

# **Theses of Doctoral (PhD) Dissertation**

## **STUDY OF THE GENE RESERVES OF HUNGARIAN TRADE -PRODUCING COMMON CARP (*CYPRINUS CARPIO* L.) STRAINS BASED ON MATERNAL AND BIPARENTAL MARKERS**

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## 1. BACKGROUND AND OBJECTIVES OF THE DOCTORAL DISSERTATION

Similarly to the breeding of domesticated species, the domestication of aquatic species is also a form of evolutionary pressure. Investigating the effects of evolutionary pressure is essential to improve aquaculture practices. The effects of these pressures can be revealed by the application of molecular genetics and used to develop aquaculture practices. Anthropogenic effects can affect the genetic structure of captive populations, especially forms bred for commercial interests. Because of all this, knowledge of genetic diversity is extremely important for professionals who want to improve their stock. Furthermore, understanding captive populations at the genetic level is essential for understanding animal husbandry practices. In addition to all this, the genetic variation of a species determines its ability to survive in nature, as well as its ability to adapt to various environmental changes. As a result, the survival and resistance of a species requires genetic variation. In order to manage genetic variations, it is necessary to characterize the genetic diversity of species, varieties, and strains, and in addition to this, constant monitoring of the genetic status of species is essential for their preservation and management.

There are worldwide attempts to improve the genetic stock of the economically important common carp (*Cyprinus carpio* L.) in various hatcheries through introductions and crossings. However, despite this, the species faces several threats, such as a homogenized gene pool due to confinement when breeders use the same genetic resource. Artificial introductions and breeding activities can also cause problems even within strains. It is also necessary to emphasize the effects of genetic drift, the founder and/or bottleneck effects, which presumably has had an influence on the introduced domesticated common carp populations.

We formulated our objectives based on the problems described above, where we took into account that local populations of farmed common carp (within species) have developed in Hungary, the reasons for which are the different environmental conditions, the different farming activities of the different hatcheries, the small size of the breeding stocks and the strictly closed breeding were systems. Despite the fact that it is a very important species from a commercial point of view and with a huge market demand, their origin and relationship are not clear, and the genetic data of the herds is incomplete. Furthermore, it is also noteworthy that the Hungarian hatcheries consider their common carp stocks as a separate strains, in which case no significant phenotypic difference can be detected. In the country, only strains with breed recognition or registered for breed

recognition, or hybrids can be commercialized for further breeding, if they have breed recognition of their origin. It is worth noting that the performance test does not include genetic screening.

With the help of molecular markers, the relationships within and between populations can be revealed, the gene sets of given populations can be characterized, and they can provide useful information for the control of populations during monitoring. In addition to all this, they are also essential in terms of determining genetic differences, understanding population structure and distinguishing the suitability of different strains. In molecular genetic studies, the microsatellite marker is widely used in aquaculture research, where changes within and between populations can be small. Also, besides in addition to the microsatellite marker, the mitochondrial marker is often used in various researches, through which information on the genetic structure and origin of the common carp can be revealed.

Knowing all this, we used these two methods in my thesis during the molecular genetic examination. We believe that it is important to get to know the genetic structure of the Hungarian common carp strains as thoroughly as possible in order to get a more accurate picture of their origin and relationships, which is essential to fill gaps in their production properties, to improve the heterosis effect, and to prevent the deterioration of inbreeding.

**During our work, we had the following objectives:**

- Examination of the genetic diversity and population structure of Hungarian common carp strains based on microsatellite markers.
- Analysis of the genetic diversity of the Hungarian common carp strains and their phylogenetic characterization by a 687 bp segment of the mitochondrial DNA cytochrome *b* region.
- Detection of possible interbreeding of Hungarian common carp strains included in the study using methods based on biparental and maternal inheritance.
- Compensating for the lack of scientific knowledge, which helps the work of practical specialists.

## 2. MATERIALS AND METHODS

### Sample collection

In the spring and winter of 2017, we collected common carp individuals from twelve Hungarian common carp strains (Biharugra mirror and scaly, Hajdúszoboszló mirror and scaly, Szeged mirror and scaly, Hortobágy mirror, scaly and wild, Szarvas 15 mirror, Szarvas P3 scaly, Tata scaly), and in the spring of 2019 from Hajdúböszörmény mirror common carp individuals for our study. We collected additional individuals from the Amur scaly wild common carp, which were used as an external control during the statistical evaluations (**Fig. 1**).



**Figure 1:** Sample collection locations of the examined strains

*Notes: The different colors indicate the hatcheries where the sampling took place and the strains that were sampled. With yellow color: Hatchery of Biharugra Ltd.; with purple color: CLARIAS Agriculture, Producer and Trade Lp.; with green color: Hatchery of Hortobágy cPlc., with orange color: Bocskai Fishing Ltd.; with blue color: Fish Biology Laboratory, Faculty of Agricultural and Food Sciences and Environmental Management, University of Debrecen; with gray color: Hungarian University of Agriculture and Life Sciences, Institute of Aquaculture and Environmental Safety, Research Center of Fisheries and Aquaculture.*

At the time of sampling, the individuals were intoxicated with clove oil at a ratio of 1 drop of concentrated oil to 1 liter of water. Tissue samples were collected by cutting pieces of 0.5-3 cm each from the caudal fin of the individuals, which were stored in 96% ethanol at -20 °C until the genomic DNA was extracted.

For the mitochondrial DNA test, we used 10 individuals from each strain (n=140). In addition, we were able to use 114 reference sequences from the NCBI database.

For our study based on microsatellite markers, we sampled 45 individuals from each strain, a total of 630 individuals were used to answer our research objectives.

### **Isolation of genomic DNA**

Isolation of genomic DNA (gDNA) from tissue samples (caudal fin) of strains was carried out using E.Z.N.A. Tissue DNA Kit (Omega Bio-Tek, Norcross, GA, USA). We followed the manufacturer's instructions during the isolation. For both procedures, the isolated genomic DNAs were stored at -20 °C until further use.

### **A study based on microsatellite markers**

Based on literature data, twenty-two most commonly used microsatellite markers were selected for our planned study, of which twenty microsatellite markers (Cca24, Cca67 (YUE et al., 2004) and MFW1, MFW2, MFW3, MFW4, MFW6, MFW7, MFW9, MFW11, MFW12, MFW13, MFW15, MFW16, MFW17, MFW20, MFW26, MFW28, MFW29, MFW31 (CROOIJMANS et al., 1997)) were used for the PCR reaction. The annealing temperature of the primer pairs was determined using gradient PCR. Among the primer pairs, fluorescent labeling was used for the forward primer, which was necessary for multiplexing and reading the fragments (**Table 1**).

