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Research Article

Genetic diversity among populations of the endangered European weatherfish *Misgurnus fossilis* in the Czech Republic, Austria and adjacent areas

Lukáš Choleva[1,2], Jörg Bohlen[1], Tomáš Dvořák[1], Anja Palandačić[3,4], Michael Jung[5], Min J. Chai[3], Veronika Labajová[1,2], Kateřina Bezányiová[1,6], Tomáš Pavlica[1,6], Alexandr Sember[1], Milan Muška[7,8], Marek Šmejkal[7,9], Vendula Šlechtová[1]

1 *Laboratory of Fish Genetics, Institute of Animal Physiology and Genetics, Czech Academy of Sciences, Liběchov, Czech Republic*
2 *Department of Biology and Ecology, Faculty of Science, University of Ostrava, Ostrava, Czech Republic*
3 *First Zoological Department, Vienna Museum of Natural History, Vienna, Austria*
4 *Department of Biology, Biotechnical Faculty, University of Ljubljana, Ljubljana, Slovenia*
5 *ezb – TB Zauner GmbH, Consulting Office for Applied Hydrobiology, Fisheries and Hydro-Engineering, Engelhartszell, Austria*
6 *Department of Zoology, Faculty of Science, Charles University, Prague, Czech Republic*
7 *Institute of Hydrobiology, Biology Centre of the Czech Academy of Sciences, České Budějovice, Czech Republic*
8 *Nature Conservation Agency of the Czech Republic, Prague, Czech Republic*
9 *Department of Zoology, Faculty of Science, University of South Bohemia, České Budějovice, Czech Republic*

Corresponding author: Jörg Bohlen (bohlen@iapg.cas.cz)

Abstract

The European weatherfish *Misgurnus fossilis* is a freshwater fish species specialised at inhabiting shallow, stagnant water bodies with dense vegetation. Owing to the widespread loss and degradation of such habitats through human-induced landscape alteration, the species has undergone a severe decline and is currently considered endangered across much of Europe. To support future conservation and management strategies, we analysed the intraspecific genetic diversity of weatherfish populations from the Czech Republic, Austria and adjacent regions. Both genetic markers, the mitochondrial cytochrome oxidase I gene (*COI*) and the nuclear recombination-activating gene (*RAG1*), revealed a remarkably low genetic diversity and shallow population structure compared with most other European freshwater fish species. Across 170 specimens from 35 populations, two common mitochondrial haplotypes and two common nuclear alleles were identified. All specimens from Austria and Bavaria exclusively carried the most common mitochondrial haplotype and the most common nuclear allele. This marker combination was also dominant in most Czech populations. However, locally restricted populations displayed rarer haplotypes and alleles. Notably, two populations from the Czech part of the Oder basin were dominated by a combination of a rare mitochondrial haplotype and rare nuclear alleles, indicating the presence of a genetically distinct lineage in the Oder basin relative to the Danube and Elbe basins. This geographic pattern was independently recovered by both mitochondrial and nuclear markers, strongly suggesting that it reflects genuine historical population structure. The observed geographic structure implies the importance of considering regional genetic units in conservation planning for this endangered species.

Key words: *COI* gene, Conservation, Danube, Elbe, freshwater fish, Oder, *RAG1* gene

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Introduction

Small standing water bodies such as pools, marshes, and wetland depressions support disproportionately high levels of biodiversity, including amphibians, aquatic insects, birds, plants, and fishes (Hill et al. 2021, Šmejkal et al. 2025). Despite their ecological importance, these valuable habitats are being lost at an alarming rate due to landscape drainage, agricultural intensification, and urban development (Kusanke et al. 2020). The Czech Republic, for example, has experienced a loss of 99% of its lowland wetlands over the past 180 years (Skaloš et al. 2017), and in neighbouring Austria, 70–90% of natural wetlands have been destroyed during the last 200 years (WWF Austria 2023). A reconstructed pre-regulation Danube River morphology showed that channelisation and hydropower led to a truncated fluvial system, a 65% decline in eupotamal side arms, massive loss of bars and islands, halving of the historical flow-pulse, and major reduction of hydrological lateral connectivity between river and floodplain (Hohensinner et al. 2004). The disappearance of these habitats has resulted in the decline of numerous specialist species (Sayer et al. 2025, Šmejkal et al. 2025), and ongoing climate change with increasing frequency of extreme heatwaves and drought events, is expected to further accelerate wetland degradation (Beranek et al. 2022).

One such specialised species is the European weatherfish *Misgurnus fossilis* (Linnaeus, 1758) (Cobitidae), which inhabits stagnant or slowly flowing waters with dense aquatic vegetation and soft, organic-rich sediments. Reaching a maximum total length of approximately 30 cm, this benthic and nocturnal species exhibits several morphological and physiological adaptations that facilitate survival in hypoxic conditions, including the ability to respire atmospheric oxygen (Pyrzanowski et al. 2019). Historically, *M. fossilis* was widely distributed across Europe, ranging from the Volga basin in Russia westward to northern France and Belgium, and southwards to the Black Sea and Caspian drainage basins (Kottelat and Freyhof 2007). The species is currently experiencing ongoing declines across its range and is classified as of high conservation concern in many countries, listed in Annex II of the EU Habitats Directive, and is considered endangered or critically endangered in several countries (Freyhof 2013; Lusk et al. 2017, Freyhof et al. 2023). In some cases, the detection of population declines has been delayed because of the presence of superficially similar congeneric non-native weatherfish species (e.g., Belle et al. 2021, Stoeckle et al. 2019).

