



Phylogeography, phylogeny, and taxonomical revision of the Midday jird (*Meriones meridianus*) species complex from Dzungaria

Olga G. Nanova¹ | Vladimir S. Lebedev¹ | Vera A. Matrosova² |
Yansanjav Adiya³ | Enkhbat Undrakhbayar³ | Alexei V. Surov⁴ | Georgy I. Shenbrot⁵

¹Zoological Museum, Moscow State University, Moscow, Russia

²Department of Structural and Functional Genomics, Engelhardt Institute of Molecular Biology, Russian Academy of Sciences, Moscow, Russia

³Institute of General and Experimental Biology of Mongolian Academy of Science, Ulaanbaatar, Mongolia

⁴Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia

⁵Mitrani Department of Desert Ecology, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Midreshet Ben-Gurion, Israel

Correspondence

Olga G. Nanova, Zoological Museum, Moscow State University, Moscow, Russia.
Email: nanovaolgag@gmail.com

Funding information

Russian Foundation for Basic Research, Grant/Award Number: 18-04-00400; and 14-50-00029; Russian Science Foundation

Abstract

The Midday jird *Meriones meridianus* sensu lato is a widely distributed and highly variable species complex, whose taxonomy is still controversial despite several genetic and morphological studies. Dzungaria is a crucial region for understanding the phylogeny and phylogeography of this species complex. In this work, the genetic variation of *M. meridianus* in Dzungaria and adjacent areas was studied based on mitochondrial (*Cytb*) and nuclear (*BRCA1* and *IRBP*) genes. To compare morphological and genetic differentiation among lineages, craniological variation of the genotyped specimens was examined. Moreover, environmental data were used to estimate the most probable dispersal routes of *M. meridianus* clades in the studied area. Three clades of *M. meridianus* with interspecific level of differentiation were found and treated as distinct species: *M. psammophilus* (Milne-Edwards, 1871); *M. meridianus* (Pallas, 1773); and *M. penicilliger* (Heptner, 1933). The distribution ranges of all three species overlap in Dzungaria. According to the molecular data, *M. psammophilus* and *M. meridianus* are sister taxa that diverged ca. 500 kya, while *M. penicilliger* separated from the common ancestor of the other two lineages ca. 800 kya. These three species have significantly different cranial measurements. Moreover, traces of hybridization between *M. psammophilus* and *M. meridianus* were detected, but not between *M. penicilliger* and the other two species. Finally, the dispersal scenarios for *M. psammophilus*, *M. meridianus*, and *M. penicilliger* are herein discussed. It is suggested that *M. meridianus* and *M. penicilliger* independently colonized Dzungaria from the west via Dzungarian gates.

KEYWORDS

Central Asian deserts, Gerbillinae, glacial cycles, speciation, species distribution modeling

1 | INTRODUCTION

Gerbils and jirds (Gerbillinae Gray, 1825) constitute an important component of the mammalian communities of the arid regions of Eurasia and Africa. Research on their phylogeography and evolutionary history can provide important insights into the Pleistocene dynamics of Old World desert fauna. Geographical variation in several wide-range Asian gerbillines has been examined based on morphometric data (Alhajeri, 2018; Tabatabaei Yazdi & Alhajeri, 2018; Tabatabaei Yazdi, Colangelo, & Adriaens, 2015); however, only a few genetic and integrative studies have been reported (Bray, Alagaili, & Bennett, 2014; Dianat, Darvish, Cornette, Aliabadian, & Nicolas, 2017).

The Midday jird *Meriones meridianus* (Pallas, 1773) species complex is widely distributed, occurring in arid Eurasia from the Caspian Sea to northeastern China. This species complex is characterized by a remarkably high genetic and morphological variation (Gromov & Erbajeva, 1995; Heptner, 1968; Neronov, Abramson, Warshavsky, Karimova, & Khlyap, 2009; Pavlinov, Dubrovsky, Rossolimo, & Potapova, 1990). Despite intensive study (Heptner, 1968; Huang & Zhou, 2012; Ito et al., 2010; Nanova, 2014; Neronov et al., 2009; Tabatabaei Yazdi, Adriaens, & Darvish, 2012; Wang, Zhao, Fang, Liao, & Liu, 2013; Zou et al., 2003), the taxonomy of the *M. meridianus* species complex is still controversial.

Based on genetic (Huang & Zhou, 2012; Ito et al., 2010; Zou et al., 2003) and morphological (Nanova, 2014) data, three widespread lineages are recognized in the *M. meridianus* species complex: *M. meridianus* (Pallas, 1773), *M. penicilliger* (Heptner, 1933), and *M. psammophilus* (Milne-Edwards, 1868–1874). While some authors regard them as distinct species (Ito et al., 2010; Nanova, 2014), others assign them subspecies rank (Wang et al., 2013).

According to morphological data (Nanova, 2014), *M. meridianus* sensu stricto inhabits the northern part of the species complex range, covering an area from the North Caspian depression to the Mongolian Dzungaria and northern Xinjiang; *M. penicilliger* inhabits the southern part of the complex range, occurring from Turkmenistan, Uzbekistan, Tajikistan, eastern Iran, northeastern Afghanistan, and southwestern to southeastern Kazakhstan, and extending eastwards toward western China. In the north, the distribution of *M. penicilliger* reaches the northern borders of Turkmenistan and Uzbekistan, and southern Kazakhstan from the northern Kyzylkum Desert (south of Zhana-Darya valley), through south Balkhash desert, to the western and southern parts of the Alakol depression. *Meriones psammophilus* inhabits most of the Mongolian and Chinese areas of the species complex range, except for the Mongolian Dzungaria and the northwestern, western, and central parts of Chinese Dzungaria. *Meriones chengi* Wang, 1964, is probably a junior synonym of *M. psammophilus* (Ito et al., 2010; Nanova, 2014).

The relationships among the three putative *Meriones* species (lineages) can be clarified via examination of the contact zone. Recent studies on both genetic (Huang & Zhou, 2012; Ito et al., 2010; Wang et al., 2013; Zou et al., 2003) and morphological (Nanova, 2014) variation of the *M. meridianus* complex revealed the existence of all

three species in Dzungaria (Dzungar Basin). Dzungaria is located in the Northern Xinjiang, and it includes Chinese and Mongolian parts, the latter restricted to Barun-Khure basin. Dzungaria also includes several large sand deserts such as Gurvan-tungut and the Karartys valley. It is bounded by Dzungarian Alatau, Tarbagatay, and Saur mountains at the west, Tian Shan Mountains at the south, and Altai Mountains at the north. There are two passages connecting Dzungaria with Kazakh Steppe (Great Dala) through the Dzungarian Gate (western) and Irtysh valley (northwestern), and one passage connecting it with arid areas of the Northern China and Southern Mongolia (eastern). Thus, jirds could migrate between Dzungaria and adjacent areas despite partial isolation of this region by mountains.

The aim of the present study was to examine the phylogeographical structure of the *M. meridianus* complex in the potential contact zone and its historical demography. Our tasks included the identification of distribution boundaries of phylogenetic lineages in Dzungaria, East Kazakhstan, and western Mongolia as well as the estimation of the time of their divergence. Furthermore, we analyzed the relative impact of Pleistocene landscape dynamics versus Quaternary orogenesis on the current phylogeographical structure of the *M. meridianus* complex. We also aimed to resolve the existing taxonomic issues using phylogenetic analyses, genetic divergence values, and data on natural hybridization and allele introgression. We employed morphological data (Nanova, 2014) from genotyped specimens to evaluate the consistency of molecular and morphological variation in the potential contact zone.

2 | MATERIALS AND METHODS

2.1 | Sample collection, DNA extraction, amplification, and sequencing

DNA samples were collected from 86 individuals of *M. meridianus* from 32 natural localities in Dzungaria and adjacent territories from 2003 to 2016 during the Joint Russian-Mongolian Biological expedition. Animals were captured with live-traps, and the trapping points were determined with a GPS navigator (Garmin, Switzerland). Genomic DNA was extracted from ethanol-preserved tissues (liver, kidney or toe clippings) using a standard protocol of proteinase K digestion, phenol-chloroform deproteinization, and isopropanol precipitation (Sambrook, Fritsch, & Maniatis, 1989).

The complete mitochondrial *cytochrome b* (*Cytb*, 1,140 bp, Alignment S1) gene and fragments of two nuclear loci—exon 11 of the breast cancer type 1 susceptibility protein (*BRCA1*, 951 bp, Alignment S2) and exon 3 of the interphotoreceptor binding protein gene (*IRBP*, 954 bp, Alignment S3) were used as genomic markers. *Cytb* was amplified using the primer pair L7 and H6 (Montgelard, Bentz, Tirard, Verneau, & Catzeflis, 2002; Appendix 1). The PCR program consisted of an initial denaturation at 94°C for 5 min, followed by 30 cycles of 30 s denaturation at 94°C, 1 min of annealing at 50°C, and 1 min extension at 72°C, followed by a final extension at 72°C for 6 min. *BRCA1* and of *IRBP* were

amplified and sequenced using forward/reverse primer combinations designed for this study (Appendix 1); the PCR program consisted of an initial denaturation at 94°C for 3 min, followed by 30–35 cycles of 30 s denaturation at 94°C, 1 min annealing at 56°C (*BRCA1*) or 62°C (*IRBP*), 1 min extension at 72°C, and followed by a final extension of 72°C for 6 min. The PCR products were visualized on a 1.5% agarose gel and then purified using ammonium–ethanol precipitation or cutoff and purified using a MinElute Gel Extraction kit (Qiagen, Germany). Approximately 10–20 ng of the purified PCR product was used for sequencing with each PCR primer. Sequencing was performed in an ABI 3,730 automated genetic analyzer using a BigDye™ Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, CA, USA) and PCR-primers. Assembly was performed manually and using SeqMan (Lasergene, USA).

The total *Cytb* dataset included 84 original sequences from *M. meridianus* specimens collected in 32 localities from Dzungaria and adjacent territories and 110 sequences downloaded from GenBank (Table 1; Table S1). Two *M. libycus* sequences (AJ851266, AB381902) and three *M. unguiculatus* sequences (AF119264, AB381901, AF159405) were used as outgroups. The total sample sets of *BRCA1* and *IRBP* included 79 and 78 individuals, respectively. All sequences generated in this study were deposited in GenBank. Accession numbers for *Cytb*, *BRCA1*, and *IRBP* are MN204228–MN204313, MN204314–MN204392, and MN204393–MN204470, respectively (Appendix 2).

2.2 | Phylogeographical structure

2.2.1 | Mitochondrial data

Tree reconstructions were performed based on the alignment of *Cytb* haplotypes containing mostly complete or nearly complete sequences (1,014–1,140 bp). Seven shorter (755 bp) GenBank sequences from a study by Wang et al. (2013) were included for comparison. Maximum likelihood (ML) reconstruction of the *Cytb* tree was performed in the Treefinder software, version October 2008 (Jobb, 2008). Appropriate models of sequence evolution were separately selected for the third and first + second codon positions under the Bayesian information criterion (BIC) employing the routine implemented in Treefinder. Bootstrap analysis employed 1,000 replicates.

A Bayesian tree reconstruction was conducted in MrBayes 3.2 (Ronquist et al., 2012). Models with either two or six rate matrix parameters were selected for each partition based on the results of the model selection for the ML analysis. The analysis included two independent runs of four chains (one cold plus three heated, following the default settings). Chain length was set to 5,000,000 generations with sampling every 2,000 generations. With these settings, the effective sample size exceeded 200 for all estimated parameters. Tracer 1.6 software (Rambaut & Drummond, 2005) was used to check for convergence and determine the necessary burn-in

fraction, which was 10% of the chain length. In addition, a neighbor-joining (NJ) tree for the extended dataset including 102 shorter *Cytb* fragments reported by Wang et al. (2013) was generated in PAUP* 4.0b10 (Swofford, 2003) using the *P*-distance method.

2.2.2 | Nuclear data

For allelic phase reconstruction, the PHASE module (Stephens & Donnelly, 2003; Stephens, Smith, & Donnelly 2001) Stephens & Donnelly, implemented in the DNAsp software v. 5 (Librado & Rozas, 2009) was used. Alleles with posterior probabilities below 0.9 were excluded from the analyses. Median-joining networks were reconstructed using Network version 5.0 under default options.

2.3 | Species tree reconstruction and molecular dating

To estimate the dates of divergence between the main lineages, the species tree was reconstructed employing a Bayesian coalescent framework as implemented in *BEAST v. 1.8.2 (Heled & Drummond, 2010). *Meriones shawi* (*Cytb*: KR089031; *IRBP*: KC953400; *BRCA1*: AF332048) was used as the outgroup. Considering that the *BEAST algorithm does not allow for allele exchange among species, all animals from Mongolian Dzungaria and western Transaltai Gobi were excluded from the analysis.

To calibrate the species tree, the approximate estimates of substitution rates in the two nuclear genes (*IRBP* and *BRCA1*) were obtained in BEAST ver. 1.8.4 (Drummond, Suchard, Xie, & Rambaut, 2012) based on the concatenation including 23 species of Gerbillinae. The list of taxa and Genbank accession numbers are shown in Table S2. Sequence data were taken mostly from Alhajeri, Hunt, and Stepan (2015). Each individual gene alignment was partitioned into two subsets corresponding to first + second and third codon positions. Substitution models for the four subsets were selected using the routine implemented in Treefinder. Strict clock and Yule tree prior were assumed. The tree was calibrated using a normal prior (mean = 10 Mya, STDEV = 1.25) for tree root age, which corresponds to the split between Gerbillini and Gerbillurini; this choice was based on the results of molecular dating in Alhajeri et al. (2015) and Stepan, Adkins, and Anderson (2004). Chain length was set to 10,000,000 generations, and the first 1,000,000 generations were discarded as burn-in. The output was examined in Tracer 1.6. Using this procedure, the substitution rates for *IRBP* and *BRCA1* were estimated at 4.46×10^{-3} (95% HPD interval = $3.15\text{--}6.10 \times 10^{-3}$) and 5.83×10^{-3} (95% HPD interval = $4.04\text{--}8.02 \times 10^{-3}$) substitutions per site per My, respectively.

