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PHYLOGEOGRAPHY OF *TERRICOLA* VOLES IN THE CAUCASUS AND EASTERN ANATOLIA, WITH A NEW SOUTHERNMOST RECORD OF *MICROTUS DAGHESTANICUS* (RODENTIA, CRICETIDAE, ARVICOLINAE)

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Phylogeography of *Terricola* Voles in the Caucasus and Eastern Anatolia, with a New Southernmost Record of *Microtus daghestanicus* (Rodentia, Cricetidae, Arvicolinae). Kalkan, K. K., Çetintaş, O., Çolak, F., Yanchukov, A., Sözen, M. — *Microtus daghestanicus* (Shidlovskiy, 1919), one of the least studied members of the subgenus *Terricola* '*subterraneus*' species group, remains poorly understood with respect to its phylogeography and genetic structure. Here, we reevaluated its evolutionary relationships, genetic diversity and distribution of the species using mitochondrial cyt*b* sequences (71 haplotypes of 77 samples) together with new field records from Türkiye. Maximum-likelihood and Bayesian analyses produced nearly similar topologies and separated three well-defined lineages corresponding to *M. daghestanicus*, *M. fingeri* (Neuhäuser, 1936), and *M. subterraneus* (Sélys, 1836). Two mitochondrial lineages were identified within *M. daghestanicus*: a Caucasian lineage (Russia–Georgia) and an Anatolian lineage including Ardahan, Artvin, Kars, and a newly recorded population from Hakkari. The Hakkari record represents the first verified occurrence of the species in southern part of Eastern Anatolia and marks the southern limit of the species' known range, extending the known distribution and highlighting the Anatolia–Caucasus phylogeographic separation. Pairwise K2P distances and F_{st} values indicated

pronounced genetic differentiation among taxa, whereas neutrality tests showed no significant deviations from mutation–drift equilibrium. Generally, observed genetic structure is consistent with long-term geographic isolation across the Pontic–Caucasian region. Our results provide a foundation for understanding the taxonomy and distribution of *M. daghestanicus*.

Key words: Arvicolinae, cytochrome *b*, phylogeny, small mammals.

Introduction

The subfamily Arvicolinae is among the most species-rich and rapidly evolving lineages within the muroid rodents (McKenna & Bell, 1997; Chaline et al., 1999; Musser & Carleton, 2005). Within this subfamily, *Microtus* is the most speciose genus and taxonomically one of the most complex groups (Jaarola et al., 2004; Baskevich et al., 2016, 2017; Bogdanov et al., 2021, 2024). It is represented by five subgenera and 37 species in the Palearctic and 60 species across the Holarctic region (Kryštufek & Shenbrot, 2022; MDD, 2025). In Türkiye, *Microtus* is known to include 11 species (Kryštufek & Shenbrot, 2022; Sözen & Çolak, 2025). Several subgenera and species groups within *Microtus* have speciated across different parts of its wide distribution range, and there are still many groups in the process of speciation (Jaarola et al., 2004). Pine voles are now recognized as members of the subgenus *Terricola*, a Palearctic taxon distributed across the Caucasus and much of Europe, living in both lowland and mountainous habitats (e. g., Chaline, 1987; Jaarola et al., 2004; Baskevich et al., 2016; Kryštufek & Shenbrot, 2022). According to Kryštufek & Shenbrot (2022), there are 14 recognized species within the subgenus *Terricola*, although their taxonomic status remains a subject of debate.

The '*subterraneus*' species group includes *M. subterraneus* (Sélys, 1836), found across Asia Minor and Europe, *M. fingeri* (Neuhäuser, 1936) in northern Anatolia, and *M. daghestanicus* (Shidlovskiy, 1919) in the Caucasus mountains (Jaarola et al., 2004; Baskevich et al., 2016, 2017; Bogdanov et al., 2021, 2024; Çetintürk, 2022; Kryštufek & Shenbrot, 2022). Cytogenetic studies have revealed substantial chromosomal variation within the group, with *M. daghestanicus* displaying particularly high polymorphism (2n = 38–54) compared to the stable karyotypes of *M. subterraneus* and *M. fingeri* (e. g., Ivanov & Tembotov, 1972; Akhverdyan et al., 1992; Macholán et al., 2001; Baskevich et al., 2007, 2018; Selçuk & Kefelioğlu, 2024).

Subsequent molecular studies have shown that *M. subterraneus*, *M. fingeri*, and *M. daghestanicus* are genetically distinct (e. g., Macholán et al., 2001; Jaarola et al., 2004; Tougard, 2017; Bogdanov et al., 2021). While earlier studies debated the position of *M. majori*, recent multilocus and karyological assessments have confirmed that it constitutes a separate species group, leaving *M. subterraneus*, *M. daghestanicus*, and the recently recognized northern Anatolian endemic *M. fingeri* as the sole members of the '*subterraneus*' species group (e. g., Baskevich, 1997; Mezhzherin et al., 1995; Jaarola et al., 2004; Tougard, 2017; Bogdanov et al., 2021). Thus, the '*subterraneus*' species group of the subgenus *Terricola* currently includes three species: *M. subterraneus* (European Pine Vole); *M. fingeri* (Anatolian Pine Vole); and *M. daghetanicus* (Dagestan Pine Vole) (Kryštufek & Shenbrot, 2022; MDD, 2025).

In contrast to the extensively sampled Caucasian populations, data from Türkiye remain scarce and limited to a few localities in the northeast (Jaarola et al., 2004;

Çetintürk, 2022). Caucasian populations of the species have been sampled much better (e. g., Ivanov & Tembotov, 1972; Akhverdyan et al., 1992; Bulatova et al., 2007; Baskevich et al., 2017; Bogdanov et al., 2024) but to date, no detailed phylogeographic study has addressed the species' distribution limits in Anatolia or its genetic connectivity with the main Caucasian range. Such limited representation of Anatolian populations and insufficient distribution data in the existing literature highlight the importance of the present study.

Here, we focus on the Caucasus–Eastern Anatolia region and integrate newly collected Turkish cyt*b* sequences with publicly available data to update the phylogeographic framework for *M. daghestanicus*. Our goal was (1) to identify new distribution areas for *M. daghestanicus* in Türkiye, (2) to assess the genetic diversity and phylogenetic relationships of newly identified Anatolian populations in respect to the existing data, and (3) to gain better insight into the phylogeographic structure of *M. daghestanicus* across its range.

Material and Methods

Samples

A total of 77 samples belonging to the subgenus *Terricola* were examined in this study (22 from *M. subterraneus*, 9 from *M. fingeri*, and 46 from *M. daghestanicus*). Additionally, two *M. arvalis* (Pallas, 1778) samples were included as the outgroup. Eleven out of 46 *M. daghestanicus* samples were collected by us from the Eastern Black Sea (Artvin) and Eastern Anatolia (Ardahan and Hakkari) regions (Fig. 1 and Table 1). Additional sequences (*M. subterraneus*, *M. fingeri*, *M. daghestanicus*, and *M. arvalis*) were obtained from GenBank. The distribution (areal) layer was redrawn based on the distribution information in Kryštufek & Shenbrot (2022) and combined with our sampling localities for visualization purposes.