Understanding the genetic diversity and population structure of threatened species represents a key component of effective conservation management (Kohout et al. 2012, Šmejkalová et al. 2026). Patterns of genetic differentiation can reveal historical connectivity among populations, identify cryptic lineages, and help to define conservation units, particularly in fragmented and rapidly changing freshwater landscapes. Bohlen et al. (2007) studied the genetic diversity of *M. fossilis* over a large part of its European distribution area using the mitochondrial cytochrome b gene marker and found only low mtDNA divergence, revealing only eight closely related haplotypes across a huge geographic range including nine European drainage basins.

In this study, we investigated the genetic diversity of *M. fossilis* across Austria, Bavaria (Germany), and the Czech Republic. Given the limited mito-

chondrial divergence reported previously, we employed a dense sampling design and analysed both a mitochondrial (cytochrome c oxidase subunit I; *COI*) and a nuclear (recombination-activating gene 1; *RAG1*) marker. We test the hypothesis that distinct genetic lineages correspond to the three major drainage basins within the study area and evaluate the implications of the observed patterns for conservation management.

Material and methods

Sampling

All Austrian samples were obtained from the collection of the Natural History Museum Vienna, Austria (**NMW**), all Bavarian samples from the Bavarian State Collection, Munich, Germany (**ZSM**), one German sample from the Leibniz Institute for the Analysis of Biodiversity Change, Bonn, Germany (**ZFMK**), and one Polish sample from the Natural History Museum, Wrocław. Poland (**UWZM**). The Czech samples were obtained from the collection of the Institute of Animal Physiology and Genetics, Liběchov, Czech Republic (**IAPG**) and from the authors' own collections. Eleven additional sequences were obtained from the Barcode of Life Data (**BOLD**) Portal.

Laboratory procedures

Genomic DNA was extracted from tissue or mucus samples using the Tissue/Blood DNA Mini Kit (Geneaid). The mitochondrial *COI* gene was amplified using the primers FishF1 5'-TCAACCAACCACAAAGACATTGGCAC-3' and FishR1 5'-TAGACTTCTGGGTGGCCAAAGAATCA-3' (Ward et al. 2005). The nuclear *RAG1* was amplified with primers RAG-1F 5'-AGCTGTAGTCAGTAYCACAARATG-3' (Quenouille et al. 2004) and RAG-Rv1 5'-TCCTGRAAGATYTTGTAGAA-3' (Šlechtová et al. 2007). An overview of the analysed samples is provided in Table 1; in total, 170 samples from 35 populations were analysed.

Polymerase chain reaction (PCR) conditions and thermal cycling profiles were identical for both genes. PCR amplification was carried out in 25 µL reaction volumes containing 10 mM Tris–HCl, 50 mM $(HN_4)_2SO_4$, 0.1% Triton X-100, 1.2–1.8 mM $MgCl_2$ (PCR Blue Buffer), 2 mM TMA oxalate (PCR enhancer), 5 nmol of each nucleotide (PCR dNTP mix), 1.25 U of Taq DNA polymerase Unis (all reagents were obtained from Top–Bio), and 12.5 pmol of each primer. PCRs were performed on a C1000 Touch™ Thermal Cycler (Bio-Rad). The cycling conditions consisted of an initial denaturation at 95 °C for 5 min, followed by a touchdown phase during which the annealing temperature decreased from 60 °C to 55 °C (–1 °C per cycle) for 1 min 30 s, followed by 30 cycles with a constant annealing temperature of 54 °C and a final extension step of 7 min at 72 °C. PCR products were purified using either the PCR Cleanup kit (Geneaid) or the NucleoSpin Gel and PCR Clean-up Kit (Macherey-Nagel). Direct Sanger sequencing was performed using the commercial sequencing service provided by SEQme s.r.o. A subset of PCR products was sequenced in-house using the BrightDye Terminator v3.1 Cycle Sequencing Kit (Carolina Biosystems) with the same primers as used for PCR amplification. Reaction setup and cycling conditions followed the manufacturer's instructions. Sequencing reactions were

Table 1. Overview of the geographic origin, number of samples per population, and observed mitochondrial haplotypes and nuclear variants of analysed *Misgurnus fossilis*. The source of the samples is either from the collection of IAPG, Liběchov, Czech Republic, from the BOLD database or from the museums: Natural History Museum Vienna, Austria (NMW), Natural History Museum Wroclaw, Poland (UWZM), the Bavarian State Collection, Munich, Germany (ZSM), or the Leibniz Institute for the Analysis of Biodiversity Change, Bonn, Germany (ZFMK). Country codes: A – Austria, CZ – Czech Republic, D – Germany, PL – Poland, SK – Slovakia.

