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GENETIC VARIATION AND TAXONOMIC STATUS OF DAHL'S JIRD (*MERIONES DAHLI*, RODENTIA, MURIDAE)[1]

© 2024 O. G. Nanova[a,*], V. S. Lebedev[a], E. N. Solovyeva[a], A. A. Lisenkova[b], V. Yu. Bogatyreva[a], E. D. Zemlemerova[c], V. A. Matrosova[d]

[a]*Zoological Museum, Lomonosov Moscow State University, Moscow, 125009 Russia*

[b]*Department of Vertebrate Zoology, Lomonosov Moscow State University, Moscow, 119234 Russia*

[c]*Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, 119081 Russia*

[d]*Department of Structural and Functional Genomics, Engelhardt Institute of Molecular Biology, Russian Academy of Sciences, Moscow, 119991 Russia*

**e-mail: nanovaolgag@gmail.com*

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Dahl's jird, *Meriones dahli*, is a critically endangered species restricted to a small area in central Transcaucasia. The phylogenetic position of Dahl's jird within the Midday jird species complex was assessed based on the DNA of museum material. Both mitochondrial and nuclear gene sequences were employed. Dahl's jird has been found to be a sister group close to *M. penicilliger*, which is distributed in Turan. This result suggests the existence of a late Middle Pleistocene dispersal corridor for psammophilic species that is known to have connected the Transcaucasian and Transcaspian regions.

Keywords: cryptic species, Central Asia, Transcaucasia, species complex, Gerbillinae

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The Dahl's jird (*Meriones dahli* Shidlovsky 1962) is a narrow endemic of the Ararat Plain where it inhabits relict sands in Armenia, Nakhichevan, and Northeastern Turkey. The historic range of the Dahl's jird was divided into several isolated patches and covered less than 300 ha in the 1960s (Bulut, 2022; Sahakyan et al., 2009). However, Sahakyan et al. (2009) report finding no specimens during an intensive study in Armenia in 2006–2007. Thus, *M. dahli* is now considered critically endangered or extinct in Armenia due to anthropogenic habitat destruction (Sahakyan et al., 2009; Wilson et al., 2017; Dando, 2021).

The Dahl's jird belongs to the species complex of the Midday jird, which also includes several Central Asian species (Heptner, 1968; Nanova, 2014; Nanova et al., 2020): the northern *M. meridianus* Pallas 1773 (distribution from the North Caucasus through North Kazakhstan to Dzungar Basin), the southern *M. penicilliger* Heptner 1933 (Karakum, Kyzylkum, and Southeast Kazakhstan), and the eastern *M. psammophilus* Milne-Edwards 1871 (most East Central Asian deserts) (Fig. 1). The Dahl's jird was first described as the subspecies *M. meridianus dahli* by Shidlovsky (1962) from Sadarak steppe in Armenia on the basis of external body traits, such as coat color and hind foot length. It has dark and brightly colored fur on the back, from brownish-ocher to brownish-ash, light abdomen, and black tail brush. Later, Dyatlov and Avanyan (1987) elevated the Dahl's jird to a full species rank based on hybridization experiments and the physiological traits associated with plague resistance. The karyotype of Dahl's jird was described by Korobitsyna (1969), highlighting the specific features of its Y-chromosome morphology.

According to the study of craniometric variation within the Midday jird superspecies complex (Nanova, 2014), cranial morphology of the Dahl's jird is similar to that of the nominative Midday Jird species *M. meridianus*.

Recently, the first genetic data on the Dahl's jird for several specimens from Turkey (Bulut, Karacan, 2021) were published, including sequences of one mitochondrial and one nuclear gene (cyt*b* and IRBP, respectively). The phylogenetic analysis confirmed that the Dahl's jird belongs to the species complex of the Midday jird, and its authors suggested to treat the Dahl's jird as a subspecies, *M. meridianus dahli*. However, that study did not discuss the relationships among the genetic lineages (species) within the Midday jird species complex.