The fragment analysis was performed by BIOMI Ltd. (Gödöllő, Hungary). Alleles were read using the PeakScanner v.1.0 program (Applied Biosystem, Foster City, CA, USA). Three microsatellite markers (MFW9, MFW12, MFW28) provided no or incomplete results during the fragment analysis, so they were excluded from the statistical evaluations (MFW9, MFW12, MFW28). During the statistical evaluation of the data, MICRO-CHECKER, FreeNA, GENEPOP v.4.3., GenAlEx 6.41., FSTAT v.2.9.3.2., POPGENE 1.32., GENECLASS v.2.0., Arlequin 3.5. 2.2. and the CLUMPP v.1.1.2 programs helped us. It is important to note that based on the fragment analysis, seventeen microsatellite markers proved to be effective, which were the starting points of our study. Among these, however, microsatellite loci with a significantly high number of null alleles

(>0.2) and non-informative alleles were excluded from further analyzes (MFW1, MFW2, MFW16, MFW20, MFW29). Pairwise  $F_{st}$  values and genetic distance (D) between strains were calculated using the Wright fixation index and the Cavalli-Sforza and Edwards genetic distance. Our results are based on POPULATION v. 1.2.28., TreeView, STRUCTURE 2.3.4. and DISTRUCT v.1.1. visualized using programs.

**Table 1:** Characteristics of microsatellite primers

| Locus | Forward and reverse sequence (5'-3')              | Fluorescent dye | Annealing temperature (°C) | Fragment range (bp) | Multiplex for fragment analysis | Reference              |
|-------|---------------------------------------------------|-----------------|----------------------------|---------------------|---------------------------------|------------------------|
| Cca24 | AAATTTTCAAGACTGGGTGGTT<br>ACAGCAAGATGACAAAATGAGTG | ATTO565         | 60                         | 210-234             | 1.                              | YUE et al., 2004       |
| Cca67 | GTAGCCCCAAAAGATGTAGCA<br>TGGTCAAAGTTCAAGGCTGTAT   | FAM             | 60                         | 209-299             | 3.                              | YUE et al., 2004       |
| MFW1  | GTCCAGACTGTCATCAGGAG<br>GAGGTGTACACTGAGTCACGC     | FAM             | 60                         | 173-267             | 4.                              | CROOLMANS et al., 1997 |
| MFW2  | CACACCGGGCTACTGCAGAG<br>GTGCAGTGCAGGCAGTTTGC      | ATTO565         | 63                         | 144-220             | 4.                              | CROOLMANS et al., 1997 |
| MFW3  | GATCAGAAGGTACAGAGAAG<br>CCTTACAGAAAACCTGTTTGC     | ATTO565         | 58                         | 134-240             | 1.                              | CROOLMANS et al., 1997 |
| MFW4  | TCCAAGTCAGTTTAATCACCG<br>GGGAAGCGTTGACAACAAGC     | HEX             | 59                         | 138-253             | 1.                              | CROOLMANS et al., 1997 |
| MFW6  | ACCTGATCAATCCCTGGCTC<br>TTGGGACTTTTAAATCACGTTG    | FAM             | 60                         | 158-212             | 2.                              | CROOLMANS et al., 1997 |
| MFW7  | GATCTGCAAGCATATCTGTCTG<br>ATCTGAACCTGCAGCTCCTC    | ATTO550         | 59                         | 132-152             | 2.                              | CROOLMANS et al., 1997 |
| MFW9  | GATCTGCAAGCATATCTGTCTG<br>ATCTGAACCTGCAGCTCCTC    | HEX             | 59                         | no data             | 2.                              | CROOLMANS et al., 1997 |
| MFW11 | GCATTGTCCTTGATGGTTGTG<br>TCGTCTGGTTTAGAGTGCTGC    | ATTO565         | 60                         | 110-196             | 2.                              | CROOLMANS et al., 1997 |
| MFW12 | TTTATTAGAATAAATTAGCA<br>GATAGAAGTCGATGGAAAGTCC    | FAM             | 60                         | no data             | 3.                              | CROOLMANS et al., 1997 |
| MFW13 | ATGATGAGAACAATTGTTACAG<br>TGAGAGAACAATGTGGATGAC   | HEX             | 58                         | 192-270             | 2.                              | CROOLMANS et al., 1997 |
| MFW15 | CTCCTGTTTGTGTTTGTGAAA<br>GTTTACAAGGTCATTTCAGC     | ATTO550         | 59                         | 159-283             | 3.                              | CROOLMANS et al., 1997 |
| MFW16 | GTCCATTGTGTCAAGATAGAG<br>TCTTCATTTCAAGGCTGCAAG    | HEX             | 60                         | 116-211             | 3.                              | CROOLMANS et al., 1997 |
| MFW17 | CAGTGAGACGATTACCTTGG<br>GTGAGCAGCCACATTGAAC       | HEX             | 60                         | 254-312             | 1.                              | CROOLMANS et al., 1997 |
| MFW20 | CAGTGAGACGATTACCTTGG<br>GTGAGCAGCCACATTGAAC       | ATTO565         | 60                         | 125-255             | 3.                              | CROOLMANS et al., 1997 |
| MFW26 | CCCTGAGATAGAAACCACTG<br>CACCATGCTTGGATGCAAAAAG    | ATTO550         | 60                         | 151-221             | 4.                              | CROOLMANS et al., 1997 |
| MFW28 | GATCCCTTTTGAATTTTCTAG<br>ACAGTGAGGTCCAGAAGTCG     | FAM             | 60                         | no data             | 1.                              | CROOLMANS et al., 1997 |
| MFW29 | GTTGACCAAGAAACCAACATGC<br>GAAGCTTTGCTCTAATCCACG   | HEX             | 60                         | 126-208             | 4.                              | CROOLMANS et al., 1997 |
| MFW31 | CCTTCCTCTGGCCATTCTCAC<br>TACATCGCAGAGAATTCGTAAG   | ATTO550         | 60                         | 283-305             | 1.                              | CROOLMANS et al., 1997 |

## Mitochondrial DNA analysis

A section of the mitochondrial DNA cytochrome *b* region was amplified by PCR according to MABUCHI et al. (2005) with a pair of primers covering a total length of 742 bp (forward primer: 5' TGAGGACAAATATCCTTTTGAGG 3' (L15172-Cytb) and reverse primer: 5' CCGATCTTCGGATTACAAGACCG 3' (H15913-Thr)).

Sequencing of the samples was performed by Macrogen Europe (Amsterdam, The Netherlands) using the forward primer used for PCR amplification as a sequencing primer.

The correctness of the read nucleotides was checked with the MEGA6 program and any errors that occurred were corrected manually. The obtained sequences and the



114 sequences available in the NCBI database were aligned and compared with the ClustalW program. We also cut the sequences to equal length (687 bp) using the MEGA6 program.

During the statistical evaluation of the data, DnaSP 5.10, PartitionFinder 2.1.1., BEAST v.2.3, Network 10.2., Arlequin 3.5.2.2., STRUCTURE 2.3.4., CLUMPP v.1.1.2. and DISTRUCT v.1.1. programs were used.