Country, province	Drainage basin	Sub-catchment	Locality	Coordinates (N,E)	No. of specimens	Individual labels	Source	*COI* haplotype(s)	*RAG1* variant(s)
A, Vienna	Danube	Danube	Wien	48.157,16.531	1	BCAFL791_22	BOLD	B	-
A, Lower Austria	Danube	Danube	Fadenbach	48.139,16.794	12	Mfos07–12, 14–16, IAPG A12443–12445	NMW	B	B
A, Styria	Danube	Drau	Kutschenitza (Mur)	46.723,15.996	3	Mfos23, IAPG A12441–12442	NMW	B, B5	B
A, Upper Austria	Danube	Inn	Innauen	48.292,13.220	3	Mfos28–30	NMW	B	-
D, Bavaria	Danube	Isar	airport Munich	48.367,11.800	2	ZSM40054	ZSM	B	B
D, Bavaria	Danube	Isar	Moosach	48.383,11.688	3	ZSM45120, 45121	ZSM	B	B
A, Burgenland	Danube	Lake Neusiedl	Neusiedler_ See	47.732,17.027	3	Mfos20, 21, 22	NMW	B	-
CZ, South Morava	Danube	Morava	Thaya	48.721,16.907	3	IAPG A12394–96	IAPG	B	B
CZ, South Morava	Danube	Morava	Bažina-Lanžhot (Thaya)	48.628,16.926	3	IFCZE882_11, IFCZE883_11, IFCZE884_11	BOLD	B, B2	-
CZ, South Morava	Danube	Morava	Hodonín	48.844,17.140	8	IAPG A526, 531, 536, 2030, 2033, 2036, 2039, 2042	IAPG	B	B
CZ, South Morava	Danube	Morava	Košárské louky	48.648,16.926	1	IAPG A075	IAPG	B	-
CZ, South Morava	Danube	Morava	Kyjovka (Thaya)	48.7Ohre18,16.981	1	IFCZE896_11	BOLD	B	-
A, Lower Austria	Danube	Morava	March	48.322,16.881	13	Mfos02–06, 17–19, 25–26, IAPG12446-12448	NMW	B, B1, B4	B
A, Lower Austria	Danube	Morava	Zwerndorf	48.320,16.850	3	BCAFL738_20, BCAFL739_20, BCAFL740_20	BOLD	B, B2	-
SK, Bratislavsky	Danube	Morava	Gajary	48.464,16.890	6	IAPG A2610–2615	IAPG	C, C1, C2	B, C
SK, Bratislavsky	Danube	Morava	Male Levare Rudava	48.493,16.970	1	RYBY064_21	BOLD	B	-
A, Burgenland	Danube	Raab	Flutmulde Lafnitz	46.973,16.248	2	Mfos13, 27	NMW	B, B3	-
A, Burgenland	Danube	Raab	Gussing (Strem)	47.053,16.318	1	BCAFL411_20	BOLD	B	-
SK, Košice	Danube	Tisza	Stary Laborec	48.542,21.904	1	IAPG A2091	IAPG	C	B, D
A, Upper Austria	Danube	Traun	Tagerbach-Graben	48.243,14.391	3	IAPG A12449–12451	NMW	B	B
CZ, Central Bohemia	Elbe	Cidlina	Žehuňský rybník	50.143,15.348	16	MM50–55, 75–78, 83–87	IAPG	A, B	A, A1, B
CZ, Karlovy Vary	Elbe	Ohre	Nebanice	50.117,12.448	4	IAPG A12221–24	IAPG	B	B
CZ, Central Bohemia	Elbe	Psovka	Pšovka	50.366,14.562	2	IAPG A2073, 2078	IAPG	B	B
CZ, South Bohemia	Elbe	Vltava	Dvory (Lužnice)	48.853,14.909	3	IAPG A12499–501	IAPG	B	B
CZ, South Bohemia	Elbe	Vltava	Na Primárně (Lužnice)	48.865,14.895	10	IAPG A12502–504, MM110-116	IAPG	B	B

Country, province	Drainage basin	Sub-catchment	Locality	Coordinates (N,E)	No. of specimens	Individual labels	Source	*COI* haplotype(s)	*RAG1* variant(s)
CZ, South Bohemia	Elbe	Vltava	Majdalena (Lužnice)	48.970,14.865	10	IAPG A079–080, 12505, 12522, MM30, 32–34, 37, 39	IAPG	A, B	A, A1, B
CZ, South Bohemia	Elbe	Vltava	Nežárka (Lužnice)	49.127,14.807	1	MM783	IAPG	-	B
CZ, South Bohemia	Elbe	Vltava	Novořecký rybník (Lužnice)	49.001,14.851	1	IFCZE891_11	BOLD	B	-
CZ, South Bohemia	Elbe	Vltava	Stropnice (Malše)	48.883,14.674	3	MM119, MM120, IAPG A12498	IAPG	B	B
CZ, South Bohemia	Elbe	Vltava	Stříbřec (Lužnice)	49.030,14.870	7	MM2, 4, 20, 23–26	IAPG	B	B
A, Lower Austria	Elbe	Vltava	Lainsitz (Lužnice)	48.782,14.988	4	Mfos1, IAPG A12437–12439	NMW	B	B
PL, Lower Silesia	Oder	Barycz	Miloslawice	51.500,17.215	1	IAPG A2176	UWZM	A	A
CZ, Moravia-Silesia	Oder	Oder	Kunín	49.634,17.990	11	IAPG A12424–12435	IAPG	A, B	A
CZ, Moravia-Silesia	Oder	Oder	Štěpán	49.863,18.193	23	IAPG A12397–12419	IAPG	A	A, A2
D, Brandenburg	Oder	Oder	Kostrzyn	52.628,14.531	2	IAPG A473, ZFMK-TIS-25041	IAPG ZFMK	A	A

purified using NucleoSEQ dye terminator removal kit (Macherey-Nagel) and analysed on an ABI Prism 3130 Genetic Analyser (Applied Biosystems).

Direct sequencing of the nuclear *RAG1* marker revealed numerous heterozygous positions in all individuals, reflecting the tetraploid structure of the genome. To verify sequence variants and assist in phase determination, PCR products of four heterozygous individuals were cloned using the pDrive Cloning Vector Kit (Qiagen) according to the manufacturer's instructions. Recombinant plasmids were isolated using a QIAprep Spin Miniprep Kit (Qiagen), and for each individual, 16 clones were sequenced using universal M13 forward and reverse vector primers of the pDrive cloning system (M13F 5'-TGTAAAACGACGGCCAGT-3' and M13R 5'-CAGGAAACAGCTATGACC-3'). Sequencing was performed partly by the commercial sequencing service SEQme s.r.o. and partly in-house using standard Sanger sequencing protocols.

