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Morphological wing templates of drone bees for populations of *Apis mellifera* in Ukraine

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The testing of morphometric templates (standards) for drone wings, obtained from previous studies of bees in Lviv, Zhytomyr, Kyiv, Sumy, Kharkiv, and Poltava regions of Ukraine, was conducted to assess their suitability for determining the subspecies and population affiliation of colonies from local honey bee populations. For this purpose, 1,492 drone wings from 14 colonies of a breeding apiary in the Khmelnytskyi region were classified into four clusters based on eight indices: Ci, Dbi, Pci, Disc. sh., Ri (traditional), and Ci.3, Ci.2.1, Ci.2.2 (proposed by the authors). Cluster identification was carried out using morphometric templates: "Carnica", representing a local population of the subspecies *A. m. carnica*; "UkrBee" – Ukrainian bees; "UkrStep" – Ukrainian steppe bees (for which subspecies identification has not been reliably established); and "HybrCaucas" – a probable hybrid of the subspecies *A. m. caucasica*, based on Mahalanobis distances between the centroids of templates and clusters. It was established that four populations of honey bees predominate at the location of the apiary. At the next stage of the study, a classification of 1,939 drone wings into two clusters was performed for each of the 22 colonies (an additional 8 colonies were included for further analysis). The identification of phenotypes for each of the clusters was carried out in a similar manner by comparison with the aforementioned templates. This made it possible to identify the subspecies and population affiliation of wing phenotypes for 28 (65%) clusters. The results of identifying subspecies and population affiliation of drone wing phenotypes using templates derived within the framework of classical morphometrics indicate the effectiveness of the applied methodology and can be used for the preliminary assessment of the probable genomic composition of drones and queens in the part related to wing morphology. In addition to its primary objective, this study expands knowledge about the racial composition of honey bees in Ukraine. The obtained information on the probable genomic composition of queens can be applied in breeding programs to increase the presence of desired populations at a given apiary and to eliminate populations or hybrids whose presence is undesirable.

Keywords: honey bee; native bees; Ukrainian steppe bees; drones; classical morphometry; discriminant analysis; Mahalanobis distances; *Apis mellifera carnica*; *Apis mellifera macedonica*; *Apis mellifera caucasica*.

Introduction

The United Nations, within its Sustainable Development Goals (SDGs) framework, has established 17 goals aimed at fostering global development. Among these, food security (Goal 2), nutrition and sustainable agriculture, as well as the protection of biodiversity and ecosystems (Goal 15), are directly related to addressing major challenges in the natural environment. An integral part of these challenges is the protection of insect pollinators. The honey bee species (*A. mellifera* L.) is an essential representative of the order Hymenoptera. Researchers from different countries increasingly consider these two goals in conjunction with respect to bees – namely, biodiversity conservation and sustainable agriculture (Geldmann et al., 2018; Adeoye et al., 2020). Anthropogenic activities and efforts to address the global food crisis have led beekeepers to adopt modern practices, including the use of large-scale apiaries (>1,000 colonies), long-distance migratory beekeeping, and the introduction of non-native bee populations into regions where they are not naturally adapted. These factors cause irreversible damage to biodiversity, which has attracted the attention of researchers in the United States (Potts et al., 2018; Alaux et al., 2019) and China (Teichroew et al., 2017). As of today, annual cases of honey bee colony collapse are reliably documented in North America and Eurasia, posing a threat of substantial declines in *A. mellifera* populations across large geographic areas. Some authors attribute these issues to a complex of abiotic factors (Wade et al., 2019; Calovi et al., 2021), while others also emphasize the influence of biotic factors (Insolia et al., 2022), as reported in studies conducted in South America (Requier et al., 2018), Europe (Chauzat et al., 2016), Saudi Arabia (Albarrak et al., 2023), and China (Tang et al., 2023). Another serious threat to colonies is the parasite *Varroa destructor* (Anderson et al., 2000). In the United States, numerous studies are being conducted on viruses transmitted by ticks (Faurot–Daniels et al., 2020). Significant attention is devoted to controlling this parasite through chemical (Jack et al., 2024) and integrated approaches (Yevstafieva et al., 2020; Sobrinho et al., 2023). Attempts to synthesize and generalize data related to these issues have been presented in the works of several authors (van Engelsdorp et al., 2010; Gray et al., 2023).

