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Cytochrome *b* yields new insight into taxonomic scope of *Microtus schidlovskii* (Rodentia, Arvicolinae, *Microtus*)

Tanya Zorenko*, Toni Koren & Boris Kryštufek

ABSTRACT. *Microtus schidlovskii* is a member of social voles (subgenus *Sumeriomys*) known from a small range in the highlands of Armenia. Similar voles were reported from Anatolia and Lebanon but were mainly ascribed to another enigmatic species *M. irani*. We assessed taxonomic position of *M. schidlovskii* from Armenia and its relationships with seven other species of social voles using molecular data. Phylogenetic reconstructions were based on a 409 bp fragment of cytochrome *b M. schidlovskii* and reference samples of *M. irani*, including *M. irani karamani* from Turkey and Lebanon. *M. irani* within its current scope emerged to be paraphyletic with respect to *M. schidlovskii*. Mean K2P distances in the *irani-schidlovskii-karamani* cluster were the highest (0.038) between the *irani* and the *schidlovskii* lineages and the lowest (0.028) between the *schidlovskii* and the *karamani* lineages; the distance separating the *irani* and *karamani* lineages was intermediate (0.032). The *irani-schidlovskii-karamani* group is genetically more variable than any other species group of social voles. We conclude that voles from Lebanon and Turkey (*M. irani karamani*) are conspecific with *M. schidlovskii* from Armenia. Furthermore, genetic divergence between *M. irani* and *M. schidlovskii* is the lowest among the species of social voles. And finally, our study restricted geographic scope of *M. irani* to its type locality in Shiraz.

KEY WORDS: *Microtus schidlovskii*, phylogeny, taxonomy, cytochrome *b*.

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Цитохром *b* приводит к новому пониманию таксономического статуса *Microtus schidlovskii* (Rodentia, Arvicolinae, *Microtus*)

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РЕЗЮМЕ. Полевка Шидловского *Microtus schidlovskii* Argyropulo, 1933, занимающая небольшой ареал в высокогорье Армении, является представителем общественных полевок подрода *Sumeriomys*. Близкие формы обнаружены в Анатолии и Ливане, однако, их обычно относят к мало изученному виду *M. irani*. С помощью молекулярного маркера оцениваются таксономические отношения *M. schidlovskii* из Армении и семи других видов общественных полевок. Филогенетические реконструкции основаны на фрагменте гена цитохрома *b* (409 bp). *M. schidlovskii* образует сестринскую группу с M. *irani*, наиболее близка оказывается *M. irani karamani* из Турции и Ливана. *M. irani* является парафилетической группой по отношению к *M. schidlovskii.* Генетическая дистанция в кластере *irani-schidlovskii-karamani* наибольшая между *irani* и *schidlovskii* (0.038), наименьшая (0.028) между линиями *schidlovskii* и *karamani*; дистанция, разделяющая линии *irani* и *karamani* промежуточная (0.032). Группа *irani-schidlovskii-karamani* генетически более изменчива по сравнению с другими видами общественных полевок. Согласно полученным результатам, полевки из Ливана и Турции (*M. irani karamani*) конспецифичны *M. schidlovskii* из Армении. При этом генетическая дистанция между *M. irani* и *M. schidlovskii* наименьшая в группе общественных полевок. Наши исследования ограничивают ареал *M. irani* областью Шираза.

КЛЮЧЕВЫЕ СЛОВА: *Microtus schidlovskii*, филогения, таксономия, цитохром *b*.

Introduction

Social voles are one of the youngest, rapidly evolving and species-rich groups from a specious arvicoline genus *Microtus* Schrank, 1798. They are either classified in a subgenus *Sumeriomys* Argyropulo, 1933 (Argyropulo, 1933; Gromov & Erbajeva, 1995; Abramson & Lissovsky, 2012; Zorenko, 2013), or as a *socialis* species groups within the subgenus *Microtus* (Jaarola *et al*., 2004). Social voles are a sister group to the *arvalis* species group (Martínková & Moravec, 2012). Rapid speciation pulse in *Sumeriomys*, which was apparently triggered towards the end of the Middle Pleistocene, produced in rather short period more than 10 extant species (Kryštufek *et al*., 2010).