Cloned sequences confirmed the presence of two *RAG1* gene copies. These sequences were used to validate allele identity and to guide haplotype phase inference for the remaining individuals. Variant phases were inferred computationally using ConvPhase (Stephens et al. 2001; Stephens and Donnelly 2003; Flot 2010) of the iTaxoTools package (Vences et al. 2021) with default settings and subsequently verified by manual inspection. Only high-quality sequences without ambiguous base calls were included in subsequent analyses. One of the detected copies exhibited very limited variation across the dataset and was therefore phylogeographically uninformative. Consequently, only phased haplotypes of the second, more variable and informative copy were retained and used for all downstream analyses.

Data analyses

Chromatograms were visually inspected, and the sequence assembly was performed using the SeqMan II module of the DNAStar software package (LASER-

GENE). In addition to newly generated data, 11 *COI* sequences that matched the geographic focus of the present study were downloaded from BOLD (Ratnasingham and Hebert 2007) and included in the analyses. Sequences of mitochondrial haplotypes and nuclear alleles have been deposited in GenBank under the accession numbers PZ462591–PZ462600 for *COI* (see Table 2) and PZ471385–PZ471390 for *RAG1* (see Table 3). Sequences were aligned using the ClustalW (Larkin et al. 2007) multiple alignment algorithm implemented in BioEdit (Hall 1999), and the alignments were checked and trimmed to equal length. Genetic diversity indices including the number of haplotypes (*h*), haplotype diversity (*Hd*), nucleotide diversity (π), number of segregating sites (*S*), and average number of nucleotide differences (*k*) were calculated in DnaSP 6.12.3 (Rozas et al. 2017). Polymorphic sites were classified as singleton or parsimony-informative. To explore the relationships among the haplotypes, we constructed a minimum spanning haplotype network in PopArt 1.7 (Leigh and Bryant 2015).

Results

The mitochondrial *COI* gene

The mitochondrial *COI* alignment (656 bp) comprised 154 sequences, including 144 newly generated sequences and 11 retrieved from BOLD. The alignment

Table 2. Haplotype-specific mutations in the mitochondrial *COI* marker and the GenBank accession numbers.

COI	Nucleotide position within alignment									GenBank accession number
Haplotype	**31**	**88**	**154**	**220**	**229**	**325**	**418**	**538**	**580**	
HapA	A	C	C	T	G	C	G	A	T	PZ462594
HapB	G	C	C	T	G	C	G	A	T	PZ462591
HapB1	G	T	C	T	G	C	G	A	T	PZ462597
HapB2	G	C	C	T	G	T	G	A	T	PZ462600
HapB3	G	C	C	C	G	C	G	A	T	PZ462599
HapB4	G	C	C	T	A	C	G	A	T	PZ462598
HapB5	G	C	C	T	G	C	G	A	C	PZ462596
HapC	A	C	A	T	G	C	G	A	T	PZ462593
HapC1	A	C	A	T	G	C	A	A	T	PZ462595
HapC2	A	C	A	T	G	C	G	T	T	PZ462592

Table 3. Allele-specific mutations in the nuclear *RAG1* marker and GenBank accession numbers.

RAG1	Nucleotide position within alignment				GenBank accession number
Allele	**556**	**595**	**727**	**816**	
VarA	C	G	G	A	PZ471386
VarA1	C	G	A	A	PZ471389
VarA2	A	G	G	A	PZ471387
VarB	C	A	A	G	PZ471385
VarC	C	A	G	G	PZ471388
VarD	C	G	G	G	PZ471390

contained only nine (1.4%) polymorphic sites, of which six (1.0%) were singletons and three (0.5%) parsimony informative (Table 2).

Analyses of the *COI* gene identified 10 haplotypes (h = 10), with moderate haplotype diversity (Hd = 0.448 ± 0.043) but very low nucleotide diversity (π = 0.00086). The average number of nucleotide differences between sequences was low (k = 0.564). Overall, the *COI* dataset revealed shallow mitochondrial divergence and limited sequence differentiation among populations within the study area.

The haplotype network showed that adjacent haplotypes differed by at most a single mutational step (Fig. 1a). Two haplotypes, A and B, were common and were found in 29 and 112 specimens, respectively. Haplotype C occurred in five specimens from two localities. The remaining haplotypes were rare (one or two individuals each) and formed satellite variants derived from haplotypes B or C. Because these satellite haplotypes likely originated directly from haplotypes B and C and have negligible influence on the main patterns observed, they are considered together with their respective parental haplotypes in the discussion (as B1 – 5 and C1 – 2).