The ability to survive and adapt to changing environmental conditions largely depends on the "quality" of populations, which is determined by their genetic components. Honey bee colonies, as structural units of *Apis mellifera* populations, are characterized by specific phenotypic traits defined by the genomic composition of queens, drones, and worker bees. Adaptation and the development of new traits (phenotypic characteristics), as well as resistance to ecosystem changes, depend on the ability of the population as a whole to stabilize an optimal configuration of nuclear chromosomal sets. In this process, recombinational variability occurs much more frequently than mutational variability and is present only in queens (Liu et al, 2015). At the

same time, mutational variability is higher in drones (Slater et al., 2022) and lower in queens, although overall it remains significantly lower than recombinational variability. In this regard, drones play an important role in maintaining desired traits. Researchers and breeders pay considerable attention to various important aspects of drone biology, including rearing conditions (Zhang et al., 2024), semen quality (Yániz et al., 2020) and its dependence on nutrition (Gontarz et al., 2016), assessment of mating areas (Woodgate et al., 2021), estimation of colony density based on drone abundance in the environment (Utaipanon et al., 2021), comparison of drone traits across different populations (Schaumann et al., 2024), reproductive quality (Rangel et al., 2019; Metz et al., 2021), and behavioral characteristics (Neubauer et al., 2023; Gilchrist et al., 2024). Researchers have also focused on the behavioral traits of drones from feral honey bee colonies (Williamson et al., 2022; Hagan et al., 2024), as the adaptive capacity of such populations may be higher than that of populations subjected to intensive selective breeding.

Genetic analysis of honey bees provides reliable information about their subspecies affiliation (Donthu et al., 2024; Leroy et al., 2024), as well as population identity (Lukić et al., 2024). Of particular importance is the modern perspective on genomic analysis related to honey productivity (Bernstein et al., 2023; Eynard et al., 2024) and genomic selection (Jones et al., 2020). The application of population genetics can facilitate the development of honey bee strains capable of withstanding various environmental stressors (Maucourt et al., 2020; Shi et al., 2020). Such studies are periodically conducted in Ukraine to determine the subspecies affiliation of honey bee populations within the Carpathian region (Metlytska et al., 2011; Cherevatov et al., 2019), as well as in other regions of Ukraine and Europe (Cherevatov et al., 2020; Roshka et al., 2021). However, these studies are limited in scope and mainly focus on mitochondrial and, less frequently, nuclear DNA. Most researchers in Ukraine face constraints in applying genetic methods. As an alternative for determining racial affiliation, the study of morphological traits of bees is widely used, as it allows the inference of probable genomic origin (Carreira et al., 2017). In this context, it is well established that wing morphology provides the most informative data compared to other morphological traits in Hymenoptera (Lorenz et al., 2015; Krtinić et al., 2016).

Using traditional, classical morphometry, introduced by Ruttner (1988), local populations of the honey bee *A. mellifera* have been studied across different countries and continents: in Turkey (Kekecoglu et al., 2023a), Africa (Meixner et al., 2011), and Iran (Rahimi et al., 2017). An example of a modified classical approach is presented in Kekecoglu et al. (2023b): "This study aimed to determine the naturally occurring honey bee biodiversity in Turkiye by measuring 7 areas (A1, A2, A3, A4, A5, A6, A7) on the right front wing". The work of Güler (2010) rightly notes: "The validity of the method depends on defining the morphological characteristics of original honeybee subspecies or lines using multiple worker bee samples and correctly determining standard morphometric canonical discriminant function coefficients and constant coefficients". We agree with this statement and consider that when using worker bee wings to determine the subspecific affiliation of local bee populations, the main challenge lies in obtaining independent information that can serve as a reference standard. For the subspecies *A. mellifera carnica*, it is possible to obtain queens with reliable pedigrees, as queens of different lines of this subspecies are widely distributed across apiaries in many countries. For other subspecies, it is necessary to rely on reference samples of worker bee wings available in the database of the German Beekeepers' Association (Morphometric Bee Data Bank, Oberursel). However, this option is technically limited, as not all researchers have access to it. This has motivated the initiation of work aimed at creating a regional information system of morphometric data for local populations of *A. mellifera* in Ukraine (Yarovets et al., 2024). In addition, in practice, bee colonies for which the exact origin is unknown are most often studied. As a rule, the queens of such colonies are inter-subspecific or inter-population hybrids. Based on phenotypic analyses of worker bee wings, reliable identification of such colonies is, in most cases, extremely difficult. However, in the case of "purebred" colonies, taxonomic identification can be performed with high reliability using both classical morphometrics of worker bee wings and geometric morphometrics (Tatsuta et al., 2018; Klingenberg, 2021). In some cases, both methods are applied (Koca et al., 2013), and comparisons are made between the data obtained by the two approaches (Bustamante et al., 2019). We are aware of several recent studies in which, alongside worker bee wings, drone wings have also been examined using geometric morphometrics (Henriques et al., 2020; Tofilski et al., 2024). These publications demonstrate that drone wing morphology provides sufficient informative value for the taxonomic identification of bee colonies and correlates with genetic analysis data. A similar conclusion was obtained when combining classical morphometrics with genetic analysis (Özdil et al., 2022). Currently, attempts are being made to automate the entire process of honey bee wing morphometrics, including the acquisition of landmark coordinates and the development of a general classifier of subspecies based on geometric morphometrics of wings (Rodrigues et al., 2022).