### 3. RESULTS

#### 3.1. Results of a study based on a microsatellite marker

In order to analyze genetic diversity and genetic distances between populations, we examined a total of 630 individuals within the fourteen strains of Hungarian common carp using twelve microsatellite markers.

The analysis with the MICRO-CHECKER program did not show allelic deletions or additional errors. The frequency of null alleles was generally low, varying between 0.000 and 0.317. Regarding the analysis of the null alleles, within the twelve microsatellite markers, a potentially debatable threshold value ( $r > 0.2$ ) was detected for the markers MFW6, MFW11, MFW13, and MFW26 in some strains. However, considering the low frequency of null alleles in all strains and the non-significant results of the program, we did not omit any locus during the further analyses.

#### Genetic diversity parameters

Data on the parameters of the genetic diversity of the examined Hungarian common carp strains are presented in **Table 2**.

**Table 2.:** Data concerning the parameters of the genetic diversity of the examined strains

| Strain                      | MNA    | Apr | Ar    | N <sub>e</sub> | dHW |
|-----------------------------|--------|-----|-------|----------------|-----|
| Hajdúszoboszló scaly        | 6.500  | 9   | 1.670 | 5.290          | 1   |
| Hajdúszoboszló mirror       | 8.450  | 2   | 1.820 | 5.670          | 2   |
| Szeged scaly                | 8.180  | 4   | 1.680 | 4.270          | 3   |
| Szeged mirror               | 9.630  | 0   | 1.770 | 4.210          | 1   |
| Hortobágy scaly             | 11.080 | 11  | 1.860 | 7.810          | 1   |
| Hortobágy mirror            | 14.000 | 4   | 1.830 | 6.470          | 2   |
| Hortobágy wild              | 12.250 | 24  | 1.890 | 9.710          | 1   |
| Biharugra scaly             | 11.500 | 8   | 1.830 | 7.090          | 3   |
| Biharugra mirror            | 17.580 | 1   | 1.800 | 5.240          | 2   |
| Szarvas P3 scaly            | 11.580 | 3   | 1.790 | 4.960          | 4   |
| Szarvas 15 mirror           | 13.000 | 1   | 1.740 | 4.640          | 3   |
| Tata scaly                  | 7.900  | 11  | 1.820 | 5.910          | 3   |
| Hajdúböszörmény mirror      | 13.080 | 22  | 1.800 | 5.360          | 5   |
| Amur scaly wild common carp | 8.500  | 17  | 1.800 | 5.870          | 1   |

**MNA:** mean number of alleles per strain; **Apr:** number of private alleles; **Ar:** mean values of allelic richness; **N<sub>e</sub>:** mean number of effective alleles; **dHW:** number of loci deviating from HWE

Based on our results, all strains showed a deviation from Hardy-Weinberg equilibrium (HWE) at at least one locus ( $p < 0.01$ ). The average number of microsatellite alleles per strains was 11. The lowest and highest average allele numbers were observed in the Hajdúszoboszló scaly (6.500) and the Biharugra mirror (17.580). A total of 117 unique alleles were detected on the twelve polymorphic markers in the 630 individuals. The smallest and largest numbers of unique alleles were observed in the Szeged mirror ( $A_{pr}=0$ ) and Hortobágy wild ( $A_{pr}=24$ ) strains. Of all the strains, the Hortobágy wild strain stands out, in which case we observed the highest number of unique alleles and the highest average allelic richness ( $A_r=1.890$ ).

The average value of the expected heterozygosity for the fourteen strains was 0.800, which value varied within the range of 0.710 (Szarvas 15 mirror) and 0.890 (Hortobágy wild) (**Table 3**).

**Table 3:** Data on the heterozygosity, inbreeding and population assignment of the examined strains

| Strain                      | H <sub>o</sub> | H <sub>e</sub> | F <sub>is</sub> | Assignment test (%) |
|-----------------------------|----------------|----------------|-----------------|---------------------|
| Hajdúszoboszló scaly        | 0.790          | 0.730          | -0.080          | 100                 |
| Hajdúszoboszló mirror       | 0.920          | 0.820          | -0.118          | 97                  |
| Szeged scaly                | 0.770          | 0.750          | -0.027          | 88                  |
| Szeged mirror               | 0.730          | 0.750          | 0.034           | 97                  |
| Hortobágy scaly             | 0.860          | 0.860          | 0.002           | 89                  |
| Hortobágy mirror            | 0.900          | 0.830          | -0.083          | 93                  |
| Hortobágy wild              | 0.900          | 0.890          | -0.007          | 83                  |
| Biharugra scaly             | 0.810          | 0.840          | 0.026           | 91                  |
| Biharugra mirror            | 0.840          | 0.800          | -0.051          | 97                  |
| Szarvas P3 scaly            | 0.900          | 0.790          | -0.140          | 88                  |
| Szarvas 15 mirror           | 0.720          | 0.710          | -0.004          | 95                  |
| Tata scaly                  | 0.930          | 0.820          | -0.134          | 93                  |
| Hajdúböszörmény mirror      | 0.990          | 0.800          | -0.250          | 100                 |
| Amur scaly wild common carp | 0.740          | 0.810          | 0.083           | 100                 |

H<sub>o</sub>: observed heterozygosity; H<sub>e</sub>: expected heterozygosity; F<sub>is</sub>: inbreeding coefficient; Assignment test: percent of individuals correctly assigned to their strain of origin (%)

Based on our results, the value of the inbreeding coefficient varied between -0.250 (Hajdúböszörmény mirror) and 0.083 (Amur scaly wild common carp).

The results of the population assignment test showed that 93.64% of the individuals were assigned to the strain corresponding to their origin.

The degree of genetic differentiation ( $F_{st}$ ) varied within the range of 0.028 (between Biharugra mirror and Hortobágy mirror) to 0.231 (between Szarvas 15 mirror and Hajdúszoboszló scaly) (**Table 4**).

**Table 4:** Pairwise  $F_{st}$  values (above the diagonal) and Dc distance (below the diagonal) between the 13 Hungarian common carp strains and the Amur scaly wild common carp based on the twelve microsatellite loci