The geographical distribution of the haplotypes revealed a strong prevalence of haplotype B. This haplotype occurred in all analysed specimens from Bavaria (5 specimens) and Austria (48 specimens) and in 98 out of 107 specimens (92%) from the Czech Republic. In the Czech Republic, haplotype A was found in all 23 specimens from locality 'Štěpán' (Oder basin), in four of 11 specimens

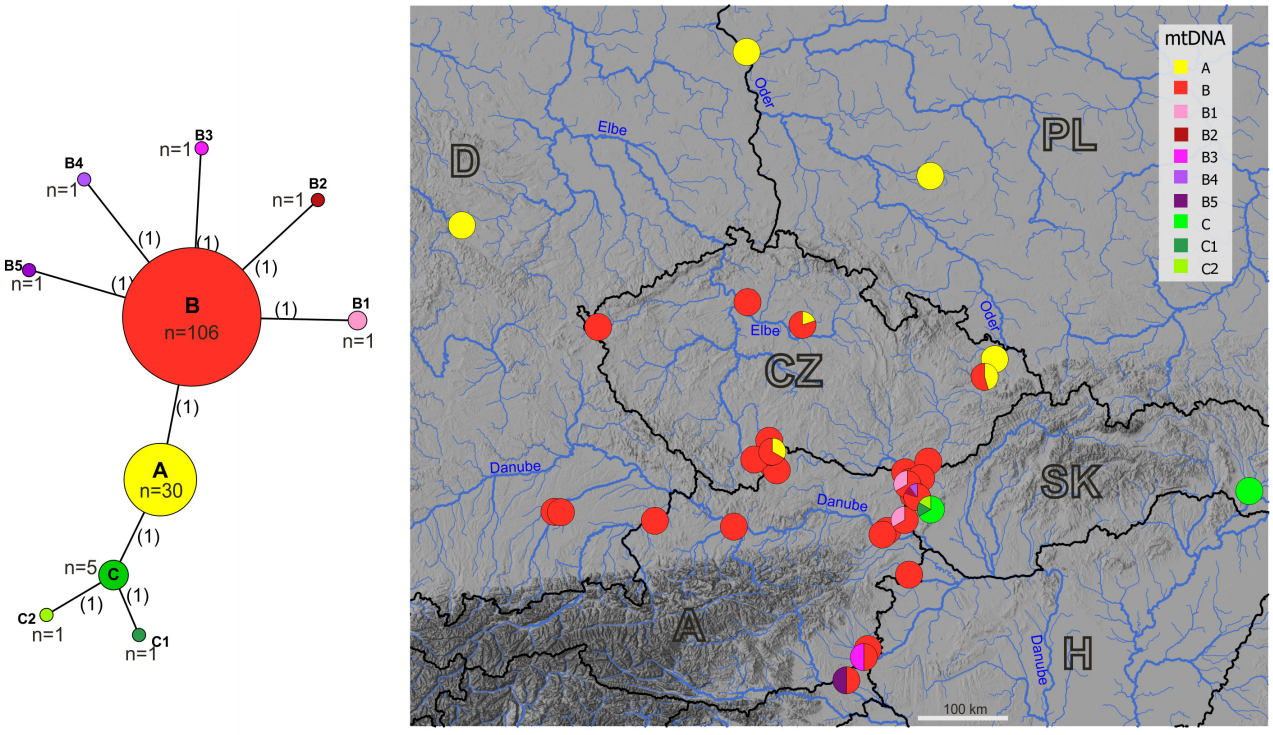

Figure 1. a. Haplotype network; **b.** Geographic distribution of the mitochondrial *COI* gene for 154 sequences of the weatherfish *Misgurnus fossilis*. Circles in the haplotype network represent haplotypes, and their size corresponds to the number of specimens with this haplotype. The number of short black lines on the branches reflects the number of mutational steps between neighbouring haplotypes. Circles in the map give the geographic point of origin of the investigated populations; the colours indicate which haplotype(s) have been found in each population. Blue lines show rivers, black lines show political borders.

(30%) from locality 'Kunín' (Oder basin), in three of 15 specimens (20%) from locality 'Žehuňský rybník' (Elbe basin) and in two of 10 specimens (20%) from locality 'Majdalena' (Elbe basin). Haplotype A was also detected in comparative material from the Polish and German parts of the Oder basin (Fig. 1b).

The nuclear *RAG1* gene

The alignment of the nuclear *RAG1* gene (947 bp) comprised 112 sequences, all generated in this study. Four positions (0.4%) were variable and all were parsimony-informative (Table 3). No singleton mutations were detected.

Analyses of the *RAG1* dataset (i.e. phased allelic sequences) identified six haplotypes (h = 6), hereafter referred to as alleles for clarity. Allele diversity (Hd = 0.602 ± 0.033) was moderate, while nucleotide diversity was low (π = 0.00169). The average number of nucleotide differences between sequences was 1.603.

The network showed that adjacent alleles differed by at most one mutational step (Fig. 2a). Two alleles, A and B, were common and represented 31 and 64 specimens, respectively. Alleles C and D each occurred in a single specimen from one locality (Table 1). Two additional alleles (A1 and A2) were closely related derivatives of allele A and were represented by seven and eight specimens, respectively.