Sampling of *M. daghestanicus* was conducted under permits issued by the Ministry of Agriculture and Forestry, Republic of Türkiye, General Directorate of Nature Conservation and National Parks (Permit Numbers: E-21264211-288.04-10350129 and E-72784983-288.04-19227738). Animal ethics approval was granted by the Ethics Committee of Zonguldak Bülent Ecevit University (Zonguldak, Türkiye) (Permit Numbers: 91330202-09 and 2025-03-20/02).

Fieldwork was carried out during the summer periods, and the samples were captured at elevations ranging from 2178 m to 3324 m. Tissues including lung, liver, heart, spleen, and kidney were preserved in RNAlater solution and stored at –80 °C until molecular analysis. Skulls were cleaned and are currently being kept with registration numbers in our mammal collection at Zonguldak Bülent Ecevit University.

Molecular DNA Analysis

DNA was extracted from the liver tissue samples preserved in RNALater, using EcoPURE Genomic DNA Kit (EcoTech, Erzurum, Türkiye) following the manufacturer's protocol. The mitochondrial cyt*b* gene was amplified by using the primer pair L7 (5'-ACCAATGACATGAAAAATCATCGTT-3') and H6 (5'-TCTCCATTTCTGGTTTACAAGAC-3') (Montgelard et al., 2002).

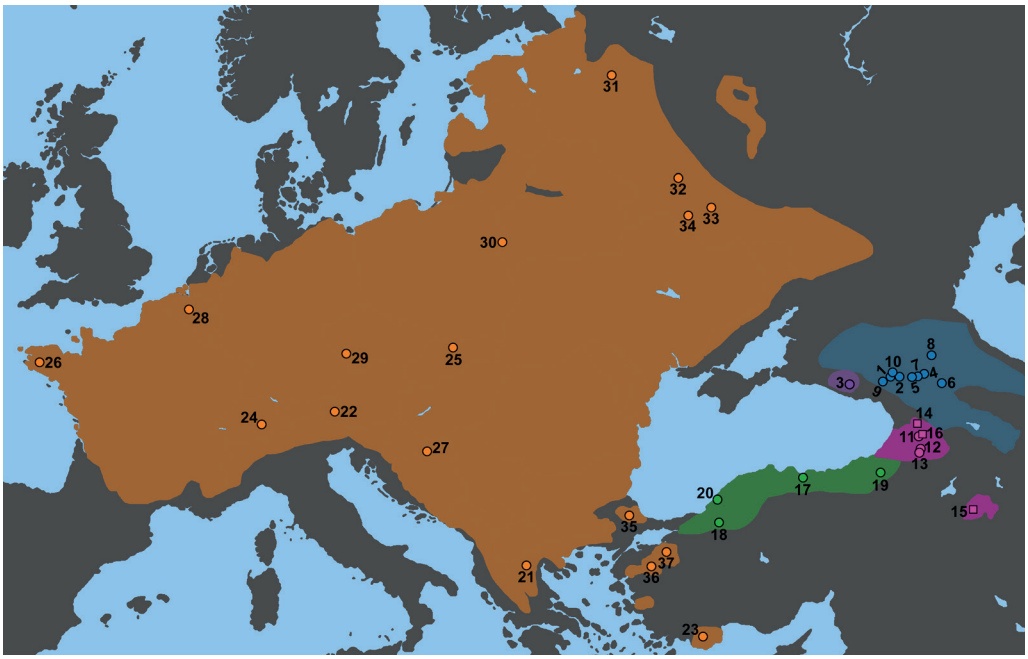

Fig. 1. Map showing the sample localities of subgenus *Terricola* ('*subterraneus*' species group) included in the present study: ● *M. subterraneus*; ● *M. fingeri*; ● *M. daghestanicus* (Anatolia); ● *M. daghestanicus* (Western Greater Caucasus); ● *M. daghestanicus* (Central and Eastern Greater Caucasus); ■ *M. daghestanicus* (Anatolia, this study). Locality numbers correspond to Table 1. Only the ■ symbol represents samples newly sequenced in this study; all other localities represent sequences obtained from GenBank. The shaded area colors follow the branch colors in Fig. 2. The distribution (areal) layer was redrawn based on the distribution information in Kryštufek & Shenbrot (2022) and combined with our sampling localities for visualization purposes

Each PCR reaction was prepared in a final volume of 25 µl, containing 2.5 µl 10× Taq buffer, 0.5 µl dNTP mixture, 0.25 µl Taq DNA polymerase, 1.5 µl $MgCl_2$, 0.5 µl DNA template, 0.5 µl of each primer, and 18.75 µl nuclease-free water. Amplifications were conducted in a gradient thermal cycler under the following conditions: an initial denaturation at 95 °C for 5 min; 35 cycles of denaturation at 95 °C for 30 s, annealing at 55 °C for 60 s, and extension at 72 °C for 90 s; followed by a final extension at 72 °C for 10 min.

PCR products were purified using the EcoPURE PCR/Gel Purification Kit (Eco-Tech, Erzurum, Türkiye) according to the manufacturer's instructions. All DNA extraction and PCR purification steps were carried out under sterile conditions to prevent contamination. The purified products were sequenced in both directions by Macrogen Europe (Amsterdam, The Netherlands).

Phylogenetic Analysis

All sequences were edited and assembled using Geneious Prime software v.2025.2.1 (Geneious Biomatters Ltd., 2025; https://www.geneious.com), and multiple sequence alignment was performed with the MAFFT v.7 (Katoh & Standley, 2013) algorithm implemented in the same software. To explore the phylogenetic relationships, we used 77 cyt*b* sequences representing *M. subterraneus*, *M. fingeri*, and *M. daghestanicus*, together with two M. arvalis (GenBank: AM991045 [Tougard, 2008b] and AY220788 [Haynes et al.,

Table 1. **Sampling localities (also shown on Fig. 1) with the corresponding cyt*b* haplotypes**

Map Number	Collection Number	Haplotype Number	GenBank Accession Number	Locality	References
M. daghestanicus (Dagestan Pine Vole)					
1	–	Hap_7	KM656486	Adyl Su, Kabardino Balkaria, Russia	Baskevich et al., 2016
1	–	Hap_3	KM656482	Adyl Su, Kabardino Balkaria, Russia	Baskevich et al., 2016
1	–	Hap_20	KM656480	Adyl Su, Kabardino Balkaria, Russia	Baskevich et al., 2017
1	–	Hap_2	KM656481	Adyl Su, Kabardino Balkaria, Russia	Baskevich et al., 2017
1	–	Hap_4	KM656483	Adyl Su, Kabardino Balkaria, Russia	Baskevich et al., 2017
1	–	Hap_1	KM656479	Adyl Su, Kabardino Balkaria, Russia	Baskevich et al., 2017
1	–	Hap_6	KM656485	Adyl Su, Kabardino Balkaria, Russia	Baskevich et al., 2017
1	–	Hap_5	KM656484	Adyl Su, Kabardino Balkaria, Russia	Baskevich et al., 2017
2	–	Hap_24	MZ198183	Kabardino Balkar, Elbrussky, Adyl Su River, Russia	Bogdanov et al., 2021
2	–	Hap_25	MZ198184	Kabardino Balkar, Elbrussky, Adyl Su River, Russia	Bogdanov et al., 2021
2	–	Hap_26	MZ198185	Kabardino Balkar, Elbrussky, Adyl Su River, Russia	Bogdanov et al., 2021
2	–	Hap_24	MZ198186	Kabardino Balkar, Elbrussky, Adyl Su River, Russia	Bogdanov et al., 2021
2	–	Hap_27	MZ198187	Kabardino Balkar, Elbrussky, Adyl Su River, Russia	Bogdanov et al., 2021
2	–	Hap_28	MZ198188	Kabardino Balkar, Elbrussky, Adyl Su River, Russia	Bogdanov et al., 2021
2	–	Hap_29	MZ198189	Kabardino Balkar, Elbrussky, Adyl Su River, Russia	Bogdanov et al., 2021
3	–	Hap_9	KM656488	Krasnaya Polyana, Krasnodar Krai, Russia	Baskevich et al., 2017
3	–	Hap_10	KM656489	Krasnaya Polyana, Krasnodar Krai, Russia	Baskevich et al., 2017
3	–	Hap_11	KM656490	Krasnaya Polyana, Krasnodar Krai, Russia	Baskevich et al., 2017
3	–	Hap_12	KM656491	Krasnaya Polyana, Krasnodar Krai, Russia	Baskevich et al., 2017
4	–	Hap_13	MZ198175	North Ossetia Alania, Alagirsky, Nizhny Tsey Village, Russia	Bogdanov et al., 2021
4	–	Hap_13	MZ198176	North Ossetia Alania, Alagirsky, Nizhny Tsey Village, Russia	Bogdanov et al., 2021

