, the next digit indicates the colony number, the next digit indicates the colony number, the digits 1 and 2 in brackets indicate the cluster number; ** – templates obtained in this study*

Table 4.

The result of the classification of drone wings (n=1546) for the combined array of features for 4 reference colonies and 13 colonies from five apiaries in Lviv region. Average values of indices according to the classification model for three clusters

Indexes	Cluster 1 means ± SE	Cluster 2 means ± SE	Cluster 3 means ± SE
Ci	2.159 ± 0.016	1.754 ± 0.014	2.136 ± 0.017
Dbi	0.913 ± 0.003	0.913 ± 0.003	1.038 ± 0.003
Pci	2.868 ± 0.006	3.005 ± 0.006	2.827 ± 0.006
Disc. sh.	0.110 ± 0.083	2.263 ± 0.081	3.639 ± 0.082
Ri	1.412 ± 0.003	1.517 ± 0.003	1.577 ± 0.004
Ci.3	1.730 ± 0.008	1.719 ± 0.008	1.711 ± 0.008
Ci.2.1	1.604 ± 0.004	1.785 ± 0.005	1.805 ± 0.006
C.2.2	3.810 ± 0.022	3.907 ± 0.024	3.842 ± 0.023
Ci.1.1	3.452 ± 0.009	3.186 ± 0.007	3.332 ± 0.009
Number of wings	581	494	471

The resulting datasets of trait-index values were used to construct small regional templates for identifying the wing phenotypes of drones originating from *A. m. carnica* queens in Lviv Oblast (Table 5). The resulting templates were designated as Cluster 1 - "Troiseck(W)", Cluster 2 - "Peschetz(W)", and Cluster 3 - "Sclenar(W)". The suffix (W) denotes the western Ukrainian origin of the templates and indicates their association with honey bee populations from western Ukraine. For the 1,780 wings obtained from the Grebeniv apiary, the optimal clustering solution comprised three clusters, designated G1, G2, and G3. Overall classification accuracy was 96.1% (Tabl. 5, 6). The resulting clusters were validated against the independent reference templates "Troiseck(W)", "Peschetz(W)" and "Sclenar(W)" (Table 7).

Table 5.

Result of classification of drone wings (n=1780) for the apiary in the village of Grebeniv. Average values of indices according to the classification model for three clusters

Indexes	Cluster G1 means ± SE	Cluster G2 means ± SE	Cluster G3 means ± SE
Ci	1.869 ± 0.016	1.847 ± 0.018	1.684 ± 0.013
Dbi	0.948 ± 0.003	0.796 ± 0.003	0.902 ± 0.003
Pci	2.907 ± 0.006	3.015 ± 0.008	2.822 ± 0.006
Disc. sh.	2.362 ± 0.074	-0.818 ± 0.118	-2.440 ± 0.081
Ri	1.517 ± 0.004	1.368 ± 0.004	1.306 ± 0.003
Ci.3	1.751 ± 0.006	1.665 ± 0.007	1.721 ± 0.007
Ci.2.1	1.795 ± 0.005	1.556 ± 0.005	1.649 ± 0.005
C.2.2	3.860 ± 0.020	4.492 ± 0.025	3.514± 0.016
Ci.1.1	3.249 ± 0.008	3.395 ± 0.010	3.273 ± 0.007
N	649	477	654

Table 6.

Coefficients of classification functions for the classification model obtained by classifying 1780 drone wings from the apiary in the village of Grebeniv into three clusters: G1, G2, G3

Classification features	Odds G1* p=.36461	Odds G2* p=.26798	Odds G3* p=.36742
Ci	11.36	12.17	10.74
Dbi	255.98	239.58	256.05
Pci	211.28	217.08	208.53
Disc. sh.	-14.72	-14.98	-15.19
Ri	300.15	286.31	283.68
Ci.3	68.02	62.81	65.81
Ci.2.1	165.32	156.46	157.53
C.2.2	37.00	39.48	36.12
Ci.1.1	119.56	124.29	118.31
Constant	-1123.81	-1110.67	-1067.07

*Note: * – G1, G2, G3 are marked in transliteration: "Peschetz(G)", "UkrBee1(G)", and "UkrBee2(G)"*

Table 7.