Studies of drones using classical wing morphometrics, both historically and at present, have been sporadic in nature. Fragmentary information can be found in the works of Ruttner (1988) and Groeneveld et al. (2020). Systematic investigations of drone wing phenotypes in populations of the honey bee *A. mellifera* distributed across the territory of Ukraine were initiated in the studies by Galatiuk et al. (2024) and Yarovets et al. (2024). The purpose of this work was to continue the study of drone wing morphology and to expand the geographical area of research. A breeding queen-rearing apiary located in Khmelnytskyi Oblast was selected as the study object. The authors sought to demonstrate the effectiveness of a template-based (reference standard) approach for determining the subspecific and population affiliation of individual colonies. It was also necessary to assess the consistency of the obtained results with previously conducted studies. In our view, the stated objectives were achieved. This made it possible to expand the experimental dataset and to obtain a basis for a comprehensive assessment of subspecific diversity of the honey bee *A. mellifera* within the territory of Ukraine.

Materials and methods

For the purpose of testing, morphometric templates obtained in previous studies (Galatiuk et al., 2024; Babenko et al., 2024a) were used. These templates represent datasets of values (multidimensional statistics) based on eight traits (indices): Cubital (Ci), Dumbbell (Dbi), Discoidal shift (Disc. sh.), Precubital (Pci), Radial (Ri) – traditional indices (Bouga et al., 2011) – as well as Ci.3, Ci.2.1, and Ci.2.2 proposed by the authors. The last three indices were calculated as ratios of distances between landmarks on the wing: Ci.3 = d(9;17) / d(9;8), Ci.2.1 = d(10;4) / d(5;6), and Ci.2.2 = d(10;4) / d(8;6), where d(m;n) denotes the distance between landmarks numbered m and n (Fig. 1).

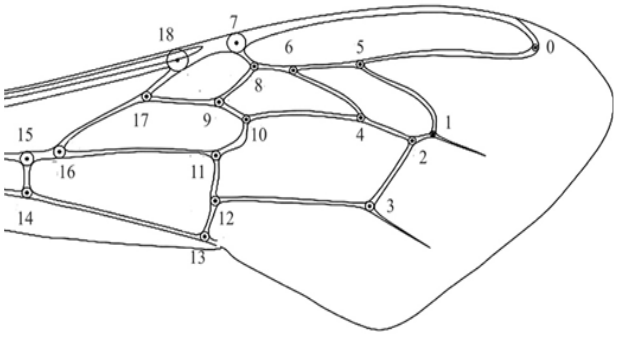

Fig. 1. Scheme of numbering and order of applying landmark points on the wing

The designations of the templates are presented in transliteration as follows: "Carnica", corresponding to the local population of the subspecies *A. m. carnica*; "UkrStep", corresponding to a local population likely belonging to the subspecies *A. m. macedonica*; "UkrBee", corresponding to a local population of Ukrainian honey bees for which subspecific affiliation has not been established; and "Troiseck",

"Peschetz", and "Sklenar", referring to European breeding lines of the subspecies *A. m. carnica*. In addition, based on the data from Galatiuk et al. (2024), an additional template designated as "HybrCaucas" was developed. This template corresponds to a local population significantly hybridized with the subspecies *A. m. caucasica*. It was constructed from wings of colony Cc.307 (58 wings), originating from Georgia, and a subset of wings primarily from the "UkrBee" template (354 wings), and was used in this study for the identification of drone wing clusters.

