



HUNGARIAN UNIVERSITY OF
AGRICULTURE AND LIFE SCIENCES

**INVESTIGATION OF THE EVOLUTIONARY ORIGIN AND
GENETIC DIVERSITY OF THE PANNONIAN BEE USING
MOLECULAR METHODS**

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1. BACKGROUND AND OBJECTIVES OF THE STUDY

Honey bees play a key role in the ecosystem and the economy (Westerkamp & Gottsberger 2000, Klein et al. 2007).

Today, several studies highlighted that bee mortality can cause serious problems in ecology and agriculture (Hopkins & Herr 2010, Harwood & Dolezal 2020).

As with other farm animals, the loss of genetic diversity is a major concern in honey bees as well, if not even a greater one due to their unique genetic and reproductive characteristics. It is important to protect the native honey bee populations and maintain their genetic diversity (Wegener et al. 2014). In order to preserve native populations with the original gene pool, several gene conservation programs have been launched around the world under *in vivo* and *in vitro* conditions (Jensen & Pedersen 2005, Strange et al. 2008).

According to Government Decree 188/2019. (VII. 30.), in Hungary only those honey bee species can be bred that have an officially approved breeding program. Therefore, currently only the Pannonian bee is allowed to be bred in Hungary, which was recognized as an independent breed by the Animal Breeding Directorate of NÉBIH (Decision No.: 02.5/2297-2/2012) on 21st August 2012.

The breeding and supervision of the Pannonian bee is carried out by members of the Hungarian Bee-Breeders' Association (HBBA) (Szalay 2017). Each year, the HBBA commissions the Department of Apiculture and Bee Biology of the Institute for Farm Animal Gene Conservation, National Centre for Biodiversity and Gene Conservation to perform the morphological breed identification (color pattern, proboscis length and cubital index) of the

reared Pannonian bee colonies. Based on these assessments, bee breeders can receive the breeding license.

In this context, our institute has begun assessing the gene pool of Pannonian bees, as it is important to determine genetically whether a given individual belongs to the Pannonian bee in Hungary.

The aim of my study was to:

- determine the evolutionary origin of the Pannonian bee based on mitochondrial DNA, which is the only breed that can be bred in Hungary,
- assess the genetic diversity of the Pannonian bee across the country using microsatellite markers,
- compare the Hungarian Pannonian bees that met the breed standard with the morphologically defective individuals, Carniolan bees (*Apis mellifera carnica*), and other subspecies present in Hungary with molecular genetic tools,
- select a relevant sample collection for the high-resolution whole genome sequencing,
- detect SNP variants that can provide a good basis for an SNP marker panel for the identification and/or separation of the Pannonian bee.

2. MATERIALS AND METHODS

According to Government Decree 40/2013 (II. 14.), no animal testing permission is required for experiments conducted on honey bees.

2.1. The groups of bees included in the study

My research was based on adult worker bee individuals, which were sent by breeders for morphological breed identification. These samples were used with the breeders' permission for further genetic investigations while preserving their anonymity.

A total of 144 samples were grouped into four categories for mitochondrial DNA and microsatellite analyses.

The first group (MF - 64 samples/16 apiaries) consisted of individuals from colonies of breeders of Hungarian Bee-Breeders' Association, that met the morphological breed standard based on the officially performed breed identification for several years. In the second group (NMF - 32 samples/8 apiaries), there were individuals from colonies that failed the official morphological breed identification, mainly selected based on the tergite color. In addition, a reference group (REF - 32 samples/4 apiaries) was established, which included Buckfast hybrids, Italian bee × Buckfast hybrids and Italian bees (*Apis mellifera ligustica*). Finally, the fourth group consisted of individuals from two colonies (*Apis mellifera carnica*, KRAJ - 16 samples/2 apiaries) of the Carniolan bee (Ukraine, Slovenia) from two other European countries.

For whole genome sequencing, 87 bees were selected from the 144 individuals described above. The reduction in sample size was based on the results of the microsatellite analysis, which mainly affected the Pannonian bee that met the morphological breed standard. The main criteria of the sample

selection was that the selected bee should have as many unique alleles as possible that occur only in the MF group. On the other hand I considered the result of the Principal Coordinate Analysis (PCoA) as well. The sample size was balanced between the three groups (MF, NMF, REF) with 29 individuals of each; the KRAJ group was not included in this sample collection for financial reasons.