Mahalanobis distances (MD) between the centroids of the three templates obtained in this work – one template obtained in a previous study and three clusters of drone wings for the apiary of the village of Grebeniv (G1, G2, G3)

Templates and clusters,	"Troiseck(W)"*	"Peschetz(W)"*	"Sklenar(W)"*	G1	G2	G3	"UkrBee"**
"Troiseck(W)"	0	2.30	>2.60	2.17	2.20	1.98	2.26
"Peschetz(W)"	–	0	2.10	0.79	2.95	3.00	3.27
"Sklenar(W)"	–	–	0	1.52	4.29	3.85	4.60
G1	–	–	–	0	3.23	2.91	3.49
G2	–	–	–	–	0	>2.60	1.57
G3	–	–	–	–	–	0	1.66
"UkrBee"	–	–	–	–	–	–	0

*Note: * – templates obtained in actual work (Table 4); ** – template used according to the work: (Galatiuk et al., 2024)*

The wing morphology of cluster G1 was assigned to the Peschetz lineage based on its high degree of similarity to the "Peschetz(W)" template (MD = 0.79). G1 also showed substantial morphological similarity to the "Sclenar(W)" template, with a Mahalanobis distance of 1.52 (Table 7). A displacement of the G1 centroid toward the "Sclenar(W)" template was also observed; the corresponding Mahalanobis distance of 1.58 indicated moderate similarity between the phenotypes. In contrast, the wing morphology of clusters G2 and G3 could not be reliably assigned using the linear, local (L), or regional (W) *A. m. carnica* templates developed in the present study. Therefore, previously established regional templates (Galatiuk et al., 2024) were additionally applied. On this basis, both clusters were assigned to Ukrainian honey bee populations designated "UkrBee1(G)" and "UkrBee2(G)". This assignment was supported by Mahalanobis distances of 1.57 and 1.66 for the respective G2/"UkrBee" and G3/"UkrBee" comparisons. To improve the reliability of subsequent analyses, 74 wings whose phenotypes could not be assigned with sufficient confidence were excluded from the overall wing pool. The remaining 1,706 wings were reclassified into three clusters: G1 (630 wings), G2 (459 wings), and G3 (617 wings). Classification accuracy remained virtually unchanged. The resulting datasets of trait-index values for G1, G2, and G3 were subsequently defined as local reference templates for the Grebeniv apiary and designated "Peschetz(G)", "UkrBee1(G)", and "UkrBee2(G)", respectively. The suffix (G) denotes the geographical origin of the templates, Grebeniv. These local templates were subsequently used to assess the wing phenotypes of individual clusters from the 18 colonies examined at the Grebeniv apiary (Table 8).

Table 8.

Cluster identification results for 18 colonies in the village of Grebeniv. MD – Mahalanobis distance between the centroids of the wing clusters under study and the templates; Degree of similarity (Ds) – wing shares, with additional classification of individual wing clusters into three clusters

Cluster names*	MD	Identific**	Ds*** "Peschetz(G)", %	Ds*** "UkrBee1(G)", %	Ds*** "UkrBee2(G)", %
1(1)	2.30	"UkrBee1(G)"	47	34	19
1(2)	1.69	"Peschetz(G) "	98	3	0
3(1)	1.81	"UkrBee2(G)"	46	3	51
3(2)	0.52	"Peschetz(G) "	100	0	0
4(1+2)	1.78	"UkrBee2(G)"	40	11	49
6(1)	2.07	"UkrBee2(G)"	0	31	69
6(2)	2.33	"UkrBee2(G)"	29	24	47
7(1)	–	No indific	–	–	–
7(2)	1.89	"Peschetz(G) "	76	17	7
10(1)	1.92	"UkrBee2(G)"	3	0	97
10(2)	0.98	"UkrBee2(G)"	0	0	100
11(1+2)	1.77	"Peschetz(G) "	43	15	43
12(1)	1.36	"UkrBee2(G)"	26	16	58
12(2)	1.04	"Peschetz(G) "	95	4	2
13(1)	1.65	"UkrBee2(G)"	2	2	97
13(2)	–	No indific	–	–	–
14(1)	2.11	"Peschetz(G) "	64	34	2
14(2)	1.55	"UkrBee1(G)"	0	99	1
15(1)	1.52	"Peschetz(G) "	93	7	0
15(2)	2.00	"UkrBee2(G)"	9	28	63
22(1)	1.42	"UkrBee2(G)"	10	22	68
22(2)	0.71	"Peschetz(G) "	94	2	4
24(1)	1.36	"Peschetz(G) "	85	15	0