[1] Supplementary material (online resource 1, 2, 3) to the article are located at the link https://doi.org/10.31857/S0044513424030116

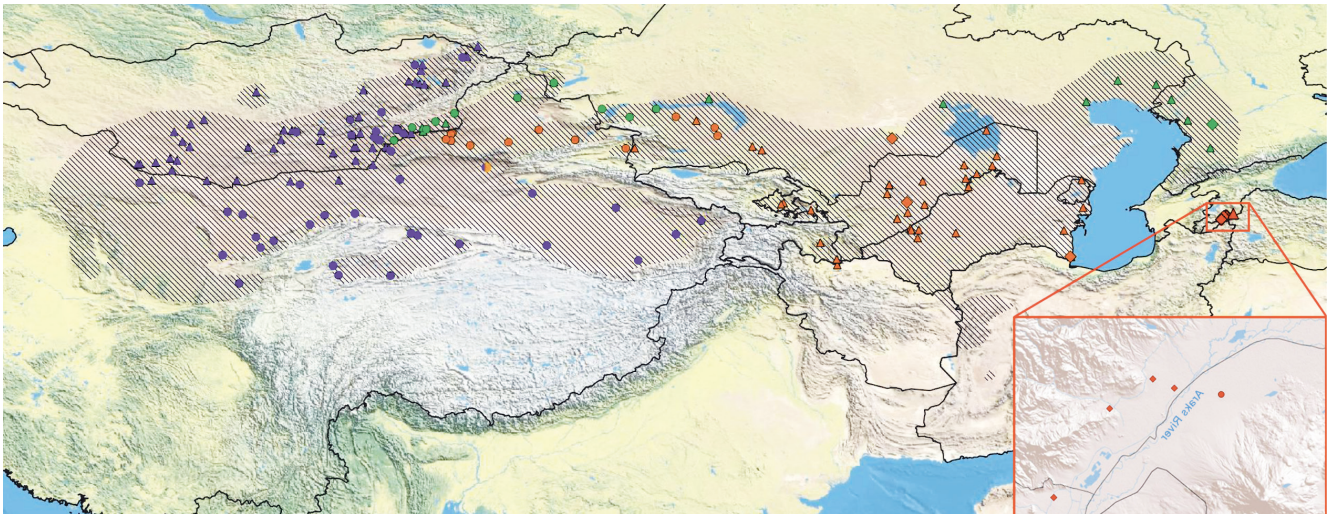

Fig. 1. Map showing distribution of taxa belonging to *Meriones meridianus* species complex. Green – *M. meridianus*, orange – *M. pennicilliger*, blue – *M. psammophilus*, red – *M. dahli*, triangle – morphological data (Nanova, 2014), circle – previous genetic data, diamond – original genetic data. Hatched area – approximate range of species complex. Red frame shows a more detailed distribution map of *M. dahli* specimens.

Thus, genetic, morphological, caryological, and hybridological data provide controversial results. In the present study, we attempt to resolve the existing taxonomic issues in the Midday jird species complex using phylogenetic analyses of extended genetic data. Here we try to elucidate relationships between Dahl's jird and *M. meridianus, M. penicilliger*, and *M. psammophilus*.

MATERIALS AND METHODS

DNA Extraction, Amplification, and Sequencing

The original sample set of *M. dahli* used in the current study included nine specimens collected in 1958–1967 in Armenia and Nakhichevan (Azerbaijan) and stored in the collection of the Section of Mammalogy of the Zoological Museum of Lomonosov Moscow State University (ZMMU) (table 1).

Small pieces of dried skin (approximately 2 × 2 mm) from the rostrum or ventral region were used for DNA extraction. To avoid contamination, we conducted extraction and amplification of DNA from the museum specimens in the ZMMU Cabinet of Historical DNA, equipped exclusively for procedures with museum DNA specimens, where no previous analysis on fresh tissues had been performed. We utilized a protocol with the QIAamp DNA MiniKit (Qiagen, Germany), modified to include an overnight lysis step at 56 °C and longer incubation with EB buffer (5 min) during the purification step. In addition, in the present study we obtained genetic data for two *M. meridianus* specimens and three *M. penicilliger* specimens collected in recent years (table). Molecular procedures using DNA extracted from the fresh tissues were performed as in Nanova et al. (2020).

We amplified the mitochondrial cytochrome *b* gene (cyt*b*) and fragments of two nuclear genes: exon 1 of the interphotoreceptor binding protein gene (IRBP, partial exon 1) and exon 11 of the breast cancer type 1 susceptibility protein gene (BRCA1, partial exon 11). In the museum specimens, the DNA was highly degraded; thus, only short fragments (~200–400 bp) were obtained using a combination of internal primers designed for this study (Online Resource 1, Table S1). The PCR program for amplification of short fragments included an initial denaturation at 95 °C for 3 min, 45 cycles of 30 s at 95 °C, 30 s at the annealing temperature (Online Resource 1, Table S2), and 30 s at 72 °C, followed by a final extension at 72 °C for 6 min. All stages of the extraction and PCR processes included a negative control.