| Strain | HaS          | SzS          | HaM          | HoS          | HoM          | HoW          | BiM          | BiS          | SZ1          | SzM          | TaS          | SzP          | AmW          | BoM          |
|--------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|
| HaS    | <b>0,000</b> | 0,164        | 0,173        | 0,158        | 0,134        | 0,131        | 0,155        | 0,152        | 0,231        | 0,188        | 0,176        | 0,181        | 0,147        | 0,174        |
| SzS    | 0,565        | <b>0,000</b> | 0,146        | 0,137        | 0,122        | 0,116        | 0,135        | 0,116        | 0,204        | 0,114        | 0,146        | 0,149        | 0,131        | 0,140        |
| HaM    | 0,702        | 0,647        | <b>0,000</b> | 0,041        | 0,056        | 0,036        | 0,066        | 0,077        | 0,176        | 0,096        | 0,080        | 0,074        | 0,112        | 0,066        |
| HoS    | 0,702        | 0,649        | 0,454        | <b>0,000</b> | 0,051        | 0,035        | 0,071        | 0,076        | 0,155        | 0,106        | 0,071        | 0,072        | 0,102        | 0,090        |
| HoM    | 0,601        | 0,570        | 0,497        | 0,479        | <b>0,000</b> | 0,043        | 0,028        | 0,040        | 0,136        | 0,067        | 0,079        | 0,074        | 0,089        | 0,111        |
| HoW    | 0,652        | 0,624        | 0,491        | 0,476        | 0,446        | <b>0,000</b> | 0,053        | 0,054        | 0,127        | 0,085        | 0,054        | 0,057        | 0,078        | 0,063        |
| BiM    | 0,605        | 0,561        | 0,476        | 0,518        | 0,347        | 0,479        | <b>0,000</b> | 0,040        | 0,131        | 0,047        | 0,101        | 0,098        | 0,084        | 0,121        |
| BiS    | 0,651        | 0,559        | 0,555        | 0,548        | 0,405        | 0,490        | 0,400        | <b>0,000</b> | 0,110        | 0,067        | 0,103        | 0,105        | 0,077        | 0,113        |
| SZ1    | 0,683        | 0,605        | 0,652        | 0,615        | 0,555        | 0,595        | 0,530        | 0,523        | <b>0,000</b> | 0,099        | 0,181        | 0,196        | 0,133        | 0,194        |
| SzM    | 0,630        | 0,465        | 0,547        | 0,615        | 0,498        | 0,585        | 0,429        | 0,493        | 0,437        | <b>0,000</b> | 0,113        | 0,131        | 0,112        | 0,139        |
| TaS    | 0,723        | 0,660        | 0,513        | 0,519        | 0,559        | 0,527        | 0,585        | 0,607        | 0,666        | 0,606        | <b>0,000</b> | 0,039        | 0,120        | 0,106        |
| SzP    | 0,714        | 0,652        | 0,496        | 0,532        | 0,521        | 0,539        | 0,559        | 0,580        | 0,683        | 0,592        | 0,389        | <b>0,000</b> | 0,126        | 0,124        |
| AmW    | 0,618        | 0,581        | 0,622        | 0,615        | 0,536        | 0,564        | 0,500        | 0,512        | 0,563        | 0,584        | 0,625        | 0,612        | <b>0,000</b> | 0,149        |
| BoM    | 0,687        | 0,632        | 0,498        | 0,561        | 0,633        | 0,538        | 0,632        | 0,660        | 0,700        | 0,665        | 0,560        | 0,600        | 0,684        | <b>0,000</b> |

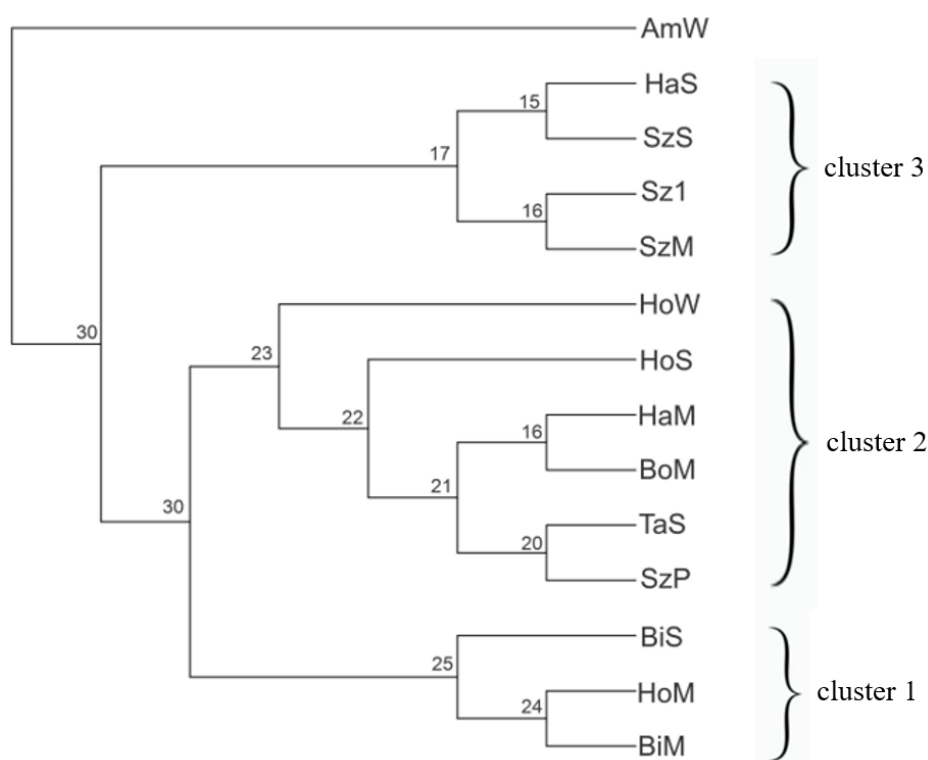
Notes: **HaS:** Hajdúszoboszló scaly, **SzS:** Szeged scaly, **HaM:** Hajdúszoboszló mirror, **HoS:** Hortobágy scaly, **HoM:** Hortobágy mirror, **HoW:** Hortobágy wild, **BiM:** Biharugra mirror, **BiS:** Biharugra scaly, **SZ1:** Szarvas 15 mirror, **SzM:** Szeged mirror, **TaS:** Tata scaly, **SzP:** Szarvas P3 scaly, **AmW:** Amur scaly wild common carp, **BoM:** Hajdúböszörmény mirror

Based on our results, the genetic distance (Dc) varied between 0.347 and 0.723 (**Table 4**). The lowest genetic distance was found between the Biharugra mirror (BiM) and Hortobágy mirror (HoM) strains, while the highest genetic difference was found between the Hajdúszoboszló scaly (HaS) and Tata scaly (TaS) strains. This difference can be explained by the geographical distance between the strains (BiM-HoM: geographical distance ~110 km; HaS-TaS: geographical distance: ~300 km).

Based on the genetic distances (Dc), we prepared a phylogenetic tree (**Fig. 2**), which shows that the populations of the examined strains formed three clusters. The Biharugra mirror, the Hortobágy mirror, and the Biharugra scaly were grouped into one

cluster (cluster 1) with the Szarvas P3 scaly, the Tata scaly, the Hajdúböszörmény mirror, the Hajdúszoboszló mirror, the Hortobágy scaly and the Hortobágy scaly strains (cluster 2). These two clusters are connected to cluster 3 (Hajdúszoboszló scaly, Szeged scaly, Szarvas 15 mirror, Szeged mirror). The Amur scaly wild common carp strain formed a separate group, which is connected to the three clusters mentioned above.