The diploid chromosome numbers of social voles vary between 46 and 64 (Zima *et al*., 2013). In late 1980s Ayrumyan *et al.* (1986) convincingly demonstrated species independence of *M. schidlovskii* Argyropulo, 1933. Their results were corroborated subsequently by Akhverdyan *et al*. (1991a, b) and Golenishchev *et al.* (2002). M. *schidlovskii* is a cryptic species and differs from *M. socialis* Pallas, 1773 in lower diploid number of chromosomes.

First cross-breeding trials among various taxa of social voles date back into 1950s (Zakharyan, 1958). Crossing of *M. schidlovskii* × *M. socialis binominatus* Ellermann, 1941 produced in the first generation sterile hybrid males and fertile hybrid females (Orlov, 1971). These results were corroborated in subsequent studies (Akhverdyan *et al*., 1991; Makaryan *et al.*, 1991; Zorenko *et al*., 1997).

Recently social voles with diploid number of chromosomes 2n = 60 were found in two localities in eastern Anatolia (Yiðit *et al*., 2006). Another population of 2n = 60 social voles from Balkusan (Taurus Mts.) appeared similar in cytochrome *b* sequence to topotypes of *M. irani* Thomas 1921 and was considered to be a divergent lineage of this species (Kryštufek *et al*., 2009). Because of genetic and morphological differences between voles from Balkusan and Shiraz, which is the type locality of *M. irani*, the former were described as a new subspecies *M. i. karamani* Kryštufek, Vohralík, Zima, Koubínova & Bužan, 2010 (Kryštufek *et al*., 2010). Karyotype of *M. irani* is not known with certainty (Zima et al., 2013). Diploid number 2n = 62 was reported from Shiraz and ascribed to *M. irani* (Golenishchev *et al*., 2002), however this may belong as well to *M. socialis*, which is known to occur in this part of Iran (Kryštufek & Kefelio□lu, 2001). Another 2n = 60 chromosomal form from Central Anatoly (Kefelio□lu & Kryštufek, 1999) was described as a new species *M. anatolicus* Kryštufek & Kefelio□lu, 2001 (Kryštufek & Kefelio□lu, 2001b). Recently *M. i. karamani* was found also in northern Lebanon. The identification was based on a partial sequence of cytochrome *b* gene but the material was not karyotyped (Kryštufek *et al*., 2013). In conference proceedings Golenishchev and Abramson (2011) report results on molecular data suggesting that Schidlovsky's vole and *M. irani karamani* may belong to the same taxon. The similar idea was advocated by Zorenko (2013) on the basis of chromosomal similarity between the two forms.

The application of molecular markers played a crucial role in stabilizing the taxonomy of social voles (Kryštufek *et al*., 2009, 2012), however, the mitochondrial sequence of *M. schidlovskii* remained unknown. This species was believed to be morphologically well defined among social voles by the excessive length of proximal stalk of baculum (Argyropulo, 1933).

The purpose of this study is to define the taxonomic scope of *M. schidlovskii* from Armenia using partial sequence of cytochrome *b* gene. Next we compared *M. schidlovskii* with a chromosomal form of *M. irani karamani* (2n = 60).

Material and Methods

We studied cytochrome *b* (cyt*b*) in a specimen of *M. schidlovskii* from Talin District in Armenia which is 40 km away from the *terra typica* of the species. Taxonomic identity of voles from Talin was confirmed in kariological analyses and hybridization trials (Golenishchev *et al*., 2002). DNA was extracted from dry museum skin using a QIAamp DNA Mini kit (Qiagen). The extracted DNA was badly degraded, which restricted our analysis to a 409 bp cyt*b* fragment. The amplification followed protocol in Kryštufek *et al*. (2013). GenBank accession number for the new sequence of *Microtus schidlovskii* is KJ739801.