PCR products were separated in 1.5% agarose gel stained with ethidium bromide, visualized in UV light, sliced, and purified using a GeneJET Gel Extraction Kit (ThermoFisher Scientific, United States), according to the manufacturer's instructions to remove primer dimers and potential non-specific products. The nucleotide sequences were determined using an ABI PRISM 3500xL automatic sequencer with BigDye Terminator Chemistry v. 3.1 (Applied Biosystems, United States) at the Genome Center for Collective Use of the Research Centre for Medical Genetics using PCR primers (Online Resource 1, Table S1).

In total, we obtained sequences of partial or complete cyt*b* and partial IRBP for nine specimens of *M. dahli* and partial BRCA1 for four of those specimens. The dataset also contained GenBank sequences originating from the Turkish population of the Dahl's jird examined previously by Bulut and Karacan (2021)

Table 1. *Meriones* samples sequenced for this study

Meriones species	Locality	Latitude	Longitude	Specimen code	cyt*b* accession number	BRCA1 accession number	IRBP accession number
M. dahli	Armenia: Ararat prov., Araks valley, S of Artashat	39.9392	44.5442	A-S85717-1967	OL448963	n/a	OL448973
M. dahli	Armenia: Ararat prov., Araks valley, S of Artashat	39.9392	44.5442	A-S85719-1967	OL448964	OL355119	OL448974
M. dahli	Armenia: Ararat prov., Araks valley, near Aygezard (Anastasavan)	39.9586	44.6034	A-S159307-1967	OL448965	n/a	OL448975
M. dahli	Armenia: Ararat prov., Araks valley, S of Artashat	39.9586	44.6034	A-S85701-1967	OL448966	n/a	OL448976
M. dahli	Armenia: Ararat prov., Araks valley, S of Artashat	39.9586	44.6034a	A-S85672-1967	OL448967	OL355120	OL448977
M. dahli	Armenia: Ararat prov., Araks valley, Vedi dis.	39.8962	44.7222	A-S77293-1958	OL448968	OL355121	OL448978
M. dahli	Armenia: Ararat prov., Araks valley, Vedi dis.	39.8962	44.7222	A-S77296-1958	OL448969	n/a	OL448979
M. dahli	Azerbaijan: Nakhchivan, Sadarak	39.7083	44.8761	Az-S77235-1963	OL448970	n/a	OL448980
M. dahli	Azerbaijan: Nakhchivan, Sadarak	39.7083	44.8761	Az-S77236-1963	OL448971	OL355122	OL448981
M. penicilliger	Uzbekistan: Bukhara reg., S slope of Kuldjuktau mnts.	40.7505	63.8294	Uz-S198857-2017	OL448958	n/a	n/a
M. penicilliger	Kazakhstan: Kyzylorda reg., 10 km W of Inkardarya	44.6005	64.7227	K-S202747-2019	OL448959	n/a	n/a
M. penicilliger	Turkmenistan: Balkan prov., near Esenguly (Gasan-Kuli)	37.4736	53.9740	Turkm-S52295-1941	OL448960	n/a	n/a
M. meridianus	Russia: Kalmykia, near Komsomolskii	45.3872	45.9968	Kalm-35	OL448961	n/a	n/a
M. meridianus	Russia: Kalmykia, near Khulkhuta	46.3081	46.3883	Kalm-200	OL448962	OL355118	OL448972

Notes. Specimen name is coded in the following format: country (K – Kazakhstan, Uz – Uzbekistan, Turkm – Turkmenistan, Kalm – Kalmykia, A – Armenia, Az – Azerbaijan) – museum (or field) number – collection year. For historical specimens, a close approximation of the geographical coordinates is given.

(three cyt*b* haplotypes and four IRBP sequences). We also included in the analysis multiple sequences of other taxa from the Midday jird species complex, in particular 28 sequences of *M. meridianus* (26 from GenBank and two sequenced de novo), 36 sequences of *M. psammophilus* (all from GenBank), and 16 sequences of *M. penicilliger* (13 from GenBank and three sequenced de novo) (table; Online Resource 2, Table S3).

All sequences were assembled in SeqMan (DNASTAR, Lasergene, United States) and the alignments were built in BioEdit v. 7.0.4.1 (Hall, 1999). The sequences obtained in this study were deposited in GenBank (see table).