**Figure 2:** Neighbor-joining phylogenetic tree, which shows the relationship of the fourteen investigated Hungarian common carp strains based on twelve microsatellite markers. Bootstrap value: 1000



Notes: **AmW**: Amur scaly wild common carp, **HaS**: Hajdúszoboszló scaly, **SzS**: Szeged scaly, **SZ1**: Szarvas 15 mirror, **SzM**: Szeged mirror, **HoW**: Hortobágy wild, **HoS**: Hortobágy scaly, **HaM**: Hajdúszoboszló mirror, **BoM**: Hajdúböszörmény mirror, **TaS**: Tata scaly, **SzP**: Szarvas P3 scaly, **BiS**: Biharugra scaly, **HoM**: Hortobágy mirror, **BiM**: Biharugra mirror

Based on all of this, it can be concluded that the observed clustering pattern was not consistent with the geographical origin and that the examined strains also showed a mixture in terms of their phenotypic appearance (scaly, mirror, wild).

### Genetic structure data

Molecular variance analysis (AMOVA) results showed that the observed heterozygous value was 3.79% between strains and 96.03% within strains (**Table 5**). The

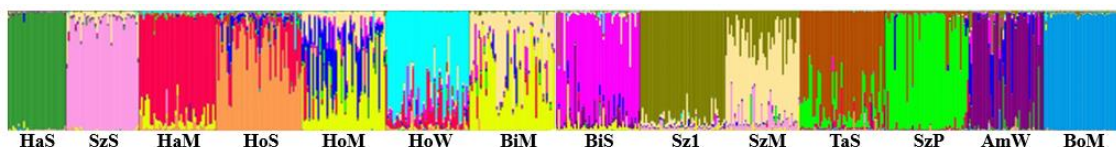
results after grouping according to strains arranged into six groups based on their origin showed that the percentage of deviation is low and not significant (0.42%,  $p=0.270$ ) between and within groups. The result showed a higher and significant value within the strains (3.62%,  $p<0.001$ ). The results show a high level of variance within the strains, which indicates high genetic diversity at the level of individuals, but does not support the traditional distinction of strains.

**Table 5:** Molecular variance analysis (AMOVA) within the studied thirteen Hungarian common carp and Amur scaly wild common carp strains

| Number of groups              | Source of variation           | d.f  | Sum of squares | Variance components | Variance (%) | p     |
|-------------------------------|-------------------------------|------|----------------|---------------------|--------------|-------|
| <b>One group</b>              | Among strains                 | 13   | 25.270         | 0.017               | 3.790        | 0.000 |
|                               | Within strains                | 1264 | 513.670        | 0.412               | 96.030       |       |
|                               | Total                         | 1259 | 538.940        | 0.429               |              |       |
| <b>Six (by origin) groups</b> | Among strains                 | 5    | 10.590         | 0.001               | 0.420        | 0.270 |
|                               | Between groups within strains | 8    | 14.680         | 0.015               | 3.620        | 0.000 |
|                               | Within strains                | 1246 | 513.67         | 0.412               | 95.960       | 0.000 |
|                               | Total                         | 1259 | 538.94         | 0.429               |              |       |

d.f.: degrees of freedom;  $p<0.001$

The cluster analysis of the studied Hungarian common carp strains was carried out using the STRUCTURE program for 630 individuals, where the highest value was obtained at  $K=14$ , followed by  $K=2$  (**Fig. 3**).



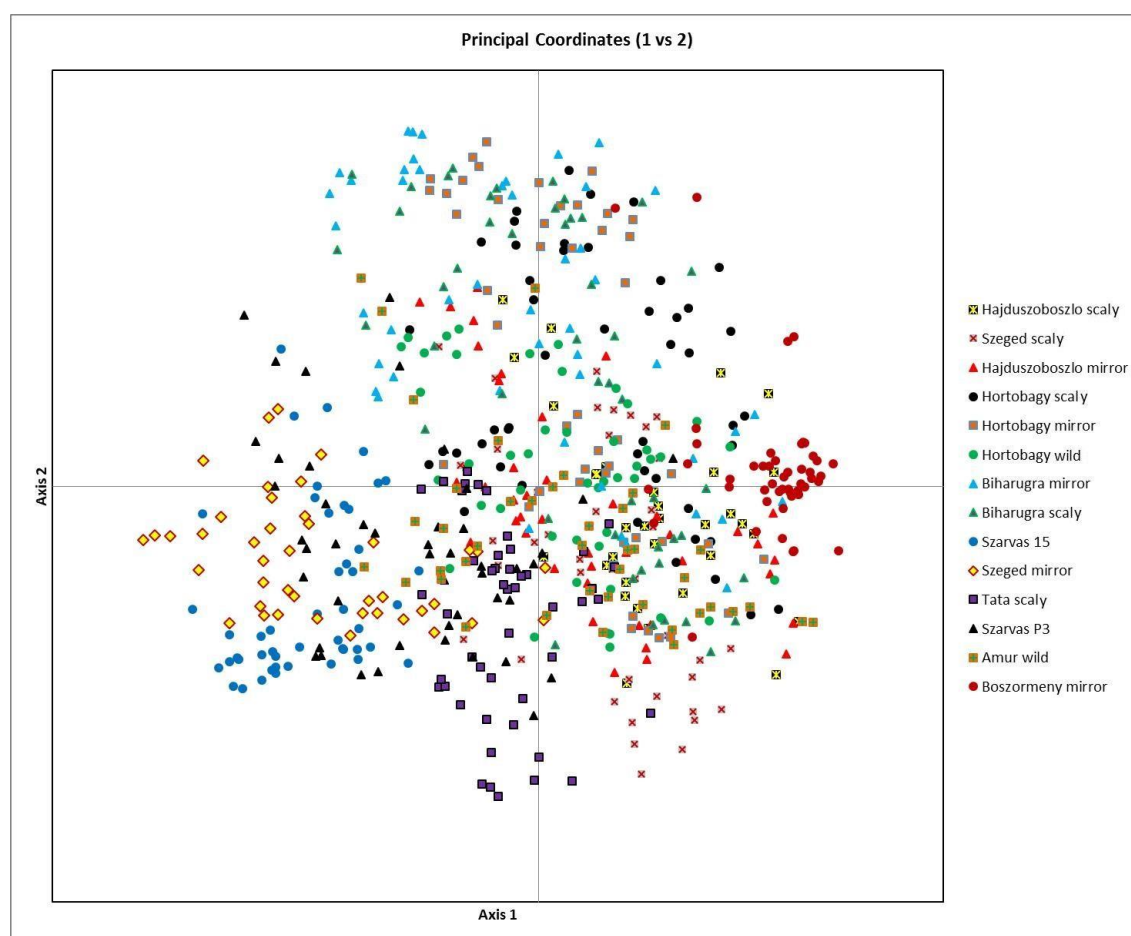
**Figure 3:** Cluster analysis of individuals analyzed with the Bayesian algorithm and 12 microsatellite markers for  $K=14$  (each cluster is marked with a unique color). Each vertical column represents an individual, and dividing the column into 14 colors represents the estimated membership coefficient of each strain.