24(2)	0.63	"UkrBee1(G)"	0	97	3
25(1)	1.75	"UkrBee2(G)"	0	2	98
25(2)	2.12	"UkrBee2(G)"	37	22	41
31(1)	1.98	"Troiseck(W)"	–	–	–
31(2)	2.19	"Sclenar(W)"	–	–	–
35(1)	1.06	"UkrBee2(G)"	27	15	58
35(2)	2.24	"Peschetz(G) "	65	35	0
41(1)	1.46	"UkrBee1(G)"	7	67	26
41(2)	1.89	"UkrBee1(G)"	0	73	27
61(1)	1.34	"UkrBee2(G)"	0	7	93
61(2)	1.93	"UkrBee2(G)"	33	3	64

*Note: * – the symbol G indicates the location of the apiary, namely: the village of Grebeniv (G), the next digit indicates the colony number, symbols 1 and 2 in parentheses indicate the cluster number, (1+2) – clusters are combined into one; ** – templates obtained in actual work (Table 6); *** – wing shares in clusters, according to the classifier obtained for 1780 drone wings (Table 7).*

Expanding the set of classification variables from five to nine indices by incorporating the four additional variables Ci.1.1, Ci.2.1, Ci.2.2, and Ci.3 substantially improved the discriminatory performance of the classification model. For the dataset comprising 545 wings, Wilks' Lambda decreased from 0.240 to 0.171, while classification correctness increased from 85.8% to 96.8%. For the 1,546-wing dataset, the corresponding values changed from 0.256 to 0.192 and from 85.4% to 97.0%, respectively. For the 1,706-wing dataset, Wilks' Lambda decreased from 0.279 to 0.169, while classification correctness increased from 83.0% to 96.0%.

To assess the possible phenotypic presence of *A. m. caucasica* in local *Apis mellifera* populations, a joint classification was performed using the templates "UkrBee1(G)", "UkrBee2(G)", and the independent reference template "Cc.307" obtained by Galatiuk et al. (2024) (Table 9). The classification correctness was 96.8%.

In addition, Mahalanobis distances were calculated between the centroids of these templates and those of the independent reference templates "Troiseck(W)", "UkrBee(R)", and "HybrCaucas(R)" (Table 10).

Based on these results, an additional classification of all the listed templates into three clusters was performed (Table 11). The classification correctness was 95.3%.

The analysis was completed by constructing a dendrogram illustrating the main patterns of the relative positions of the template centroids in morphospace (Fig. 2).

At the initial stage of the study, the results of a previous attempt to develop morphometric templates for *Apis mellifera* populations in Ukraine (Babenko et al., 2024) were critically re-evaluated (Tables 1–2).

The eight linear templates developed in that study demonstrated high classification accuracy and resolution. However, the high discriminatory resolution of such templates may also constitute a limitation when they are applied to highly admixed populations or inter-line hybrids, in which increased phenotypic variability can reduce classification robustness. To address this limitation, it is methodologically reasonable to construct templates with lower discriminatory resolution but based on a broader empirical dataset that incorporates morphometric variation among multiple queens assigned to the same lineage or population. Following this approach, local templates (designated by the suffix “L”) were developed for three established lineages of *A. m. carnica* by pooling data from four queens and subsequently classifying the combined dataset of 545 wings into three clusters (Table 2). Given the *a priori* assumption of three lineages, this clustering scheme was considered biologically justified. The redistribution of wings among the resulting clusters, which were initially represented by two phenotypic classes per colony reflecting alternative paternal contributions to the drone offspring of diploid queens, is consistent with inter-line admixture contributing to increased morphological variability (Table 3).