2.4 | Species validation

To test for significant nuclear differentiation between the two closest sister lineages, we used the species validation method

TABLE 1 List of localities analyzed in the present study. No—locality number; Locality—geographical description; Lat—latitude; Long—longitude; *n*—number of specimens; Source—source of data (a—our data; b—Wang et al., 2013; c—Ito et al., 2010; d—Chevret & Dobigny, 2005); Species—definition of the specimens from this study

No	Locality	Lat	Long	<i>n</i>	Source	Species
1	Kazakhstan, southern Balkhash, Topar	44.7711	75.2486	2	a	<i>M. pencilliger</i>
2	Kazakhstan, southern Balkhash, Boztobe	45.2572	75.4254	2	a	<i>M. pencilliger</i>
3	Kazakhstan, southern Balkhash, Ushkara	45.9083	77.7647	2	a	<i>M. pencilliger</i>
4	Kazakhstan, eastern Balkhash, Sarykurak	46.3813	78.9566	2	a	<i>M. meridianus</i>
5	Kazakhstan, eastern Balkhash, Kabanbai	45.8869	80.5558	2	a	<i>M. meridianus</i>
6	eastern Kazakhstan, eastern Balkhash, right bank of Emily river	46.3704	82.2203	2	a	<i>M. meridianus</i>
7	eastern Kazakhstan, Zaysan depression, Chernyi Irtys river, Buran	47.9502	85.1271	4	a	<i>M. meridianus</i>
8	China, Dzungar basin, Xinjiang, Musowan Field Station	45.1256	86.0278	1	a	<i>M. pencilliger</i>
9	China, Dzungar basin, Xinjiang, Baytag-Bogdo southern slope, 23 km to the northeast from Turungy-khuduk	44.9141	91.2474	1	a	<i>M. pencilliger</i>
10	China, Dzungar basin, Xinjiang, Baytag-Bogdo southern slope, 29 km to the East from Turungy-khuduk	44.8564	91.3297	2	a	<i>M. pencilliger</i>
11	China, Dzungar basin, Xinjiang, Uzuntag Mt., 10 km to the southeast	44.4636	91.3218	2	a	<i>M. pencilliger</i>
12	China, Dzungar basin, Xinjiang, Zhifan, 18 km to the northwest	44.5476	91.6312	1	a	<i>M. pencilliger</i>
13	Mongolia, Mongolian Dzungaria, right bank of Bulgan river	46.1166	91.1164	5	a	<i>M. meridianus</i>
14	Mongolia, Mongolian Dzungaria, Elhon	45.6167	92.2653	3	a	<i>M. meridianus</i>
15	Mongolia, Mongolian Dzungaria, northern slope of the Huh-Unduriyn-Nuuru	45.1493	92.8185	1	a	<i>M. meridianus</i>
16	Mongolia, Mongolian Dzungaria, Gun-Tamga-Bulak spring	45.2569	93.6731	5	a	<i>M. meridianus</i>
17	Mongolia, northwestern Transaltai Gobi, Govi-Altai aimag, Nogon-davon	44.8926	94.1919	2	a	<i>M. psammophilus</i>
18	Mongolia, northwestern Transaltai Gobi, 55 km to the northwest from Altai	44.8003	94.2359	5	a	<i>M. psammophilus</i> , <i>M. meridianus</i>
19	Mongolia, northwestern Transaltai Gobi, Alag-Nuur	45.1673	94.5488	1	a	<i>M. psammophilus</i>
20	Mongolia, northwestern Transaltai Gobi, Alag-Nuur	45.1677	94.6032	1	a	<i>M. psammophilus</i>
21	Mongolia, northwestern Transaltai Gobi, Alag-Nuur	45.1264	94.5757	10	a	<i>M. psammophilus</i>
22	Mongolia, northwestern Transaltai Gobi, 19 km to the southwest from Altai	44.4838	94.7669	1	a	<i>M. meridianus</i>
23	Mongolia, northwestern Transaltai Gobi, southwestern Harmagtain-Hutag	44.5012	95.6165	3	a	<i>M. psammophilus</i>
24	Mongolia, northwestern Transaltai Gobi, northern Harmagtain-Hutag	44.5205	95.7039	3	a	<i>M. psammophilus</i>
25	Mongolia, northwestern Transaltai Gobi, Toroin-Holoi	45.0023	95.8452	2	a	<i>M. psammophilus</i>
26	Mongolia, northwestern Transaltai Gobi, Harin-Shand	44.6735	95.9578	10	a	<i>M. psammophilus</i>
27	Mongolia, northwestern Transaltai Gobi, Ih-Dzarmag	44.7977	97.3199	1	a	<i>M. psammophilus</i>
28	central and northwestern Mongolia, the Great lake basin, the southeastern bank of Aчит-Nuur lake	49.4832	90.6326	2	a	<i>M. psammophilus</i>
29	central and northwestern Mongolia, the Great lake basin, the southeastern bank of Hyargas-Nuur lake	49.0312	93.5035	2	a	<i>M. psammophilus</i>
30	central and northwestern Mongolia, Sharga Gobi, 20 km to the southeast from Sharga	46.1743	95.5174	2	a	<i>M. psammophilus</i>
31	central and northwestern Mongolia, the Lake Valley, 18 km to the East from Biger	45.7205	97.4106	3	a	<i>M. psammophilus</i>
32	Central and northwestern Mongolia, the Lake Valley, northern slope of the Ih-Bogdin-Nuuru	44.9855	100.6517	1	a	<i>M. psammophilus</i>
-	China, Gansu, Anxi	40.0775	97.1234	9	b	<i>M. psammophilus</i>
-	China, Gansu, Jinta	39.9662	98.9547	9	b	<i>M. psammophilus</i>
-	China, Gansu, Gaotai	39.4131	99.8356	10	b	<i>M. psammophilus</i>
-	China, Gansu, Dongdashan	38.4225	102.0295	6	b	<i>M. psammophilus</i>

(Continues)

TABLE 1 (Continued)

No	Locality	Lat	Long	n	Source	Species
-	China, Gansu, Minqin	38.6619	103.0885	16	b	<i>M. psammophilus</i>
-	China, Gansu, Wuwei	38.0169	102.8058	5	b	<i>M. psammophilus</i>
-	China, Gansu, Yuzhong	35.8683	104.0984	14	b	<i>M. psammophilus</i>
-	China, Qinghai, Huatugou	38.2395	90.8209	8	b	<i>M. psammophilus</i>
-	China, Qinghai, Suganhu	38.8739	93.7218	13	b	<i>M. psammophilus</i>
-	China, Qinghai, Lenghu	38.7526	93.3496	6	b	<i>M. psammophilus</i>
-	China, Qinghai, Ulan	36.9229	98.4375	9	b	<i>M. psammophilus</i>
-	China, Qinghai, Dulan	36.3581	98.1132	3	b	<i>M. psammophilus</i>
-	China, Qinghai, Golmud	36.3324	94.9719	15	b	<i>M. psammophilus</i>
-	China, Nei Mongol, Ejin	41.8109	100.4526	10	b	<i>M. psammophilus</i>
-	China, Nei Mongol, Menggen	40.0196	103.8792	11	b	<i>M. psammophilus</i>
-	China, Nei Mongol, Nuoergong	40.1694	104.8062	10	b	<i>M. psammophilus</i>
-	China, Nei Mongol, Bayanzhuoer	41.9383	110.0997	11	b	<i>M. psammophilus</i>
-	China, Ningxia, Shapotou	37.5774	105.0968	13	b	<i>M. psammophilus</i>
-	China, Xinjiang, Naomaohou	43.8240	94.9368	15	b	<i>M. psammophilus</i>
-	China, Xinjiang, Nanhu	42.1342	94.4118	8	b	<i>M. psammophilus</i>
-	China, Xinjiang, Yuli	41.2909	86.4243	16	b	<i>M. psammophilus</i>
-	China, Xinjiang, Qiemo	38.1525	85.5543	13	b, c	<i>M. psammophilus</i>
-	China, Xinjiang, Alaer	40.4104	81.3932	13	b	<i>M. psammophilus</i>
-	China, Xinjiang, Maigaiti	38.8286	77.7613	5	b	<i>M. psammophilus</i>
-	China, Xinjiang, Huocheng	44.0062	80.7877	19	b, c	<i>M. pencilliger</i>
-	China, Xinjiang, Guertu	44.5128	83.8493	18	b	<i>M. pencilliger</i>
-	China, Xinjiang, Queren	44.1750	90.1715	15	b	<i>M. pencilliger</i>
-	China, Xinjiang, Turpan	42.8540	89.1884	31	b, c	<i>M. psammophilus</i> , <i>M. pencilliger</i>
-	China, Xinjiang, Artux	39.6349	76.2366	1	c	<i>M. psammophilus</i>
-	China, Xinjiang, Khotan	37.2482	80.0306	1	c	<i>M. psammophilus</i>
-	China, Xinjiang, Fukang	44.3711	87.8581	1	c	<i>M. pencilliger</i>
-	China, Xinjiang, Fuhai	47.0475	87.3157	1	d	<i>M. meridianus</i>

implemented using the BPP2.2 software (Yang & Rannala, 2010). The analysis was conducted based on the phased nuclear data using the guide tree containing a single ancestral node. The relative rates of the two loci were fixed at values produced by BEAST. Gamma priors $G(2, 100)$ and $G(1, 100)$ were specified for the θ and τ parameters, respectively. The reversible jump MCMC algorithm 0 was used with default parameters. The MCMC chain length was set to one million generations, and the burn-in period was 100,000 generations.

2.5 | Isolation with migration analysis (IMA)

The relationships among the three lineages of the *M. meridianus* species complex were also examined using the isolation-migration model as implemented in the IMA2 software version 5.1 (Hey, 2005; Hey & Nielsen, 2007). The specimens were attributed to one of the three groups in accordance with the affinity of their mitotypes. The topology of the phylogenetic tree followed the one inferred in

the species tree analysis. Two independent runs were performed. Migration was assumed to occur only between sister populations. The burn-in period was set at 100,000 generations. Analysis was run until convergence was reached (i.e., effective sample size (ESS) larger than 200). The rates of *BRCA1* and *IRBP* were set at values corresponding to posterior estimates produced in species tree reconstruction.

2.6 | Neutrality tests and analyses of demographic history

The hypothesis of demographic stability was tested by calculating Fu's neutrality statistic F_s (Fu, 1997) and Tajima's D test (Tajima, 1989) in Arlequin 3.5 (Schneider, Roessli, & Excoffier, 2000). The significance of the statistics was tested by generating 1,000 random samples under neutrality. Demographic histories of the main *Cytb* phylogroups were inferred by pairwise mismatch distribution analyses (Rogers & Harpending, 1992) as implemented in Arlequin.

The validity of the stepwise expansion model was tested using parametric bootstrapping with 1,000 replicates. Skyline plots for the three lineages were generated in BEAST using the Extended Bayesian Skyline Plot (EBSP) method (Heled & Drummond, 2008) based on the alignments of the three genes. The analysis was run for 100,000,000 steps under a strict clock model. The times of expansion were estimated based on tau parameters of the demographic expansion model using the *Cytb* rate as estimated in the species tree analysis and assuming a generation time of one year.

In addition, the neutrality tests were performed for the following six geographic populations: *meridianus* from Mongolian Dzungaria, *meridianus* from East Kazakhstan, *penicilliger* from the South Balkhash area, *penicilliger* from Chinese Dzungaria, *psammophilus* from northwestern Transaltai Gobi, *psammophilus* from the Valley of Lakes, and northwestern Mongolia.

2.7 | Skull variation

Morphometric analyses were performed on 719 specimens using 29 skull measurements. The main pool of data (665 specimens) and methods of analysis were obtained from Nanova (2014). A total of 45 skulls of newly genotyped specimens were added.

Skulls were classified employing the Mclust procedure (Fraley & Raftery, 1998, 2003) described in Nanova (2014). Principal component (PC) scores of age-corrected data were used as input (Novanova, 2014). The modified Bayesian information criterion (BIC) (Lebedev & Lissovsky, 2008; Nanova, 2014; Table S3) was employed as a measure of model optimality. The placement of specimens in a cluster was determined using the matrix of posterior probabilities (PP). A specimen was classified as unambiguously belonging to a cluster if the corresponding PP exceeded 0.90 and as probably belonging to a cluster if the corresponding maximum PP was below 0.90. Uncertainty of case-wise classification was evaluated as 1 minus the value of the maximum posterior probability for each observation. Total uncertainty (TU) was calculated for different geographic regions as the sum of all uncertainties of the specimens. Average uncertainty (AU) was calculated as ratio of TU and the number of specimens included in the analysis. AU of the sample from the potential contact zone between *penicilliger* and *meridianus* (Dzungaria and Transaltai Gobi, $n = 45$) was compared with samples from other parts of the range (parts inhabited by a single lineage) with similar number of specimens: northern Caspian and northern Aral region (inhabited by *meridianus*, $n = 46$); northeastern Turkmenistan and southeastern Uzbekistan (inhabited by *penicilliger*, $n = 46$); and Mongolia, Lake Valley (inhabited by *psammophilus*, $n = 50$). The classification of the genotyped specimens was compared using morphometric and *Cytb* data.

2.8 | Estimation of population connectivity

The idea of integrating data from landscape ecology, population genetics, and geographic information systems (GIS) emerged

during the last decade, when GIS data and tools become available (Chan, Brown, & Yoder, 2011). In particular, several different algorithms were proposed to estimate the most probable dispersal routes between existing localities based on landscape properties (Chan et al., 2011; McRae & Beier, 2007; Ray, 2005). Chan et al. (2011) proposed the use of results from species distribution modeling (SDM) to estimate landscape properties; they built SDM using the MAXENT software, used obtained values of the relative habitat suitability (RHS) to calculate the "friction landscape" as $1/\text{RHS}$, and measured landscape connectivity among populations by estimating least-cost paths among sites with "friction landscape" as cost raster layer. This approach was implemented in SDM Toolbox for ArcGIS (Brown, Bennett, & French, 2017). We attempted to use SDM Toolbox and found it extremely time and computer-resource consuming. Moreover, in cases where two lowland desert populations were divided by high-altitude mountain ranges, the tool presented least-cost paths across habitats that were non-suitable for the analyzed species. To avoid such effects, "friction landscape" was herein calculated as $1/\text{RHS}$.

The occurrence records of *Meriones* species used in the SDM were obtained from our field observations, from the Zoological Museum of Moscow State University collections, and from publications. A total of 461, 229, and 574 points were used for *psammophilus*, *meridianus*, and *penicilliger*, respectively (Table S4).

The environmental data used in the SDM were 30 arc-second grids (approximately 1 km resolution) of climate, relief, sand cover, and vegetation variables. The climate variables (annual mean temperature, mean monthly temperature range, mean temperatures of coldest and warmest quarters, maximal temperature of warmest month, minimal temperature of coldest month, temperature annual range, annual precipitation, and precipitation of wettest quarter) were obtained from WORLDCLIM Version 2.0 (Fick & Hijmans, 2017; available at <http://www.worldclim.org>). Slope data were derived from altitude data, extracted from the GTOPO30 dataset distributed with ArcGIS, using the Spatial Analyst module of ArcMap. Data on the percentage area covered by sand were obtained using ArcGIS Desktop 10.1 from the land-use layer of the Digital Chart of the World corrected with satellite images (available at <http://landsatlook.usgs.gov>). Obtained polygons of sand dune areas were converted to raster with 3 arc-second-resolution, and this raster was resampled to a 30 arc-second-resolution (Shenbrot, 2013). This operation resulted in values of the percentage area covered by sand for each grid cell. Ten-day estimate data on the Normalized Difference Vegetation Index (NDVI) averaged by seasons (winter, spring, summer, and autumn) for 1998–2007 were obtained from the VEGETATION Program (<http://www.vito-eodata.be>). NDVI is an index of greenness that is directly correlated with productivity and green vegetation biomass and is widely used in ecological and evolutionary studies (Alhajeri, Porto, & Maestri, 2019; Pettorelli et al., 2005).