2.2. Genomic DNA isolation and equalization

DNA samples were extracted using a modified method described by Latorre et al (1986).

DNA quantity and quality were measured and then equalized to 30 ng/μL for mitochondrial DNA and to 6 ng/μL for microsatellite and SNP analysis.

2.3. Mitochondrial DNA analysis

Three different regions of the mtDNA were examined in this study. The cytochrome oxidase I (*COI*) and the rRNA (*16S*) genes were used for assessing the mitochondrial genetic variance, while the tRNA^{Leu}-cox2 (*COI-COII*) intergenic region (E2/H2) was used for determining the evolutionary origin.

The PCR products were stored at –20 °C until further processing. The purification of the PCR products and the Sanger sequencing of the samples were performed by the BIOMI Ltd. (Godollo, Hungary).

2.4. Microsatellite genotyping

In total the same 144 samples were genotyped using 20 microsatellite markers: A29, A35, A88, A107, A113 (Estoup et al. 1995), A007, A(B)24, Ac011, Ac306, Ap049, Ap218, Ap226, Ap289, Ap307 (Solignac et al. 2003), Ap033, Ap043 (Garnery et al. 1998), A008 (Franck et al. 1998), Ap055,

Ap066, and Ap081 (Techer et al. 2015). The markers were selected from the literature based on their polymorphism information content (PIC).

The use of universal sequences and three different fluorescent dyes enabled to establish three marker sets, allowing the genotyping with 6–7 markers at the same time. PCR products were detected using an automatic DNA sequencer and capillary gel electrophoresis, according to the manufacturer's instructions.

2.5. Whole genome sequencing

The sequencing of the samples was performed by iBioScience Ltd. (Pécs, Hungary) on the Illumina NovaSeq 6000 platform with 20x coverage, as well as the bioinformatic analysis, since the huge amount of data requires high computer capacity.

2.6. Statistical methods used for data

2.6.1. Mitochondrial DNA analysis

The *COI* and *16S* genes were assessed both separately and jointly by generating synthetic sequences per individual to measure the diversity of mitochondrial DNA in the bee groups studied. The tRNA^{leu}-cox2 intergenic region (*COI-COII*) was used for determining the evolutionary origin of the Pannonian bee.

The quality of the raw sequences was checked, then haplotypes and diversity indices were determined, such as the nucleotide and haplotype diversity, Fu's F_s value, Tajima's genetic distance (D) and their significance level.

The haplotypes determined were compared to sequences available in the NCBI (National Center for Biotechnology Information) database by the nucleotide BLAST (Basic Local Alignment Search Tool) program.

To visualize the relationships between haplotypes, a Median-Joining network was created using the Network 10 software (Bandelt et al. 1999), while the phylogenetic tree was generated by the MEGA 11 (version 11.0.13) software (Tamura et al. 2021).

2.6.2. Population genetic analyses based on microsatellite markers

The results for the microsatellite markers were analyzed using the GenomeLab Genetic Analysis System 10.2 software. Genetic diversity parameters within bee groups, such as the mean number of alleles, unbiased expected and observed heterozygosity, inbreeding coefficients and the Hardy-Weinberg test were calculated with the Microsatellite Toolkit program (Park 2001).

Pairwise F_{ST} estimates of the studied honey bee groups were measured by the Analysis of Molecular Variance (AMOVA) using GenAlEx 6.5 software (Peakall & Smouse 2006, Peakall & Smouse 2012). In addition, Principal Coordinate Analysis (PCoA), Discriminant Analysis of Principal Components (DAPC) (Jombart 2008) and STRUCTURE analysis (Pritchard et al. 2000) were performed.

2.6.3. Bioinformatic analysis of SNP data

The sequences of the honey bee samples used in this study were compared to the reference genome of *Apis mellifera* (Amel_HAv3.1, Génbanki azonosító: GCF_003254395.2) in the NCBI database.

The results were visualized by Principal Component Analysis (PCA) using the PLINK 1.07 software (Purcell et al. 2007). Extreme values were excluded from the PCA analysis, variants with allele frequencies above 2 % and below 5 %, so the very monomorphic and fairly rare SNP alleles.