Phylogenetic Analyses of Mitochondrial Data

Phylogenetic trees were reconstructed under maximum likelihood (ML) and Bayesian inference (BI) criteria. The alignment consisted of 92 sequences of gerbils belonging to the Midday Jird species complex. Nucleotide sequences from *Meriones unguiculatus* and *M. libycus* were used as outgroups. The ML reconstructions were performed in IQTree version 1.6 (Nguyen et al., 2015). The ModelFinder routine (Kalyaanamoorthy et al., 2017) was used to identify the optimum partitioning scheme and best-fit substitution models for each subset under the Bayesian information criterion (see Online Resource 3 for the command lines used). Clade stability was estimated using Ultrafast Bootstrap (Minh et al., 2013) with 10 000 replicates.

Bayesian tree reconstruction was conducted in BEAST version 1.10 (Drummond et al., 2012) under a strict clock. Substitution models and partitioning scheme were set as in the ML analysis. Birth-death prior on tree shape was employed. The tree was calibrated using a prior distribution on the cyt*b* clock rate (lognormal, mean =0.1, standard deviation= 0.023), which corresponds to the posterior distribution generated in our previous analysis of phylogenetic relationships in the Midday jird species complex (Nanova et al., 2020). Chain and burn-in lengths were set at 30,000,000 and 3,000,000 generations, respectively. Convergence diagnostics were performed using Tracer version 1.7. Nucleotide diversity was estimated in Arlequin 3.5 (Excoffier, Lischer, 2010).

Nuclear Data Analyses

To examine the relationships among nuclear gene variants, we reconstructed median-joining networks (MJ) using PopART v.1.7 (Leigh, Bryant, 2015; https://popart.maths.otago.ac.nz). Prior to the analyses, sequences with heterozygous positions were manually phased using a parsimony approach (minimizing the total number of observed haplotypes) as suggested by Clark (1990). Alongside the sequences obtained de novo, the alignment contained sequences of *M. meridianus*, *M. psammophilus*, and *M. penicilliger*, the haplotypic phase in which was inferred using PHASE algorithm in our previous study (Nanova et al., 2020). With the IRBP data, networks were reconstructed based on either a shorter alignment containing sequences from museum specimens or a longer alignment containing GenBank sequence of *M. dahli* from Turkey.

RESULTS

Mitochondrial Data

Phylogenetic relationships among the cyt*b* haplotypes are illustrated in Fig. 2 (cyt*b*_tree). In the ML tree, all sequences of *M. dahli* form a compact highly supported cluster with pi (nucleotide diversity) estimated at 0.0004. For comparison, nucleotide diversity in regional populations of *M. meridianus, M. penicilliger*, and *M. psammophilus* is noticeably higher, ranging from 0.001 to 0.005 (median 0.004). Five of eight Dahl's jird specimens with complete cyt*b* sequences have identical haplotypes. Two other haplotypes differ from the most common variant by single transitions at the third codon positions. The *M. dahli* cluster is placed with high support as the sister group to the lineage comprising all sequences of *M. penicilliger* from West Central Asia. The latter includes haplotypes from southern Dzungar Basin, East Kazakhstan, and also newly obtained sequences from Southwestern Turkmenistan and Kyzylkum desert. The *p*-distance between the *M. dahli* and *M. penicilliger* clusters is ~3.2%, which is significantly lower than the *p*-distance between *M. dahli* + *M. penicilliger* and *M. meridianus* + *M. psammophilus* (~9.8%) or between the latter two lineages (~7.6%). It should be noted that the sequences of midday jirds from Kalmykia, which represent populations geographically most proximal to *M. dahli* range, definitely belong to the *M. meridianus* lineage. The topology of the Bayesian ultrametric tree reconstructed in BEAST is concordant with the ML tree. The divergence time between *M. dahli* and *M. penicilliger* was estimated at ~205 kya (95% HPD = 103–316 kya). However, we suggest that this result should be treated with caution, as it may be an overestimate due to the rate decay phenomenon (Ho et al., 2005).