The SDMs were built using the MAXENT 3.4.0 software (Phillips, Anderson, & Schapire, 2006). The extent of the study area or of the "landscape of interest" significantly affects SDM results (Anderson & Raza, 2010; Elith et al., 2011). To define the

study area of a species, the kernel density of occurrence points of this species was calculated with a search radius of 4°; then, the obtained raster was reclassified so that the original kernel density values equal to or over 0.05 were converted to 1, and the values under 0.05 were converted to "NoData"; this reclassified raster was used as the mask for clipping environmental variables to the study area. Models were constructed with default MAXENT settings as these settings were demonstrated to be the most appropriate for wide-ranging data (Phillips & Dudik, 2008). The MAXENT logistic output, which provides estimates of relative habitat suitability (Elith et al., 2011), was used.

Least-cost paths between each pair of genetically dated points for each species were estimated using the "Cost connectivity" tool from the standard Arc Toolbox, Spatial Analyst Tools (ArcGIS Desktop 10.6.1) with coast raster layer calculated as 1/RHS.

3 | RESULTS

3.1 | Mitochondrial variation in the *M. meridianus* species complex

Three well-supported clades were obtained in the phylogenetic reconstructions (Figure 1, Figure S1). These clades were distributed as follows (Figure 2, Figure S2): Clade 1 was distributed in all studied parts of Mongolia (Transaltai Gobi, Great lake basin, and Lake Valley) and China (Taklamakan Desert and Alashan Desert), except Dzungaria; Clade 2 occurred in the Mongolian Dzungaria, the northernmost part of the Dzungarian basin in Xinjiang, and Eastern Kazakhstan, from Zaysan depression to Alakol depression; Clade 3 occurred in the Dzungarian basin and Southern Kazakhstan between the Ili river and the interfluvium of the Aksu and Lepsy rivers. Clade 3 was consistently placed as sister to the clade combining Clades 1 and 2. No significant structure was observed within the three main lineages. However, haplotypes of Clade 2 originated from the eastern part of the Balkhash depression were separated from those from northern Dzungaria and the Zaysan hollow. Haplotypes of the Clade 3 were also separated into those from Balkhash and those from Dzungaria.

Clades 1, 2, and 3 corresponded the *psammophilus*, *meridianus*, and *penicilliger* lineages, respectively (Nanova, 2014). In general, clades were allopatrically distributed. Only near the border between the Mongolian Dzungaria and Transaltai Gobi, haplotypes of both Clades 1 and 2 were found at the same locality (locality 18, Figure 2; Appendix 2).

3.2 | Nuclear variation in the *M. meridianus* species complex

A total of 140 and 122 operational units (phased alleles) corresponding to 21 and 26 distinct haplotypes were found for *BRCA1* and *IRBP*, respectively. Both nuclear networks (Figure 3) indicated the isolated position of *penicilliger*, which had no common alleles with *psammophilus* and *meridianus*. The latter lineages share

several alleles (5 for *BRCA1* and 4 for *IRBP*), which are present at high frequencies in *psammophilus* and at low frequencies in *meridianus* from the Mongolian Dzungaria, being nearly absent in East Kazakhstan. The BPP analysis, however, strongly supported Clades 1 and 2 as separate entities with posterior probability equal to 1.0.

3.3 | Species tree

The species tree (Figure 4) was concordant with the mitochondrial tree. The *penicilliger* branched off at ca. 800 kya, whereas *psammophilus* and *meridianus* diverged at ca. 500 kya. The *Cytb* substitution rate was estimated at ca. 10% per My per bp.

3.4 | Isolation with migration

The results of the IMA are presented in Table 2 and Figure 5. Migration from *psammophilus* to *meridianus* was found to be significant, whereas the gene flow in the opposite direction was effectively zero. The number of migrants with the highest posterior density (HiPt) was estimated as 0.83 migrant per generation (95% HPD: 0.44–1.75), and the effective population number was significantly higher for *psammophilus* and *penicilliger* than for *meridianus*. The divergence times obtained in this analysis were more recent than those from the species tree reconstructions; this may be explained by the insufficient complexity of the substitution models used in IMA.

3.5 | Skyline plots

The skyline plots demonstrated a significant population growth for all three lineages (Figure 6a); however, the onset of expansion was earlier in *psammophilus* and *penicilliger* than in *meridianus*. Considering a *Cytb* substitution rate of 10% per My, as estimated by *BEAST, the expansion time is 15–20 kya (95% HPD: ~10–35 kya) for *psammophilus* and *penicilliger* and only 4 kya (2–7 kya) for *meridianus*.

3.6 | Molecular diversity and neutrality tests

The results produced by Arlequin are presented in Tables 3 and 4. The results of the neutrality tests indicated recent expansion in all three main clades. However, while the mismatch plot for *psammophilus* was characteristically bell-shaped, that for *penicilliger* had multiple peaks (Figure 6b). Population-level analyses supported significant expansion only of populations from Dzungaria (*meridianus* and *penicilliger*) and northwestern Transaltai Gobi (*psammophilus*). The mismatch analyses demonstrated that the time of expansion corresponds approximately to the end of Late Pleistocene in *psammophilus* and *penicilliger*, contrasting with a

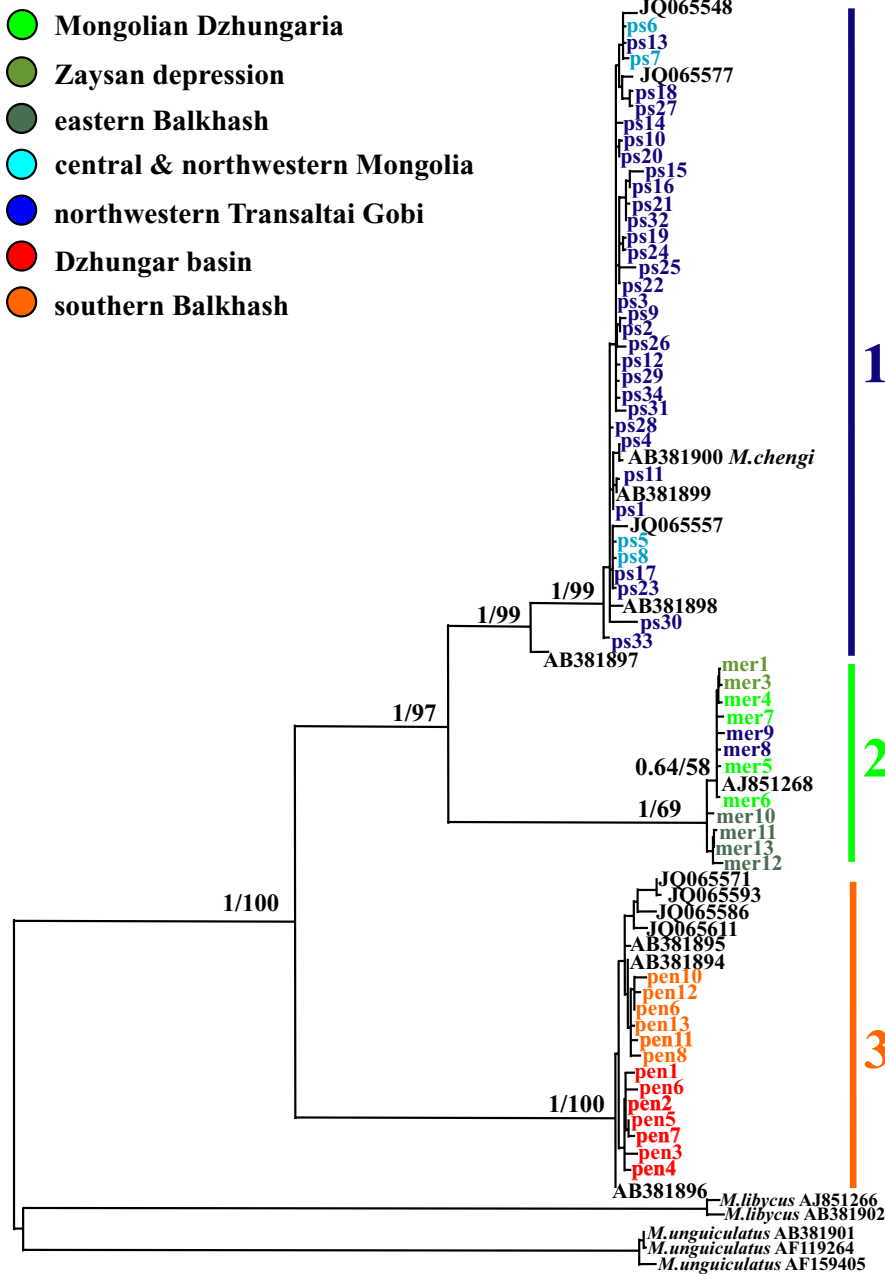


FIGURE 1 Maximum likelihood (ML) tree inferred from the *Cytb* alignment of 104 haplotypes using TREEFINDER; 84 specimens are from our sample and 20 specimens are from GenBank, including 2 specimens of *Meriones libycus* and 3 specimens of *M. unguiculatus*, which were used as the outgroup. Values above branches correspond to Bayesian posterior probabilities as estimated in MrBayes and maximum likelihood bootstrap support. Clades: 1, *psammophilus*, 2, *meridianus*, 3, *penicilliger*

significantly more recent (Holocene) expansion in *meridianus* from Mongolian Dzungaria. The latter population also had lower values of diversity indices.

3.7 | Comparison between cranial variation and *Cytb* differentiation

The classification of specimens is presented in Table 5. The optimal model for morphological data (Figure S3) resulted in four clusters, as previously proposed by Nanova (2014): cluster 1 corresponds to *psammophilus*; two clusters—2a and 2b—correspond to *meridianus* (cluster 2a comprises nominative subspecies *M. m. meridianus* and *M. m. buechneri*, whereas cluster 2b comprises *M. m. nogaorum* and *M. dahli*); and cluster 3 comprises *penicilliger*. The distribution of the

45 genotyped specimens in the space defined by the first two principal components is shown in Figure S4.

Of 45 specimens, 41 (91.1%) had identical affiliation based on the morphological and *Cytb* classification. The average uncertainty (AU) of classification was higher at the studied range at Dzungaria and Transaltai Gobi (AU = 0.106) than in the other localities—that is, northern Caspian and northern Aral region (0.075), northeastern Turkmenistan and southeastern Uzbekistan (0.023), and Mongolia, Lake Valley (0.035).

3.8 | Population connectivity

The estimations of population connectivity for each species are presented in Figure 7. Populations of *meridianus* and *penicilliger* from Balkhash Basin (including Ili River Hollow) are connected with

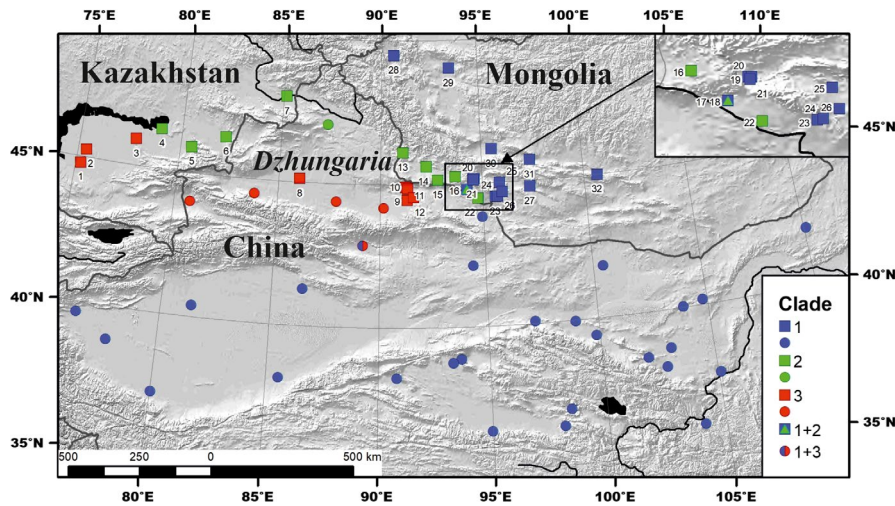


FIGURE 2 *Cytb* geographical variation in the *Merione meridianus* complex in Dzungaria and adjacent regions. Rectangles—data from the present study; circles—GenBank data. Blue symbols (1)—Clade 1 (*psammophilus*); green symbols (2)—Clade 2 (*meridianus*); red symbols (3)—Clade 3 (*penicilliger*). Green triangle in blue square (1 + 2)—both haplotypes of Clade 1 and Clade 2 are found at the same locality (locality 18, our data). Red-blue circle (1 + 3)—both haplotypes of Clade 1 and Clade 3 are found at the same locality (Wang et al., 2013). The numbering of the localities (original data only) is as in Table 1

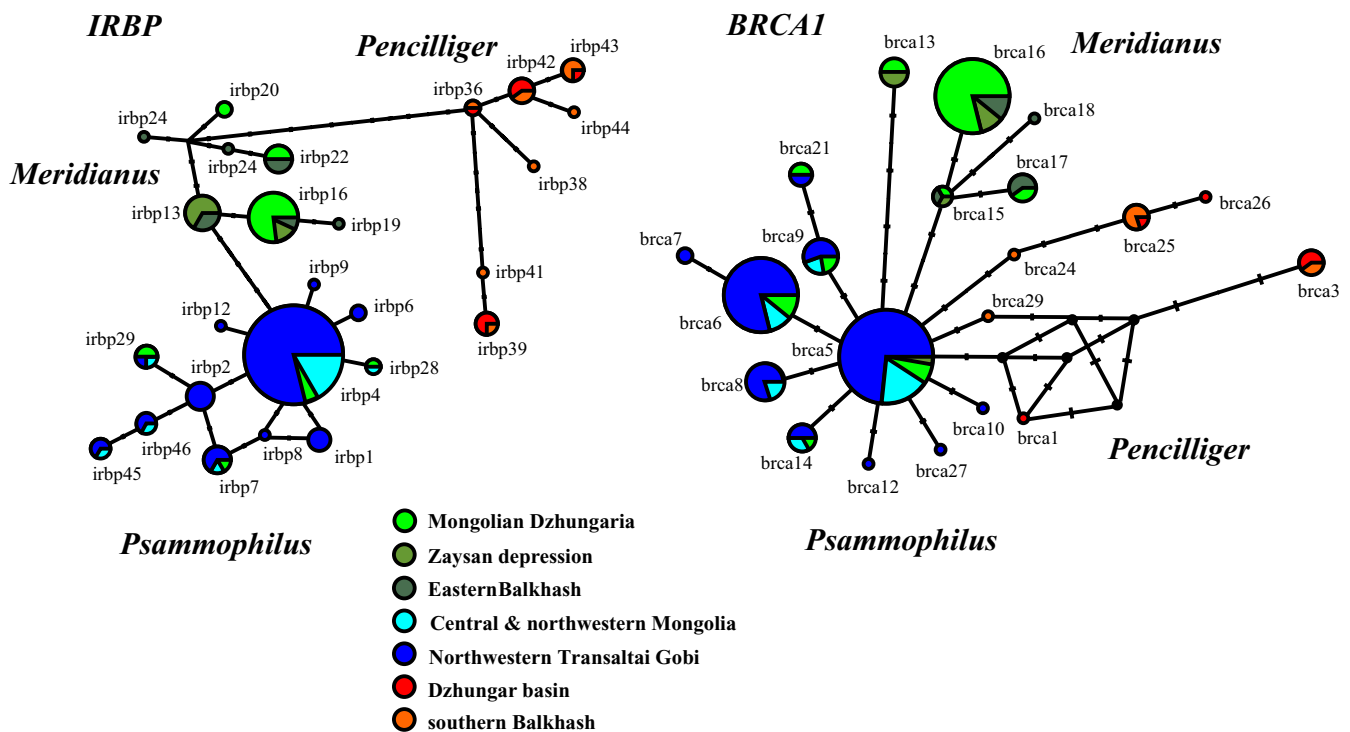


FIGURE 3 Median-joining haplotype networks of haplotypes of *IRBP* and *BRCA1*. Each circle represents a unique haplotype; the size of the circle is proportional to haplotype frequency. Colors represent the geographical regions. Small black circles represent hypothetical haplotypes. Hatches on the internodes represent nucleotide substitutions. For details, see Appendix 2

populations from Dzungarian Basin only via Dzungarian Gates. The population of *meridianus* from Zaysan Hollow is connected only with populations from Dzungarian Basin, and it is isolated from other Kazakhstan populations. Populations of *psammophilus* from the northwestern part of Transaltai Gobi are connected with populations from southern foothills of Gobian Altai at the east and with populations from southeastern foothills of Tian Shan at the southeast.