As part of the bioinformatics service, an application software was developed that is suitable for filtering variants by chromosome. After trying several screening ranges, I obtained a sufficient number of variants (Wilkinson et al. 2012) for allele frequencies of 70-30 % (MF - NMF, REF). The resulting filtered variants were plotted on a bar chart for each chromosome to represent their distribution in the genome.

3. RESULTS AND DISCUSSION

3.1. Mitochondrial DNS analysis

3.1.1. Variability of the *COI* and *16S* mitochondrial regions

In the case of the *COI* gene, 142 evaluable sequences were obtained (GenBank Acc. no.: PQ686393 - PQ686534). Based on a total of six polymorphic sites, the individuals could be classified into five haplotypes, none of which were found in the NCBI database; thus, they can be considered as new and unique. Two polymorphisms resulted in amino acid changes compared to the reference sequence in the NCBI database: one at position 180. in the HC4 haplotype (methionine instead of isoleucine) and the other at position 181. in the HC3 haplotype (isoleucine instead of valine).

The samples examined for the *16S* gene (n=141, GenBank Acc. no.: PQ721124 - PQ721264) were classified into four haplotypes based on four polymorphic sites, two of which were not found in the NCBI database.

I merged the sequences of the two genes (*COI* and *16S*) for each individual, resulting in 141 synthetic sequences. A total of ten polymorphic sites were identified among the haplotypes. Among the samples, the H1 haplotype was the most common, representing 75,2 % of individuals. The H6 haplotype, which differed from H1 by five base pairs, was found only in Buckfast hybrids. Four different haplotypes were identified in the MF group.

The *COI* and *16S* genes were assessed both separately and jointly by generating synthetic sequences per individual to determine the diversity values. Haplotype diversity was the highest in the KRAJ group and the lowest in the MF. Nucleotide diversity was also the lowest in the MF group, while the highest value was detected in the REF individuals. In the MF group, the

values indicating the population history processes were negative (Fujima's F_u and Tajima's D).

The synthetic sequences of the *COI* and *16S* genes from the studied bee samples were compared with 45 sequences belonging to several *Apis mellifera* subspecies available in the NCBI database.

The H1, H2, H3, H4, and H5 haplotypes showed a high degree of similarity to well-known subspecies, such as the Italian and Carniolan bees, and the Buckfast hybrid. In contrast, the H6 haplotype indicated genetic similarity to subspecies mainly distributed in Africa.

3.1.2. Determination of the evolutionary origin based on the tRNA_{Leu}-Cox2 intergenic region (*COI-COII*)

The analysis of the tRNA_{Leu}-cox2 intergenic region (*COI-COII*) resulted a total of 124 evaluable sequences (GenBank Acc. no.: PQ724159 – PQ724284). Six haplotypes were determined based on six polymorphic sites. All of them belonged to the C evolutionary lineage and have been described previously in the NCBI database as follows: HE1 – C1, HE2 – C2p, HE3 – C2i, HE4 – C2d, HE5 – C2e, HE6 – C2l.

Most of the samples were classified into the C1 and C2d haplotypes, while only one MF individual belonged to the C2l haplotype. All individuals from the examined groups were represented in the C1 haplotype. Although the C2d and the C2e haplotypes included a relatively large number of individuals, no samples from the REF group were present there. The C2p haplotype consisted of Italian bees, a few Buckfast hybrids and one MF individual. Two Buckfast hybrid individuals belonged to the C2i haplotype.

Based on the analysis of the tRNA_{Leu}-cox2 intergenic region (*COI-COII*), the highest haplotype diversity was detected in the MF and REF groups, while the lowest value was found in the KRAJ. Nucleotide diversity

was also lowest in KRAJ, while the highest value was measured in the REF group. The values indicating the population history processes of the MF group were positive (Fujima's F_u and Tajima's D) in case of the intergenic region.

The sequences obtained were compared with 62 *Apis mellifera* sequences from the NCBI database. The sequences were classified into a total of 45 haplotypes belonging to four evolutionary lines: A, C, O and M (Figure 1.).