Continued Table 1

Map Number	Collection Number	Haplotype Number	GenBank Accession Number	Locality	References
4	–	Hap_14	MZ198177	North Ossetia Alania, Alagirsky, Nizhny Tsey Village, Russia	Bogdanov et al., 2021
4	–	Hap_15	MZ198178	North Ossetia Alania, Alagirsky, Nizhny Tsey Village, Russia	Bogdanov et al., 2021
4	–	Hap_32	MZ198179	North Ossetia Alania, Alagirsky, Nizhny Tsey Village, Russia	Bogdanov et al., 2021
5	–	Hap_21	MZ198180	Karachay Cherkess, Dombay Village, Gonachkhir River, Russia	Bogdanov et al., 2021
5	–	Hap_22	MZ198181	Karachay Cherkess, Dombay Village, Gonachkhir River, Russia	Bogdanov et al., 2021
5	–	Hap_23	MZ198182	Karachay Cherkess, Dombay Village, Gonachkhir River, Russia	Bogdanov et al., 2021
6	–	Hap_18	AY513790	Beniani, Georgia	Jaarola et al., 2004
7	–	Hap_33	LT222300	Cew Valley, Central Caucasus, Russia	Tougard, 2017
8	–	Hap_8	KM656487	Nizhniy Tsei, North Ossetia, Russia	Baskevich et al., 2016
9	–	Hap_30	MZ198190	Kabardino Balkar, Elbrussky, Terskol Village, Russia	Bogdanov et al., 2021
10	–	Hap_31	MZ198191	Kabardino Balkar, Zolsky Ekiptsoko Russia	Bogdanov et al., 2021
11	–	Hap_16	AY513791	Bağdaşan, Ardahan, Türkiye	Jaarola et al., 2004
12	–	Hap_17	AY513792	Handere, Kars, Türkiye	Jaarola et al., 2004
13	–	Hap_19	MZ198174	Sarıkamış, Kars, Türkiye	Bogdanov et al., 2021
14	9421	Hap_62	PX637176	Ilgar Dağı, Ardahan, Türkiye	Present Study
14	9430	Hap_63	PX637177	Ilgar Dağı, Ardahan, Türkiye	Present Study
14	9432	Hap_64	PX637178	Ilgar Dağı, Ardahan, Türkiye	Present Study
14	9433	Hap_65	PX637179	Ilgar Dağı, Ardahan, Türkiye	Present Study
15	9563	Hap_66	PX637180	Berçelan Yaylası, Hakkari, Türkiye	Present Study
15	9564	Hap_67	PX637181	Berçelan Yaylası, Hakkari, Türkiye	Present Study

Continued Table 1

Map Number	Collection Number	Haplotype Number	GenBank Accession Number	Locality	References
15	9565	Hap_68	PX637182	Berçelan Yaylası, Hakkari, Türkiye	Present Study
15	9566	Hap_69	PX637183	Berçelan Yaylası, Hakkari, Türkiye	Present Study
15	9594	Hap_68	PX637184	Berçelan Yaylası, Hakkari, Türkiye	Present Study
15	9595	Hap_70	PX637185	Berçelan Yaylası, Hakkari, Türkiye	Present Study
16	10094	Hap_71	PX637186	Ardanuç, Artvin, Türkiye	Present Study
			M. fingeri (Anatolian Pine Vole)		
17	–	Hap_34	MZ198173	Samsun, Türkiye	Jaarola et al., 2004
18	–	Hap_35	FR869843	Bolu, Türkiye	Martínková et al. (unpubl.)
18	–	Hap_36	FR869844	Bolu, Türkiye	Martínková et al. (unpubl.)
19	–	Hap_37	AY513836	Gümüşhane, Türkiye	Jaarola et al., 2004
19	–	Hap_38	FR869836	Gümüşhane, Türkiye	Martínková et al. (unpubl.)
19	–	Hap_39	FR869838	Gümüşhane, Türkiye	Martínková et al. (unpubl.)
20	–	Hap_40	FR869839	Zonguldak, Türkiye	Martínková et al. (unpubl.)
20	–	Hap_41	FR869840	Zonguldak, Türkiye	Martínková et al. (unpubl.)
20	–	Hap_42	FR869842	Zonguldak, Türkiye	Martínková et al. (unpubl.)
			M. subterraneus (Common Pine Vole)		
21	–	Hap_43	AY513832	Seli, Greece	Jaarola et al., 2004
22	–	Hap_44	AY513833	Glocknerhaus, Austria	Jaarola et al., 2004
23	–	Hap_45	AY513834	Çığlıkara, Antalya, Türkiye	Jaarola et al., 2004
23	–	Hap_45	AY513835	Çığlıkara, Antalya, Türkiye	Jaarola et al., 2004
24	–	Hap_46	AJ717745	Val Piora, Ticino, Switzerland	Tougard et al., 2008a, b

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25	–	Hap_47	LT222310	Úzka dolina Valley, Western Tatra Mts, Slovakia	Tougard, 2017
26	–	Hap_48	LT222311	Tourch, Finistère, France	Tougard, 2017
27	–	Hap_49	FR869858	Nova Kapela, Croatia	Martínková et al. (unpubl.)
28	–	Hap_50	FR869862	Brussels, Waterloo, Belgium	Martínková et al. (unpubl.)
29	–	Hap_51	FR869878	Kasperske, hory Mts, Czech Republic	Martínková et al. (unpubl.)
30	–	Hap_52	FR869884	Bialowieza, Poland	Martínková et al. (unpubl.)
31	–	Hap_53	MZ198155	Novgorod, Valdaysky, Krenye Lake, Russia	Bogdanov et al., 2021
31	–	Hap_54	MZ198156	Novgorod, Valdaysky, Krenye Lake, Russia	Bogdanov et al., 2021
32	–	Hap_55	MZ198159	Kaluga, Ulyanovsky, Nagaya Village, Russia	Bogdanov et al., 2021
32	–	Hap_55	MZ198160	Kaluga, Ulyanovsky, Nagaya Village, Russia	Bogdanov et al., 2021
33	–	Hap_56	MZ198161	Voronezh, Verkhnekhavsky, Usmanka River, Russia	Bogdanov et al., 2021
33	–	Hap_57	MZ198165	Voronezh, Verkhnekhavsky, Usmanka River, Russia	Bogdanov et al., 2021
34	–	Hap_58	MZ198169	Belgorod, Gubkinsky, Gubkin, Russia	Bogdanov et al., 2021
34	–	Hap_58	MZ198168	Belgorod, Gubkinsky, Gubkin, Russia	Bogdanov et al., 2021
35	–	Hap_59	MZ198170	Kırklareli, Türkiye	Bogdanov et al., 2021
36	–	Hap_60	MZ198171	Balıkesir, Türkiye	Bogdanov et al., 2021
37	–	Hap_61	MZ198172	Bursa, Türkiye	Bogdanov et al., 2021

2003]) used as outgroups (Table 1). The final alignment included sequences with ungapped lengths ranging from 976 to 1143 bp. Since the missing data constituted less than 5% of the total alignment, all sequences were retained without trimming, and used in subsequent phylogenetic analysis.