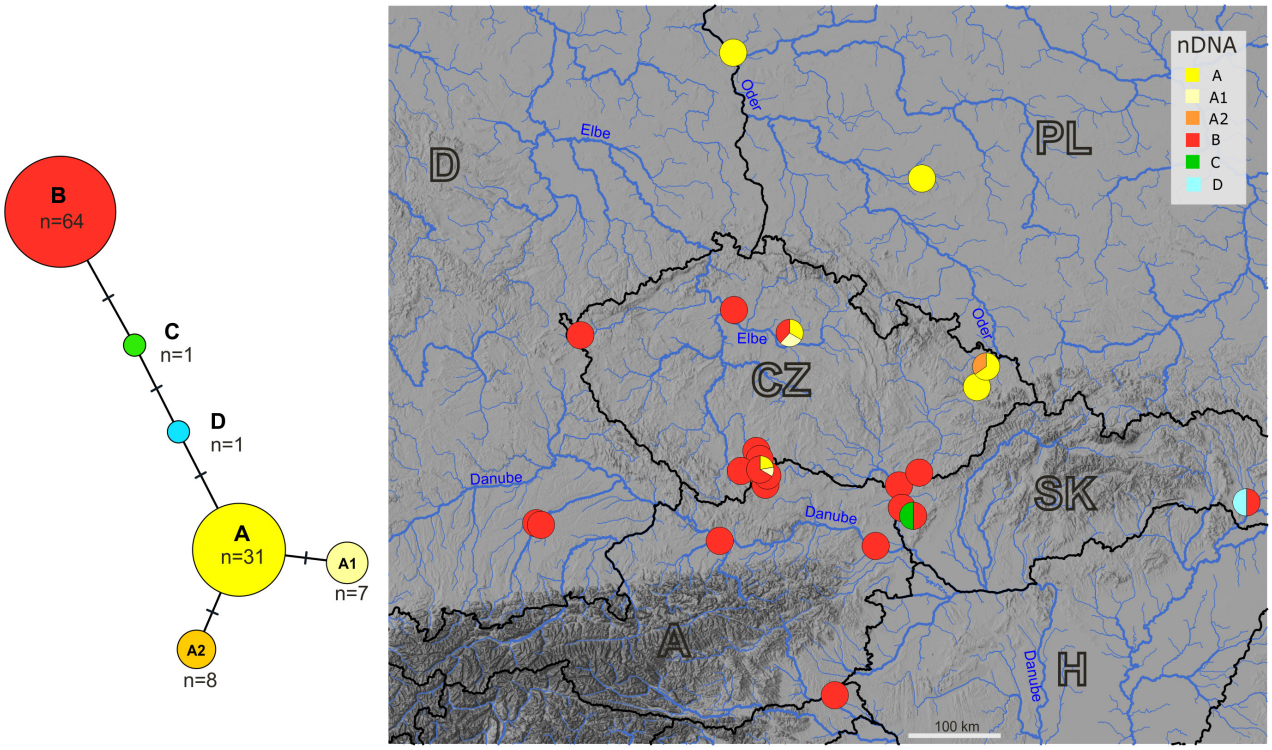

Figure 2. a. Haplotype network; **b.** Geographic distribution of the nuclear *RAG1* gene for 112 sequences of the weatherfish *Misgurnus fossilis*. Circles in the haplotype network represent alleles, and their size corresponds to the number of specimens with this allele. The number of short black lines on the branches reflects the number of mutational steps between neighbouring alleles. Circles in the map give the geographic point of origin of the investigated populations; the colours indicate which allele(s) have been found in each population. Blue lines show rivers, black lines show political borders.

Cloning and phasing revealed that eight individuals were heterozygous for alleles A and A1 (genotype A/A1) and one individual was heterozygous for alleles B and D (genotype B/D). All remaining individuals were homozygous. Overall, the *RAG1* data revealed low nuclear sequence divergence within the study area.

The geographic distribution of *RAG1* variants was largely congruent with the distribution of *COI* haplotypes (Fig. 2). Variant B occurred in all analysed specimens from Bavaria (4 specimens) and Austria (11 specimens), and in 47 of 93 specimens (50%) from the Czech Republic. In the Czech Republic, alleles A, A1, and A2 were present in all 23 specimens from locality 'Štěpán' (Oder basin), in all five specimens from locality 'Kunín' (Oder basin), in 13 of 21 specimens (62%) from locality 'Žehuňský rybník' (Elbe basin) and in two of nine specimens (22%) from locality 'Majdalena' (Elbe basin). Alleles C and D occurred in a single specimen each from the Slovak localities 'Gajary' and 'Laborec', respectively.

Fig. 3 provides an overview of the geographic distribution of haplotypes and alleles according to major drainage basins and subcatchments.