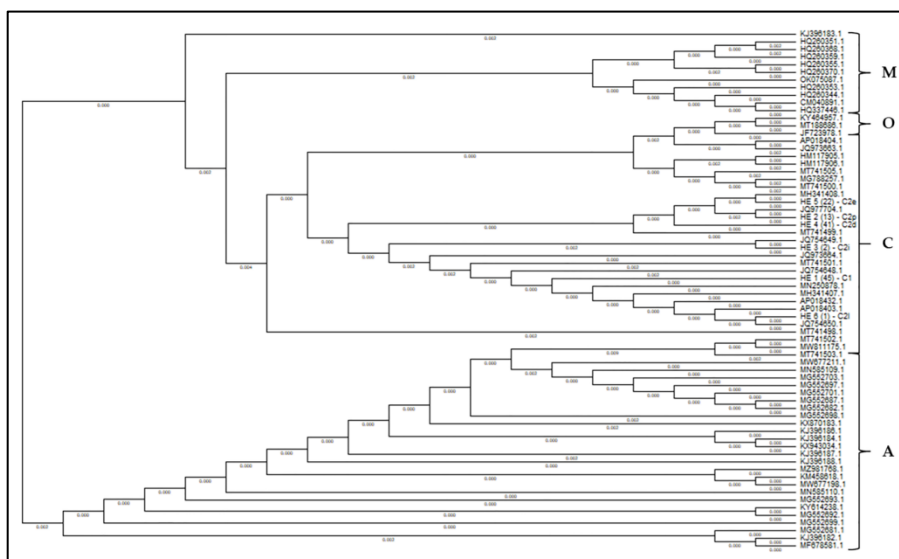


Figure 1. Phylogenetic analysis of the tRNA^{Leu}-cox2 intergenic region (*COI-COII*) for determining the evolutionary origin of the Pannonian bee in Hungary

HE1 – 6: haplotypes containing samples of the bee groups studied. The numbers in parentheses correspond to the number of individuals with a certain haplotype, which were identified using the commonly used nomenclature in the NCBI database.

A, C, O and M: different evolutionary lineages

Eight Buckfast hybrid individuals, that showed similarity to African bees based on the investigation of the *COI* and *16S* regions, were not included in the analysis of the intergenic region. This is due to the poor quality and different lengths of the sequences, which were almost twice as long as in the other samples.

3.2. Microsatellite marker analysis

A total of 224 different alleles were identified during the microsatellite marker analysis. The lowest average number of alleles was observed in the KRAJ group, while the highest allele diversity was found in the MF group. In general, all examined groups showed high heterozygosity and only the MF and NMF groups deviated from Hardy–Weinberg equilibrium significantly. The level of inbreeding was low in all groups.

Several rare alleles (frequency below 10 %) were detected, including more that were found only in one bee group.

Population genetic statistical analyses (pairwise F_{ST} , PCoA, DAPC, STRUCTURE) revealed that the REF was clearly separated from the other bee groups examined. A partial overlap was observed between the MF and NMF; however, it was noticeable that NMF individuals were more similar to the Carniolan bees than to the Pannonian bees that met the breed standard (MF) (Figure 2.).

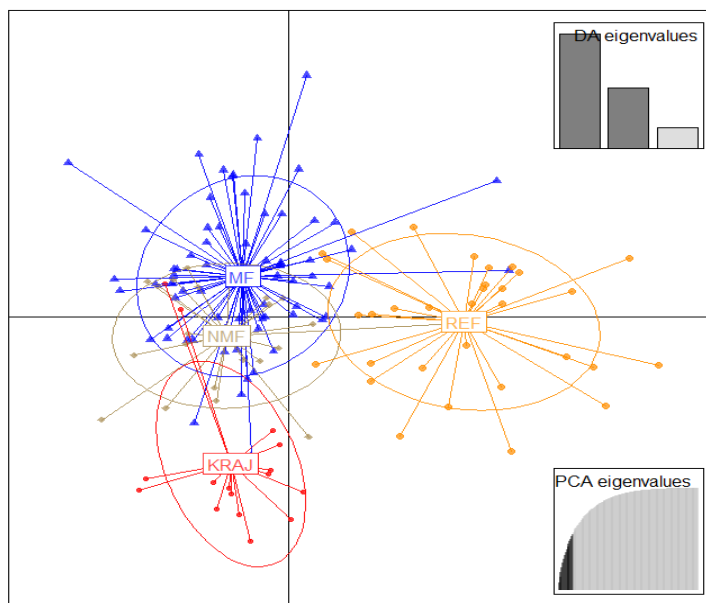


Figure 2. Graphical illustration of the population structure presented by Discriminant Analysis of 15 Principal Components (DAPC)