The experimental material intended for testing was obtained from a breeding queen-producing apiary. This apiary is positioned as one that focuses on breeding populations of indigenous honey bees and has never been subjected to artificial introduction. The apiary was established in the 1980s in the village of Volytsia, Khmelnytskyi Oblast, and initially comprised 25–30 colonies. In 1994, bee packages were introduced from the Starosyniava district of Khmelnytskyi Oblast, with queens of local breeding. In 2010, two additional queens of local selection were acquired from the Horodok district of Khmelnytskyi Oblast. Thereafter, reproduction was carried out exclusively using in-house breeding material. The current state of the apiary was formed during the period 2011–2016. At present, the apiary consists of 320–340 colonies; the nucleus stock includes 1700–2600 mating units depending on the season. Queens are produced by manual grafting into wax cups, rearing queen cells in starter-finisher colonies, and natural mating in two-frame nuclei of ¼ Dadant frame format (classical four-unit nuclei). The apiary's activities include the sale of bee packages, mated queens, and the production of marketable honey. The surrounding apiary density within a 5 km radius is low, consisting predominantly of small-scale hobby apiaries with 20–30 colonies or fewer. Previously, nearly every agricultural enterprise maintained apiaries with 40–100 colonies, but since the 2000s these have ceased to exist. This decline is associated with relatively low honey yields in the region. These factors explain why predominantly local honey bee *Apis mellifera* populations have been preserved in this area, with origins tracing back to the mid-20th century. The apiary owners distribute their own queens free of charge within their settlement and neighboring villages, which is important for maintaining the "purity" of indigenous populations.

A total of 1,939 drone wings from 22 colonies were analyzed. For the study, 60–100 drones were sampled from each colony. The method of drone maintenance ensured sufficient isolation to prevent inter-colony migration. In particular, one honeycomb containing a small amount of sealed drone brood was placed in the second hive body, and a Hahnemann grid was installed between the first and second bodies. After completion of the biological development cycle, dead drones were collected to obtain wings for analysis. In this way, the requirements of EU Directive 2010/63/EU on the Protection of Animals used for Scientific Purposes were adhered to. The research protocol was approved by the Commission on Bioethics and Scientific Research at Yuriy Fedkovych Chernivtsi National University (protocol No. 2 dated May 15, 2025).The right wings of drones were mounted on microscope slides using glycerol. High-quality images of the wings were obtained using a POCO M5 digital camera (50 MP resolution) mounted on a stereoscopic microscope MST 131 (PZO Warszawa) at 25× magnification and stored in a computer database. Landmark placement to obtain coordinate data was performed according to Figure 1 using the TpsDig2 software. Based on the obtained coordinates, values of eight traits (indices) were calculated and used for discriminant analysis in the Statistica software package, followed by classification into four clusters. The identification of drone wing clusters for each bee colony was carried out using morphometric templates. The criterion for determining subspecific and population affiliation was the Mahalanobis distance (MD) between the centroids of the templates and the centroids of the wing clusters. The empirical scale of similarity was as follows: MD values within 0–2 indicate high similarity between datasets; 2–2.6 indicates moderate similarity; 2.6–3.5 indicates low similarity; and values >3.5 indicate no similarity (Babenko et al., 2023).

Results

At the initial stage of the study, a general classification of 1,492 wings from 14 bee colonies into four clusters was performed. Pairwise correlations between most of the analyzed indices, within each cluster, ranged from 0 to 0.25, and in some cases from 0.25 to 0.38 ($P < 10^{-7}$). This indicates that correlations between indices are generally weak, and occasionally moderate. These findings demonstrate the importance of all eight indices for data classification.

The contribution of each index to the classification was assessed using the "Partial Lambda" criterion and, in ascending order, was as follows: Ci.3, Ri, Ci, Ci.2.2, Ci.2.1, Disc. sh., Pci, Dbi. Thus, the indices Ci.3 and Ri had the least influence on the classification of this dataset of drone wings, whereas Pci and Dbi had the greatest influence. The classification correctness (reliability) reached 96.3% (Table 1, Fig. 1).