Nuclear Data

The data on the short fragment of the IRBP gene (159 bp) shows that majority of *M. dahli* specimens (five of nine) were homozygous for the allele diagnostic of *M. penicilliger* (Fig 3*a*). At the same time, three specimens were heterozygous for the penicilliger-like and meridianus-like alleles, the latter being most common variant found across both *M. meridianus* and *M. psammophilus*. Finally, one specimen was homozygous for the meridianus-like allele. The four longer (954 bp) sequences from Turkey can be interpreted as a homozygote for the meridianus-like allele, a homozygote for the penicilliger-like allele, and two

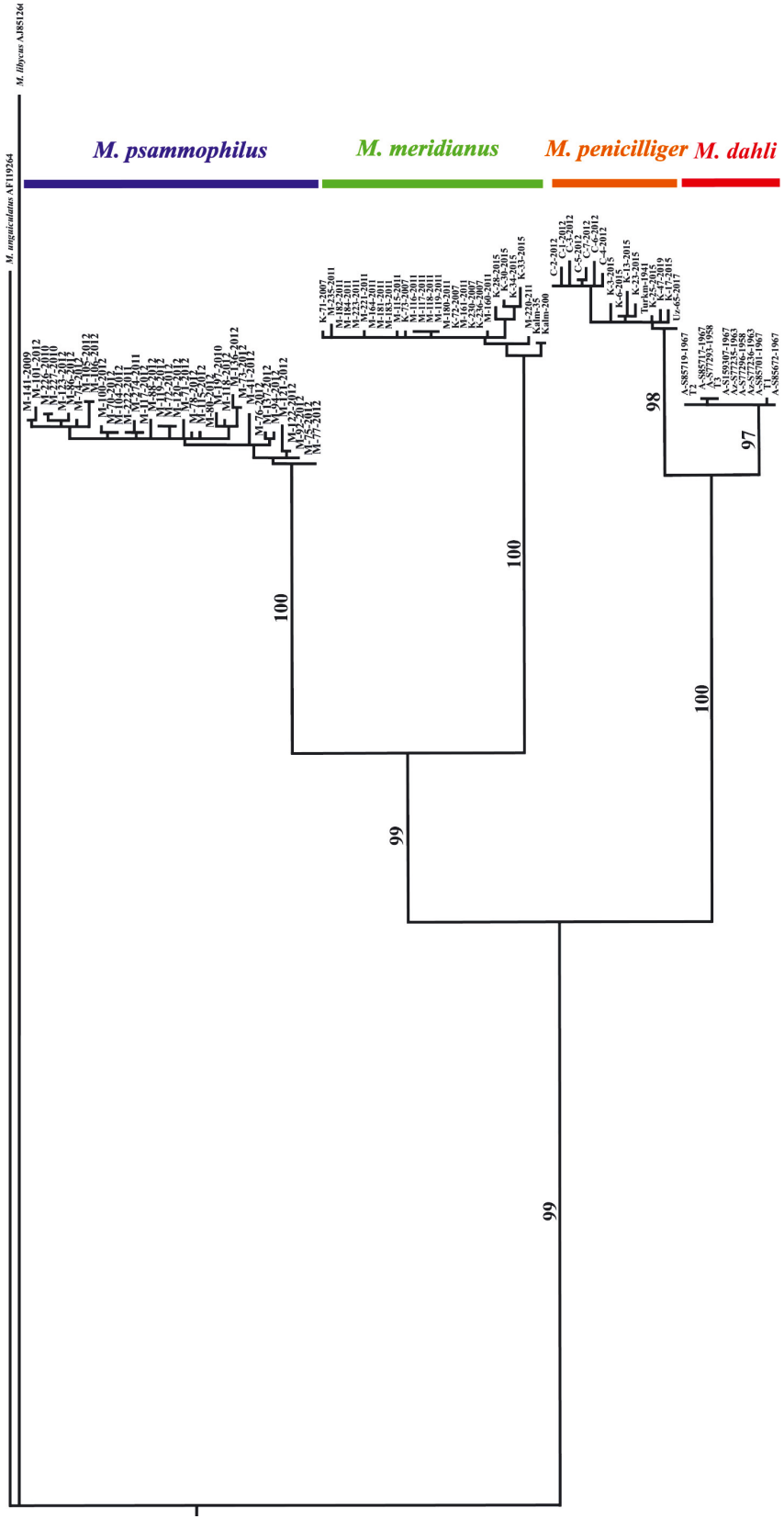

Fig. 2. Maximum likelihood tree reconstructing phylogenetic relationships among cyt*b* haplotypes in the *M. meridianus* complex. For color codes, see Fig. 1.