The Maximum Likelihood (ML) phylogenetic tree was constructed in IQ-TREE v.3 (Wong et al., 2025). The best-fit nucleotide substitution models were determined by ModelFinder (Kalyaanamoorthy et al., 2017) implemented in IQ-TREE for both the Bayesian

Information Criterion (BIC) and the Akaike Information Criterion (AICc). Node supports were evaluated using ultrafast bootstrap (UFBoot; 3000 replicates) (Hoang et al., 2018) and the Shimodaira–Hasegawa approximate likelihood ratio test (SH-aLRT; 1000 replicates) and the approximate Bayesian support (aBayes), with the –bnni option to minimize potential bootstrap overestimation. Based on the BIC, the GTR+F+I+G4 model was selected as the best-fit model for the ML analysis, whereas AICc favored GTR+F+I+R3 for Bayesian Inference (BI). Since MrBayes does not explicitly implement the "+R3" rate scheme, the Bayesian analysis was conducted under the GTR+I+G model, which represents an equivalent formulation using a gamma distribution with four rate categories. The BI was constructed in MrBayes v.3.2.7 (Ronquist et al., 2020). Two independent Markov Chain Monte Carlo (MCMC) analyses were run, each consisting of four chains (one cold and three heated) for 10 million generations, sampling every 1,000 generations, discarding the initial 25% as burn-in. Convergence between the runs and adequate mixing were verified by ensuring that the average standard deviation of split frequencies was below 0.01 and that potential scale reduction factors (PSRF) approached 1.0 for all parameters. The resulting posterior distribution was summarized as a 50% majority-rule consensus tree, with branch lengths proportional to the mean posterior estimates. The Effective Sample Size (ESS) values were evaluated in TRACER v.1.7.2 (Rambaut et al., 2018), and only parameters with ESS ≥ 200 were considered reliable. The ML and Bayesian trees were not combined into a single consensus topology. Instead, the ML tree was used as the reference, and posterior probability (PP) values obtained from the Bayesian analysis were manually added to the corresponding nodes using FigTree v.1.4.4 (Rambaut, 2018). To match the nodes, clades were compared based on their taxon composition and overall tree structure. When a node received a support value of ≥ 70 in both analyses, the two support values were shown together on the same branch. If only one analysis provided support (≥ 70), the unsupported one was indicated with a (–) symbol. No changes were made to the branch structure, and no nodes were repositioned during this process. The resulting consensus trees were visualized, and editing PP were used to assess nodal support in FigTree v.1.4.4 software (Rambaut, 2018). Although SH-aLRT and aBayes metrics were calculated to internally evaluate node stability, only UFBoot and Bayesian posterior probability (PP) values were added onto the final consensus tree. This approach was taken to prevent visual clutter, avoid potential confusion among multiple support values, and enhance the overall comprehensibility of the phylogenetic relationships (Fig. 2).

To examine haplotype relationships within the '*subterraneus*' species group, cyt*b* sequences were analyzed using a parsimony approach. For this purpose, the TCS algorithm (Clement et al., 2000) implemented in PopART v.1.7 (Leigh & Bryant, 2015) was applied. The dataset includes both newly generated sequences (10 haplotypes of 11 samples) and the sequences obtained from GenBank (61 haplotypes among 66 samples; Table 1). *M. arvalis* outgroup samples were excluded from the haplotype network. The resulting network was then visualized to examine the overall genealogical structure and to assess the relative frequencies of haplotypes among lineages.

Population Structure

Neutrality tests, including Fu and Li's F*, Fu's Fs, Fu and Li's D*, and Tajima's D, were performed to assess deviations from neutrality across the identified lineages. Haplotype and nucleotide diversity indices were estimated using DnaSP v.6.12.03 (Nei &

Li, 1979; Tajima, 1989; Fu & Li, 1993; Fu, 1997; Rozas et al., 2017). Population differentiation was evaluated through pairwise F_{ST} values calculated in DnaSP v.6.12.03 (Rozas et al., 2017), while intra- and interspecies mean genetic distances were computed using the Kimura 2-parameter (K2P) model implemented in MEGA X (Kumar et al., 2018). Analysis was performed using the aligned cyt*b* dataset, including all sequences used in the phylogenetic reconstruction, and analyses were performed under the pairwise deletion option to exclude gaps and ambiguous sites. Pairwise distances were computed both within *M. daghestanicus* (separated into Anatolian and Caucasian subclades defined by ML and Bayesian trees) and between clades/species (*M. daghestanicus*, *M. fingeri*, and *M. subterraneus*). Standard deviations of mean distances were estimated through 1000 bootstrap replicates.

Results

Phylogenetic Analysis

The ML tree based on the mitochondrial cyt*b* sequences from 77 individuals, with *Microtus arvalis* included as an outgroup, recovered the following major lineages within the '*subterraneus*' species group of the subgenus *Terricola* (Fig. 2). The outgroup *M. arvalis* (from France and Spain) was placed basally, clearly separating it from the ingroup clade comprising *M. daghestanicus*, *M. fingeri*, and *M. subterraneus*. Within the ingroup, three well-supported lineages were recovered, corresponding to the three main species.

M. daghestanicus formed a diverging lineage, sister to the clade uniting *M. fingeri* and *M. subterraneus*. The separation among these three lineages was strongly supported (UFBoot ≥ 94–98 across the backbone node), confirming their reciprocal monophyly and the robustness of the inferred topology. Two main geographic lineages within *M. daghestanicus* were identified. Sequences from the Greater Caucasus region, including localities within the Russian Federation (Kabardino-Balkaria, Karachay-Cherkess, North Ossetia, Nizhny Tsey, Elbrussky region, Zolsky Ekiptsoko, and Cew Valley) and Georgia, formed a major geographic lineage characterized by long internal branches and multiple nested hierarchical splits. Within this core region, node support ranged from moderate to maximal (UFBoot = 70–100, PP = 0.71–1.0); however, a few minor internal nodes exhibited lower or unsupported UFBoot values (< 70) despite holding moderate Bayesian posterior probabilities (PP = 0.71–0.84). The Anatolian populations (Ardahan, Artvin, Kars, and Hakkari), together with the western Caucasian sample from Krasnaya Polyana, constituted a second subclade with moderate-to-strong support (UFBoot = 82, PP = 0.98). Within this subclade, the northeastern populations (Ardahan, Artvin, and Kars) and Krasnaya Polyana clustered into a distinct 'North' group (UFBoot = 70, PP = 0.98), standing as a sister to the Hakkari lineage with moderate-to-strong supported divergence (Fig. 2). The population (Berçelan Yaylası, 3324 m a. s. l.) formed a distinct peripheral branch at the southernmost limit of the species' distribution, i.e., the northwestern end of the Zagros Mountain range, and above its known high elevation limit. This group appeared as a genetically cohesive and well-supported lineage, represented by closely related haplotypes and short internal branches.