For the phylogenetic analysis, further 36 haplotypes belonging to seven species were downloaded from GenBank (Jaarola *et al*., 2004; Kryštufek *et al*., 2009, 2012, 2013): *M. hartingi* Barret-Hamilton, 1903 from Macedonia (Accession No. FJ767744), Greece (AY513804), and Turkey (FJ767745-7, FJ767751-2); *M. guentheri* Danford & Alston, 1880 from Syria (FJ767743, AY513805), Israel (AY513806) and Lebanon (KC953620-1); *M. dogramacii* Kefelio□lu & Kryštufek, 1999 from Turkey (AY513793-5); *M. anatolicus* Kefelio□lu, 2001 from Turkey (FJ767740-2); *M. irani* from Turkey (FJ767748-50), Lebanon (KC953617-9) and Iran (FJ767739); *M. paradoxus* Ognev et Heptner, 1928 from Turkmenistan (KC953622-4); and *M. socialis* from Georgia (AY513829-30), Ukraine (KC953625-6), Russia (KC953627) and Iran (AY513831).

Nucleotide, amino acid composition and genetic distances were analyzed assuming a Kimura 2 parameter (K2P) sequence evolution with 10^4 bootstraps in the MEGA v. 4 program (Tamura *et al*., 2011). The most appropriate models of DNA substitution for the data were identified using MRMODELTEST 2.3 (Nylander, 2004). Both the Akaike Information Criterion (AIC) and the hierarchical Likelihood Ratio Test (hLRT) were used. Phylogenetic analysis was conducted with the Bayesian inference (BI), using the program MRBAYES 3.1.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003), and Maximum Likelihood (ML) as implemented in the program PhyML 2.4.5 (Guindon & Gascuel, 2003; Anisimova & Gascuel, 2006).

The phylogenetic inferences were performed with a general time-reversible model (GTR+G+I) (G = 0.5804 and I = 0.5479). Four Monte Carlo Markov chains were run simultaneously for 6.5 x 10^6 generations, with the resulting trees sampled every 500 generations. Bayesian posterior probabilities (BPP) were used to assess branch support of the BI tree. Convergence for posterior probabilities was checked by examining the generation plot visualized with TRACER v1.4 (Rambaud & Drummond, 2007).

The GTR+G model was used for ML analysis. Branch support (BP) in the ML tree was estimated by 10^3 bootstrap replicates. The topologies resulting from these two methods were compared using a Shimodaira–Hasegawa test (Shimodaira & Hasegawa, 1999) imple-