MF (blue) – Pannonian bees that met the breed standard, NMF (grey) – Pannonian bees with morphological disorders, REF (yellow) – different varieties of *Apis mellifera*: Buckfast hybrid, *Apis mellifera ligustica* × Buckfast hybrid and *Apis mellifera ligustica*, KRAJ (red) – *Apis mellifera carnica* from other European countries, DA eigenvalues – eigenvalues of the discriminant analysis, PCA eigenvalues – eigenvalues of the principal component analysis

3.2.1. Population genetic analysis of the sample collection selected for whole genome sequencing using microsatellite markers

The basic diversity parameters of the bee groups selected for SNP analysis (87 individuals) did not differ significantly from those of the collection (144 samples) based on microsatellite marker analysis.

Similar results were obtained from the PCoA and STRUCTURE analyses: the MF and NMF groups showed partial overlap, while the REF was clearly separated from the Pannonian bees.

3.3. High-resolution marker analysis based on point mutations

The study revealed variants at a total of 6.533.718 loci in the 87 samples analyzed in three groups of bees (MF, NMF, REF).

The PCA was based on alternative alleles with frequencies between 5 % and 98 %, resulting in a total of 5.912.008 SNPs (Figure 3.).

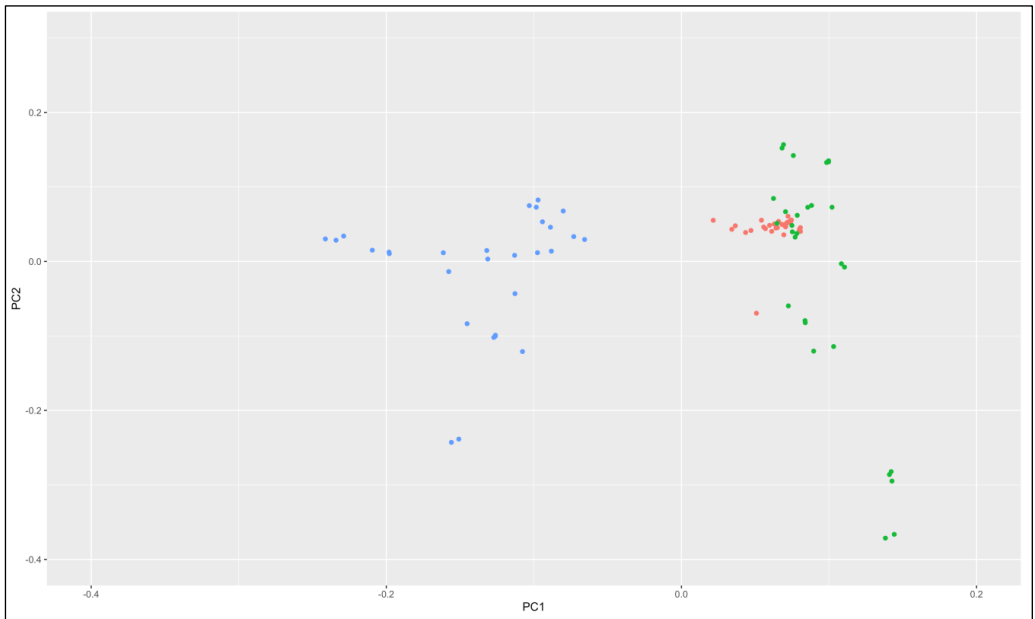


Figure 3.: Principal Component Analysis (PCA): relationship between individuals of three studied bee groups (MF, NMF, REF) based on SNP variants with frequencies of 5-98 %

MF (red) – Pannonian bees that met the breed standard, NMF (green) – Pannonian bees with morphological disorders, REF (blue) – different varieties of *Apis mellifera*: Buckfast hybrid, *Apis mellifera ligustica* × Buckfast hybrid, *Apis mellifera ligustica*

As a result, the REF group was clearly separated from the MF and NMF individuals, while those showed some overlap, which is consistent with the findings from the microsatellite analysis. However, it should be noted that the MF group formed a more concentrated cluster, while NMF individuals were more scattered across the figure.