The *M. fingeri* lineage was recovered as a monophyletic group with strong support

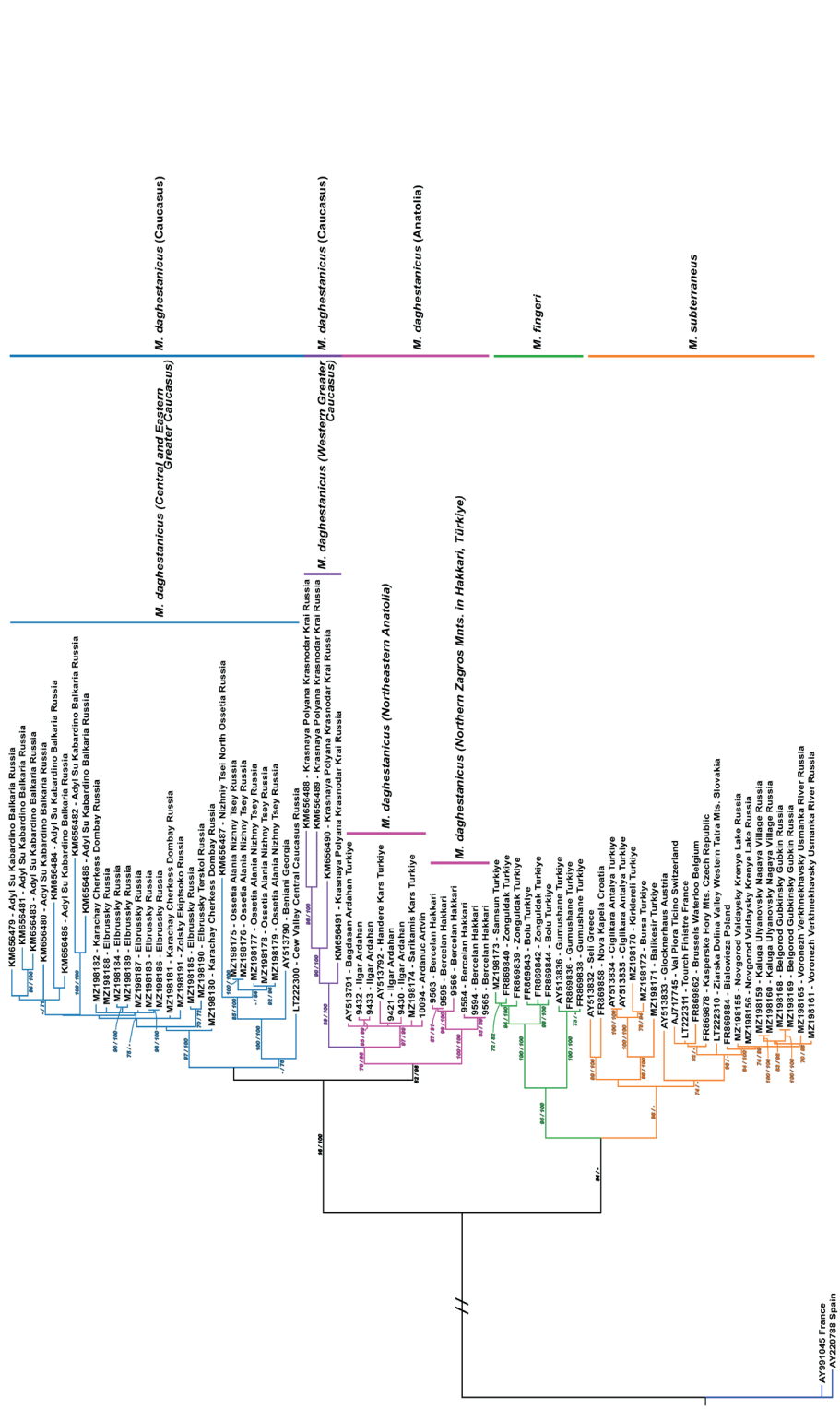

Fig. 2. Combined ML and BI phylogeny of the '*subterraneus*' species group (subgenus *Terricola*) inferred from mitochondrial cyt*b*. Labels above the nodes indicate ML ultrafast bootstrap (UFBoot ≥ 70% are shown); values below nodes are Bayesian posterior probabilities (PP ≥ 0.70 are shown). *M. arvalis* (France and Spain) used as the outgroup. Scale bar indicates substitutions per site

(UFBoot = 95, PP = 1.0). Two well-defined subclades were observed within this lineage: the first clustered the western and central Black Sea populations (Zonguldak, Bolu, and Samsun), while the second comprised the eastern Black Sea populations from Gümüşhane. Both subclades received maximal support (UFBoot = 100, PP = 1.0), indicating limited but geographically structured genetic divergence across northern Türkiye (Bogdanov et al., 2021) (Fig. 2).

The *M. subterraneus* lineage was strongly supported (UFBoot = 98, PP = —) and displayed two well-defined geographic subdivisions. The first subclade included European and Balkan samples (Greece, Croatia, and Türkiye: Kırklareli, Antalya, Bursa, and Balıkesir), showing high support (UFBoot = 98–99, PP = 1.0). The second subclade included European populations from Austria, Switzerland, France, Slovakia, Belgium, the Czech Republic, Poland, and the Russian Federation, separated from the Anatolian–Thracian lineage with moderate support (UFBoot = 74, PP = —) (Fig. 2). The divergence between the European and Balkan-Anatolian clades suggests a long-term geographic isolation likely maintained since the Pleistocene glacial cycles (Jaarola et al., 2004; Abramson et al., 2021).

The BI analysis based on the same cyt*b* dataset yielded a nearly identical topology to the ML tree. Both inference methods resolved the same three major monophyletic lineages corresponding to *M. daghestanicus*, *M. fingeri*, and *M. subterraneus*. The posterior probabilities (PP ≥ 0.70) were largely congruent with the ML bootstrap values (UFBoot ≥ 70), indicating moderate to strong statistical support across principal nodes (Fig. 2).