Table 1
Mean values of indices for four clusters of drone wings (n = 1492)

Indexes*	Cluster 1 means ± SE	Cluster 2 means ± SE	Cluster 3 means ± SE	Cluster 4 means ± SE
Ci	1.595 ± 0.015	1.873 ± 0.019	1.840 ± 0.017	1.522 ± 0.014
Dbi	0.799 ± 0.003	0.921 ± 0.004	0.890 ± 0.003	0.785 ± 0.003
Pci	3.022 ± 0.006	2.909 ± 0.008	2.824 ± 0.007	3.031 ± 0.009
Disc. sh.	-0.139±0.085	1.955 ± 0.096	-1.539±0.092	-4.541±0.117
Ri	1.445 ± 0.004	1.543 ± 0.004	1.367 ± 0.003	1.269 ± 0.004
Ci.3	1.734 ± 0.009	1.761 ± 0.011	1.801 ± 0.008	1.919 ± 0.009
Ci.2.1	1.581 ± 0.005	1.731 ± 0.006	1.530 ± 0.005	1.445 ± 0.005
C.2.2	4.741 ± 0.034	4.137 ± 0.033	3.868 ± 0.024	3.941 ± 0.028
Number of wings	407	330	403	352

Note: * see the Materials and methods section for the designation of indices.

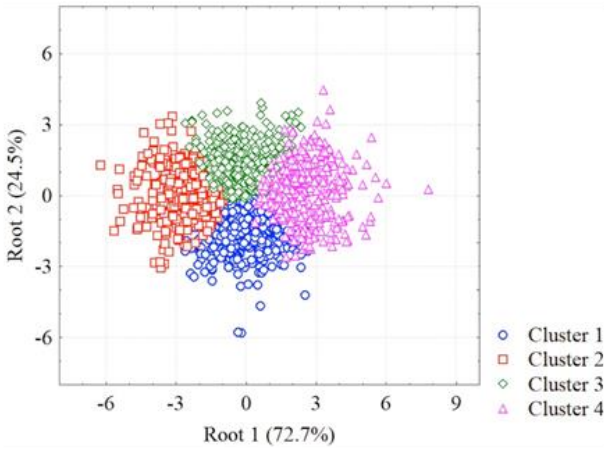

Fig. 2. Distribution of 1,492 drones wings into four clusters in the space of the first two canonical variables (the percentage of total data variance explained by the respective canonical variables is given in parentheses)

Table 2
Mahalanobis distances (MD) between the centroids of four drones wing clusters and three centroids of the reference templates used as standards

Clusters	"Carnica"*	"UkrBee"*	"UkrStep"*
Cluster 1	>2.13	>2.13	1.59
Cluster 2	1.75	>2.13	>2.13
Cluster 3	>2.13	1.51	>2.13
Cluster 4	>2.13	2.13	>2.13

Note: * – data on templates is taken from the work: (Galatiuk et al., 2024).

Analysis of the data presented in Table 2 indicates that the wing phenotypes of Cluster 1 correspond to the population described by the "UkrStep" template, Cluster 2 to the population described by the "Carnica" template, and Clusters 3 and 4 to the populations described by the "UkrBee" template. The slightly higher value of MD=2.13, compared to the others, indicates a certain ambiguity in the interpretation of the population affiliation of the wings of cluster 4.

Subsequently, samples of drone wings from an additional eight colonies were included in the analysis. Thus, at the second stage of the study, the wings from each of the 22 bee colonies were classified into two clusters. Subspecific affiliation for the two wing clusters of each colony was performed by comparison with the same templates that we used to identify the four clusters of 1,492 wings, and the additional template "HybrCaucas". The results of this identification are presented in Table 3.

Table 3
Mahalanobis distances (MD) between two centroids of drone wing clusters for individual colonies (n = 22, total number of wings: n = 1939), and the centroids of the four templates

Colony, no.	Clusters, no.	MD	Templates, names*
12	1	1.95	"UkrBee"
	2	2.04	"UkrBee"
17	1	1.40	"UkrBee"
	2	>2.60	Not identified
21	1	2.11	"HybrCaucas"
	2	>2.60	Not identified
35	1	1.76	"HybrCaucas"
	2	1.88	"UkrStep"
40	1	2.11	"HybrCaucas"
	2	2.10	"Carnica"
50	1	>2.60	Not identified
	2	2.21	"UkrBee"
62	1	1.95	"UkrBee"
	2	2.17	"HybrCaucas"
70	1	2.05	"Carnica"
	2	1.80	"UkrBee"
76	1	>2.60	Not identified
	2	2.28	"UkrBee"
77	1	>2.60	Not identified
	2	>2.60	Not identified
79	1	>2.60	Not identified
	2	1.75	"UkrBee"
81	1	1.95	"UkrStep"
	2	2.28	"Carnica"
84	1	2.10	"UkrBee"
	2	2.19	"HybrCaucas"
174	1	1.61	"UkrBee"
	2	2.38	"HybrCaucas"
122	1	2.08	"UkrBee"
	2	2.00	"Carnica"
402	1	>2.60	Not identified
	2	>2.60	Not identified
422	1	>2.60	Not identified
	2	2.23	"UkrBee"
472	1	1.66	"Troiseck"
	2	>2.60	Not identified
672	1	1.50	"UkrStep"
	2	1.86	"HybrCaucas"
682	1	2.16	"UkrBee"
	2	2.09	"UkrStep"
692	1	>2.60	Not identified
	2	>2.60	Not identified
942	1	1.91	"UkrBee"
	2	1.68	"Carnica"