The screening of variants with a frequency of at least 70 % in the MF group and at most 30 % in the NMF and REF groups resulted in the detection of 31 alternative alleles (SNPs). In contrast, the opposite screening (30 – 70 %) identified 69 variants that are more typical of individuals with morphological defects and of other subspecies present in our country.

After filtering the variants using two different approaches, the identified SNPs showed relatively good coverage across the genome. In the first screening, no SNPs were detected on chromosomes 6 and 15, whereas in the second screening, the highest number of variants was found on chromosomes 6 and 12.

4. CONCLUSIONS AND SUGGESTIONS

4.1. Understanding and relevance of mitochondrial DNA data

The investigation of the origin of Pannonian bees showed that all examined individuals belonged to the C evolutionary lineage, which is typical of North Mediterranean subspecies.

Based on the synthetic sequences (*COI*, *16S*), most haplotypes were classified into one group, with the exception of H6. This haplotype showed more than 99.7 % genetic similarity to subspecies belonging to the evolutionary lineage A, which represents African bee subspecies. In this case, the sequence length – unlike the others, which were approximately 400 bp – was 800 bp, as confirmed by agarose gel electrophoresis. This difference may be due to length polymorphism between evolutionary lineages (Garnery et al. 1992), heteroplasmy (Meusel & Moritz 1993), or the presence of NUMTs (Zhang & Hewitt 1997); however, further investigations are needed to confirm this.

Based on the mitochondrial diversity values of the synthetic sequences, I found that the Pannonian bees that met the breed standard were genetically more homogeneous, while the REF showed a higher level of variability. This finding is consistent with the results of the microsatellite analysis. The reason can be that the REF group included individuals from different subspecies, while the MF group consisted only of Pannonian bees from 16 queen breeders from geographically well-distributed apiaries across Hungary. Values indicating the population history processes suggest that population growth or positive selection could have happened in the Pannonian bees in the recent past.

4.2. Genetic diversity of the studied bee groups based on microsatellite markers

Based on the results of the microsatellite analysis, it can be concluded that the genetic variability of Pannonian bees that met the breed standard is at an appropriate level and their genetic status is satisfactory.

The different population genetic analyses (pairwise F_{ST} , PCoA, DAPC, STRUCTURE) showed that MF individuals consistently clustered together and were clearly separated from other subspecies present in our country (REF).

A slight but detectable difference was observed between MF and NMF groups at the genetic level, not only phenotypically. The genetic overlap between these groups suggests that if foreign genetic material was admixed into the Hungarian Pannonian bees, it could have happened most likely in the past across several generations.

Similarities could be found between NMF and KRAJ, while the MF group showed a greater genetic distance from the Carniolan bees. This difference is likely to be resulted by past hybridizations between the two groups, which may have been influenced by natural and artificial selection over several generations.

Based on these findings, it can be concluded that the long-established morphological breed identification is probably effective for preserving the genetic purity of Pannonian bees, with no significant genetic contamination detected in the population. However molecular genetics can be of great help in selecting bees with foreign genetic material, complementing the phenotypical selection. These results support classifying the Pannonian bee as a separate breed.

4.3. Conclusions from the analysis of SNP variants

SNP-based analyses confirmed the results of the microsatellite analysis, indicating that the REF group showed a relatively large genetic difference from the MF and NMF groups; however, partial overlap was observed between the latter two.

From all these observations, we can conclude that although SNP-based marker analysis provides a more precise picture of the gene pool, similar results can be expected when using a sufficient number of microsatellite markers. Moreover, the higher-resolution SNP-based marker research is more expensive and requires appropriate laboratory infrastructure, bioinformatics background and computer capacity. Moreover, microsatellite markers are very useful for indicating changes in genetic variability with monitoring the populations from time to time, which is of great importance in gene conservation.

100 SNPs were identified in the bioinformatic analysis that could be used to identify the Pannonian bee and/or to select bees with foreign genetic material. It is very important that genetic mutations identified in genome-wide SNP studies can only be used in practice after proper validation.

However, it should be noted that reduced point mutation panels are more suitable for breed identification and detection of the possible presence of foreign genetic material than for classical population genetic analyses (Muñoz et al. 2015).