Local templates can likewise be constructed for individual apiaries or geographically proximate groups of apiaries. The number of such templates is constrained by the diversity of subspecies and populations represented within the area under investigation. This approach was applied to construct morphometric templates for the apiary located in Grebeniv (Tables 5–8). A critical prerequisite for obtaining reliable templates is a sufficiently large empirical dataset, including an adequate number of colonies, to capture the underlying within-population

variation. The Grebeniv apiary represents an open population system. Established in 1982, it is surrounded within a radius of approximately 5 km by several smaller apiaries comprising 5–12 colonies each. Colony reproduction is predominantly swarm-based, while the exchange of virgin and mated queens among neighboring apiaries is common. In addition, queens originating from breeding centers in Zakarpattia (e.g., Hoverla and Vuchkivsky types) and from the Stryi district, including European-selected breeding lines, are occasionally introduced. These conditions facilitate continuous gene flow and may promote admixture among local honey bee populations. In the present study, 18 of the 35 colonies maintained at the apiary were analyzed, providing a substantial empirical dataset for population-level morphometric assessment.

Table 9.

The result of the distribution of drone wings (n = 1027), with a joint classification of two templates, for the apiary from the village of Grebeniv and the linear template for the subspecies A.m.caucasica, into three clusters

Templates	Cluster 1, (%)***	Cluster 2, (%)***	Cluster 3, (%)***	N wings, pcs.
"Cc.307"**	59(79.73)	1(1.35)	14(18.92)	74
"UkrBee1(G)"*	148(34.34)	5(1.16)	278(64.50)	431
"UkrBee2(G)"*	47(9.00)	403(77.20)	72(13.79)	522
Total wings	254	409	364	1027

*Note: * – templates obtained in the actual work (Tables 5, 6); ** – – templates formed by merging clusters (1+2) (Yarovets et al., 2024); *** – number and shares of wings*

Table 10.

Mahalanobis distances (MD) between the centroids of the three patterns obtained in this work and the three patterns in previous works

Templates	"Cc.307"** *	"UkrBee1(G)" *	"UkrBee2(G) " *	"Troiseck(W) " *	"UkrBee(R)"** *	"HybrCaucas(R)"** **
"Cc.307"	0	1.63	3.03	3.51	2.84	1.38
"UkrBee1(G)"	–	0	2.71	2.53	2.38	1.47
"UkrBee2(G)"	–	–	0	2.24	1.80	2.44
"Troiseck(W)"	–	–	–	0	2.01	3.07
"UkrBee(R)"	–	–	–	–	0	2.71
"HybrCaucas(R "	–	–	–	–	–	0

*Note: * – templates obtained in actual work (Table 6); ** – template: "Cc.307" formed by merging clusters (1+2) (Yarovets et al., 2024); *** – templates obtained in (Galatiuk et al., 2024)*

Table 11.

Result of distribution of drone wings (n = 2182) for three local patterns obtained in the current work and two regional patterns obtained in the previous work, when classifying the data into three clusters

Templates	Cluster 1, (%)***	Cluster 2, (%)***	Cluster 3, (%)***	N wings, pcs.
UkrBee1(G)**	302(70.07)	14(3.25)	115(26.68)	431
UkrBee2(G)**	3(0.74)	378(93.80)	22(5.46)	403
UkrBee(R)*	81(22.82)	125(35.21)	149(41.97)	355
Troiseck(W)**	39(6.71)	90(15.49)	452(77.80)	581
HybrCaucas(R)*	321(77.91)	86(20.87)	5(1.21)	412
Total wings	746	693	743	2182

*Note: * – templates obtained from experimental data in (Galatiuk et al., 2024); ** – templates obtained in actual work (Table 6); *** – number and proportions of wings*