Individuals from different hatcheries differed significantly from each other at  $K=14$ . This result can serve as evidence of the relatively high genetic diversity of the Hungarian common carp strains. Eight analyzed strains (Amur scaly wild common carp, Biharugra scaly, Hajdúböszörmény mirror, Hajdúszoboszló scaly, Hajdúszoboszló mirror, Szeged scaly, Szarvas 15 mirror, Szarvas P3 scaly) are characterized by a very high relationship coefficient, and they all seem to have different sets of genes. In the case

of the other six strains (Biharugra mirror, Hortobágy wild, Hortobágy scaly, Hortobágy mirror, Szeged mirror, Tata scaly) we can already observe genetic evidence of mixing.

Our previously presented results were also illustrated with principal component analysis, which provides information on the separation of individuals of the investigated Hungarian common carp strains (**Fig. 4**).

**Figure 4:** Principal component analysis (PcoA) carried out at the individual level based on the twelve microsatellite markers



The analysis carried out at the individual level also supports our result, namely, that the Hungarian common carp strains we examined are mixed with each other, almost melting into each other, also in **Figure 4**. It can be seen that the examined individuals are not clearly separated according to their genetic or geographical distances. In accordance with our previous results, the results of the principal component analysis also shows a close relationship between the examined Hungarian common carp strains.

### 3.2. Results of the study based on the mitochondrial cytochrome *b* marker

#### Genetic diversity parameters

For our study based on the mitochondrial DNA cytochrome *b* marker, we included a total of 138 individuals from Hungarian common carp strains and another 112 sequences (belonging to common carp lines from the United States, Greece, Japan, China, Germany and Russia), which were downloaded from the NCBI gene bank. We identified 83 haplotypes in a total of 250 sequences on the 687 bp section of cytochrome *b*. We detected 43 haplotypes within the 138 sequences from the Hungarian common carp strains, of which 40 were new haplotypes not yet reported (**Table 6**).

**Table 6:** Evolution of the haplotypes detected based on the sequences of the investigated common carp strains

| Strains  | AmW | BiS | BiM | BoM | HoW | HoS | HoM | Sz1 | SzP | SzS | SzM | HoS | HoM | TaS | Total     |
|----------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----------|
| <i>h</i> | 10  | 2   | 3   | 4   | 8   | 1   | 2   | 2   | 4   | 3   | 3   | 2   | 10  | 5   | <b>43</b> |

Notes: HaS: *Hajdúszoboszló scaly*, SzS: *Szeged scaly*, HaM: *Hajdúszoboszló mirror*, HoS: *Hortobágy scaly*, HoM: *Hortobágy mirror*, HoW: *Hortobágy wild*, BiM: *Biharugra mirror*, BiS: *Biharugra scaly*, Sz1: *Szarvas 15 mirror*, SzM: *Szeged mirror*, TaS: *Tata scaly*, SzP: *Szarvas P3 scaly*, AmW: *Amur scaly wild common carp*, BoM: *Hajdúböszörmény mirror*

The average haplotype diversity value of the Hungarian common carp strains sequences was  $0.566 \pm 0.052$ , and the nucleotide diversity value was  $0.00474 \pm 0.00083$ . The highest haplotype diversity value ( $H_d$ ) was found in the Amur scaly wild common carp ( $H_d = 1.000 \pm 0.045$ ) and the Hajdúszoboszló mirror ( $1.000 \pm 0.045$ ), and the highest nucleotide diversity value ( $\pi = 0.02054 \pm 0.00442$ ) was also found in the Amur scaly wild common carp. The lowest  $H_d$  and  $\pi$  values were found in the Hortobágy scaly strain ( $H_d = 0.000 \pm 0.000$  and  $\pi = 0.00000 \pm 0.00000$ ). The haplotype and nucleotide diversity values were high (**Table 7**).



**Table 7:** Genetic parameters of the thirteen Hungarian common carp strains and the Amur scaly wild common carp based on the 687 bp cyt *b* sequences

| Strains                     | <i>Hd</i> ± <i>SD</i> | $\pi$ ± <i>SD</i>      | <i>P</i>  | <i>k</i>     |
|-----------------------------|-----------------------|------------------------|-----------|--------------|
| Biharugra scaly             | 0.433±0.180           | 0.00088±0.00035        | 3         | 0.600        |
| Biharugra mirror            | 0.511±0.113           | 0.00269±0.00153        | 10        | 2.017        |
| Hajdúböszörmény mirror      | 0.607±0.163           | 0.00313±0.00146        | 10        | 2.322        |
| Hajdúszoboszló scaly        | 0.222±0.166           | 0.00032±0.00024        | 1         | 0.222        |
| Hajdúszoboszló mirror       | 1.000±0.045           | 0.01513±0.00288        | 37        | 10.378       |
| Hortobágy scaly             | 0.000±0.000           | 0.00000±0.00000        | 0         | 0.000        |
| Hortobágy mirror            | 0.278±0.162           | 0.00061±0.00041        | 2         | 0.516        |
| Hortobágy wild              | 0.972±0.064           | 0.00515±0.00124        | 11        | 3.528        |
| Szarvas 15 mirror           | 0.200±0.154           | 0.00175±0.00135        | 6         | 1.200        |
| Szarvas P3 scaly            | 0.533±0.180           | 0.00227±0.00128        | 7         | 1.556        |
| Szeged scaly                | 0.511±0.164           | 0.00081±0.00030        | 2         | 0.556        |
| Szeged mirror               | 0.378±0.181           | 0.00117±0.00060        | 4         | 0.800        |
| Tata scaly                  | 0.648±0.125           | 0.00559±0.00190        | 17        | 3.756        |
| Amur scaly wild common carp | 1.000±0.045           | 0.02054±0.00442        | 51        | 14.067       |
| <b>TOTAL</b>                | <b>0.566±0.052</b>    | <b>0.00474±0.00083</b> | <b>85</b> | <b>3.226</b> |

***Hd***: haplotype diversity;  **$\pi$** : nucleotide diversity; ***P***: polymorphic sites, ***k***: average number of nucleotide differences; ***SD***: standard deviation.  $p < 0.05$  significant

Our results showed that the number of polymorphism sites was low in the Biharugra scaly, Hajdúszoboszló scaly, Hortobágy scaly, Hortobágy wild, Szarvas 15 mirror, Szarvas P3 scaly, and Tata scaly strains.

The Tajima *D* value of the fourteen strains (**Table 8**), with the exception of Hortobágy scaly strain (0.0000), was negative. However, it is important to note that the value of only five strains (Hortobágy mirror, Szarvas 15 mirror, Szarvas P3 scaly, Szeged mirror, Tata scaly) was significant ( $p < 0.05$ ).