4 | DISCUSSION

4.1 | Phylogeographical structure and hybridization in nature

The genetic differentiation in the *M. meridianus* complex constitutes an example of the high diversity of Palearctic desert rodents. Three

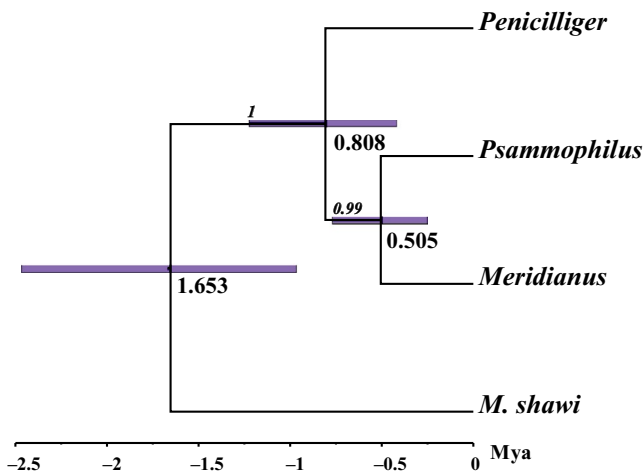


FIGURE 4 Species tree generated using the *BEAST algorithm. Divergence times correspond to the median posterior estimate of the age in Mya. Blue bars represent the 95% highest probability density intervals. Values above the branches correspond to posterior probabilities for each node

lineages of the *M. meridianus* complex—*psammophilus*, *meridianus*, and *penicilliger*—are allopatrically distributed throughout the range of the superspecies complex. Similarly to Ito et al. (2010), we herein found all three clades in Dzungaria, whereas Wang et al. (2013) found only *penicilliger* and *psammophilus* (designated as Clades A and B in their study). Two of these three lineages—*meridianus* and *penicilliger*—are the most common in Dzungaria and inhabit its northern and southern part, respectively, whereas *psammophilus* inhabits the surroundings of Dzungaria and contacts both *meridianus* and *penicilliger* at its eastern and southern borders.

Several contact zones between lineages were detected in Dzungaria, Transaltai Gobi, and eastern Kazakhstan. The contact zone between is in northwestern Transaltai Gobi (localities 18 and 22: Honin-Us-Sair and southern foothills of Adzh-Bogdo). The Tahiyn Shar Nuruu mountains may act as a partial barrier to gene flow between *psammophilus* and *meridianus* restricting the eastward dispersal of the latter from Mongolian Dzungaria. No stable populations were detected in Honin-Us-Sair because, as a hyperarid sandy-gravel desert, it is a suboptimal environment for *M. meridianus*—this was confirmed by the fact that few individuals (six specimens in two

years) were captured in this location. In 2011, individuals with *Cytb* haplotypes from both *psammophilus* (specimen M-222-2011) and *meridianus* lineages (specimens/M221-2011, M-223-2011, M-235-2011) were captured in Honin-Us-Sair and in the southern Adzh-Bogdo area. Two of these specimens (M-221-2011 and M-235-2011) were morphologically misclassified. Specimen M-222-2011 has the mitochondrial haplotype of *psammophilus* and nuclear haplotypes of *meridianus*, and it was morphologically identified as *psammophilus*. All specimens with *Cytb* haplotypes of *meridianus* have nuclear haplotypes specific for the *meridianus* lineage. In 2012, only animals (35 specimens) with both mitochondrial and nuclear haplotypes of *psammophilus* were captured in localities in Transaltai Gobi adjacent to Honin-Us-Sair: Nogon-Davon, Harin-Shand, Harmagtai-Hutag, Alag-Nuur, and Toroi-holoy.

IMa results revealed a significant but low nuclear gene flow from *psammophilus* to *meridianus*. The analysis of nuclear data indicated an evident signature of intensive flow in Mongolian Dzungaria. However, the results of the present study as well as those of Wang et al. (2013) do not allow the hypothesis about the ongoing hybridization between lineages to be either accepted or rejected. Further studies should focus on the timing (present or ancient) and frequency of hybridization between *psammophilus* and *meridianus*.

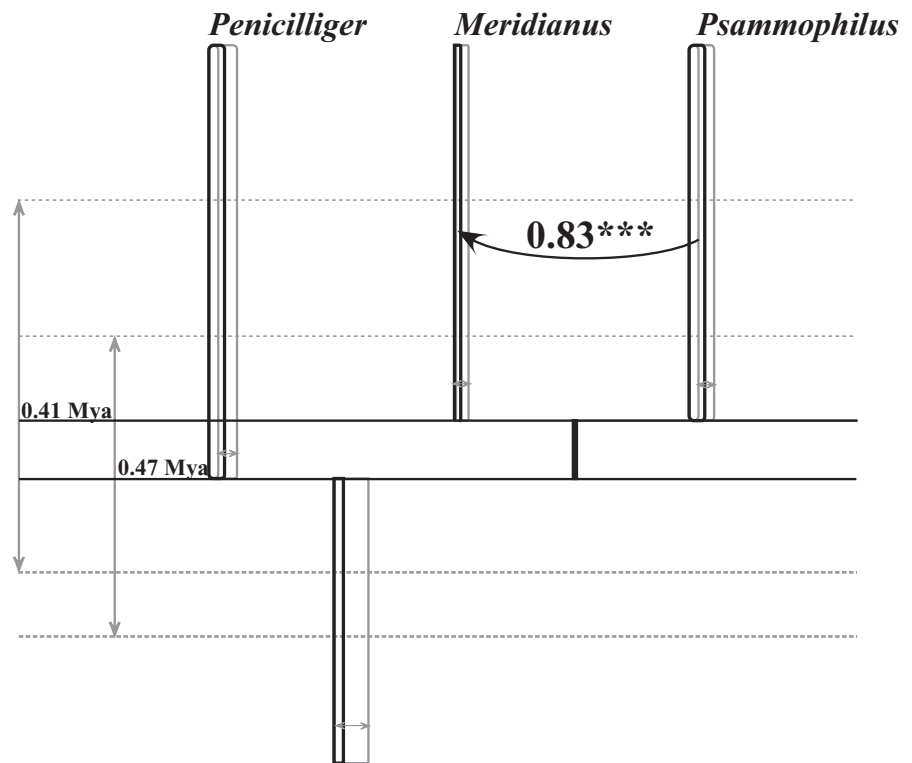
No shared haplotypes between *penicilliger* and both *psammophilus* and *meridianus* were found. However, *penicilliger* contacts *meridianus* in the Dzungaria Basin sands and in southern Kazakhstan between the Lepsy and Aksu rivers (Balkhash basin); *penicilliger* contacts *psammophilus* in southern Dzungaria and the northern Tarim basin. The latter contact zone is discussed by Wang et al. (2013).

In our study, no areas of sympatry between lineages were found other than Honin-Us-Sair. In particular, sympatry between *penicilliger* and *psammophilus* was not detected. In contrast, Wang et al. (2013) reported mitochondrial haplotypes of both clades A (corresponds to *penicilliger*) and B (*psammophilus*) in several localities of southwestern Dzungaria, Tarim Basin, and in the upper course of the Ili River. However, our IRBP data reveal the existence of distinct allelic groups corresponding to the *psammophilus* and *penicilliger* lineages. No heterozygotes were found that contained alleles from both the *psammophilus* and *penicilliger* allelic groups. Therefore, the coexistence of different mitochondrial haplotypes may be explained by limited hybridization in the past.

TABLE 2 Results of the isolation with migration analysis (IMa). Abbreviations: *psam*—*psammophilus* (Clade 1); *mer*—*meridianus* (Clade 2); *pen*—*penicilliger* (Clade 3)

	Split time T (kya)		Effective population number N_e (/1,000)						
			Contemporary			Ancestral		Migrant number	
	<i>psam/mer</i>	<i>pen/(psam + mer)</i>	<i>mer</i>	<i>psam</i>	<i>pen</i>	(<i>psam + mer</i>)	(all)	<i>psam > mer</i>	<i>mer > psam</i>
Value	t0	t1	N1	N2	N3	N4	N5	2N0m0 > 1	2N1m1 > 0
HiPt	409.4	476.7	75.3	181.6	172.8	31.0	101.9	0.83	0.00
Mean	384.5	478.7	77.4	185.3	188.9	3,760.9	168.4	0.96	0.11
95%Lo	179.0	327.8	48.7	128.5	110.8	57.6	31.0	0.44	0.00
95%Hi	586.6	653.9	119.6	252.5	296.8	8,581.5	474.0	1.75	0.41

FIGURE 5 The results of the isolation–migration analysis performed in the IMA2 software. Widths of the tree branches correspond to the estimated effective population sizes. The arrow shows the direction of gene flow. The value with asterisks denotes significant ($p < .05$) gene flow from *psammophilus* to *meridianus* (number of migrants per generation)



4.2 | Comparison between genetic and morphological variation

A high correspondence between genetic and cranial identification of genotyped specimens was herein detected. This finding is consistent with our previous results on morphological variation in the *M. meridianus* complex throughout this distribution range (Nanova, 2014). However, the level of uncertainty regarding the identification of specimens based on skulls was higher in Mongolian Dzungaria and Translatai Gobi than in the western part of the range (Caspian depression). This may be a result of hybridization between lineages in the Mongolian Dzungaria–Transaltai Gobi contact zone, or it may be explained by a similar impact of ecological factors on skull morphology in both lineages.

4.3 | Historical demography and dispersal scenarios

4.3.1 | The problem of the origin of the *M. meridianus* complex

The area of origin of the *M. meridianus* complex cannot be defined based on currently available data. Wang et al. (2013) proposed the eastern part of Central Asia as this taxon's place of origin based on the existence of *M. meridianus*-like fossil records in China from the early Pleistocene–middle Pleistocene (see references in Wang et al., 2013). The fact that *M. meridianus* cannot be confidently distinguished by isolated molars from its closest relative, *M. unguiculatus* must be considered; however, fossils reliably identified as *M. cf. meridianus* from the beginning of the early Pleistocene (MN 17) were recorded in southeastern Kazakhstan

(Sotnikova, Dodonov, & Pen'kov, 1997). Thus, we can assume that the *M. meridianus* complex probably originated in the deserts of Turan and southern Kazakhstan.

4.3.2 | Ecological and geographical aspects of the evolutionary scenario for the *M. meridianus* complex

Meriones meridianus is a desert-adapted, sand-dwelling species. Its psammophily is not very strong, and it is able to disperse across large areas of stony-gravel desert with dry riverbeds, which is evidenced by the species' occupation of small isolated patches of sand on stony-gravel deserts along the northern shore of Balkhash Lake (Burdelov & Leontyeva, 1956). The high dispersal ability of *M. meridianus* is supported by its population social structure and by its particularly low aggressiveness (Tchabovsky, 2006).

Our estimations of population connectivity demonstrated that, under current environmental conditions, there is one western passage connecting Dzungarian Basin with western deserts of Kazakhstan (Dzungarian Gates) and one eastern passage connecting Dzungarian Basin with Gobi, Alashan, and Tarim Basin deserts (between eastern foothills of the Tian Shan Mountains and southern foothills of the Gobian Altai Mountains). Zaysan Hollow in Kazakhstan is connected at the east with the Dzungarian Basin, but its western region is isolated from other Kazakhstan deserts by Kalbinskiy Altai and Tarbagatay Mountains.

Wang et al. (2013) suggested that the divergence between the *psammophilus* and *penicilliger* lineages resulted from the uplift of the Tian Shan Mountains and from climate-induced environmental changes, namely the expansion of forests and grasslands during

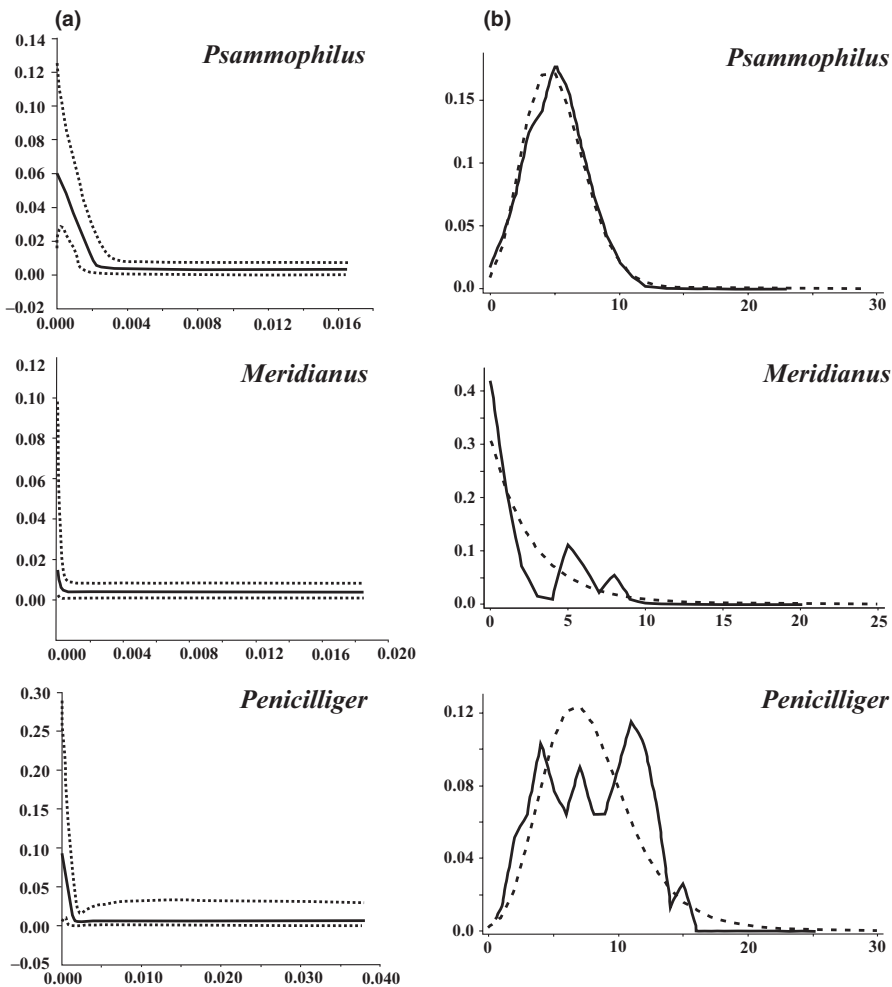


FIGURE 6 Demographic history analysis. Bayesian skyline plots (a) and mismatch distribution (b) for *Cytb* of the three phylogroups, that is, *psammophilus* (Clade 1), *meridianus* (Clade 2), *penicilliger* (Clade 3). (a) Solid lines represent median values for the \log_{10} of the population size ($N_e \tau$) (τ , generation time); dashed lines mark the 95% highest probability density intervals in all panels. (b) The dashed line represents the expected distribution, and the solid line represents the observed distribution

interglacial periods; these factors may have led to the isolation of northern and southern populations of the *M. meridianus* complex. However, modern geological data indicate that the last intensive uplift of Tian Shan and Altai Mountains was 2–3 Mya (Buslov, Kokh, & De Grave, 2008), and thus, regional orography at the time of the divergence of genetic lineages of the *M. meridianus* complex (800–500 kya) was close to modern.