Note: * – data on templates are taken from the works (Babenko et al., 2024a; Galatiuk et al., 2024).

According to visual observations, the coloration of the majority of drones was as follows: two orange (yellow-brown) tergites in colony no. 21; striped with broad orange (yellow-brown) bands in colonies nos. 35, 40, 17, 50, 76, 61; striped with narrow bands in nos. 79, 84, 174, 12; and dark, with almost no visible banding, in nos. 70, 77, 81. Comparison of observational data with the results presented in Table 3 shows that, for colony no. 21 – where one of the clusters belongs to the population described by the "HybrCaucas" template – the external characteristics of drones exhibit the highest proportion of yellow-brown coloration. For colonies nos. 35, 40, 17, 50, 76, 61, 79, 84, and 174, where the queen genomes are assigned to populations described by the "UkrBee" and "UkrStep" templates, various coloration patterns are observed, ranging from distinct yellow-brown stripes to barely noticeable markings. For the population described by a template the "Carnica", the color of the drones is predominantly black, with barely noticeable streaks (nos.70, 77, 81).

Additionally, the similarity of phenotypes of the local "Carnica" population to local reference templates of European-selected lines of the subspecies *A. m. carnica* was examined (Table 4).

Table 4
Mahalanobis distances (MD) between the centroids of the three templates "Troiseck", "Peschetz", and "Sklenar", corresponding to distinct European breeding lines of the subspecies *A. m. carnica*, and the centroid of the "Carnica" template, which represents the local population of the subspecies *A. m. carnica*

Templates	"Troiseck"	"Peschetz"	"Sclenar"	"Carnica"
"Troiseck"*	0	2.55	3.41	2.26
"Peschetz"*	–	0	2.78	2.05
"Sclenar"*	–	–	0	2.15
"Carnica"**	–	–	–	0

Note: * – data on templates are taken from (Babenko et al., 2024a); ** – from the work (Galatiuk et al., 2024).

Discussion

In this study, the authors employed classical wing morphometrics using a limited number of traits, along with the Statistica software package, whose analytical toolkit enables the required analyses and whose interface is sufficiently user-friendly. In addition to the traditional indices (Ci, Dbi, Pci, Disc. sh., and Ri) three additional indices were proposed (Ci.3, Ci.2.1, and Ci.2.2). The effectiveness and reliability of their application have been confirmed in previous studies.

The fundamental principles underlying our research, which determined both the choice of study objects and the methodology for analyzing experimental data, can be formulated as follows:

First postulate. The morphology of wings in Hymenoptera, in terms of significance and discriminative power, surpasses all other morphological traits (Lorenz et al., 2015; Krtinic et al., 2016). "The ability of wing traits to capture a genetic pattern so strikingly similar to that inferred from hundreds of molecular loci spread across the 16 honey bee chromosomes …. could be explained by a high heritability and a polygenic nature of wing shape" (Henriques et al, 2020).

Second postulate. The informational value of the phenotype–genotype relationship inferred from morphological traits is higher for drones than for worker bees. This is because the phenotypes of drones are determined by the haploid genome, whereas the phenotypes of worker bees are determined by the diploid genome. As a result, phenotypic variability in workers increases while informational resolution decreases. Only in cases of high chromosomal homozygosity in the diploid genome do the informational components become comparable. Based on drone wing phenotypes, it is possible to infer the probable subspecific affiliation of chromosomal sets for both drones and queens, at least for the genomic regions associated with wing morphology. Establishing a similar correspondence between phenotype and subspecific genomic affiliation in worker bees is only feasible in specific cases – namely, when both the queen's genome and the drone sperm genome belong to the same subspecies and exhibit substantial homozygosity.