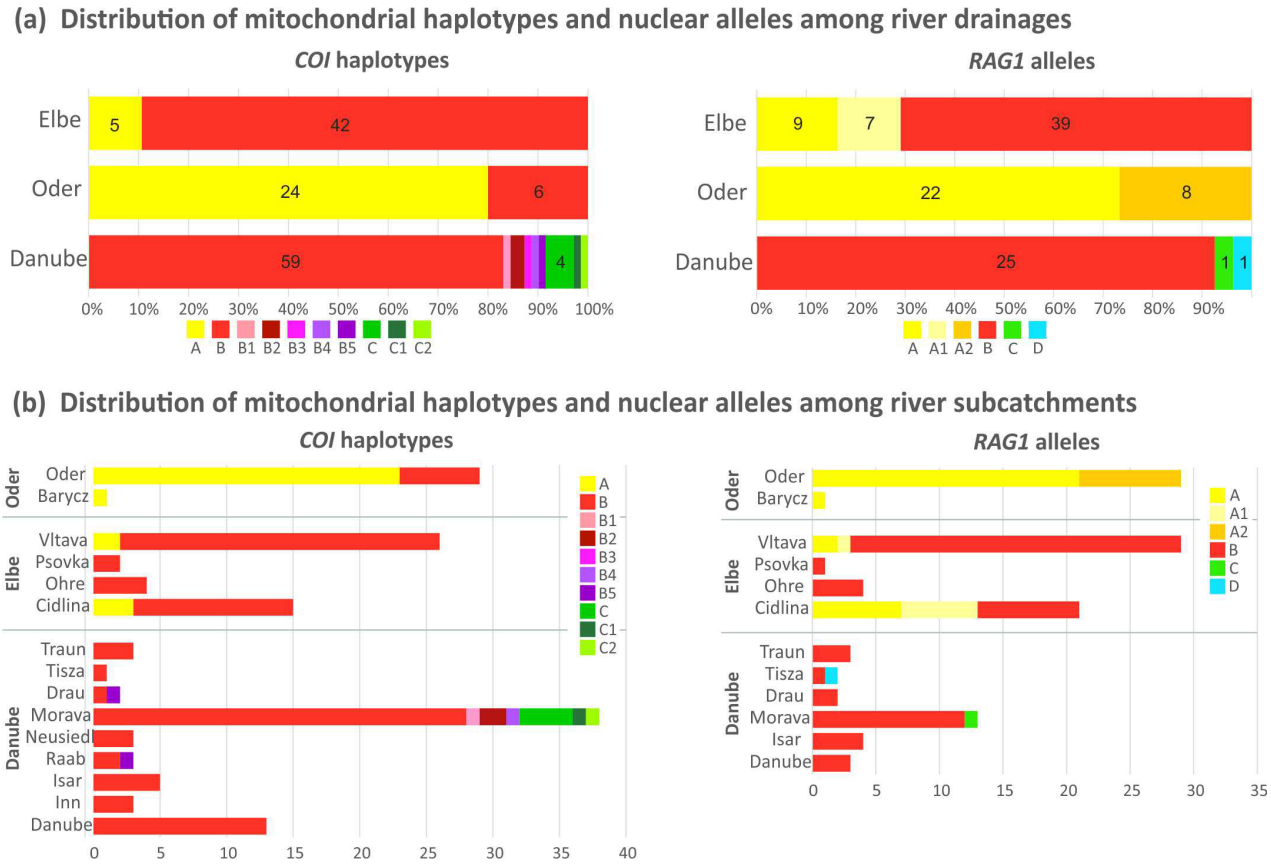

Figure 3. a. Relative frequencies of mitochondrial *COI* haplotypes and nuclear *RAG1* alleles in the three major drainage basins included in this study. Each bar represents the proportional contribution of individual alleles to the total number of analysed specimens within a drainage basin. Numbers within the bars specify numbers of specimens. **b.** Distribution of mitochondrial *COI* haplotypes and nuclear *RAG1* alleles among individual drainage subcatchments. Each coloured segment represents the number of specimens carrying a particular mitochondrial haplotype or nuclear allele. Subcatchments are arranged according to the Danube, Elbe and Oder drainage basins. Colours of haplotype and alleles correspond to colours used in Figs 1, 2.

Discussion

The most important finding of this study is the complete concordance between mitochondrial and nuclear markers. Both markers consistently revealed two major genetic groups (A and B), demonstrating that the species is not genetically homogeneous within Central Europe. In all investigated Bavarian and Austrian populations, and most Czech populations, exclusively B/B (first letter referring to the mitochondrial haplotype, second letter to the nuclear allele) combinations were detected, whereas populations within the Oder drainage basin were dominated by A/A combinations, with only limited zones of admixture. The agreement between independently evolving mitochondrial and nuclear markers strongly suggests that this pattern reflects genuine historical geographic structure rather than stochastic variation or marker-specific artefacts.

The distribution of genetic markers broadly corresponds to major drainage basins. All analysed populations from the Danube drainage basin carried predominantly the combination B/B, suggesting long-term genetic cohesion within this drainage basin. Most populations from the Elbe basin were also dominated by B/B markers, however, two Czech localities 'Žehuňský rybník' and 'Majdalena' showed admixture of A and B markers. The highly localised nature of this admixture, particularly within otherwise genetically homogeneous wetland systems, makes a purely historical explanation unlikely. The presence of A markers is most plausibly explained by recent anthropogenic translocations. Considering the long tradition of carp aquaculture in the Třeboňsko area (Majdalena) and Central Bohemian (Žehuňský rybník) pond systems (Lyach 2023), unintentional introduction of weatherfish together with stocked carp represents a plausible explanation. The absence of A markers in neighbouring wetlands without apparent dispersal barriers further supports a recent origin of these mixed populations. The widespread occurrence of only a few haplotypes across extensive geographic areas may indicate that historical dispersal during large flood events was more effective than previously assumed, particularly during the postglacial period when extensive alluvial wetlands connected river systems.

In contrast, populations within the Oder drainage basin were largely dominated by A/A combinations. Identical mitochondrial and nuclear markers were found in comparative material from Poland and Germany, consistent with a shared evolutionary history within the Oder basin. The 'Štěpán' population, located close to the Czech-Polish border, consisted exclusively of A/A individuals, whereas 'Kunín' (situated upstream and near the watershed divide between the Oder and Danube basins) exhibited mixed mitochondrial haplotypes but only the nuclear allele A. This pattern may reflect secondary contact and asymmetric introgression between lineages, although additional sampling would be required to clarify this process. In general, a clear geographic pattern emerges from our data, with the B/B lineage dominating the Elbe and Danube basins and the A/A lineage predominating in the Oder basin.

The two Slovak populations 'Gajary' (Morava) and 'Laborec' (Tisza) represent striking genetic outliers. All individuals carried mitochondrial haplotypes of group C, which were absent from all other analysed populations despite dense regional sampling. In the nuclear marker, alleles B, C, and D were detected in the populations 'Gajary' and 'Laborec', with alleles C and D not observed elsewhere. This distinct genetic composition is particularly surprising in the

case of the 'Gajary' population, located in the Morava/Thaya system. Given the genetic uniformity of several neighbouring populations within this drainage basin, long-term persistence of such a distinct lineage *in situ* appears unlikely. Instead, the data suggest a relatively recent founder event from an unsampled source population. Importantly, the 'Gajary' and 'Laborec' populations demonstrate the presence of additional, previously undocumented genetic diversity in the eastern part of the species' range, indicating that the overall genetic diversity of *M. fossilis* is still underestimated.