Estimated times of divergence of the genetic lineages of the *M. meridianus* complex coincide with several Middle Pleistocene glacial cycles (Hughes & Gibbard, 2018). Glaciation during these cycles in Central Asia was restricted to mountains; the modeling of environments during glacial and interglacial phases (Böhner & Lehmkuhl, 2005) has demonstrated that the desert environment was suitable for dispersal of *M. meridianus* across the western passages only during interglacial phases, whereas dispersal across the eastern passages was possible during both glacial and interglacial phases. Moreover, if the configuration and altitude of the mountains surrounding Dzungarian Basin did not significantly change during the Pleistocene, we may infer that the dispersal routes of the *M. meridianus* complex during previous interglacial phases were similar to the current ones. The Dzungarian Gates cannot currently serve as a dispersal route because their northwestern end is occupied by *M. meridianus sensu stricto* whereas the southeastern end is occupied by

M. penicilliger. To operate as a dispersal route, this passage should be free of representatives of the *M. meridianus* complex at least at one end. Such conditions probably occurred in the early stages of interglacial phases, when forest areas at the northwestern entrance of Dzungarian Gates became desert areas (Böhner & Lehmkuhl, 2005). Concurrently, large areas including Alakol Hollow, Dzungarian Gates, and some parts of the Dzungarian Basin were flooded as a result of intensive thawing of mountain glaciers. Records of this flooding episode were found in Dzungar Basin as alluvial–diluvial sediments (Zhu et al., 2014). Based on these data, we can hypothesize that the drying of these temporal lakes opened the passage through the Dzungarian Gates, which could then have served as a dispersal route for species previously unable to enter this passage.

4.3.3 | Hypothesis of speciation and dispersal of the *M. meridianus* complex

Low haplotype diversity of both *psammophilus* and *meridianus* in Dzungaria evidenced the recent colonization of Dzungaria by these lineages. The negative neutrality statistics, bell-shaped mismatch distribution, and skyline results indicate the existence of a significant signal of expansion in both *psammophilus* and *meridianus* in

TABLE 3 Neutrality estimates and expansion time estimate for *psammophilus*, *meridianus*, and *penicilliger* identified in the phylogenetic analyses

	<i>Psammophilus</i>	<i>Meridianus</i>	<i>Penicilliger</i>
Sample size	45	26	13
Tajima's <i>D</i>	-1.99887	-1.84669	-1.09158
Tajima's <i>D</i> <i>p</i> -value	.0057**	.0157*	.1387
FS of Fu	-25.16184	-6.03427	-6.77658
FS <i>p</i> -value	.0000**	.0019**	.0013**
τ (95% CI)	4 (3.02734–9.76183)	41.50463 (4.85641–84.00453)	4 (2.73634–15.86527)
Expansion time (Mya)	0.01754	0.18204	0.01754
95% CI (Mya)	0.04282–0.01328	0.36844–0.02130	0.06958–0.01200

Note: Significant values are in bold. CI, confidence interval.

*Indicates significance at $p < .05$;

**Indicates significance at $p < .01$.

TABLE 4 Neutrality estimates and expansion time estimate for different populations: *psammophilus* N—*psammophilus* from the Valley of Lakes and northwestern Mongolia; *psammophilus* SW—*psammophilus* from northwestern Transaltai Gobi; *meridianus* Kaz—*meridianus* from eastern Kazakhstan; *meridianus* Dzungaria—*meridianus* from Mongolian Dzungaria; *penicilliger* Kaz—*penicilliger* from southern Balkhash area; *penicilliger* Dzungaria—*penicilliger* from Chinese Dzungaria

	<i>Psammophilus</i> N	<i>Psammophilus</i> SW	<i>Meridianus</i> Kaz	<i>Meridianus</i> Dzungaria	<i>Penicilliger</i> Kaz	<i>Penicilliger</i> Dzungaria
Sample size	10	35	9	17	6	7
Tajima's <i>D</i>	-0.20468	-1.66858	-0.39329	-1.86628	-1.17419	-1.31438
Tajima's <i>D</i> <i>p</i> -value	.433	.029*	.37	.011*	.13	.093
FS of Fu	-1.95214	-18.37424	-1.54367	-3.52566	-2.32822	-3.1805
FS <i>p</i> -value	.114	.0000**	.155	.004**	.039	.012*
τ	6.8184	4.45313	6.7422	1.0000	5.0000	4.0000
95%CI	3.05666–11.06062	2.77148–11.22469	2.64844–11.24419	0.0000–2.03910	2.67188–7.52742	2.75777–8.38288
Expansion time (Mya)	0.02991	0.01953	0.02957	0.00439	0.02193	0.01754
95% CI (Mya)	0.04851–0.01341	0.04923–0.01216	0.04932–0.01162	0.00894–0.0000	0.03302–0.01172	0.03677–0.01210

Note: Significant values are in bold. CI, confidence interval.

*Indicates significance at $p < .05$;

**Indicates significance at $p < .01$.

Dzungaria. The *meridianus* lineage invaded Dzungaria most recently (ca. 2–7 thousand years ago). Based on the estimated time of divergence, we can propose how speciation and dispersal of the *M. meridianus* complex occurred. Apparently, at the first stage, during the series of glacial cycles 500–800 kya BP, the glaciation of the Tian Shan, Tarbagatai, and Altai Mountains divided a single population into two isolated populations: the western ancestors of the *penicilliger* lineage and the eastern ancestors of the *psammophilus* and *meridianus* lineages. These two isolated populations adapted to the local environments (warmer in the west and cooler in the east). Most probably, at the second stage, during the interglacial phase approximately 500 kya BP, the cold-adapted eastern *psammophilus* + *meridianus* lineage penetrated the west (probably via the Dzungarian Gates) and dispersed further westwards across Kazakhstan and the northern edges of Turan. Distributional limits in Turan (northern for

penicilliger and southern for *psammophilus* + *meridianus*) were probably established as a result of competitive exclusion. Such stable distributional limits between the two lineages can be observed now in the area to the east of the Aral Sea (Heptner, 1968). If the competitive exclusion is considered to be based on different temperature optima, the distribution limits may be displaced northward or southward because of climate fluctuations. At the third stage, during a glacial phase 480–420 kya BP, the western and eastern parts of the range of the common ancestor of the *psammophilus* + *meridianus* lineage were isolated by mountain glaciation and evolved, forming the separate *psammophilus* and *meridianus* lineages. The *meridianus* and *penicilliger* lineages may have penetrated the Dzungarian Basin via Dzungarian Gates during one of the interglacial phases of the Late Pleistocene, probably during marine isotope stage 3 (MIS3) or even after the last glacial maximum (LGM). The contemporary pattern of

TABLE 5 Results of the Mclust classification of 45 skulls and its comparison with the Cytb classification. Specimen No and Loc (locality). No corresponds to those shown in Appendix 2. Regions: TG—northwestern Transbaikai Gobi; MD—Mongolian Dzungaria; Db—Dzungar basin. Museum number (ZMMU)—specimen number in the collection of the Zoological Museum of Moscow State University of M. V. Lomonosov. Cytb haplotype—clade selected for each specimen by the Cytb analysis. Morphological classification—clade selected for each specimen by the “mclust” analysis of crania: psam—*psammophilus*, mer—*meridianus*, pen—*penicilliger*. Specimens with incongruent genetic and morphological classification are marked with an asterisk (*)

Specimen No	Loc No	Region	Museum number (ZMMU)	Cytb haplotype	Morphological classification	Posterior probabilities of belonging of specimens to a cluster			
						1-psam	2a	2b	3-pen
M-75-2006	27	TG	S-180958	psam	psam	0.989	0.000	0.002	0.009
M-274-2011	32	TG	S-189098	psam	psam	1.000	0.000	0.000	0.000
M-116-2011	16	MD	S-189100	mer	mer	0.027	0.004	0.952	0.017
M-117-2011	16	MD	S-189101	mer	mer	0.003	0.034	0.797	0.166
M-160-2011	14	MD	S-189104	mer	mer	0.000	0.333	0.633	0.034
M-161-2011	14	MD	S-189105	mer	mer	0.073	0.002	0.374	0.550
M-164-2011	14	MD	S-189106	mer	mer	0.000	0.676	0.314	0.010
M-182-2011	13	MD	S-189109	mer	mer	0.010	0.005	0.954	0.031
M-184-2011	13	MD	S-189110	mer	mer	0.050	0.293	0.472	0.185
M-220-2011	15	MD	S-189111	mer	mer	0.000	0.056	0.943	0.000
M-221-2011*	18	TG	S-189094	mer	pen	0.014	0.002	0.425	0.559
M-222-2011	18	TG	S-189095	psam	psam	1.000	0.000	0.000	0.000
M-235-2011*	22	TG	S-189097	mer	pen	0.037	0.000	0.019	0.944
M-41-2012	21	TG	S-191012	psam	psam	1.000	0.000	0.000	0.000
M-70-2012	21	TG	S-191013	psam	psam	0.937	0.000	0.001	0.062
M-72-2012	21	TG	S-191015	psam	psam	1.000	0.000	0.000	0.000
M-73-2012	21	TG	S-191016	psam	psam	0.999	0.000	0.000	0.001
M-74-2012	20	TG	S-191017	psam	psam	0.994	0.000	0.001	0.005
M-75-2012	21	TG	S-191018	psam	psam	0.988	0.000	0.000	0.012
M-76-2012	21	TG	S-191019	psam	psam	0.750	0.000	0.000	0.249
M-77-2012	21	TG	S-191020	psam	psam	0.999	0.000	0.000	0.001
M-79-2012	21	TG	S-191022	psam	psam	0.999	0.000	0.001	0.000
M-80-2012	19	TG	S-191023	psam	psam	0.597	0.000	0.061	0.342
M-86-2012	17	TG	S-191024	psam	psam	0.991	0.000	0.000	0.009
M-88-2012	17	TG	S-191025	psam	psam	1.000	0.000	0.000	0.000
M-91-2012	18	TG	S-191026	psam	psam	0.997	0.000	0.002	0.001
M-92-2012	18	TG	S-191027	psam	psam	0.614	0.000	0.105	0.280
M-94-2012	23	TG	S-191028	psam	psam	1.000	0.000	0.000	0.000
M-100-2012	23	TG	S-191029	psam	psam	0.995	0.000	0.001	0.004
M-101-2012	23	TG	S-191030	psam	psam	0.992	0.000	0.000	0.008
M-103-2012	26	TG	S-191031	psam	psam	0.999	0.000	0.000	0.000

(Continues)

TABLE 5 (Continued)

Specimen No	Loc No	Region	Museum number (ZMMU)	Cytb haplotype	Morphological classification	Posterior probabilities of belonging of specimens to a cluster			
						1-psam	2a	2b	3-pen
M-104-2012	26	TG	S-191032	psam	psam	1.000	0.000	0.000	0.000
M-105-2012	26	TG	S-191033	psam	psam	0.766	0.000	0.025	0.208
M-106-2012*	26	TG	S-191034	psam	mer	0.012	0.036	0.774	0.178
M-118-2011	16	TG	S-191038	psam	psam	1.000	0.000	0.000	0.000
M-119-2011	16	TG	S-191039	psam	psam	1.000	0.000	0.000	0.000
M-120-2012	26	TG	S-191040	psam	psam	1.000	0.000	0.000	0.000
M-122-2012	26	TG	S-191042	psam	psam	0.942	0.000	0.000	0.058
M-123-2012	26	TG	S-191043	psam	psam	0.998	0.000	0.001	0.002
M-136-2012	25	TG	S-191044	psam	psam	0.990	0.000	0.000	0.009
M-137-2012	25	TG	S-191045	psam	psam	0.646	0.000	0.269	0.085
C-2-2012	9	Db	S-191547	pen	pen	0.027	0.000	0.016	0.957
C-3-2012	10	Db	S-191548	pen	pen	0.009	0.000	0.000	0.991
C-4-2012	10	Db	S-191549	pen	pen	0.017	0.000	0.055	0.928
C-5-2012*	12	Db	S-191550	pen	psam	0.923	0.000	0.000	0.077

distribution of *meridianus* and *penicilliger* suggests a complex scenario of range shifts or colonization, the details of which remain to be elucidated. The following sequence of events can be hypothesized. After the end of the LGM, temperatures gradually increased from 20 to 10 kya and then abruptly decreased (8–0 kya; Stott, Poulsen, & Lund, 2002). The initial increase in temperature after the LGM allowed *penicilliger* to recolonize the southern and central parts of the Dzungarian Basin and to push *meridianus* northward. At that time, *meridianus* remained only in the Zaysan Hollow refugium. Concurrently, *psammophilus* started to disperse westward along the southern foothills of Altai, across the eastern edge of Dzungarian Basin. Finally, as temperatures decreased 7–2 kya, *meridianus* dispersed from Zaysan Hollow to the northern part of the Dzungarian Basin and to Mongolian Dzungaria.

4.3.4 | Comparison with other widespread Central Asian psammophilous species

Two other widespread psammophile species complexes occur in Central Asia and have known phylogeographic patterns: *Dipus sagitta* Pallas, 1773 and *Phodopus roborovskii* Satunin, 1903. *Salpingotus kozlovi* Vinogradov, 1922 and *Salpingotus crassicauda* Vinogradov, 1924 are also widespread Central Asian psammophile species complexes, but their phylogeographic patterns have not yet been studied.