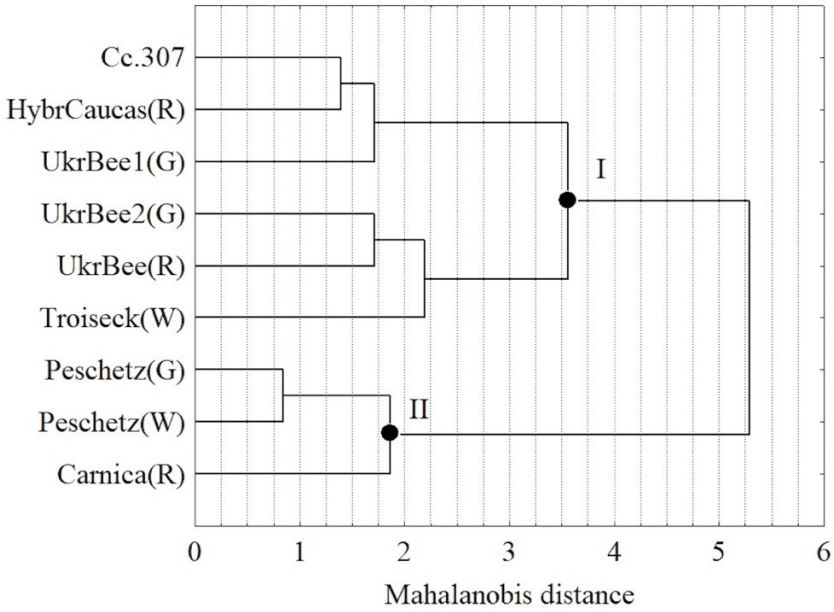


Fig.2. Dendrogram of centroid distribution into two groups, for linear: "Cc.307", local: "UkrBee1(G)", "UkrBee2(G)", "Peschetz(G)" and regional: "UkrBee(R)", "Carnica(R)", templates by Mahalanobis distances (full linkage rule). I and II are critical points characterizing the distribution of templates in each group

Given the geographic position of the apiary within the Carpathian region, the study population was expected to be predominantly associated with *A. m. carnica*. This expectation was only partially supported by the morphometric data. A total of 1,780 drone wings from 18 colonies were classified into three clusters (G1, G2, and G3; Table 8). Unexpectedly, the identification analysis indicated that two of the resulting micropopulations, designated UkrBee1(G) and UkrBee2(G), exhibited a high degree of morphological similarity to the *A. m. caucasica* reference template (Galatiuk et al., 2024). These two clusters showed strong morphometric signals consistent with admixture involving *A. m. caucasica* and together accounted for 58.8% of the sampled population, with UkrBee2(G) predominating. Overall, 426 (23.9%) of the 1,780 examined drone wings from this apiary exhibited phenotypic similarity to *A. m. caucasica* and were assigned to this subspecies on the basis of the morphometric classification. This finding, together with the results of the previous study, raises the possibility of regional differences in the distribution of phenotypes morphometrically similar to *A. m. caucasica* between Central European countries and Ukraine. In particular, colony-level analyses of wing morphology have indicated only a minor representation of phenotypes assigned to *A. m. caucasica* in Poland and Moldova (Oleksa et al., 2023).

To further clarify the taxonomic status of these populations, an additional classification was performed using the "UkrBee1(G)", "UkrBee2(G)" templates together with the linear template "Cc.307", derived from a queen originating from a mountainous region near Kutaisi, Georgia (Yarovets et al., 2024). The results (Table 9) showed that most of the wings used to construct the "UkrBee1(G)" template were assigned to clusters corresponding to the subspecies *A. m. caucasica*. In contrast, the "UkrBee2(G)" template formed a separate cluster with only minor overlap with the other two clusters. This distinction was supported by the Mahalanobis distance between the "UkrBee1(G)" and "UkrBee2(G)" templates (MD > 2.6; Table 10), indicating substantial phenotypic divergence between the two populations. Notably, the Mahalanobis distances between "Troiseck(W)" and clusters G2 and G3 (MD = 2.20 and 1.98, respectively) indicated moderate morphological similarity (Table 7). To further investigate the subspecies and population affiliations of the wing phenotypes, an additional joint classification was performed using the "UkrBee1(G)", "UkrBee2(G)", "Troiseck(W)", "HybrCaucas(R)", and "UkrBee(R)" templates together with the corresponding regional reference templates. The "HybrCaucas(R)" template represents *A. m. caucasica*, whereas "UkrBee(R)" represents Ukrainian honey bees of unresolved subspecies status originating from populations in eastern and central Ukraine (Galatiuk et al., 2024). The combined dataset was subsequently classified into three clusters (Table 11), with an overall classification correctness of 96.1%. The results showed that 46.6% of the wings from "UkrBee1(G)" and 83.0% of those from "HybrCaucas(R)" were

assigned to the same cluster, supporting the morphometric association of "UkrBee1(G)" with *A. m. caucasica*. In contrast, "UkrBee(R)" and "Troiseck(W)" showed partial overlap, with 43.9% and 76.6% of wings, respectively, assigned to the same cluster. This pattern suggests that "UkrBee(R)" is morphometrically more closely associated with *A. m. carnica*, while also exhibiting a component consistent with introgression: 22.5% of its wings were assigned to the cluster supported by the "HybrCaucas(R)" reference. The "UkrBee2(G)" template remained largely distinct, with 73.3% of wings showing self-assignment, and its subspecies affiliation could not be conclusively resolved on the basis of the present morphometric data.