Third postulate. Phenotype identification is based on morphometric templates (reference standards). This represents a distinction, though not a fundamental one, from traditional approaches where reference standards are based on physical samples or scans of worker bee wings, for example in the Morphometric Bee Data Bank (Bundesland Hessen, Oberursel, Germany). In the available literature, we found no indication that comparable reference data for drones are present in this database. Even in publications where drone wing morphology has been studied (Henriques et al., 2020; Tofilski et al., 2024), this is not mentioned. The use of morphometric templates instead of direct wing references is motivated by a key consideration: for bee populations present in Ukraine, there are no effective barriers to reproductive isolation, as discussed in Oleksa et al. (2013), and Tofilski et al. (2021). This is also supported by our own studies (Ba-

benko et al., 2024b; Yarovets et al., 2024). An exception may be the population of Polesie bees of the subspecies *A. m. mellifera*, which we found only in the wooded and swampy area of Zhytomyr region. As a rule, queens of local populations are inter-subspecific or inter-population hybrids. Therefore, obtaining queens that could serve as sources of reference data for such populations and interpopulation hybrids is extremely challenging. For the subspecies *A. m. carnica*, *A. m. mellifera*, and *A. m. caucasica*, such queens were obtained. This is important because they were used to create local morphometric templates for specific lines.

To standardize the workflow and for reasons of practical efficiency, it was decided to create an in-house bank of morphometric templates. Templates generated using the proposed procedure may correspond either to populations belonging to specific subspecies or to populations that have undergone hybridization under the influence of other subspecies (Galatiuk et al., 2024). In practice, it is considerably more efficient for researchers to use compact, pre-established templates than to rely on large-scale databases of wing images from local populations. It should be noted that a similar approach has been adopted by other researchers (Węgrzynowicz et al., 2020), who developed databases of landmark coordinates to address the problem of inter-subspecific and inter-population hybridization using geometric morphometrics of worker bee wings.

The classification of the dataset of 1,492 wings demonstrates that, within this apiary, most drones belong to four types in approximately equal proportions (25%:25%:25%:25%) (Table 1). Since drone genomes are haploid, this enables the prediction of probable phenotype–genome correspondence. Specifically, drones with predominantly four genomic types are simultaneously present in the apiary: those corresponding to the subspecies *A. m. carnica*, represented by the "Carnica" reference pattern; likely *A. m. macedonica*, represented by the "UkrStep" pattern; a population of unknown subspecific origin, represented by the "UkrBee" pattern; and *A. m. caucasica*, represented by the "HybrCaucas" pattern. As a result, the number of possible chromosomal combinations in the diploid genomes of the majority of worker bees and queens in the apiary is estimated to be 10. It is likely that natural selection stabilizes those types that are currently adaptive under given environmental conditions. This explains why morphometric analyses reveal a limited number of dominant phenotypes within a given geographical area. From the analysis of Figure 2, it can be observed that clusters 2 and 4 do not share common boundaries. This indicates that the wing phenotypes of these clusters differ substantially from each other, whereas clusters 1 and 3 share boundaries with all three other clusters. Wing phenotypes from different clusters located in boundary regions may be highly similar, forming transitional forms. This phenomenon can be explained by the interaction and hybridization of genomes of different subspecies, populations, and lines. It should be noted that the boundary regions between clusters 1 and 2, 1 and 4, and 3 and 4 are somewhat diffuse. Phenotypes are present that are markedly distant from the canonical positions of their respective clusters and occur within the space of neighboring clusters. This is likely due to the fact that, in some colonies, phenotypes were observed that deviated substantially from typical ones and could not be reliably identified.

According to the data presented in Table 3, of the 44 clusters, 14 (31.81%) were assigned to the population of Ukrainian bees described by the "UkrBee" template; 4 (9.09%) to the population of Ukrainian steppe bees ("UkrStep"); 5 (11.36%) to the local population of the subspecies *A. m. carnica* ("Carnica"); 7 (15.91%) to the Ukrainian population significantly hybridized with the subspecies *A. m. caucasica* ("HybrCaucas"); and 1 (2.27%) to the local population of the subspecies *A. m. carnica* ("Troiseck"). For 13 clusters (29.55%), subspecific or population affiliation could not be determined. According to information provided by beekeepers, the method used for obtaining drones for the study was not always followed precisely, which likely contributed to the inability to identify the phenotypes of some wing clusters.