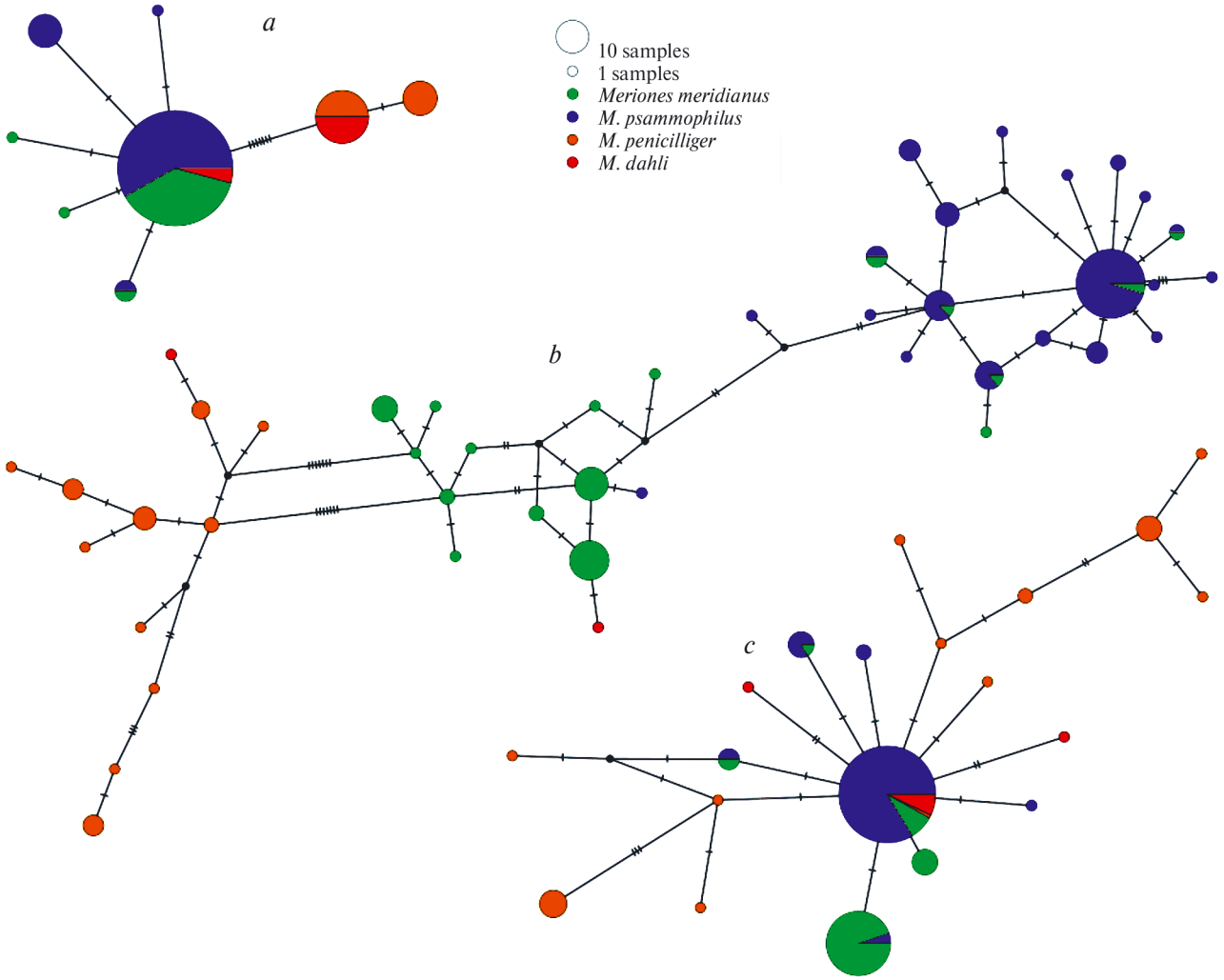

Fig. 3. Median-joining network reconstructions in PopART of relationships among nuclear gene alleles: *a* – short fragment of IRBP gene from museum specimens, *b* – longer fragment of IRBP gene using longer sequences of *M. dahli* specimens from Turkey (Bulut, Karacan, 2021), *c* – short fragment of BRCA1 gene. Circle size corresponds to the number of samples, color denotes the species (see scale and color reference in the legend). Number of streaks on branches marks mutational steps between nodes.

heterozygotes. The position of the *M. dahli* sequences in the MJ network reconstructed for the longer fragment is consistent with the reconstruction for the shorter fragment (Fig 3*b*).

The results on the short fragment of BRCA1 (355 bp) are less clear (Fig 3*c*). Two of the four *M. dahli* sequences are homozygous for the allele occurring in the most of *M. meridianus* and *M. psammophilus* but found also in one *M. penicilliger*. The same allele is present in the other two *M. dahli*, however, in combination with some unique alleles. Thus, the results for the BRCA1 gene should be regarded as indeterminate.