Overall, the results demonstrate that classical wing morphometry provides sufficient statistical reliability for the development and validation of morphometric templates required to address the objectives of this study. Geometric morphometrics may provide additional information on the spatial configuration of wing-shape features; however, its use is not a necessary condition for addressing the objectives of the present study. Comparative studies of classical and geometric morphometrics of honey bee wings indicate that both approaches can be effective for discriminating morphologically differentiated groups, with the choice of method depending on the specific research objectives and the nature of the traits being analysed (Cherevatov et al., 2026).

To further explore the relationships among the developed templates, a dendrogram based on Mahalanobis distances using complete linkage was constructed (Fig. 2). The analysis revealed two principal groups, consistent with the results of the additional classifications of the two corresponding groups of wing samples (Tables 9–11). The first principal group (critical point I) was further divided into two subgroups. One subgroup comprised the "Cc.307", "UkrBee1(G)", "HybrCaucas(R)" templates. Their identification was determined by the linear "Cc.307" template and was associated with the subspecies *A. m. caucasica*. The second subgroup comprised the "UkrBee2(G)", "UkrBee(R)" and "Troiseck(W)" templates. The inclusion of "Troiseck(W)" in this subgroup is noteworthy given its established association with *A. m. carnica*. This pattern may reflect introgression among local populations, potentially resulting from gene flow involving *A. m. caucasica*, as suggested by both previous and present studies.

The second principal group (critical point II) comprised the "Carnica(R)", "Peschetz(W)", and "Peschetz(G)" templates, which showed a consistent association with *A. m. carnica*.

The results obtained for the Grebeniv apiary are consistent with previous findings (Yarovets et al., 2023b) and support two principal conclusions: (1) the presence of at least three coexisting morphometrically differentiated populations of *Apis mellifera* within the study area and (2) the apparent temporal stability of this population structure. These findings provided a basis for applying the analytical system for assessing interpopulation admixture described by Babenko et al. (2024) to 30 clusters. The distribution of wing phenotypes among the three clusters was analyzed using degree of similarity (D_S) values, which provide a quantitative measure of the morphological similarity of a phenotype to its principal reference lineage (Table 8). In 12 clusters (40.0%), the dominant lineage accounted for more than 90% of the wings, indicating a limited contribution of other populations. In 13 clusters (43.3%), the dominant lineage accounted for 50–90% of the wings, suggesting a moderate degree of admixture. In several clusters, including 6(2), 1(1), and 25(2), no single component showed a pronounced predominance over the other two. The resulting lower classification confidence was associated with relatively high Mahalanobis distance values (MD = 2.12–2.33) and may reflect complex patterns of phenotypic admixture and introgression.

An additional outcome of the study was the development of two regional reference templates by integrating data from independent reference templates. For the phenotype associated with *A. m. caucasica*, data from the "UkrBee1(G)" and "HybrCaucas(R)" templates, comprising 459 and 412 wings, respectively, were combined to form the regional reference template "HybrCaucas(U)" (871 wings in total). Similarly, for the phenotype associated with *A. m. carnica*, data from the "UkrBee(R)" and "Troiseck(W)" templates, comprising 355 and 581 wings, respectively, were combined to form the regional reference template "Troiseck(U)" (936 wings in total). The suffix (U) denotes the Ukrainian origin of the template.

Based on the results obtained, a hierarchical framework for the application of morphometric templates can be proposed. Linear templates supported by well-documented pedigree information represent the primary reference level and provide the basis for constructing higher-order templates. In the present study, they were used as markers for the identification of local morphometric patterns. Local templates, including apiary-level datasets, are derived from aggregated empirical data and capture population-specific phenotypic variation. Regional templates, constructed from larger datasets, provide lower discriminatory resolution but may be particularly effective for preliminary classification

when subspecies affiliation is unknown. Accordingly, a sequential application of templates-from regional through local to linear-may provide an effective balance between robustness and taxonomic resolution in the preliminary assessment of subspecies and population affiliation. Such a hierarchical approach allows broad morphometric patterns to be identified at the regional level before progressively higher-resolution templates are applied to resolve local and lineage-level variation.