The geographic distribution of the *Dipus* complex is almost the same as that of the *M. meridianus* complex. As with *M. meridianus*, the *Dipus* complex in the western part of its geographic range has two different phylogenetic Turano-Kazakh lineages; however, these are not separated into northern and southern lineages (as *M. meridianus* is) but into eastern and western lineages (Lebedev et al., 2018). Moreover, rather than one widespread eastern phylogenetic lineage, as with *M. meridianus* s.l. (*psammophilus* lineage), *Dipus* populations within the same distributional limits are subdivided into two deeply divergent genetic lineages, the northeastern and southwestern lineages, which co-occur at the eastern edge of the Tarim Basin; nevertheless, *Dipus* and *M. meridianus* in these regions are not strong psammophiles (i.e., they do not occur only in sand massifs). Finally, the Dzungarian *Dipus* group has a single phylogenetic line. The Dzungarian and Turano-Kazakh populations of *Dipus* are not currently connected via the Dzungarian Gates because of the absence of sand massifs and of the strong psammophily of these populations. Thus, the distribution patterns of *Dipus* and *M. meridianus* significantly differ; however, the history of both complexes probably includes several independent dispersal events across the Tian Shan–Altai Mountain border.

The third species, *Ph. roborovskii*, has a narrower distribution (it occurs only to the east of the Tian Shan–Altai Mountain border) and simpler phylogeographic patterns than the other two species complexes, without significant genetic differentiation across almost the entire Central Asian area (Lv et al., 2016). The genetic similarity in this species complex is clear despite the geographical separation

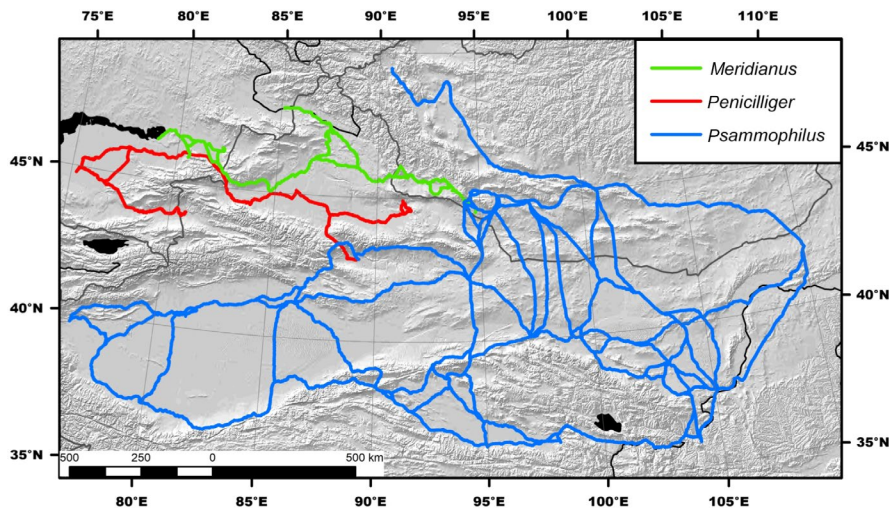


FIGURE 7 The most probable routes connecting the occurrence points of the species of the *Meriones meridianus* complex (see Figure 1) based on estimations of least-cost path for population connectivity

between Dzungarian populations and Gobian populations. Notably, the geographic distribution of *Ph. roborovskii* in Dzungaria is practically identical to that of the *meridianus* lineage of *M. meridianus*; this may indicate that common environmental factors affect the geographic distribution of both species.

4.4 | Taxonomical implications

There are two points of view regarding the systematics of the *M. meridianus* complex. According to Ito et al. (2010), the three clades of *M. meridianus* complex should be treated as species. At the same time, Wang et al. (2013) regarded the two taxa examined in their study (*penicilliger* and *psammophilus*) as subspecies based on the belief that the lower boundary of the degree of divergence between valid sister species is close to 13%.

In our opinion, the three clades should be considered as distinct species—*M. psammophilus* (Milne-Edwards, 1868–1874); *M. meridianus* (Pallas, 1773); and *M. penicilliger* (Heptner, 1933). There is no direct evidence of ongoing hybridization between these taxa in nature, and hybridization between *M. penicilliger* and the other species of the complex appears to be very rare or absent. Moreover, the genetic consequences of hybridization between *M. psammophilus* and *M. meridianus* are low and local. Next, the genetic distances between the lineages correspond to interspecific levels of differentiation (Baker & Bradely, 2006). The *Cytb* K2P distances between *M. psammophilus* and *M. penicilliger*, *M. psammophilus*, and *M. meridianus*, and *M. meridianus* and *M. penicilliger* were 10.5%, 8.1%, and 11.8%, respectively. These values are comparable to those between some other valid species of *Meriones* such as *M. libycus*/*M. arimalius* (8.9% K2P) or *M. rex*/*M. crassus* (5.4% K2P). Distances between subspecies usually fall below 5% (e.g., Dianat et al., 2017; Gu et al., 2011). (Two highly divergent lineages within *M. persicus* (9.5% K2P) revealed in the latter study may also represent distinct species). The divergence time of the *M. meridianus* species complex is estimated to be the first half of the middle Pleistocene. Finally, chromosomal (Korobitsina & Kartavtseva, 1988) and cranial (Nanova,

2014; this study) differences exist between the three species of *M. meridianus* s.l.

ACKNOWLEDGEMENTS

We are sincerely grateful to A.B. Poltarau (Engelhardt Institute of Molecular Biology RAS) for providing the possibility of DNA sequencing. We thank Ryurikov G., Khlyap L.A., Bogomolov P.L., Sukhchuluun G., and Adiya Yad. for their help with collecting jirds. We are also grateful to Meschersky I.G. and Sorokin P.A. for their help with DNA extraction. This study was supported by the Russian Foundation for Basic Research, grant 18-04-00400; Russian Science Foundation, grant 14-50-00029. This work was also supported by Moscow State University Grant for Leading Scientific Schools "Depository of the Living Systems" in frame of the MSU Development Program. We would like to thank Editage (www.editage.com) for English language editing.

ORCID

Olga G. Nanova  <https://orcid.org/0000-0001-8886-3684>
 Vladimir S. Lebedev  <https://orcid.org/0000-0003-4943-7097>
 Vera A. Matrosova  <https://orcid.org/0000-0003-2325-8584>
 Georgy I. Shenbrot  <https://orcid.org/0000-0002-5075-7349>

REFERENCES

- References marked with * are cited in Supporting Information.
- Afanasyev, A. V. (1960).* *Zoogeography of Kazakhstan (Based on Mammalian Distribution)*. Alma-Ata: Kazakhstan Acad. Sci: Press, USSR. [in Russian].
- Ageyev, V. S., Burdelov, A. S., Kozlova, T. A., Osipov, V. P., Sarayev, F. A., Tanitovskiy, V. A., & Shevchenko, V. A. (2001).* Species composition and some indexes of abundance of fleas parasitizing *Meriones* jirds in different parts of Volga-Ural sandy natural plague focus. *Quarantable and Zoonotic Infections in Kazakhstan*, 3, 39–44. [in Russian].
- Akimzhanov, R. K., Aysautov, B. N., Malikov, B. M., Akhmetov, B. B., Songuliyev, U. K., Konyrbayev, B. K., ... Kulseitova, L. Z. (2004).* About mass reproduction of *Meriones meridianus* in the ancient valley of the Zhanadarya River in 2002–2003. *Quarantable and Zoonotic Infections in Kazakhstan*, 9, 99–100. [in Russian].

- Alhajeri, B. H. (2018). Cranial variation in geographically widespread dwarf gerbil *Gerbillus nanus* (Gerbillinae, Rodentia) populations: Isolation by distance versus adaptation to local environments. *Journal of Zoological Systematics and Evolutionary Research*, 57, 191–203. <https://doi.org/10.1111/jzs.12247>
- Alhajeri, B. H., Hunt, O. J., & Steppan, S. J. (2015). Molecular systematics of gerbils and deomyines (Rodentia: Gerbillinae, Deomyinae) and a test of desert adaptation in the tympanic bulla. *Journal of Zoological Systematics and Evolutionary Research*, 53, 312–330. <https://doi.org/10.1111/jzs.12102>
- Alhajeri, B. H., Porto, L. M. V., & Maestri, R. (2019). Habitat productivity is a poor predictor of body size in rodents. *Current Zoology*. <https://doi.org/10.1093/cz/zo037>
- Allen, G. M. (1940).* *The Mammals of China and Mongolia*. Part 2. New York, NY: The American Museum of Natural History.
- Anderson, R. P., & Raza, A. (2010). The effect of the extent of the study region on GIS models of species geographic distributions and estimates of niche evolution: Preliminary tests with montane rodents (genus *Nephelomys*) in Venezuela. *Journal of Biogeography*, 37, 1378–1393. <https://doi.org/10.1111/j.1365-2699.2010.02290.x>
- Andrushko, A. M. (1939).* *Rodent activity on dry pastures of Middle Asia*. Leningrad, Russia: Leningrad University Press. [in Russian].
- Artykbaeva, A. I. (1999).* Faunistic complexes of the plague hosts in different habitats of north-western part of Aktyubinsk Oblast. *Quarantable and Zoonotic Infections in Kazakhstan*, 1, 182–184. [in Russian].
- Baker, R. J., & Bradley, R. D. (2006). Speciation in mammals and the genetic species concept. *Journal of Mammalogy*, 87, 643–662. <https://doi.org/10.1644/06-MAMM-F-038R2.1>
- Bekenov, A., Yeszhanov, B., Mazin, V. N., & Zhapbarov, M. P. (1989).* Data on distribution and abundance of midday jird in Southern Balkhash region. In: V. E. Sokolov (Ed.), *Gerbils – most important rodent of arid zone of USSR* (pp. 214–216). Tashkent: Fan Press. [in Russian].
- Böhner, J., & Lehmkuhl, F. (2005). Environmental change modelling for Central and High Asia: Pleistocene, present and future scenarios. *Boreas*, 34, 220–231. <https://doi.org/10.1111/j.1502-3885.2005.tb01017.x>
- Bondar, E. P. (1956).* Data on the mammals of the Betpakdala desert and south-western part of Kazakh Upland. *Proceedings of the Middle Asian Scientific Anti-Plague Institute*, 3, 107–122. [in Russian].
- Bray, T. C., Alagaili, A. N., & Bennett, N. C. (2014). A widespread problem: Cryptic diversity in the Libyan jird. *Zoological Studies*, 53, 33. <http://www.zoologicalstudies.com/content/53/1/33>. <https://doi.org/10.1186/s40555-014-0033-3>
- Brown, J. L., Bennett, J. R., & French, C. M. (2017). SDMtoolbox 2.0: The next generation Python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *PeerJ*, 5, e4095. <https://doi.org/10.7717/peerj.4095>
- Burdelov, A. S. (1995).* Rodents and Lagomorphs in the depression of the Ala-Kul' Lake. *Selevinia*, 3, 3–11. [in Russian, English summary].
- Burdelov, A. S., & Leontyeva, M. N. (1956). Gerbils of northern Balkhash. *Proceedings of the Middle Asian Scientific Anti-Plague Institute*, 3, 57–62. [in Russian].
- Burdelov, A. S., & Levoshina, A. I. (1959).* Ecological and faunistic data on mammals of Alakul' Basin. *Proceedings of the Middle Asian Scientific Anti-Plague Institute*, 6, 175–184. [in Russian].
- Burdelov, A. S., Sabilayev, A. S., Sapozhnikov, V. I., Makhnin, V. B., Larionov, G. I., Zveryansky, G. I., & Kasenova, A. K. (1999).* On significance of separate parts of North-West Pribalkhash region in natural focality of plague. *Quarantable and Zoonotic Infections in Kazakhstan*, 1, 64–66. [in Russian].
- Burdelov, A. S., Zaykovskiy, V. B., Grube, A. S., Makhnin, B. V., Klassovskiy, N. L., Savelov, Y. V., & Grigorash, V. I. (1989).* Discovery of Libyan jird in the north Balkhash region. In V. E. Sokolov (Ed.), *Gerbils – most important rodent of arid zone of USSR* (pp. 32–33). Tashkent: Fan Press. [in Russian].
- Buslov, M. M., Kokh, D. A., & De Grave, J. (2008). Mesozoic-Cenozoic tectonics and geodynamics of Altai, Tien Shan, and Northern Kazakhstan, from apatite fission-track data. *Russian Geology and Geophysics*, 49, 648–654. <https://doi.org/10.1016/j.rgg.2008.01.006>
- Chan, L. M., Brown, J. L., & Yoder, A. D. (2011). Integrating statistical genetic and geospatial methods brings new power to phylogeography. *Molecular Phylogenetics and Evolution*, 59, 523–537. <https://doi.org/10.1016/j.ympev.2011.01.020>
- Cheng, J., & Ren, D. (1998).* Mammals survey in Aral area, Xinjiang, China. *Journal of Talimu University of Agricultural Reclamation*, 10, 39–40. [in Chinese].
- Chevret, P., & Dobigny, G. (2005). Systematics and evolution of the subfamily Gerbillinae (Mammalia, Rodentia, Muridae). *Molecular Phylogenetics and Evolution*, 35, 674–688. <https://doi.org/10.1016/j.ympev.2005.01.001>
- Chugunov, Y. D. (1962).* Mammals of the Gobi Altai. Part 1. Jirds, hamsters, voles. *Zoologicheskii Zhurnal*, 41, 1719–1730. [in Russian, English summary].
- Darvish, J., Siahsarvie, R., Mirshamsi, O., Kayvanfar, N., Hashemi, N., & Shakib, F. S. (2006).* Diversity of the rodents of northeastern Iran. *Iranian Journal of Animal Biosystematics*, 2, 57–76.
- Davydov, G. S. (1964).* *Rodents of Northern Tajikistan*. Dushanbe: Tajikistan Acad. Sci. Press, USSR. [in Russian].
- Dementyev, G. P. (1955).* Data on mammals of south-western Turkmenistan. *Archives of Moscow State University, Biology*, 171, 15–51. [in Russian].
- Dianat, M., Darvish, J., Cornette, R., Aliabadian, M., & Nicolas, V. (2017). Evolutionary history of the Persian Jird, *Meriones persicus*, based on genetics, species distribution modelling and morphometric data. *Journal of Zoological Systematics and Evolutionary Research*, 55, 29–45. <https://doi.org/10.1111/jzs.12145>
- Drummond, A. J., Suchard, M. A., Xie, D., & Rambaut, A. (2012). Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution*, 29, 1969–1973. <https://doi.org/10.1093/molbev/mss075>
- Egorov, S. A., Rasin, B. V., Davydenko, L. S., & Shyngysbayev, K. S. (2001).* Some characteristics of populational dynamic of midday gerbil in Ily-Karatal rivers divide. *Quarantable and Zoonotic Infections in Kazakhstan*, 4, 133–137. [in Russian].
- Elith, J., Phillips, S. J., Hastie, T., Dudik, M., Chee, Y. E., & Yates, C. J. (2011). A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, 17, 43–57. <https://doi.org/10.1111/j.1472-4642.2010.00725.x>
- Fenyuk, B. K., & Kamnev, P. I. (1957).* Notes on the mammalian fauna of Mangyshlak and Ustyurt. *Rodents and Its Control*, 5, 387–397. [in Russian].
- Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37, 4302–4315. <https://doi.org/10.1002/joc.5086>
- Formozov, A. N. (1929).* *Mammals of the Northern Mongolia based on collections of 1926 expedition*. Leningrad: USSR Academy of Sciences Press. [in Russian].
- Fotteler, E. R., Mitropolskiy, O. V., Lobyzova, V. P., Tretyakov, G. P., & Polyanskiy, A. V. (1989).* Distribution and abundance of midday jird in Surkhan-Darya Oblast (southern Uzbekistan). In: V. E. Sokolov (Ed.), *Gerbils – most important rodent of arid zone of USSR* (pp. 68–70). Tashkent: Fan Press. [in Russian].
- Frale, C., & Raftery, A. E. (1998). How many clusters? Which clustering method? Answers via Model-based cluster analysis. *The Computer Journal*, 41, 578–588. <https://doi.org/10.1093/comjnl/41.8.578>
- Frale, C., & Raftery, A. E. (2003). Enhanced software for model-based clustering, discriminant analysis, and density estimation: MCLUST. *Journal of Classification*, 20, 263–286. <https://doi.org/10.1007/s00357-003-0015-3>
- Fu, Y. X. (1997). Statistical tests of neutrality of mutations against population growth, hitchhiking and background selection. *Genetics*, 147, 915–925.