It is noteworthy that the results of drone wing studies are consistent with and complement previous investigations conducted in Lviv, Zhytomyr, Kyiv, Sumy, Kharkiv, and Poltava Oblasts, which are geographically separate from Khmelnytskyi Oblast (Galatiuk et al., 2024). According to the obtained data, drone wing phenotypes distributed across Ukraine predominantly fall into four main types. Since the morphological traits of drone wings are determined by haploid genomes, these findings support the hypothesis of the existence of two distinct Ukrainian bee populations, provisionally designated as UkrBee and UkrStep, without attempting to assign them strict taxonomic status.

The significant presence of bees of the subspecies *A. m. caucasica* in the studied apiary (15.91% according to Table 3) correlates with historical information regarding the targeted and organized import of queens of gray mountain Caucasian bees in the 1970s–1980s to agricultural enterprises in the Khmelnytskyi region. However, this explanation for the presence of *A. m. caucasica* in the studied area cannot be considered unequivocal. Migration pathways of the honey bee *Apis mellifera* from the Caucasus are not strongly constrained by geographic barriers. The subspecies has successfully spread across Anatolia and nearly to the Balkans (Kekecoglu et al., 2023a) and could, with similar probability, have expanded into Ukraine. Therefore, the conclusion regarding hybridization of the Ukrainian bee population UkrBee by *A. m. caucasica* (Galatiuk et al., 2024) is not unambiguous. The interpretation may in fact be reversed, assuming that *A. m. caucasica* itself has been hybridized by the Ukrainian bee population UkrBee, which is plausible according to Han et al. (2012). To obtain a definitive conclusion on this issue, further high-precision large-scale studies of drone wing morphology are required, or genetic analyses should be conducted on queens whose genomes consist of hybridized chromosomal sets of *A. m. caucasica* and the UkrBee population.

Analysis of Mahalanobis distance (MD) values between the centroids of three clusters of local templates ("Troiseck", "Peschetz", "Sklenar") and the centroid of the local "Carnica" population indicates substantial similarity (Table 4). Although this similarity cannot be considered complete correspondence, it is particularly high for the "Peschetz" template. Overall, this observation may be interpreted as supporting the assumption of comparability between the phenotypes of *A. m. carnica* bees of European breeding origin and the local population described by the "Carnica" template, thereby also suggesting a common origin. This interpretation is consistent with the position of Lukic et al. (2024): “We have observed genetic homogeneity of the Carniolan honey bee population when considered in a broader genetic/geographical context. However, the Carniolan honey bee has sufficient genetic diversity in its geographical home range that needs to be carefully monitored and maintained… admixture analysis revealed varying levels of gene flow and genetic admixture within the Carniolan honey bee populations, demonstrating closer relationships between specific geo-graphic regions”. These conclusions are also consistent with data reported by Tofilski et al. (2021).

The results presented in Table 3 allow the following interpretations. For queens from colonies nos. 12, 35, 40, 62, 70, 81, 84, 174, 122, 672, 682, and 942, the probable subspecific affiliation of both chromosomal sets of their genomes – specifically the components associated with wing morphology – has been established. For colonies nos. 17, 21, 50, 76, 422, and 472, subspecific affiliation was established for only one of the two chromosomal sets. For colonies nos. 77, 402, and 692, subspecific affiliation could not be determined. The inability to assign phenotypic affiliation can be explained by two main factors. First, insufficient isolation of drones within colonies may lead to uncontrolled migration. Second, it is possible that a small proportion of phenotypes from unidentified clusters belong to populations of introduced bees.

Due to genetic deviations, up to 5% of wings exhibited defects in venation, including missing vein intersections, and were excluded from the analysis. For individual colonies Nos. 79, 84, and 672, the defect rate was significant, namely ~30%, ~30%, and ~40%, respectively. These observations have a logical explanation: “…drones usually exhibit a higher number of wing venation anomalies due to their haploid condition … Drones are haploid, allowing more frequent phenotypic expression of deleterious alleles, which were identified here as missing landmarks” (Henriques et al., 2020).

Conclusion

The study of drone wing morphology for one large apiary accomplished two tasks. First, it expanded information on the subspecies and population composition of honey bees in Ukraine. Second, drone wing samples from this apiary were used as an independent object for testing templates.

The proposed method of obtaining templates for local bee populations does not require queens, which must meet the quality of the reference ones. The results of using these templates indicate that they successfully identified the subspecies and population affiliation of the studied clusters of drone wings. This gives grounds to recommend them as regional morphometric templates (standards) of drone wings for bee populations present in Ukraine.

An important consequence of the successful subspecies and population identification of drone wing phenotypes is the ability to predict the likely diversity of diploid queen genomes in the part responsible for wing morphology.

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