The Fu *FS* values of five populations (**Table 8**) were also negative, however, only two of these values (Hajdúszoboszló mirror and Hortobágy wild) showed significant values ( $p < 0.05$ ).

**Table 8:** Genetic diversity parameters of Tajima *D* and Fu *FS* based on the 687 bp cyt *b* sequences of the thirteen Hungarian common carp strains and the Amur scaly wild common carp

| Strains                     | Tajima <i>D</i> | Fu <i>FS</i> |
|-----------------------------|-----------------|--------------|
| Biharugra scaly             | -1.1117         | -0.3393      |
| Biharugra mirror            | -1.4731         | 2.3554       |
| Hajdúböszörmény mirror      | -1.5345         | 0.9197       |
| Hajdúszoboszló scaly        | -1.0882         | -0.2635      |
| Hajdúszoboszló mirror       | -1.0082         | -3.3275*     |
| Hortobágy scaly             | 0.0000          | 0.0000       |
| Hortobágy mirror            | -1.4008*        | 0.5862       |
| Hortobágy wild              | -0.6355         | -3.4267*     |
| Szarvas P3 scaly            | -1.5728*        | 0.0477       |
| Szarvas 15 mirror           | -1.7963*        | 2.6067       |
| Szeged scaly                | -0.1297         | 0.5197       |
| Szeged mirror               | -1.6671*        | 0.4773       |
| Tata scaly                  | -1.7439*        | 0.9773       |
| Amur scaly wild common carp | -1.0597         | -2.4354      |

\*p<0.05

### Genetic structure data

AMOVA results showed that the genetic variance within strains (86.22%) was higher than the variance between strains (13.78%) (**Table 9**).

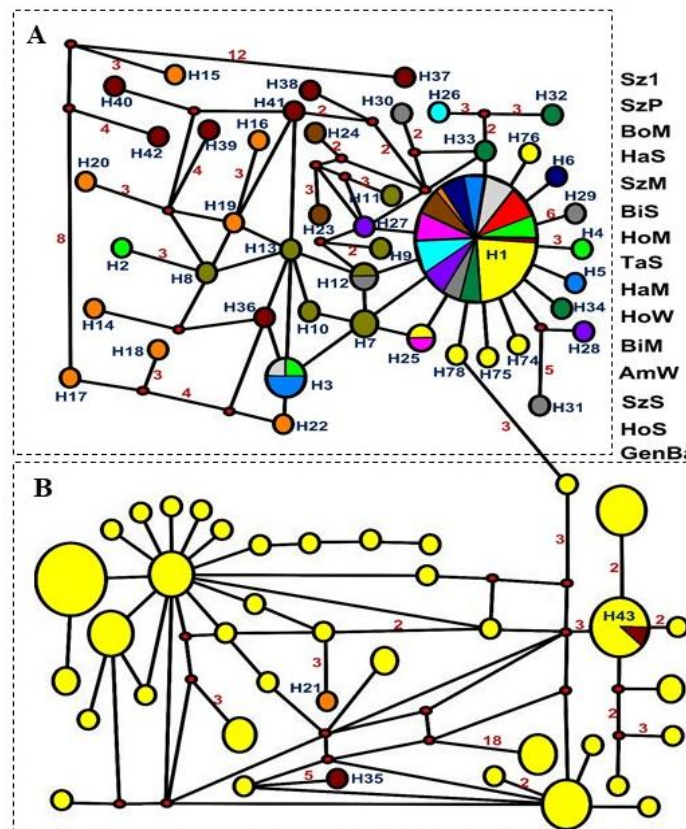
**Table 9:** AMOVA results of the thirteen Hungarian common carp strains and the Amur scaly wild common carp based on the 687 bp cyt *b* sequences

| Source of variance | <i>d.f.</i> | Sum of squares | Variance components | Variance (%) |
|--------------------|-------------|----------------|---------------------|--------------|
| Among strains      | 13          | 52.443         | 0.250               | 13.78***     |
| Within strains     | 124         | 194.267        | 1.566               | 86.22***     |
| Total              | 137         | 246.710        | 1.817               |              |

*d.f.*: degree of freedom; \*\*\*p<0.001

The relationships between haplotypes were visualized in the Median-Joining Network (MJ) figure (**Fig. 5**). The MJ network produced two major haplogroups in all haplotypes identified in our study. The sequences of the Hungarian common carp strains fell into the same two haplogroups, where haplogroup „A” was the dominant one. Only three individuals (Hajdúszoboszló mirror 8.: H21, Amur scaly wild common carp 1.: H35 and Amur scaly wild common carp 10.: H43) appeared in haplogroup „B” from the sequences from Hungary that we sampled. With the exception of H1, H3, H12, H25 and

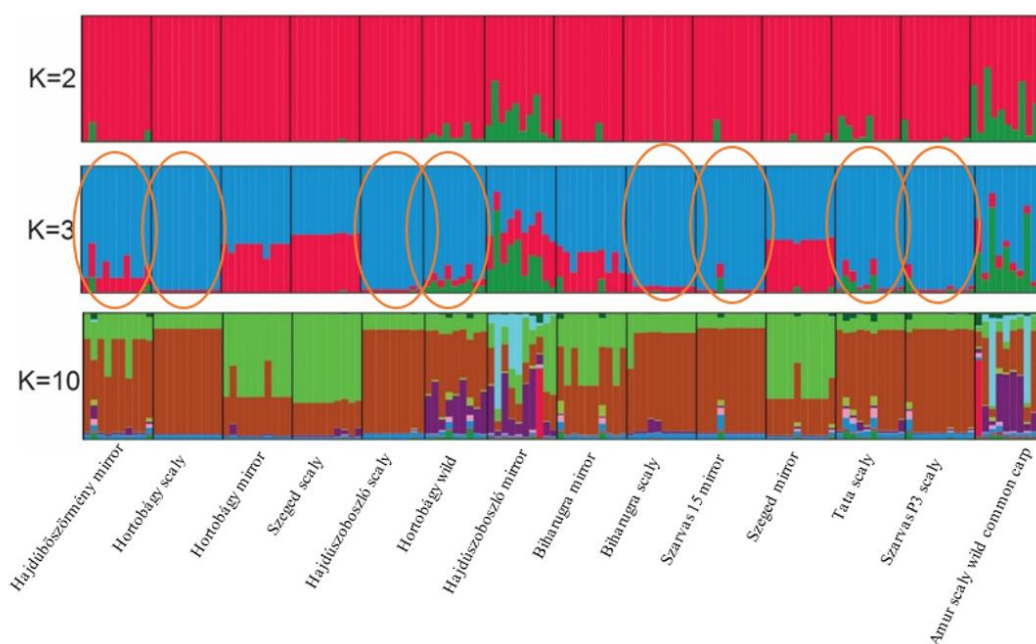
H43, 38 haplotypes were found in a single population of Hungarian common carp. Of the fourteen Hungarian common carp populations and the common carp populations available in the NCBI gene bank, the most common haplotype H1 was grouped. In addition to the Hungarian common carp populations we investigated, Hungarian common carp (KJ511883) from the NCBI gene bank, German mirror carp (KP993139: *C. c. carpio*), American Lake Erie common carp (MG570427 and MG570435), wild common carp from the Volga River (AY347295: *C. c. carpio*), with Greek wild common carp (EU689059-EU689072 and DQ868871-DQ868875: *C. c. carpio*) and Oregon common carp (EU676848) formed a common haplotype (H1). Another common haplotype (H43) was detected, which included nine individuals, including one individual of the Hungarian Amur scaly wild common carp (AmW10), the Oujiang colored common carp (JX188253 and NC\_018366: *C. c. color*), the Japanese koi carp (KJ511882 and AB158806: *C. c. koi*), Zujiang wild common carp (KP993137), KP013086, KU159761 and KY949559.