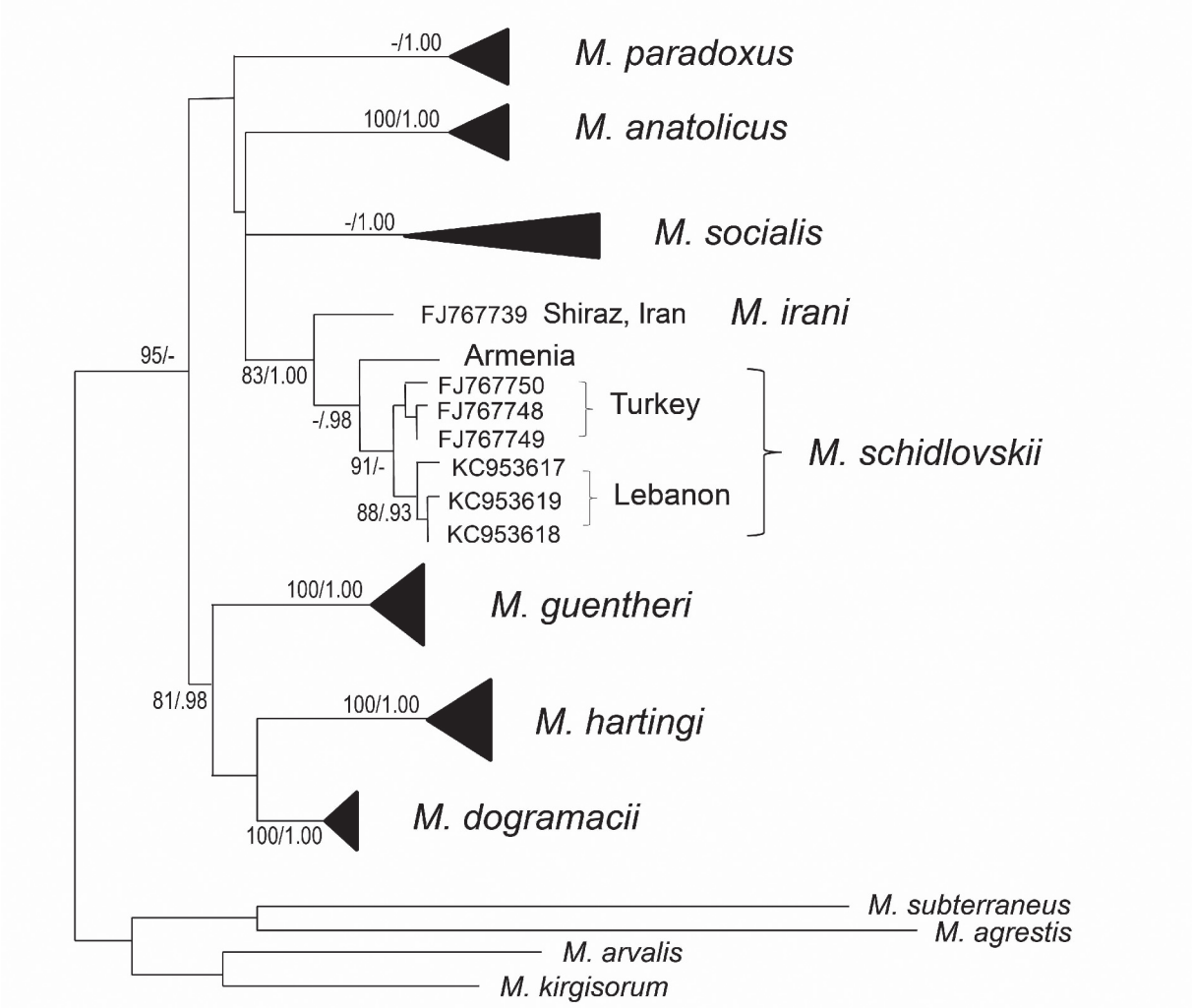

Figure 1. Maximum likelihood tree reconstructed from a 409 bp cytochrome *b* sequences of social voles and rooted with *Microtus agrestis, M. subterraneus, M. kirgisorum,* and *M. arvalis*. The numbers on the branches correspond to bootstrap supports (BP > 80%) and posterior probability values (BPP > 0.90). The triangles represent species of social voles which are based entirely on published haplotypes.

mented in PAUP* 4.010b (Swofford, 2002) with 10^3 bootstrap replicates. We considered BPP > 0.95 as "good", and BPP = 0.90–0.95 as "moderate" support, in line with other authors. For branch support in the ML tree we accepted BP > 90% as "good" support, and BP = 80–90% as "moderate" support.

Trees were rooted with four *Microtus* species (Jaarola *et al*., 2004): *M. arvalis* Pallas, 1779 (AY220766), *M. subterraneus* Selys-Longchamps, 1836 (AJ717745), *M. kirgisorum* Ognev 1950 (AY513809), and *M. agrestis* Linnaeus, 1761 (AY167213).

Results

The trees obtained with the two probabilistic methods (ML and BI) present an inconsistency at a deeper node but yielded congruent results at terminal nodes. Therefore, the basal division into two major lineages (the *socialis* and the *guentheri* lineage sensu Kryštufek *et al*., 2012) was supported only in the ML tree (BP = 95%), while the BI phylogenetic reconstruction placed *M. paradoxus* into well supported (BPP = 1.00) sister position against all other social voles. Because the Shimodaira-Hasegawa test did not reveal significant differences between these trees (P=0.33) only the ML tree is shown (Figure 1). In line with published results (Kryštufek *et al*., 2012) seven major groups emerged which matched species recognized in earlier studies: *M. paradoxus*, *M. anatolicus*, *M. socialis*, *M. irani*, *M. guentheri*, *M. hartingi,* and *M. dogramacii*. New sequence of *M. schidlovskii* clustered with reference samples of *M. irani*, specifically as a sister group to *M. irani karamani* from Turkey and Lebanon. Therefore, *M. irani* within its current scope (Kryštufek *et al*., 2009) is paraphyletic with respect to *M. schidlovskii*. The monophyly of the *irani-schidlovskii* lineage was