DISCUSSION

The genetic data analysis from both current and previous (Bulut, Karacan, 2021) studies shows that Dahl's jird individuals from Armenia, Azerbaijan, and Turkey are genetically homogeneous, thus suggesting that animals from all studied localities may have belonged to a single population, despite separation of the Turkish segment by the Aras River. The species is now passing through a severe bottleneck accompanied by range fragmentation, which is illustrated by its likely extinction in Armenia in the most recent past (Sahakyan et al., 2009).

Affiliation of the Dahl's jird with the Midday jird complex is strongly supported by genetic (Bulut, Karacan, 2021; current study), morphological (Nanova, 2014), and physiological (Dyatlov, Avanyan, 1987) data. However, the fact that the Dahl's jird is a close relative of *M. penicilliger* is rather unexpected. The latter taxon is distributed exclusively in the West Central Asian deserts such as Karakum, Qyzylkum, and Saryesik-Atyrau (Heptner, 1968; Pavlinov et al., 1990; Nanova

et al., 2020). The range of *M. dahli* is separated from most proximal populations of *M. penicilliger* by more than 800 kilometers. At the same time, the molecular pattern does not agree with morphological data (Nanova, 2014) that suggests that the Dahl's jird is close to the nominative species *M. meridianus* and in particular, to its western subspecies *M. m. nogaiorum*, distributed in the North Caucasus (minimum distance to *M. dahli* is approximatey 400 km). Nonetheless, our mitochondrial data robustly support the close relationship between the Dahl's jird and *M. penicilliger*, while the available nuclear data are consistent with this pattern. The genetic distance (cyt*b* *p*-distance = 3.2%) between these two clades can correspond to either close sister species or intraspecific lineages, the latter interpretation being more probable (Baker, Bradley, 2006).

The most interesting question that arises from the genetic data is how the distribution pattern observed in *M. dahli*–*M. penicilliger* could have evolved. A plausible scenario would imply an episode of colonization of Transcaucasia from Turan by the ancestor of *M. dahli* in the late Middle Pleistocene. West Central Asia in general, and Turan in particular, is a major center of diversity of arid fauna (Heptner, 1945) that harbors a plethora of specialized psammophiles. In contrast, the latter category is poorly represented among vertebrates of Transcaucasian deserts. The most likely colonization route is through Iran; however, the exact position of dispersal pathways suitable for psammophile species and the climatic conditions at that time remain unclear. One may hypothesize, even, that the dispersal corridor emerged during a regression along the Caspian Sea shore. It should be emphasized that no range disjunction comparable to that in *M. dahli*–*M. penicilliger* is found in the West Central Asian terrestrial psammophile tetrapods (mammals and reptiles) such as jerboas (*Paradipus*, *Eremodipus*, and *Dipus*), ground squirrels (*Spermophilopsis leptodactylus* and *Spermophilus fulvus*), piebald shrew (*Diplomesodon*), toad-head agamas *Phrynocephalus mystaceus* and *Ph. interscapularis*, racerunners *Eremias grammica* and *E. lineolata,* fringe-toed gecko *Crossobamon eversmanni*, or sand boas (*Eryx* spp.) (Bannikov et al., 1971; Gromov, Erbajeva, 1995; Ananjeva et al., 2006; Zaitsev et al., 1995). To some extent, this pattern can be attributed to relative paucity of Transcaucasian psammophile fauna. Instead, a disjunct distribution is observed in the Strauch's racerunner *Eremias strauchi* Kessler 1878 (Hosseinian Yousefkhani et al., 2016), which is, however, not a psammophile but a sclerophile. Its nominative subspecies inhabits Transcaucasia and adjacent regions of East Turkey and Northwest Iran, while *E. s. kopetdaghica* occurs in Northeast Iran and Turkmenistan, the two subspecies being separated by a gap in North Iran. High level of divergence between these taxa suggests that this dichotomy is significantly older than the *M. penicilliger* / *M. dahli* split, and thus corresponds to a different biogeographic event.

The presence of two divergent alleles (penicilliger-like and meridianus-like) in the IRBP gene of *M. dahli* can be attributed to an episode of hybridization between the Dahl's jird and *M. meridianus*, which may have dispersed from the Northern Caucasus deserts. However, this hypothesis should be tested with more loci. Dyatlov and Avanyan (1987) used two subspecies *M. m. meridianus* and *M. m. nogaiorum* in their experiments on hybridization between the Dahl's jird and the Midday jird. The results of this study indicated a significant reduction of fertility in the mixed pairs.