**Figure 5:** The relationship between the haplotypes of the thirteen Hungarian common carp strains and the Amur scaly wild common carp and other common carp lines based on the sequences of the 687 bp sections of the cytochrome *b* region

It should be highlighted in **Figure 5** that the Hungarian common carp populations have a common haplotype with lines from Germany, the United States, Russia and Greece, and a Hungarian common carp population from the gene bank also appeared in the most common haplotype.

In the cluster analysis (STRUCTURE), the logarithmic probability of the data (LnPD) showed the highest value for K=3 and then for K=10 (**Fig. 6**). Based on the K=2 value, all but two individuals (Hajdúszoboszló mirror and Amur scaly wild common carp) were grouped into the same cluster. Therefore, there appeared to be no evidence for a K=2 partitioning of the populations. Based on the K=3 grouping, eight of the studied strains (Biharugra scaly, Hajdúböszörmény mirror, Hajdúszoboszló scaly, Hortobágy wild, Hortobágy scaly, Szarvasi 15 mirror, Szarvas P3 scaly, Tata scaly) were grouped into one cluster with very high membership coefficients. The other strains were grouped into the three inferred clusters and showed a certain level of mixing ratio. Taking the K=10 value into account, the results of the mentioned strains (with the exception of Hortobágy wild) were the same as the K=3 values.



**Figure 6:** Bayesian cluster analysis in STRUCTURE for K=2, 3 and 10. Each vertical bar represents an individual, and the separation of columns into different colors represents individual membership to each cluster. Individuals grouped in the same cluster are marked in orange.

Based on the results of the cluster analysis (STRUCTURE) (**Fig. 6**) with very high membership coefficients at  $K=3$ , the eight studied strains (Biharugra scaly, Hajdúböszörmény scaly, Hajdúszoboszló scaly, Hortobágy wild, Hortobágy scaly, Szarvas 15 mirror, Szarvas P3 scaly, Tata scaly) were grouped into the same cluster with very high membership coefficients from the fourteen strains, which proves the great genetic diversity of common carp strains in Hungary.

#### **4. NEW SCIENTIFIC RESULTS OF THE DISSERTATION**

*New scientific results based on microsatellite markers:*

1. Using twelve polymorphic microsatellite markers, I proved that 93.64% of the individuals of the thirteen Hungarian common carp strains and the Amur scaly wild common carp that I examined belong to the strains corresponding to their origin.
2. I found that there is a lot of heterozygosity within the Hungarian common carp strain I examined, which indicates that we do not have to fear inbreeding deterioration in our country at the moment.
3. I showed that the Hungarian common carp strains I examined, with a few exceptions, are different from common carp populations from other countries.

*New scientific results based on mitochondrial DNA markers:*

1. Based on the sequences of the 687 bp long section of the mitochondrial region of cytochrome *b*, I identified 43 haplotypes in the Hungarian common carp strains I examined, of which 40 appeared as new haplotypes. I proved that the Hungarian common carp strains I examined are grouped into a common haplotype, the Hortobágy wild common carp strain was an exception.

*Together, the new scientific results based on the two markers:*

1. With the help of the twelve polymorphic microsatellite markers and the cytochrome *b* mitochondrial marker, I proved that the Hungarian common carp strains mix with each other, and their genetic variance between individuals is significant.
2. Based on the results of the cluster analysis, individuals of the same five strains (Biharugra scaly, Hajdúböszörmény mirror, Hajdúszoboszló scaly, Szarvas 15 mirror, Szarvas P3 scaly) were similarly grouped in the same cluster with very high membership coefficients, which proves the real existence of these strains.
3. The Median-Joining Network analysis based on the microsatellite method and the data on the genetic diversity parameters (number of unique alleles and allele richness), as well as the cluster analysis based on the mitochondrial DNA marker, proved that the Hortobágy wild common carp strain can be considered the most genetically distinct strain.

## **5. PRACTICAL USEFULNESS OF THE RESULTS**

1. Hatcheries around the world are trying to improve their common carp stock through introductions and crossings. The valuable genetic stock of strains with separate gene sets can be endangered by crossings with strains with different gene sets and different phenotypic appearance. Therefore, we believe that in order to preserve Hungarian common carp strains, it is essential to know the genetic diversity and structure of strains, as well as to identify and characterize the genetically separate strains of hatcheries.

2. The genetic background of the common carp species is threatened by the homogenized gene pool. Detention can result in the development of a homogenized gene pool and the fact that breeders use the same genetic resource during breeding. The discovery of the gene set is important in order to improve the production properties, the heterosis effect and to prevent the deterioration of inbreeding. Based on these, we believe that our results can be used to improve the stocks of the hatcheries we examined.

3. Increasingly intensive fish farming, selective breeding programs and reintroductions can lead to a significant degradation of the genetic base of the given strains, to the disappearance of genetically distinct strains, and to the dilution and standardization of the genetic background characteristic of each strains. Based on all of this, our results can be used to review and possibly improve traditional breeding practices.

4. We explored the relationships within and between the strains we examined and characterized their gene pool using several approaches. Our results can provide useful information in the breeding of strains and during their continuous monitoring.

5. We believe that the results of our molecular genetic examination fill in gaps and can form the basis of further investigations. Furthermore, they can help fill the gap in scientific knowledge about the genetic diversity and population structure of common carp.

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## 7. LIST OF PUBLICATIONS



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Doctoral School: Doctoral School of Animal Husbandry  
MTMT ID: 10074985

### List of publications related to the dissertation

#### Hungarian book chapters (1)

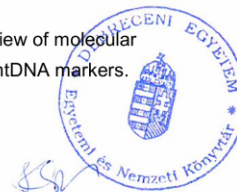
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In: Multidisciplinary Conference on Sustainable Development Section: Animal Resources Bioengineering, Banat University of Agricultural Sciences and Veterinary Medicine, Temesvár, 20, 2021.

**Total IF of journals (all publications): 36,608**

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The Candidate's publication data submitted to the iDEa Tudóstér have been validated by DEENK on the basis of the Journal Citation Report (Impact Factor) database.

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