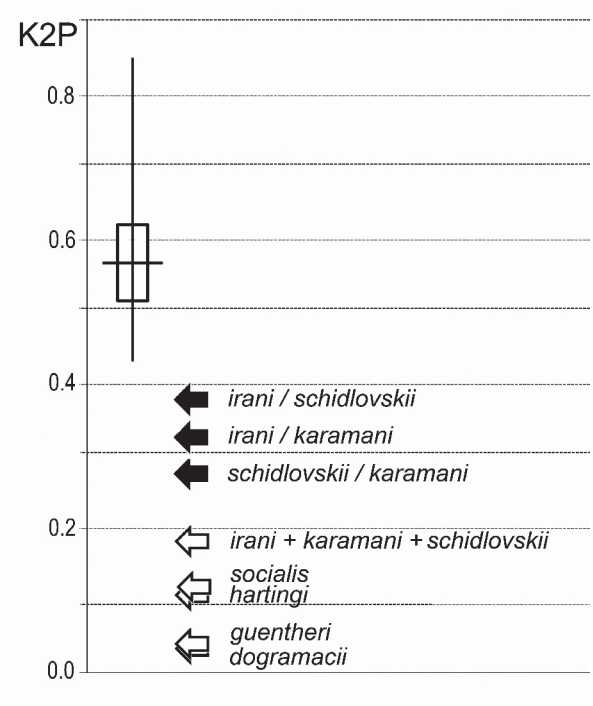

Figure 2. Box and whiskers plot of mean K2P genetic distances between the seven major lineages of social voles shown in Fig. 1. Bold line represents total range, boxes are central quartiles and horizontal line is median value. Black arrows point on distances between major sublineages of the *irani-schidlovskii-karamani* group. White arrows show within-species divergences. This distance was zero in *M. paradoxus* and *M. anatolicus* (not shown).

not supported due to unresolved polytomy in the *socialis*-group of species. On the other hand, all branches within this lineage benefited good support. *M. irani* from the type locality (Shiraz, Iran) hold strongly supported (BP = 83%, BPP = 1.00) basal position in the group.

Mean K2P genetic distances between the major lineages were from 0.043 (between *M. socialis* and *M. dogramacii*) and 0.085 (between *M. hartingi* and *M. anatolicus*), and within group distances (excluding *irani-schidlovskii-karamani* group) were 0.017 (in *M. socialis*) and lower. Genetic distances between the three major monophiletic lineages of the *irani-schidlovskii-karamani* group were between the K2P distances separating major lineages (i.e. species) and distances within these groups (Figure 2). Mean K2P distance was the highest (0.038) between the *irani* and the *schidlovskii* lineages and the lowest (0.028) between the *schidlovskii* and the *karamani* lineages; the distance separating the *irani* and *karamani* lineages was intermediate (0.032). This pattern may suggest a stepping stone expansion of the lineage, but more evidence is required for firm conclusions. In any case, the *irani-schidlovskii-karamani* group is genetically more variable than any other species group of social voles.

Discussion

Our analysis of a 409 bp fragment of cyt*b* gene placed the sequence of *M. schidlovskii* from Armenia inside the *M. irani* cluster, more specifically as a sister group of *M. irani karamani*. Such a result is not sursprising considering that both taxa share identical diploid number of chromosomes. Evidently, *karamani* is conspecific with *schidlovskii* In accordance with the Principle of Priority as stipulated in the Article 23 of the International Code for Zoological Nomenclature (1999), *schidlovskii* is the senior name for the species and *karamani* is its junior synonym. There are morphological differences between *schidlovskii* and *karamani*, particularly so in the shape of baculum, in addition to a relatively large K2P genetic divergence, which suggest significant intraspecific structuring and the existance of well differentiated subspecies. This, however, is task for further research. For the time being we can claim with confidence, that the range of *M. schidlovskii* extends from the Armenian highlands in the east, to the Lebanese mountains in the west (Figure 3).