Our results further show that *M. fossilis* has a low genetic diversity in the analysed mt and nuclear genes. In comparison to other freshwater fishes in the central Europe, the number of mitochondrial haplotypes in *M. fossilis* falls into the lower part of the range. Species such as *Salmo trutta* Linnaeus, 1758, *Cottus gobio*, *Rhodeus amarus* (Bloch, 1782), *Cobitis taenia* Linnaeus, 1758 and *Phoxinus* sp. exhibit exceptionally high mitochondrial diversity within Central Europe (Bernatchez 2001, Šlechtová et al. 2004, Bohlen et al. 2006, Culling et al. 2006, Palandačić et al 2020), whereas *Vimba vimba* (Linnaeus, 1758), *Carassius carassius* (Linnaeus, 1758) and *Rutilus rutilus* (Linnaeus, 1758) display intermediate levels (Hänfling et al. 2009, Rylková et al. 2013, Levin et al. 2025). In contrast, *Misgurnus fossilis* resembles only a few species, including *Tinca tinca* (Linnaeus, 1758), *Perca fluviatilis* Linnaeus, 1758 and *Esox lucius* Linnaeus, 1758, in possessing comparatively few haplotypes (Lajbner et al. 2011, Nesbø et al. 1999, Skog et al. 2014).

The most striking feature of *M. fossilis* is the absence of deep phylogeographic structure. Its haplotypes differ from one another by only a single mutational step, a pattern that contrasts sharply with the classic phylogeographic scenario described for many European freshwater fishes, in which populations survived the Pleistocene glaciations in multiple isolated refugia, resulting in deeply divergent mitochondrial lineages. Two deeply separated major clades have been found in *Rhodeus amarus* (Bohlen et al. 2006), *Vimba vimba* (Hänfling et al. 2009), *Tinca tinca* (Lajbner et al. 2011) and *Carassius carassius* (Jeffries et al. 2016), while three refugial lineages are present in *Cobitis taenia* (Culling et al. 2006), and many such lineages in *Salmo trutta* (Bernatchez 2001), *Cottus gobio* (Šlechtová et al. 2004), *Squalius cephalus* Linnaeus, 1758 (Seifertová et al 2012), and *Phoxinus* sp. (Palandačić et al 2017). Nevertheless, our geographic sampling represents only part of the species' distribution, and broader sampling across Europe may reveal additional phylogeographic structure.

From a conservation perspective, the species appears particularly endangered. Although overall genetic diversity is low, populations are not genetically uniform, and the presence of geographically structured lineages (A, B, and locally C) indicates that regional genetic units should be considered in conservation and biodiversity management planning. Recent field observations in Bohemia revealed a rapid decline of small and isolated populations, with four out of six monitored localities drying out or losing suitable habitat within only a few years (Choleva, Bohlen, personal observations). Similar observations have been made in Austria, where several populations have died out during droughts within the last years and many of the remaining populations comprise alarmingly few individuals (M. Jung, personal observation). Given projections of an increasing frequency of extreme heat and drought events in Central Europe (Suarez-Gutierrez et al. 2023), further habitat degradation is expected.

The combination of low genetic variability, strong habitat specialisation, and ongoing wetland loss will substantially increase the risk of local extinction. Taken together, these findings highlight the urgency of conserving the remaining wetland habitats and maintaining the genetic integrity of regional populations throughout Central Europe.

Conclusions

The European weatherfish *Misgurnus fossilis* exhibits an unusual combination of remarkably low overall genetic diversity and distinct geographic structuring. Both mitochondrial and nuclear markers independently recovered the same phylogeographic pattern, providing strong evidence that populations in the Oder basin are genetically differentiated from those in the Danube and Elbe basins. These results demonstrate that, despite limited genetic diversity, the species is not genetically homogeneous across Central Europe and comprises geographically structured evolutionary lineages that should be considered in conservation planning. Given the rapid loss of wetland habitats throughout Central Europe, preserving the genetic integrity of these regional lineages should become an integral component of future conservation and management strategies for this endangered species.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Artificial Intelligence (AI) use

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.
No AI tools were used in the preparation of this manuscript.

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Author contributions

Conceptualization: VŠ, JB. Data curation: TD, KB, AP, TP, MJC, VL. Formal analysis: VŠ. Funding acquisition: LC. Investigation: AP. Methodology: VŠ. Project administration: LC. Resources: MM, MŠ, MJ. Writing – original draft: JB. Writing – review and editing: AP, MJ, MŠ, MJC, LC, TD, VŠ, TP, JB, MM, KB.

Author ORCIDs

L. Choleva https://orcid.org/0000-0002-3603-0266
J. Bohlen https://orcid.org/0000-0002-7068-2321
T. Dvořák https://orcid.org/0000-0001-8151-2144
A. Palandačić https://orcid.org/0000-0002-4555-5240
M. Jung https://orcid.org/0009-0007-4611-9487
M.J. Chai https://orcid.org/0009-0003-6213-2973
V. Labajová https://orcid.org/0000-0002-4156-0392
K. Bezányiová https://orcid.org/0000-0002-9639-7967
T. Pavlica https://orcid.org/0000-0003-3333-3787
A. Sember https://orcid.org/0000-0003-4441-9615
M. Muška https://orcid.org/0000-0001-6659-986X
M. Šmejkal https://orcid.org/0000-0002-7887-6411

Data availability

All of the data that support the findings of this study are available in the main text.