Population Structure Analysis

Pairwise Kimura 2-parameter (K2P) distances revealed a consistent pattern of genetic divergence among taxa within the subgenus *Terricola*, as summarized in Table 2. The mean divergence between the Anatolian and Caucasian lineages of *M. daghestanicus* was 0.0404 ± 0.0043, indicating moderate intraspecific differentiation. Genetic distances between *M. daghestanicus* (Caucasus) and *M. fingeri* and *M. subterraneus* were 0.0955 ± 0.0085 and 0.0890 ± 0.0081, respectively, whereas the Anatolian lineage showed slightly lower divergences from the same species (0.0850 ± 0.0083 and 0.0803 ± 0.0081). The interspecific distance between *M. fingeri* and *M. subterraneus* averaged 0.0573 ± 0.0056. Collectively, these values support a clear genetic separation between the Anatolian and Caucasian *M. daghestanicus* lineages, with divergence levels lower than those observed among distinct *Terricola* species (Jaarola et al., 2004; Tougard, 2017; Bogdanov et al., 2021). This pattern is fully consistent with the phylogenetic tree topology and the known

Table 2. **Mean Kimura 2-parameter (K2P) genetic distances based on cyt*b***

Taxon / Lineage	Mean K2P distance with ± SD
M. daghestanicus (Anatolia and Caucasus)	0.0404 ± 0.0043
M. daghestanicus (Anatolia) — *M. fingeri*	0.0850 ± 0.0083
M. daghestanicus (Caucasus) — *M. fingeri*	0.0955 ± 0.0085
M. daghestanicus (Anatolia) — *M. subterraneus*	0.0803 ± 0.0081
M. daghestanicus (Caucasus) — *M. subterraneus*	0.0890 ± 0.0081
M. fingeri — *M. subterraneus*	0.0573 ± 0.0056

± SD: Standard Deviation.

geographical distribution of the taxa.

Patterns of genetic diversity were broadly comparable across the examined lineages within the subgenus *Terricola*, although the magnitude of variation differed among groups (Table 3). As expected from a wide and topographically complex distribution, *M. daghestanicus* (Caucasus) displayed the highest nucleotide diversity ($\pi = 0.03627$) and one of the richest haplotype pools (30 haplotypes among 32 individuals). This diversity was not evenly distributed; most of it was concentrated within the Central and Eastern Greater Caucasus, a cluster characterized by deep internal splits and an abundance of unique haplotypes — consistent with a long-term, stable population history in the eastern Greater Caucasus.

In contrast, the Anatolian lineage of *M. daghestanicus* exhibited markedly lower nucleotide diversity ($\pi = 0.01444$), despite maintaining high haplotype richness (13 of 14 individuals). The finer subdivision within Anatolia reflected more structured dynamics: the Northeastern Anatolia (Ardahan, Artvin, and Kars) and Western Greater Caucasus (Krasnaya Polyana) showed the highest haplotype diversity (Hd = 1.000) but only moderate nucleotide diversity (0.02783), whereas the Hakkari lineage, located at the species' southernmost limit, retained fewer haplotypes (5 of 6 individuals) and the lowest nucleotide diversity (0.00658) (Table 3). This gradient — deep divergence in the Caucasus, intermediate diversity in the Northeastern Anatolia, and shallow diversity in Hakkari — mirrors the branching pattern in the phylogeny and the geometry of the haplotype network, where the North group forms a star-like cluster and Hakkari emerges as a compact peripheral unit (Figs 2, 3).

Both *M. fingeri* (9 of 9 individuals) and *M. subterraneus* (19 of 22 individuals)

Table 3. **Neutrality and genetic diversity tests for the subgenus *Terricola* ('*subterraneus*' species group) taxa based on cyt*b* sequences**

Taxon / Lineage	N	h	Hd	π	Tajima's D	Fu & Li's D*	Fu & Li's F*
M. daghestanicus (Anatolia)	14	13	0.989	0.01444	+0.234 (n.s.)	−0.270 (n.s.)	−0.152 (n.s.)
M. daghestanicus (Caucasus)	32	30	0.996	0.03627	−1.370 (n.s.)	1.102 (n.s.)	−1.416 (n.s.)
M. daghestanicus (Central and Eastern Greater Caucasus)	28	26	0.995	0.02881	−1.259 (n.s.)	−1.478 (n.s.)	−1.661 (n.s.)
M. daghestanicus (NE Anatolia and West Greater Caucasus)	12	12	1.000	0.02783	−0.843 (n.s.)	−0.494 (n.s.)	−0.668 (n.s.)
M. daghestanicus (Northern Zagros Mnts. in Hakkari, Türkiye)	6	5	0.933	0.00658	+0.630 (n.s.)	+0.342 (n.s.)	+0.437 (n.s.)
M. fingeri	9	9	1.000	0.02647	+0.983 (n.s.)	+0.896 (n.s.)	+1.031 (n.s.)
M. subterraneus	22	19	0.987	0.02251	−1.195 (n.s.)	−1.706 (n.s.)	−1.813 (n.s.)

N: Number of samples, h: Number of haplotypes, Hd: Haplotype diversity, π (pi): Nucleotide diversity, n.s., not significant at $p > 0.10$.

Table 4. **Genetic differentiation (F_{ST}) among *Terricola* ('*subterraneus*' species group) taxa based on cyt*b* sequences. (Fixation index; Hudson et al., 1992)**

Taxon / Lineage	*M. daghestanicus* (Anatolia)	*M. daghestanicus* (Caucasus)	*M. daghestanicus* (Central and Eastern Greater Caucasus)	*M. daghestanicus* (**NE** Anatolia and West Greater Caucasus)	*M. daghestanicus* (Northern Zagros Mnts. in Hakkari, Türkiye)	*M. fingeri*	*M.subterraneus*
M. daghestanicus (Anatolia)	—	0.36103 ***	0.44183 ***	0.13438 **	0.30278 ***	0.75105 ***	0.77621 ***
M. daghestanicus (Caucasus)	0.36103 ***	—	–0.01654	0.28575 ***	0.46585 ***	0.65954 ***	0.67360 ***
M. daghestanicus (Central and Eastern Greater Caucasus)	0.44183 ***	-0.01654	—	0.38255 ***	0.54375 ***	0.69745 ***	0.71559 ***
M. daghestanicus (NE Anatolia and West Greater Caucasus)	0.13438 **	0.28575 ***	0.38255 ***	—	0.45894 ***	0.68991 ***	0.70493 ***
M. daghestanicus (Northern Zagros Mnts. in Hakkari, Türkiye)	0.30278 ***	0.46585 ***	0.54375 ***	0.45894***	—	0.79179 ***	0.81970 ***
M. fingeri	0.75105 ***	0.65954 ***	0.69745 ***	0.68991 ***	0.79179 ***	—	0.55402 ***
M. subterraneus	0.77621 ***	0.67360 ***	0.71559 ***	0.70493 ***	0.81970 ***	0.55402 ***	—

* $0.01 < P < 0.05$; ** $0.001 < P < 0.01$; *** $P < 0.001$.