More puzzling are taxonomic relationships between the *schidlovskii-karamani* cluster and *irani* from Shiraz. Genetic distances among the three major monophyletic lineages of the *irani-schidlovskii-karamani* group in our study were between the K2P divergences which separate species of social voles and the distances within them. Therefore, based on molecular markers, *M. irani* and *M. schidlovskii* can be classified either as two deeply divergent infraspecific lineages or as two weakly defined species. Morphological differences between the type series of *M. irani* and *M. schidlovskii-karamani* are obvious (Kryštufek & Kefelio□lu, 2001b, Kryštufek *et al*., 2010). Karyotype of *M. irani*, on the other hand, is not known with certaintainty (Zima *et al*., 2013). Clearly, we need to gain more information in order to stabilize species taxonomy in *Sumeriomys*.

Though karyological data do not allow one to directly reconstruct phylogeny, the trend of reduction of number of chromosomes from high 64 and 62 to low 46 is clear. The first pair of autosomes in *M. schidlovskii* is large (Akhverdyan *et al*., 1991; Golenischev *et al*., 2002), similarly as in *M. socialis* and *M. paradoxus*. Emergence of taxa with diploid number 54 (*M. hartingi* and *M. guentheri*) possibly resulted from three simple translocations. The largest pair of autosomes in these voles consists of elements which are homologous to autosomes in 62-chromosomal voles (Golenischev *et al.,* 2002b). Distribution of heterochromatin blocks in *M. hartingi* and *M. socialis* suggests that differences between their karyotypes are due to centromeric transformations.

Two voles with 60 chromosomes, both from the *socialis* group (*M. schidlovskii* and *M. anatolicus*) were found in different localities in the Armenian uplands and in Anatolia. Their karyotypes, which differ in a single translocation, were achieved independently in each species from a hypothetical ancestral karyotype by