4.4. Suggestions

Based on my results, I make the following recommendations:

- Based on the microsatellite markers used in the study, I recommend systematic monitoring of the Hungarian Pannonian bee from time to time, which can be used to track their genetic diversity and control their purity, providing useful information for bee breeders.
- I recommend further analyses of the SNP variants with allele frequencies between 5 % and 98 % using additional population genetic statistical methods (e.g., DAPC, STRUCTURE) to obtain as accurate picture as possible of the genetic status of breeding stocks in Hungary.
- I suggest validating the SNP variants typical of Pannonian bees that meet the breed standard (31 SNPs), as well as those associated with other subspecies found in Hungary (69 SNPs), to establish a reliable SNP panel which can be used to identify Pannonian bees bred in Hungary and select bees with foreign genetic material.
- After establishing a stable breed profile, I recommend complementing the morphological breed identification with genetic analyses. This would allow the molecular genetic identification and selection of individuals with ambiguous phenotypes that may carry foreign genetic material.
- Overall, my results support the acceptance of the Hungarian Pannonian bee as a unique, separate breed. However, I suggest comparing it with the Carniolan bee (*Apis mellifera carnica*) populations native to neighbor countries based on SNP variants to get a more accurate picture.

5. NEW SCIENTIFIC RESULTS

1. I determined the evolutionary origin of the Pannonian bee bred in Hungary that meet the breed standard, according to which they belong to the evolutionary lineage C based on the tRNA^{Leu}-cox2 intergenic region of mitochondrial DNA (*COI-COII*). I identified three haplotypes that have been detected only in foreign bee populations so far.
2. I identified five new unique haplotypes in the *COI* region of mitochondrial DNA and two in the *16S* region in the Hungarian Pannonian bee that are not yet available in the NCBI database.
3. I compared Pannonian bees that phenotypically meet the breed standard derived from the major beekeeping regions in Hungary to individuals with morphological disorders. I found that there was a slight but detectable genetic difference between them.
4. Using molecular genetic methods, I confirmed that the breed identification of Pannonian bees in Hungary based on morphological characteristics is appropriate, and I verified the importance and relevance of the phenotypic selection method in the conservation and maintenance of purebred Pannonian bee stocks.
5. I identified 31 SNP variants in the genome of Pannonian bees bred in Hungary that meet the breed standard. After appropriate validation, these variants may be suitable for molecular genetic identification, thereby facilitating the preservation of the breed's purity.
6. I identified 69 point mutations in the genomes of individuals of Pannonian origin with morphological disorders, as well as in individuals belonging

to other subspecies present in Hungary (Italian bee and the Buckfast hybrid). After validation, these variants can be used reliably for detecting the presence of possible foreign genetic material in the Pannonian bees maintained in Hungary that meet the breed standard.

6. RELEVANT SCIENTIFIC PUBLICATIONS

Journal articles with an impact factor related to the topic of the thesis:

Balazs, R.; Molnar, T.G.; Meleg, E.E.; Hidas, A.; Zajacz, E.; Racz, T.; Palinkas-Bodzsar, N. (2025): Evolutionary Origin and Genetic Diversity of the Pannonian Ecotype of *Apis mellifera carnica* Colonies in Hungary Based on Mitochondrial DNA and Microsatellite Markers. **Biology**, 14 (5), 475.

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Journal articles without an impact factor related to the topic of the thesis:

Balázs R., Edviné Meleg E., Hidas A., Zajác E., Rác T., Pálincás-Bodzsár N. (2023): Magyarországon élő pannon méh családok genetikai összetételének vizsgálata molekuláris markerek alapján. **ACTA AGRONOMICA ÓVÁRIENSIS**, 64 (Ksz 2): 199-209. (ISSN 1416-647X)

Educational articles without an impact factor related to the topic of the thesis:

Balázs R., Edviné Meleg E., Hidas A., Rác T., Zajác E., Pálincás-Bodzsár N. (2023): Pannon méh állományok genetikai diverzitásának vizsgálata molekuláris markerekkel. **Magyar Mezőgazdaság – Méhészet**, 71 (111): 22-24.

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Balázs R., Edviné Meleg E., Hidas A., Rácz T., Zajác E., Pálincás-Bodzsár N. (2024): Magyarországon élő pannon méh populációk molekuláris genetikai elemzése mikroszatellit markerekkel. Absztrakt kötet. Biotechnológus Napok, Budapest, 2024. április 26-27., p. 4.

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