A previous craniometric study showed that the Midday jird complex includes three large clusters corresponding to *M. meridianus*, *M. penicilliger*, and *M. psammophilus.* These three species are all well distinguishable by skull measurements in contrast to *M. dahli*, which falls into the *M. meridianus* cluster (Nanova, 2014). The reason for the discordance between genetic and cranial morphometric data remains to be clarified. In theory, it can be explained by the retention of the plesiomorphic cranial shape in both *M. dahli* and *M. m. nogaiorum* or, alternatively, by adaptive convergence of skull morphology between these two westernmost forms of the Midday Jird complex. A correlation between habitat aridity and adaptive changes of several cranial traits was previously shown by Alhajeri and Steppan (2018). Finally, morphological similarity can be partly attributed to the consequences of the hypothetical hybridization with *M. meridianus.*

CONCLUSION

The Dahl's jird is genetically homogeneous throughout its narrow range. The genetic data indicate its close relationship with Turanian *M. penicilliger*, the divergence level is consistent with the subspecies rank for the Dahl's jird. Most probably, the current distribution range of the Dahl's jird in Transcaucasia evolved as a result of colonization from Turan via Iran, followed by range fragmentation. Based on limited nuclear data, one may hypothesize a gene flow event from North Caucasian *M. meridianus* into the Dahl's jird, which should be tested using a multilocus approach.

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COMPLIANCE WITH ETHICAL STANDARDS

No live animals were used in this work, the research is based on legal museum material.

CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

SUPPLEMENTARY INFORMATION

Online Resource 1 consists of Tables S1 and S2, which both accompany the subsection "Extraction, Amplification, and Sequencing" in the Materials and Methods section of the main text and describe the primers used in the present study. Table S1 lists all primers with the respective marker genes, sequences, and sources. Table S2 provides information on the pairwise primer combinations, as well as corresponding annealing temperatures and lengths (bp) of the target fragments of the genes used in the study.

Online Resource 2 is Table S3, which provides additional information referenced in the "Phylogenetic Analyses of Mitochondrial Data" subsection of the Materials and Methods section; it contains specimen codes (or in some cases haplotypes) with corresponding geographical localities and country of origin, species identification, GenBank accession numbers for the relevant sequences, and the references.

Online Resource 3 provides the command lines used for the ML reconstructions performed in IQTree version 1.6 (Nguyen et al., 2015) with application of ModelFinder routine (Kalyaanamoorthy et al., 2017) used to search for the optimum partitioning scheme and best-fit substitution models for each subset under the Bayesian information criterion.

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ГЕНЕТИЧЕСКАЯ ИЗМЕНЧИВОСТЬ И ТАКСОНОМИЧЕСКИЙ СТАТУС ПЕСЧАНКИ ДАЛЯ (*MERIONES DAHLI*, RODENTIA, MURIDAE)

О. Г. Нанова[1,*], В. С. Лебедев[1], Е. Н. Соловьева[1], А. А. Лисенкова[2], В. Ю. Богатырева[1], Е. Д. Землемерова[3], В. А. Матросова[4]

[1]Зоологический музей Московского государственного университета, Москва, 125009 Россия

[2]Кафедра зоологии позвоночных, Биологический факультет Московского государственного университета имени М.В. Ломоносова, Москва, 119234 Россия

[3]Институт проблем экологии и эволюции имени А.Н. Северцова Российской академии наук, Москва, 119071 Россия

[4]Лаборатория структурно-функциональной геномики, Институт молекулярной биологии имени В.А. Энгельгардта Российской академии наук, Москва, 119991 Россия

**e-mail: nanovaolgag@gmail.com*

Песчанка Даля (*Meriones dahli*) – вид, находящийся под угрозой исчезновения и обитающий на небольшой территории в центральном Закавказье. Филогенетическое положение песчанки Даля в пределах видового комплекса полуденных песчанок оценено с помощью анализа музейной ДНК. Исследовались последовательности как митохондриальных, так и ядерных генов. Мы обнаружили, что песчанка Даля является близкой сестринской группой к *M. penicilliger*, распространенной в Туране. Результат позволяет предположить существование в конце среднего плейстоцена коридора расселения псаммофильных видов, который соединял Закавказье и Закаспий.

Ключевые слова: криптический вид, Центральная Азия, Закавказье, комплекс видов, Gerbillinae