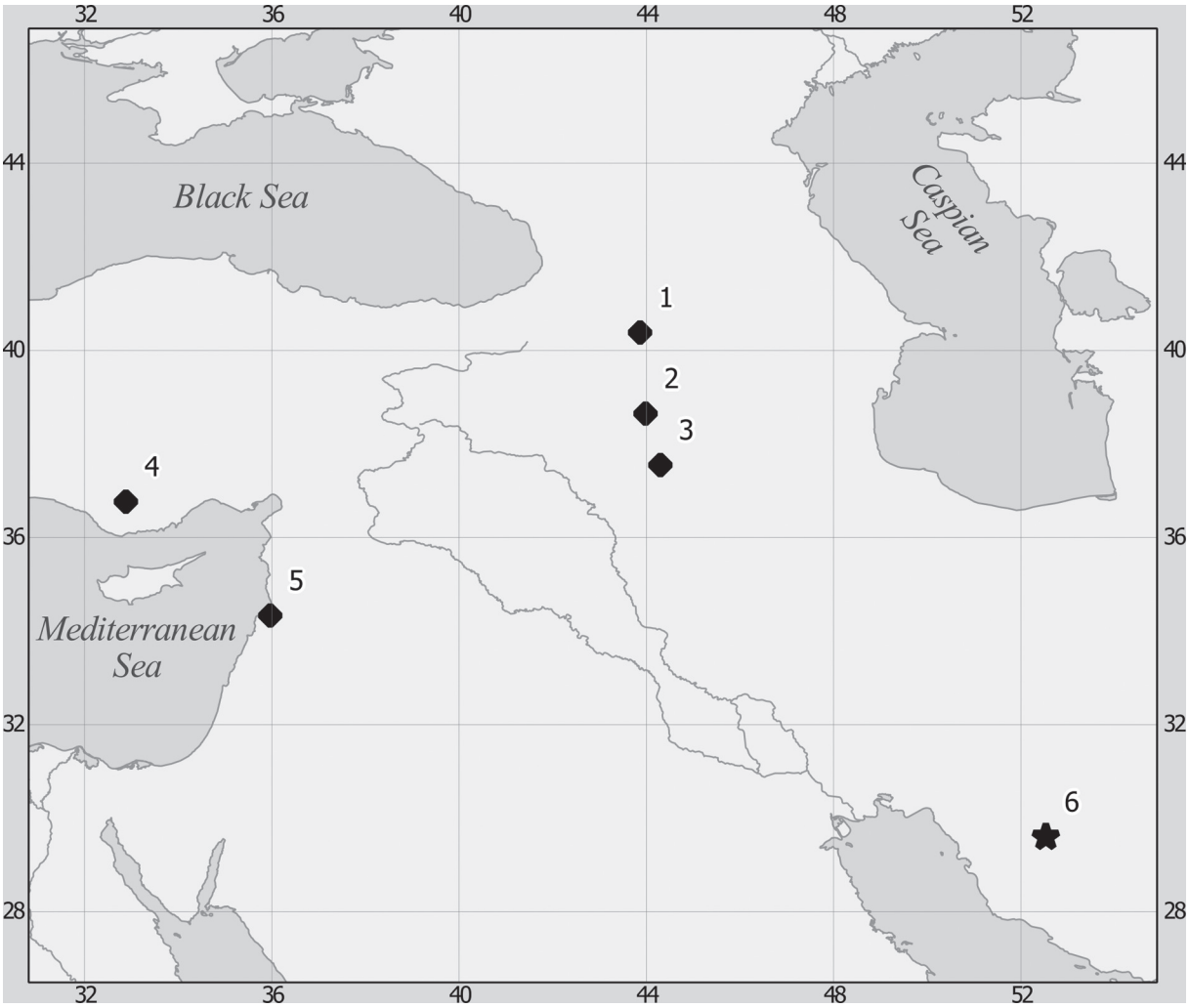

Figure 3. A map of distribution of samples of *Microtus irani-schidlovskii-karamani* group used in this study. *M. schidlovskii*: 1 — Armenia, Talin, 2 — Turkey, Yüksekova*, 3 — Özalp*, 4 — Balkusan, 5 — Lebanon; 6 — *M. iran:* Iran, Shiraz.
* species identification is based on chromosomal evidence (Yi□it *et al*., 2006).

a simple centromeric-telomeric tandem fusion of two acrocentric autosomes.

The distribution range of *M. schidlovskii* in western Armenia (Nalbandsky and Leninakan basins), northern spurs of Ararat, the Pambaksky ridge) is mountain isolate, probably from the Quaternary Period. According to a number of authors (Shidlovsky, 1941; Vereschagin, 1942) isolation was connected with lifting of the Armenian uplands. *M. schidlovskii* is allopathric to *M. socialis* (subspecies *binominatus*) which occupies eastern and southeastern parts of Armenia. The two species are segregate along the elevational gradient: *M. schidlovskii* penetrates into higher elevations (up to 1400–1700 m) while *M. s. binominatus* does not live above 600 m above sea level.

Our study again restricted the geographic scope of *M. irani* to its type locality in the Zagros Mts (Iran). It is puzzling to guess whether the range is genuinely so small or we are simply ignorant of its real extent for a shortage of reliable data. Environmental heterogeneity in the area is outstanding and this effect was further exacerbated in the past by geological and climatic dynamics. Mountains, normally detaining streams of damp air masses from the Arabian and Mediterranean seas, periodically turned dry which desiccate the entire Iranian Plateau and formed extensive saline deserts and semi-deserts. Areas of excessively arid habitat fragmented previously contiguous populations of voles, interrupted genes flow between these fragments and promoted speciation in allopatry. We may presume that populations went extinct in great number of fragments when conditions for mesophilic taxa further deteriorated. Small range of *M. irani* near Shiraz is possibly just one of originally many fragments which for some reason escaped fate of extinction.

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