- Giraudoux, P., Zhou, H., Quere, J. P., Raoul, F., Delattre, P., Volobouev, V., ... Craig, P. S. (2008). Small mammal assemblages and habitat distribution in the northern Junggar Basin, Xinjiang, China: A pilot survey. *Mammalia*, 72, 309–319. <https://doi.org/10.1515/MAMM.2008.048>
- Gromov, I. M., & Erbaeva, M. A. (1995). *The Mammals of Russia and Adjacent Territories (Lagomorphs and Rodents)*. St. Petersburg: Zoological Institute of Russian Academy of Sciences (pp. 366–369).
- Gu, D., Zhou, L., Ma, Y., Ning, S., Hou, Y., & Zhang, B. (2011). Geographic variation in mitochondrial DNA sequences and subspecies divergence of the Tamarisk Gerbil (*Meriones tamariscinus*) in China. *Acta Theriol Sinica*, 31, 347–357.
- Habibi, K. (2004). *Mammals of Afghanistan*. Kabul, Afghanistan: Zoo Outreach Organisation with assistance from U.S. Fish and Wildlife Service.
- Heled, J., & Drummond, A. J. (2008). Bayesian inference of population size history from multiple loci. *BMC Evolutionary Biology*, 8, 289. <https://doi.org/10.1186/1471-2148-8-289>
- Heled, J., & Drummond, A. J. (2010). Bayesian inference of species trees from multilocus data. *Molecular Biology and Evolution*, 27, 570–580. <https://doi.org/10.1093/molbev/msp274>
- Heptner, V. G. (1933). Notizen über die Gerbillinae (Mammalia, Muridae). V. Diagnosen von einer neuen Gattung und neun neuen Unterarten aus Turkestan. *Zeitschrift Für Säugetierkunde (Mamm Biol)*, 8, 150–155.
- Heptner, V. G. (1968). Some theoretical aspects of conceptions of subspecies, subspecies' traits and borders of range by the example of geographical variability of two palearctic mammal species. *Proceeding Zoological Museum MSU*, 10, 3–36. [in Russian].
- Hey, J. (2005). On the number of new world founders: A population genetic portrait of the peopling of the Americas. *PLoS Biology*, 3, 0965–0975. <https://doi.org/10.1371/journal.pbio.0030193>
- Hey, J., & Nielsen, R. (2007). Integration within the Felsenstein equation for improved Markov chain Monte Carlo methods in population genetics. *Proceedings of the National Academy of Sciences*, 104, 2785–2790. <https://doi.org/10.1073/pnas.0611164104>
- Huang, J., Ju, H., Te, M., Song, G., & Zhao, S. (2004). Monitoring on controlling effect of *Rhombomys opimus* in *Haloxylon ammodendron* Bunge stands using remote sensing TM imagery in Alashan. *Scientia Silvae Sinica*, 40, 107–110. [in Chinese, English summary].
- Huang, X., & Zhou, L. (2012). Genetic diversity and genetic structure of the mid-day gerbil population in Inner Mongolia-Xinjiang Plateau. *Acta Theriologica Sinica*, 32, 179–187.
- Hughes, P. D., & Gibbard, P. L. (2018). Global glacier dynamics during 100 ka Pleistocene glacial cycles. *Quaternary Research*, 90, 222–243. <https://doi.org/10.1017/qua.2018.37>
- Ismagilov, M. I. (1961). *Ecology of Rodents of the Betpakdala and South Balkhash Deserts*. Alma-Ata: Kazakhstan Acad. Sci. Press, USSR. [in Russian].
- Ito, M., Jiang, W., Jun, J. S., Zhen, Q., Jiao, W., Goto, K., ... Kamiya, H. (2010). Molecular Phylogeny of the subfamily Gerbillinae (Muridae, Rodentia) with emphasis on species living in the Xinjiang-Uygur autonomous region of China and based on the mitochondrial *Cytochrome b* and *Cytochrome c Oxidase Subunit II* Genes. *Zoological Science*, 27, 269–278.
- Jobb, G. (2008). *TREEFINDER, version of October 2008 [computer software and manual]*. Munich. Retrieved from www.treefinder.de.
- Kasatkina, N. V. (1958). Data on distribution of rodents in the foothills of Trans-Ili Alatau. *Proceedings of the Middle Asian Scientific Anti-Plague Institute*, 4, 217–222. [in Russian].
- Kashkarov, R. D., & Urmanov, R. A. (1989). Some aspects of long-term population dynamics of midday jird in north-eastern Uzbekistanian Kyzylkum. In V. E. Sokolov (Ed.), *Gerbils – most important rodent of arid zone of USSR* (pp. 53–55). Tashkent: Fan Press. [in Russian].
- Khamzin, T. K., Khamzin, S. K., Radchenko, G. A., & Kausov, S. G. (1999). On activation of plague focus in the Volga-Ural sands after a twenty-year interepizootic period. *Quarantable and Zoonotic Infections in Kazakhstan*, 1, 240–242. [in Russian].
- Khodasheva, K. S. (1953). Life forms of rodents of the Kazakhstan plains and some patterns of their geographic distribution. *Proceedings of the Geography Institute of the Academy of Sciences of USSR*, 54, 33–194. [in Russian]
- Kopbaev, E. S., Davydova, V. N., Sapozhnikov, V. I., Musirepov, T., & Stogov, L. I. (2001). Detection of new plague focality area on the left bank of the Ili depression. *Quarantable and Zoonotic Infections in Kazakhstan*, 3, 310–312. [in Russian].
- Korobitsina, K. V., & Kartavtseva, I. V. (1988). Karyotype variation and evolution of jird (Rodentia, Cricetidae, Gerbillinae): I. karyotypic differentiation of midday gerbil (*Meriones meridianus*) from the fauna of the soviet union. *Russian Journal of Zoology*, 67, 1889–1899. [in Russian].
- Koshenov, U. A., & Shvetsov, V. A. (1989). Patterns of infection process in midday jirds from Trans-Aral autonomous plague focus. In: V. E. Sokolov (Ed.), *Gerbils – most important rodent of arid zone of USSR* (pp. 241–243). Tashkent: Fan Press. [in Russian].
- Kovtun, I. P., Shokputov, M. T., & Rapoport, L. P. (1999). On a role of the jird, *Meriones meridianus* in epizootology of plague in Moinkum. *Quarantable and Zoonotic Infections in Kazakhstan*, 1, 198–200. [in Russian].
- Kucheruk, V. V., Mitropolskyi, O. V., Promptov, V. P., Tretyakov, G. P., & Shishov, A. A. (1989). Distribution and abundance of rodents in Fergana valley. *Fauna and Ecology of Rodents*, 17, 144–179. [in Russian].
- Kuznetsov, B. A. (1948). *Mammals of Kazakhstan*. Moscow: Moscow Natur. Soc. Press, USSR. [in Russian].
- Lay, D. M. (1967). A study of the mammals of Iran resulting from the Street Expedition of 1962–63. *Fieldiana: Zoology*, 54, 1–282.
- Lebedev, V. S., Bannikova, A. A., Lu, L., Snytnikov, E. A., Adiya, Y., Solovyeva, E. N., ... Shenbrot, G. I. (2018). Phylogeographical study reveals high genetic diversity in a widespread desert rodent, *Dipus sagitta* (Dipodidae: Rodentia). *Biological Journal of the Linnean Society*, 123, 445–462. <https://doi.org/10.1093/biolinnean/blx090>
- Lebedev, V. S., & Lissovsky, A. A. (2008). The geographical variability of cranial characteristics and systematics of striped-back hamsters (*Cricetulus arabensis*, Rodentia, Cricetidae). *Russian Journal of Zoology*, 87, 361–374. [in Russian].
- Li, J. S., Song, Y. L., & Zeng, Z. G. (2003). Elevational gradients of small mammal diversity on the northern slopes of Mt. Qilian, China. *Global Ecology and Biogeography*, 12, 449–460. <https://doi.org/10.1046/j.1466-822X.2003.00052.x>
- Librado, P., & Rozas, J. (2009). DnaSP v5: A software for comprehensive analysis of DNA polymorphism data. *Bioinformatics*, 25, 1451–1452. <https://doi.org/10.1093/bioinformatics/btp187>
- Liu, M., Li, Y., Wang, G., & Liu, H. (2005). Studies on rodent fauna in Zhangjiakou City. *Endemic Diseases Bulletin*, 20, 16–17. [in Chinese, English summary].
- Lv, X., Xia, L., Ge, D., Wen, Z., Qu, Y., & Lu, L. (2016). Continental refugium in the Mongolian Plateau during quaternary glacial oscillations: Phylogeography and niche modelling of the endemic desert hamster, *Phodopus roborovskii*. *PLoS ONE*, 11, e0148182. <https://doi.org/10.1371/journal.pone.0148182>
- Marinina, L. S. (2005). Midday Jird (*Meriones meridianus* Pallas, 1773). In: V. V. Kucheruk, & L. A. Khlyap (Eds.), *Lagomorpha and Rodents of the Middle Asia's deserts* (pp. 232–245). Moscow: GEOS. [in Russian].
- McRae, B. H., & Beier, P. (2007). Circuit theory predicts gene flow in plant and animal populations. *Proceedings of the National Academy of Sciences*, 104, 19885–19890. <https://doi.org/10.1073/pnas.0706568104>
- Medzykhovskiy, G. A., Parfenov, A. V., Parshin, B. M., Grazhdanov, A. K., Andryutshenko, V. V., & Tanitovskiy, V. A. (1999). To characteristics of plague epizootics in north-east of the Volga-Ural sands over