Conclusions. Based on the analysis of drone wing morphology in western Ukraine, local and regional morphometric templates associated with *Apis mellifera carnica* were developed. For the first time in the Carpathian region, a distinct morphometric population component exhibiting a high degree of similarity to *A. m. caucasica* was identified. The subspecies affiliation of the micropopulation detected at the mountain apiary and represented by the morphometric template "UkrBee2(G)" could not be conclusively determined. Its taxonomic status requires further investigation using independent molecular markers, including SNP and mitochondrial DNA (mtDNA) analyses.

The taxonomic interpretation of the previously established regional template "UkrBee(R)", derived from samples collected across four regions of Ukraine, was revised. Although this template was initially considered to represent a Ukrainian honey bee population with unresolved subspecies affiliation, the present results indicate a heterogeneous morphometric structure. A substantial proportion of wing phenotypes exhibited morphological similarity to *A. m. carnica*, particularly the Troiseck lineage, whereas another fraction showed affinity to *A. m. caucasica*. This pattern is consistent with admixture and ongoing gene flow among local honey bee populations.

The developed drone-wing morphometric templates for the Lviv region provide a practical framework for the identification and monitoring of local *A. mellifera* populations and may contribute to their conservation and management across Ukraine. Their application should be complemented by molecular genetic diagnostics where definitive subspecies or population assignment is required.

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МОРФОМЕТРИЧНІ ШАБЛОНИ КРИЛ ТРУТНІВ ДЛЯ ПОПУЛЯЦІЙ *APIS MELLIFERA* У ЛЬВІВСЬКІЙ ОБЛАСТІ УКРАЇНИ

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Метою роботи було розробити морфологічні шаблони (еталонні стандарти) крил трутнів для використання як інструменту для визначення підвидової та популяційної належності колоній з локальних популяцій медоносної бджоли.

Загалом було проаналізовано 3206 крил трутнів з 31 колонії на 6 пасіках у Львівській області. Морфологію крил було описано в рамках класичної морфометрії з використанням набору індексних ознак, включаючи традиційні індекси (Ci, Dbi, Pci, Disc. sh., Ri) та додаткові індекси, запропоновані авторами (Ci.1.1, Ci.2.1, Ci.2.2, Ci.3). Кластерна ідентифікація зразків крил для досліджуваних колоній була проведена на основі відстаней Махаланобіса між центроїдами еталонних шаблонів та емпіричних кластерів.

Одержано лінійні, локальні, та регіональні морфологічні шаблони для крил трутнів, асоційовані з лініями розведення Troiseck, Peschetz і Sklenar підвиду A. m. carnica. Крім того, для пасіки в поселенні Гребенів визначено локальні шаблони, позначені як: "Peschetz(G)" (A. m. carnica), "UkrBee1(G)" (ймовірно A. m. caucasica) та "UkrBee2(G)", для якого підвидова приналежність залишається невизначеною. Це дозволило ідентифікувати 51(85.0%) досліджених кластерів крил, та оцінити ступінь морфологічної подібності (DS) для 30(88.2%) кластерів на окремій пасіці, що пояснює змішування між лініями або популяціями.

Встановлено, що на території Львівської області присутні кілька популяцій медоносних бджіл, віднесені до підвидів: A. m. carnica та A. m. caucasica. Результати визначення підвидів та популяцій фенотипів крил трутнів на основі класичної морфометрії демонструють ефективність застосованого підходу. Запропонована методологія може бути використана для попередньої оцінки ймовірного складу гаплоїдних геномів у трутнів та маток, зокрема щодо геномного компонента, пов'язаного з морфологією крила.

Ключові слова: Apis mellifera carnica, Apis mellifera caucasica, карпатські бджоли, українські степові бджоли, трутні, морфологія крил, класична морфометрія, дискримінантний аналіз, жилкування крил, відстань Махаланобіса, Західна Україна

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