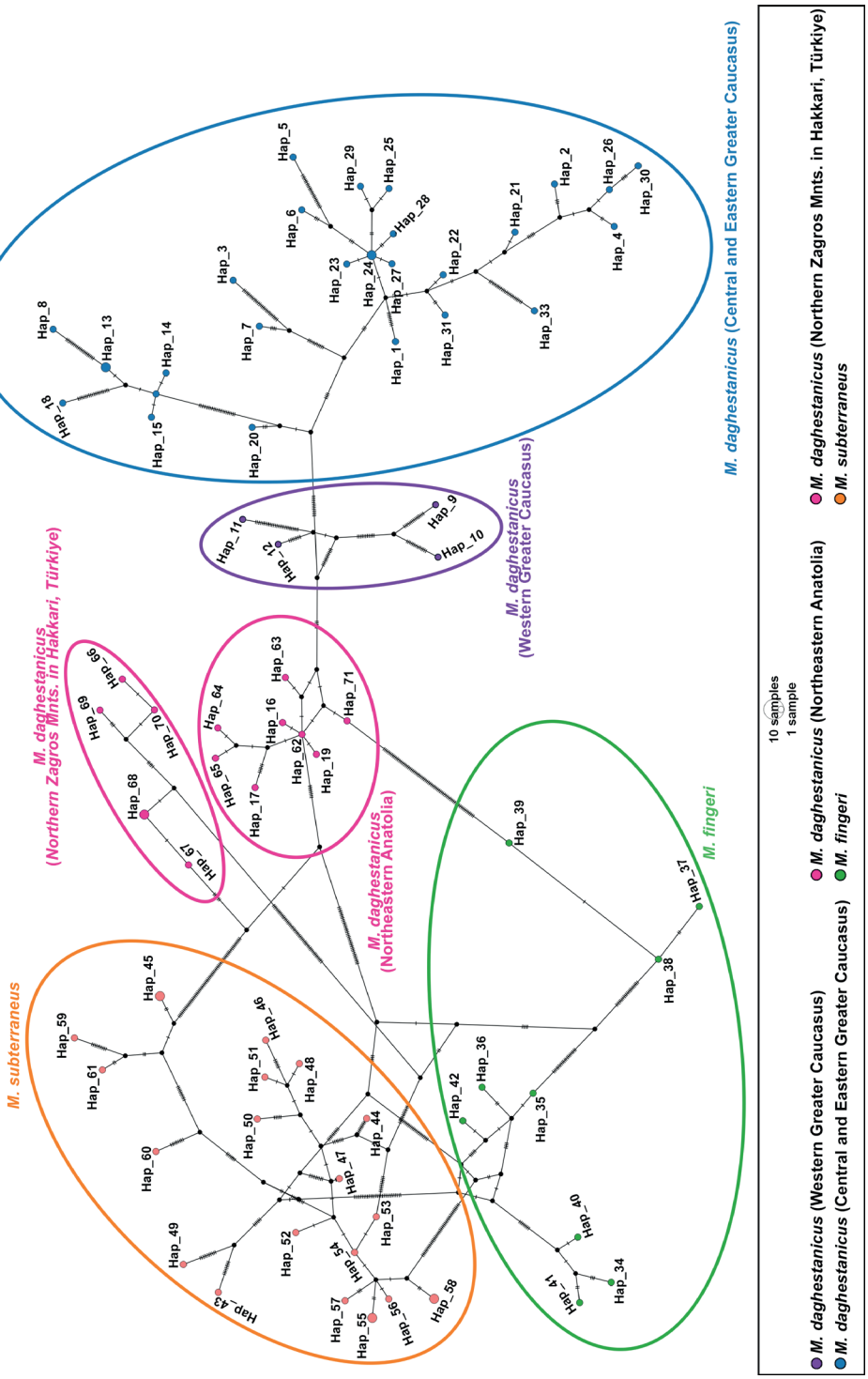

***Fig.* 3.** Haplotype network constructed using the TCS method. The shaded area colors follow the branch colors in Fig. 2

also exhibited high haplotype diversity (Hd = 1.000 and 0.987, respectively), with intermediate nucleotide diversity values, fitting their broad distributions and long-term demographic stability (Table 3).

Neutrality statistics (Tajima's D, Fu & Li's D*, and Fu & Li's F*) were non-significant across all groups, and their values fluctuated around zero. Slightly positive estimates in some lineages (e. g., *M. daghestanicus* (Northern Zagros Mnts. in Hakkari, Türkiye) and *M. fingeri*) contrast with moderately negative values in others (e. g., *M. daghestanicus* (the Central and Eastern Greater Caucasus) and *M. subterraneus*), yet none approached statistical significance (Table 3).

Most notably, the differences among the three *M. daghestanicus* sublineages — the Central and Eastern Greater Caucasus, the Northeastern Anatolia–Western Greater Caucasus, and the southern marginal population from Hakkari located within the Zagros Mountains — are reflected more clearly in phylogenetic and network topologies than in neutrality indices, which are less sensitive to deep geographic structuring (Figs 2, 3).

Pairwise F_{ST} values revealed a clear and geographically structured pattern of differentiation among lineages within the subgenus *Terricola* (Table 4). As expected for intraspecific comparisons, a relatively moderate level of differentiation was observed between the Anatolian and Caucasian groups of *M. daghestanicus* (F_{ST} = 0.361), indicating restricted historical connectivity across the eastern Black Sea–southern Caucasus corridor. When the finer sublineages are considered, differentiation becomes more structured: the NE Anatolia and West Greater Caucasus showed moderate divergence from the Central and Eastern Greater Caucasus (F_{ST} = 0.383), whereas its separation from the Hakkari lineage was stronger (F_{ST} = 0.459), mirroring the phylogenetic branching order and the topology of the haplotype network (Figs 2, 3). The Eastern Anatolian population from Hakkari consistently displayed the highest genetic differentiation paired with clear isolation from all northern groups (F_{ST} = 0.303–0.544). These values align with the distinct peripheral placement of Hakkari haplotypes in the network and support its interpretation as a geographically isolated, range-edge sublineage shaped by topographic and historical barriers (Table 4).

Interspecific comparisons were markedly higher. Differentiation between *M. daghestanicus* with *M. fingeri* (F_{ST} = 0.660–0.792) and *M. subterraneus* reached (F_{ST} = 0.674–0.820), reflecting deep and longstanding genetic separation. The contrast was strongest between *M. daghestanicus* (Northern Zagros Mnts. in Hakkari, Türkiye) and *M. subterraneus* FST = 0.820), congruent with their pronounced mitochondrial divergence and fully non-overlapping haplotype pools. Even the closest species pair, *M. fingeri* and *M. subterraneus*, retained substantial structure (F_{ST} = 0.554), in line with previous phylogenetic assessments (Table 4).

As a result, F_{ST} values support the evolutionary scenario inferred from the phylogenetic tree and haplotype network (Figs 2, 3, Table 4): (1) three internally coherent but geographically separated sublineages within *M. daghestanicus*, (2) limited or no gene flow at the scale of the species complex, and (3) strong species-level boundaries among the *Terricola* taxa.

Haplotype Network Analysis

The haplotype network (Fig. 3) revealed a clear genetic structuring among the *Terricola* taxa. A total of 71 haplotypes among 77 individuals were identified, each forming well-delimited species-level clusters separated by several muta-

tional steps. In particular, *M. fingeri* and *M. subterraneus* formed compact, non-overlapping haplotype groups, fully consistent with the deep divergence observed in the ML phylogeny.

Within *M. daghestanicus*, the northeastern Anatolian populations (Ardahan, Artvin, and Kars), together with the Western Greater Caucasian sample from Krasnaya Polyana, consistently clustered into a coherent group. This lineage displayed a star-like configuration centered on a high-frequency haplotype (Hap_62), from which several closely related haplotypes (Hap_63–65 and Hap_71) radiated outward. GenBank sequences from Ardahan and Kars (Hap_16, Hap_17, and Hap_19) were also embedded within this cluster, reinforcing the genetic integrity of the northeastern Anatolian lineage (Fig. 3). The placement of the Krasnaya Polyana haplotypes (Hap_9–12) within this group is particularly noteworthy, revealing a previously unrecognized connection between the Western Greater Caucasus and northeastern Anatolia — a pattern not detected in earlier studies due to the absence of combined sampling from these regions (Figs 2, 3).

By contrast, the southeastern Anatolian/Zagros Mnts. population (Hakkari) formed a compact peripheral cluster composed of a small number of closely related haplotypes (Hap_66–70) (Fig. 3). Although not fully star-shaped, the low internal divergence within this group points toward a potential scenario of refugial isolation or a localized founder event at the southernmost limit of the species' distribution.

Discussion

M. daghestanicus has a restricted distribution across the Greater and Lesser Caucasus in Georgia and the Russian Federation, northeastern Türkiye, Armenia, Azerbaijan, and northwestern Iran (Kryštufek & Shenbrot, 2022). Its taxonomic placement within the genus *Microtus* has been repeatedly reassessed, largely due to the complex biogeographic and phylogenetic history of the '*subterraneus*' species group (Jaarola et al., 2004; Tougard, 2017; Bogdanov et al., 2021). Our study expands this framework by providing new mitochondrial data from northeastern and southeastern Türkiye, thereby refining the species' phylogeographic structure and extending its known distribution in Anatolia.

A key biogeographic outcome of this work is the first confirmed record of *M. daghestanicus* from Hakkari, which represents both the southeasternmost Anatolian locality and the global southernmost range limit of the species. The occurrence of *M. daghestanicus* in Hakkari, localized within the Zagros orogenic belt, indicates that this lineage extends into one of the most geologically complex mountain ranges of the Middle East. The presence of *M. daghestanicus* at elevations of up to 3324 m a. s. l. (Berçelan Yaylası), substantially exceeds earlier records near 2900 m (Baskevich et al., 2017, 2021; Kryštufek & Shenbrot, 2022), and thus underscores its ecological plasticity within the montane environments. In Ardahan, Artvin, Kars, and Hakkari, the species co-occurs with *M. obscurus* in alpine meadows and rocky slopes above the forest belt, offering insights into sympatric dynamics and habitat partitioning involving the subgenus *Terricola*.

Both ML and Bayesian phylogenetic analyses, supported by previously publis-

hed datasets (e. g., Jaarola et al., 2004; Tougard, 2017; Bogdanov et al., 2021) consistently resolved three major species within the '*subterraneus*' species group — *M. subterraneus*, *M. fingeri*, and *M. daghestanicus* — with moderate to strong nodal support (UFBoot ≥ 70%; PP ≥ 0.70). Within *M. fingeri*, the presence of geographically structured clades across the Black Sea region aligns with Bogdanov et al. (2021), who suggested possible hidden diversity. In contrast, the deep and well-supported subdivisions within *M. subterraneus* are consistent with previous phylogeographic reconstructions (e. g., Jaarola et al., 2004; Baskevich et al., 2017; Bogdanov et al., 2021; Çetintürk, 2022).

Our analysis also corroborates the pronounced mitochondrial structuring reported in *Terricola* voles (e. g., Jaarola et al., 2004; Martínková & Moravec, 2012; Baskevich et al., 2016; Bogdanov et al., 2024). Divergence values between *M. daghestanicus* (Anatolian and Caucasian) and *M. subterraneus* (8.0–8.9%) closely match estimates in Baskevich et al. (2021), while F_{ST} values ranging from 0.36 (Anatolia–Caucasus) to 0.82 (*M. daghestanicus* (Northern Zagros Mnts. in Hakkari, Türkiye) — *M. subterraneus*) clearly exceed thresholds for strong population differentiation (Wright, 1978) (Tables 2, 4).

Our results resolve three geographically coherent sublineages within *M. daghestanicus*: (i) a highly diverse Central and Eastern Greater Caucasus lineage, (ii) a Northeastern Anatolia–Western Greater Caucasus lineage, and (iii) a distinct southeastern Anatolian/Zagros lineage in Hakkari. This structure has likely been shaped by the rugged topography of the Caucasus—Türkiye—Iran (CTI) region, where deep valleys, high mountain ridges, and habitat mosaics restrict dispersal and promote lineage divergence (Bogdanov et al., 2021). Importantly, the network and tree topologies converge on the same pattern: the Caucasus core harbors long internal branches and high haplotype diversity, whereas northeastern Anatolia exhibits reduced diversity and a star-like structure indicative of a relatively recent peripheral expansion (Figs 2, 3).

A key finding is the placement of the Krasnaya Polyana sample in the Western Greater Caucasus. We show that Krasnaya Polyana clusters tightly with Ardahan, Artvin, and Kars rather than with the Central and Eastern Greater Caucasus localities. This relationship points to a shared Western-Caucasian mitochondrial ancestry and suggests that Northeastern Anatolia is genetically linked not to the Georgian populations from the Central and Eastern Greater Caucasus (e. g., Beniani) but to the Western Greater Caucasus corridor. Similar interpretations appear in Macholán et al. (2001) and Tougard (2017), who emphasized that Caucasus is the primary center of origin for *M. daghestanicus* and *Terricola* lineages in general. This conclusion also coincides with the previous result based on multilocus data showing decreasing diversity toward range margins (Bogdanov et al., 2021) and with Turkish datasets demonstrating the limited haplotype richness of Anatolian populations (Çetintürk, 2022).

Taken together, our results strongly indicate that Northeastern Anatolia should not be regarded as an independent evolutionary lineage but rather as an extension of the Western Greater Caucasian mitochondrial radiation (Figs 2, 3). The identification of a distinct Hakkari lineage further highlights the role of the southeastern Anatolian mountains as biogeographic isolates along the southern fringe of the spe-

cies' distribution. The combination of phylogenetic, network, and population-genetic evidence underscores the CTI region as a dynamic and historically structured landscape, where elevational gradients and climatic oscillations jointly shape lineage divergence within the '*subterraneus*' species group (Tougard, 2017; Bogdanov et al., 2021, 2024).

We note that some parts of the species' distribution remain under-sampled; therefore, broader range-wide sampling will be required to fully resolve phylogeographic structure across the entire range. Notably, our sampling did not include a large portion of the known range of *M. daghestanicus* in the Lesser Caucasus mountains in Georgia and Armenia, which are geographically close to the sampled locations in Ardahan, Artvin, and Kars provinces in Türkiye. It is likely that the Lesser Caucasus will show genetic similarity to the Anatolian population, but obtaining the genetic material from the remaining range of the species is necessary to complete the phylogeographic framework.

Future studies integrating multilocus or SNP-based genomic datasets, wider geographic sampling, and targeted investigations of potential contact zones will be essential to test for historical introgression and to clarify the deeper demographic history of these lineages. Coupling such data with calibrated molecular clocks will allow a more precise reconstruction of divergence times and help illuminate how Pleistocene climatic changes and regional geomorphology contributed to the diversification of *Terricola* voles across the Caucasus—Türkiye—Iran region.

Authors Contribution. Conceptualization, M.S. and K.K.K.; formal analysis, M.S., A.Y. and K.K.K.; investigation, M.S., F.Ç., O.Ç. and K.K.K.; writing — original draft preparation, K.K.K.; writing — review and editing, M.S., F.Ç., O.Ç., A.Y. and K.K.K.; project administration, M.S. This study forms part of K.K.K.'s PhD thesis. All authors approved the final version of the manuscript.

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Conflict of interest. The authors declare no conflict of interests.

Data Availability. The data supporting Table 1 of this study have been deposited and are publicly accessible in the Zenodo repository under the DOI: https://doi.org/10.5281/zenodo.20630827. Additionally, the newly generated mitochondrial cyt*b* sequence data have been deposited in the GenBank database under accession numbers PX637176–PX637186.

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