- 1989-1998. *Quarantable and Zoonotic Infections in Kazakhstan*, 1, 101-104. [in Russian]
- Milne-Edwards, M. A. (1868-1874). *Recherches Pour Servir a l'histoire Naturelle des Mammiferes* (2 vols). Paris: Masson, pp 394; vols I, atlas.
- Ming, M., Leptez, S., Idriss, A., & Guo-rui, L. (2005).* Records on the vertebrates in the desert at the lower reaches of Keriya River and at the ruins of Yuansha City. *Arid Land Geography*, 28, 638-641. [in Chinese, English summary].
- Minin, N. V. (1938).* *Ecological and Geographic Review of Rodents of Central Asia*. Leningrad: Leningrad Univ. Press, USSR. [in Russian].
- Montgelard, C., Bentz, S., Tirard, C., Verneau, O., & Catzeffis, F. M. (2002). Molecular systematics of Sciurognathi (Rodentia): The mitochondrial cytochrome *b* and 12S rRNA genes support the Anomaluroidea (Pedetidae and Anomaluridae). *Molecular Phylogenetics and Evolution*, 22, 220-233. <https://doi.org/10.1006/mpev.2001.1056>
- Nanova, O. (2014). Geographical variation in the cranial measurements of the midday jird *Meriones meridianus* (Rodentia: Muridae) and its taxonomic implications. *Journal of Zoological Systematics and Evolutionary Research*, 52, 75-85. <https://doi.org/10.1111/jzs.12032>
- Naumov, N. P., Lobachev, V. S., Dmitriev, P. P., & Smirin, V. M. (1972).* *Natural plague focus in Aral Karakum*. Moscow: Moscow University Press. [in Russian].
- Neronov, V. M., Abramson, N. I., Warshavsky, A. A., Karimova, T. Y., & Khlyap, L. A. (2009). Chorological structure of the range and genetic variation of the midday gerbil (*Meriones meridianus* Pallas, 1773). *Doklady Biological Sciences*, 425, 135-137. <https://doi.org/10.1134/S0012496609020148>
- Neronov, V. M., & Aleksandrov, D. Y.. (2004). Patterns of habitat use by midday (*Meriones meridianus* Pallas, 1773) and tamarisk (*M. tamariscinus* Pallas, 1773) jirds in semidesert of southern Kalmykia. *Povolzhskiy Ekologicheskyy Zhurnal*, 1, 69-78. [in Russian, English summary].
- Neronov, V. M., Farhang-Azad, A., & Teslenko, E. B. (1974).* Distribution and abundance of gerbils of the genera *Meriones*, *Tatera* and *Gerbillus* in Iran and problems of zoogeographical zonation of the country. *Bulleten Moskovskogo Obshchestva Ispytateley Prirody, Otdel Biologicheskyy*, 79, 41-71. [in Russian].
- Nurgeldyev, O. N. (1960).* *Data on Fauna and Ecology of Mammals of the First Stage of the Karakum Canal Line and their Practical Importance*. Ashkhabad: Turkmenistan SSR Acad. Sci. Press, USSR. [in Russian]
- Nurgeldyev, O. N. (1969).* *Ecology of mammals of Turkmenistan plains*. Ashkhabad: Ylym Press. [in Russian].
- Nurgeldyev, O. N., Shcherbina, E. I., Marinina, L. S., & Penchuckovskaya, T. I. (1988).* *Mammals of the Region between the Murgab and Tedzhen Rivers*. Ashkhabad: Ylym Press, USSR. [in Russian].
- Pak, M. I. (1989).* On the study of diet of midday jird in the Amu-Darya - Syr-Darya Rivers divide. In V. E. Sokolov (Ed.), *Gerbils - most important rodent of arid zone of USSR* (pp. 108-110). Tashkent: Fan Press. [in Russian].
- Pallas, P. S. (1773). *Reise Durch Verschiedene Provinzen des russischen Reichs*. Zweiter Theil. St. Petersburg, Russia: St. Petersburg Press (pp. 702).
- Parfenov, A. V., & Parfenova, E. A. (2001).* The problem of interrelation of midday gerbil's flea abundance and plague epizootic manifestation on the North of Volga-Ural sands. *Quarantable and Zoonotic Infections in Kazakhstan*, 3, 202-205. [in Russian]
- Pavlinov, I. Y., Dubrovsky, Y. A., Rossolimo, O. L., & Potapova, E. G. (1990). *Gerbils of the world*. Moscow: Nauka, 300-306.
- Petrova, A. A. (1967).* Rodents. In: G. I. Ishunin (Ed.), *Vertebrate Ecology in Karshi Steppe* (pp. 19-51). Tashkent: FAN Press. [in Russian].
- Pettorelli, N., Vik, J. O., Mysterud, A., Gaillard, J. M., Tucker, C. J., & Stenseth, N. C. (2005). Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology & Evolution*, 20, 503-510. <https://doi.org/10.1016/j.tree.2005.05.011>
- Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, 190, 231-259. <https://doi.org/10.1016/j.ecolmodel.2005.03.026>
- Phillips, S. J., & Dudik, M. (2008). Modeling of species distributions with Maxent: New extensions and a comprehensive evaluation. *Ecography*, 31, 161-175. <https://doi.org/10.1111/j.0906-7590.2008.5203.x>
- Privalov, V. N. (1956).* On the stational distribution of rodents in the Central Kyzylkum Desert. *Proceedings of the Middle Asian Scientific Anti-Plague Institute*, 3, 93-100. [in Russian].
- Przewalskyi, N. M. (1888).* *From Kyakhta to the sources of the Yellow River, study of the northern borderland of Tibet and the way via Lob Nor along Tarim Basin*. S. Peterburg: Imperial Russian Geograpic Society.
- Rambaut, A., & Drummond, A. (2005). *Tracer version 1.5. Computer program distributed by the authors*. Oxford, UK: Department of Zoology, University of Oxford. <http://evolve.zoo.ox.ac.uk/software.html>.
- Rapoport, L. P., Rakhimov, K. R., Nuriyev, K. K., Trofimov, A. S., Shokputov, T. M., Shishkina, T. S., ... Dzhiembayev, R. S. (2003).* Plague epizooty in East Kyzylkum. *Quarantable and Zoonotic Infections in Kazakhstan*, 8, 46-51. [in Russian].
- Ray, N. (2005). Pathmatrix: A geographical information system tool to compute effective distances among samples. *Molecular Ecology Resources*, 5, 177-180. <https://doi.org/10.1111/j.1471-8286.2004.00843.x>
- Reymov, R. (1987).* *Rodents of the Southern Aral Region*. Tashkent: FAN Press, USSR. [in Russian].
- Rogers, A. R., & Harpending, H. (1992). Population growth makes waves in the distribution of pairwise genetic differences. *Molecular Biology and Evolution*, 9, 552-569. <https://doi.org/10.1093/oxfordjournals.molbev.a040727>
- Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D. L., Darling, A., Höhna, S., ... Huelsenbeck, J. P. (2012). MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61, 539-542. <https://doi.org/10.1093/sysbio/sys029>
- Rotshild, E. V., Smirin, V. M., Shilov, M. N., & Kamyshev, A. I. (1967).* Mammals of the northern Kyzylkum desert. *Fauna and Ecology of Rodents*, 8, 85-174. [in Russian].
- Sambrook, J., Fritsch, E. F., & Maniatis, T. (1989). *Molecular cloning: A laboratory manual*. New York, NY: Cold Spring Harbor Lab Press.
- Schneider, S., Roessli, D., & Excoffier, L. (2000). *Arlequin: A software for population genetics data analysis*. User manual. ver. 2. Geneva: Genetics and Biometry Lab, Dept. of Anthropology, University of Geneva. 2496-2497.
- Scatter, W. L. (1891).* *Catalogue of Mammalia in the Indian Museum, Calcutta*. Part II. Rodentia, Ungulata, Proboscidea, Hyracoidea, Carnivora, Cetacea, Sirenia, Marsupialia, Monotremata. Calcutta: The Trustees of the Indian Museum.
- Shao, M., & Liu, N. (2008). The diet of the little owl (*Athene noctua*) in the desert habitats of northwest China. *Journal of Raptor Research*, 42, 61-64. <https://doi.org/10.3356/JRR-05-17.1>
- Shashkov, V. D., Klassovskaya, Y. V., Sapozhnikov, V. I., Barchuk, T. G., Molbayev, D. Y., Abdullayev, M. A., & Shayngyshbayev, K. S. (2003).* To landscape and epizootological regionalization of Karatal - Aksu interfluvial area. *Quarantable and Zoonotic Infections in Kazakhstan*, 8, 55-59. [in Russian].
- Shenbrot, G. (2013). Geographic range, morphometric variation and niche differentiation in greater Egyptian jerboa, *Jaculus orientalis*. *Mammalia*, 77, 317-328. <https://doi.org/10.1515/mammalia-2012-0035>
- Shuai, L., Song, Y., Li, J., Zeng, Z., & Liu, J. (2006).* Rodent community structure of desert-oasis landscape in the middle reaches of the Heihe River. *Biodiversity Science*, 14, 525-533. [in Chinese, English summary]. <https://doi.org/10.1360/biodiv.060052>
- Sludskiy, A. A., Borisenko, V. A., Kapitonov, V. I., Makhmutov, S., Mokrousov, N. Y., Orlov, G. I., ... Shubin, I. G. (1978).* *Mammals of Kazakhstan*, Vol. 1 Part 3. Alma-Ata: Nauka Press Kazakh SSR, USSR. [in Russian].
- Song, Y. L., Li, J. S., Zheng, Z. G., & Zhang, J. S. (2002). Diversity of rodents communities in different habitats in Hexi Corridor, Gansu Province. *Biodiversity Science*, 10, 386-392. [in Chinese, English summary].

- Sotnikova, M. V., Dodonov, A. E., & Pen'kov, A. V. (1997). Upper Cenozoic bio-magnetic stratigraphy of Central Asian mammalian localities. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 133, 243–258. [https://doi.org/10.1016/S0031-0182\(97\)00078-3](https://doi.org/10.1016/S0031-0182(97)00078-3)
- Stalmakova, V. A. (1975). *Fauna of Tadzhik SSR. Vol. 20, Part 2. Gerbillinae. Dushanbe: Donish Press. [in Russian].
- Stephens, M., & Donnelly, P. (2003). A comparison of Bayesian methods for haplotype reconstruction from population genotype data. *American Journal of Human Genetics*, 73, 1162–1169. <https://doi.org/10.1086/379378>
- Stephens, M., Smith, N. J., & Donnelly, P. (2001). A new statistical method for haplotype reconstruction from population data. *American Journal of Human Genetics*, 68, 978–989. <https://doi.org/10.1086/319501>
- Steppan, S., Adkins, R., & Anderson, J. (2004). Phylogeny and divergence date estimates of rapid radiations in murid rodents based on multiple nuclear genes. *Systematic Biology*, 53, 533–553. <https://doi.org/10.1080/10635150490468701>
- Stott, L., Poulsen, C., & Lund, S. (2002). Super ENSO and global climate oscillations at millennial time scales. *Science*, 297, 222–226. <https://doi.org/10.1126/science.1071627>
- Swofford, D. L. (2003). PAUP. Phylogenetic analysis using parsimony (and other methods). Version 4. Sunderland, MA: Sinauer Associates.
- Tabatabaei, Y. F., Adriaens, D., & Darvish, J. (2012). Geographic pattern of cranial differentiation in the Asian Midday Jird *Meriones meridianus* (Rodentia: Muridae: Gerbillinae) and its taxonomic implications. *Journal of Zoological Systematics and Evolutionary Research*, 50, 157–164.
- Tabatabaei Yazdi, F., & Alhajeri, B. H. (2018). Sexual dimorphism, allometry, and interspecific variation in the cranial morphology of seven *Meriones* species (Gerbillinae, Rodentia). *Hystrix*, 29, 162–167. <https://doi.org/10.4404/hystrix-00018-2017>
- Tabatabaei Yazdi, F., Colangelo, P., & Adriaens, D. (2015). Testing a long-standing hypothesis on the relation between the auditory bulla size and environmental conditions: A case study in two jird species (Muridae: *Meriones libycus* and *M. crassus*). *Mammalia*, 79, 185–200. <https://doi.org/10.1515/mammalia-2013-0043>
- Tajima, F. (1989). Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. *Genetics*, 123, 585–595.
- Tchabovsky, A. V. (2006). *Evolution of the sociality of rodents of open spaces: Ecological aspects*. Unpublished Doctoral Thesis, Moscow, Russian Academy of Science. 203 pp. [in Russian].
- Tembotov, A. K. (1972). *Geography of Mammals of North Caucasus. Nal'chik: Elbrus Publishing House, USSR. [in Russian].
- Tinnin, D. S., Dunnum, J. L., Salazar-Bravo, J., Batsaikhan, N., Burt, M. S., Gardner, S. L., & Yates, T. L. (2002). *Contributions to the mammalogy of Mongolia, with a checklist of species for the country. *Special Publications the Museum of Southwestern Biology*, 6, 1–38.
- Wang, G., Wang, Z., Zhou, Q., & Zhong, W. (1999). *Relationship between species richness of small mammals and primary productivity of arid and semi-arid grasslands in north China. *Journal of Arid Environments*, 43, 467–475. <https://doi.org/10.1006/jare.1999.0572>
- Wang, Y., Zhao, L.-M., Fang, F.-J., Liao, J.-C., & Liu, N.-F. (2013). Intraspecific molecular phylogeny and phylogeography of the *Meriones meridianus* (Rodentia: Cricetidae) complex in northern China reflect the processes of desertification and the Tianshan Mountains uplift. *Biological Journal of the Linnean Society*, 110, 362–383.
- Wu, X., & Fu, H. (2005). *Rodent communities in desert and semi-desert regions in Inner Mongolia. *Acta Zoologica Sinica*, 51, 961–972. [in Chinese, English summary].
- Wu, X., & Fu, H. (2008). *Fluctuations and patterns of desert rodent communities under human disturbance: Fluctuating tendency and sensitive response of their population. *Frontiers of Biology in China*, 3, 89–100. <https://doi.org/10.1007/s11515-008-0010-5>
- Xia, L., Yang, Q., Xiang, Y., & Feng, Z. (2003). *Distribution pattern and zoogeographical analysis of mammals in Qilian Mountain Areas, Qinghai, China. *Acta Theriologica Sinica*, 23, 295–303. [in Chinese, English summary].
- Yang, Z., & Rannala, B. (2010). Bayesian species delimitation using multi-locus sequence data. *Proceedings of the National Academy of Sciences*, 107, 9264–9269. <https://doi.org/10.1073/pnas.0913022107>
- Yin, Y., Jiang, W., Zhang, Z., Li, Y., Twenke, B., Turghan, M., ... Liu, B. (2014). *The divergence of small mammals in Xinjiang, China, as revealed by phylogenetic analyses of COI and Cytb. *Animal Biology*, 64, 163–176. <https://doi.org/10.1163/15707563-00002435>
- Yudin, B. S., Galkina, L. I., & Potapkina, A. F. (1979). *Mammals of Altai and Sayan Mountains. Novosibirsk: Nauka Press Siberian Branch, USSR. [in Russian].
- Zakhidov, T. Z. (1971). *Biocenoses of Kyzylkum Desert. Tashkent: Fan Press. [in Russian].
- Zakirov, R. K., & Tretyakov, G. P. (1989). Some aspects of long-term population dynamics of midday jird in the western sandy area of Uzbekistanian Kyzylkum. In V. E. Sokolov (Ed.), *Gerbils - most important rodent of arid zone of USSR* (pp. 47–48). Tashkent: Fan Press. [in Russian].
- Zhang, F., Fu, H., Wu, X., Yang, Z., Yuan, S., & Zang, X. (2011). *Spatial synchrony in population dynamics of desert rodents. *Acta Theriologica Sinica*, 31, 211–218. [in Chinese, English summary].
- Zhang, Y., Jin, S., Quan, G., Li, S., Ye, Z., Wang, F., & Zhang, M. (1997). *Distribution of Mammalian Species in China. Beijing, China: China Forestry Publ. House.
- Zholnerovskaya, E. I., & Koyasu, K. (1997). *Catalogue of the Collection of Mammals in the Siberian Zoological Museum (Novosibirsk, Russia). Nagoya, Japan: Nagoya Society of Mammalogist Special Publication No. 1.
- Zhou, X., Zhang, Y., Huang, J., & Zhang, D. (2004). *Analysis for community structure and change of the rodents at Ganjiahu Natural Reserve in Xinjiang. *Chinese Journal of Zoology*, 39, 58–61. [in Chinese, English summary].
- Zhu, B., Yu, J., Qin, X., Rioual, P., Zhang, Y., & Xiong, H. (2014). Formation and evolution of sand deserts in Xinjiang, Northwest China: II. The palaeo-environmental reconstruction. *Journal of Geographical Sciences*, 24, 539–559. <https://doi.org/10.1007/s11442-014-1105-3>
- Zou, G. B., Zhou, L., Zha, X., Zhang, B., Zhao, T., & Liang, J. (2008). Geographical pattern and historical demography of Midday gerbil *Meriones meridianus* (Gerbillidae, Rodentia) inferred from the sequences of the mitochondrial DNA control region. *Russian Journal of Theriology*, 7, 25–32. <https://doi.org/10.15298/rusjtheriol.07.1.04>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Alignment S1. Alignments employed in the present study, *Cytb*.

Alignment S2. Alignments employed in the present study, *BRCA1*.

Alignment S3. Alignments employed in the present study, *IRBP*.

Table S1. List of GenBank accession numbers of sequences of *Meriones meridianus* sensu lato used in the phylogenetic analysis.

Table S2. List of taxa and GenBank accession numbers of sequences used in the molecular clock analysis of Gerbillinae. *Meriones meridianus* sensu lato was represented by specimens/K25-2015, K-28-2015, M-106-2012.

Table S3. Modified Bayesian Information Criterion (*BIC*) (Lebedev & Lissovsky, 2008; Nanova, 2014).

Table S4. Points used for estimation of least-cost path for population connectivity. Source: ZM MU - Zoological Museum of Moscow State University of Lomonosov M.V.; MSB - University of New Mexico, Museum of Southwestern Biology, Albuquerque; ZIN - Zoological Institute of Russian Academy of Sciences in St.-Petersburg; FMNH - Field Museum of Natural History, Chicago, IL, USA; MVZ - Museum of Vertebrate Zoology, University of California, Berkeley.

Figure S1. Neighbor-joining (NJ) reconstruction of the *Cytb* tree: a) original tree; b) original tree with collapsed clades and separated clades.

Figure S2. Map with main geographical names employed in the present study.

Figure S3. Evaluation of model optimality for different numbers of axes using Mclust with Principal Components (PCs). Solid line: *BIC*. The inferred optimal number of clusters is indicated above the points on the *BIC* plot.

Figure S4. Distribution of 45 genotyped specimens from Transaltai Gobi, Mongolian Dzhungaria, and Dzhungar basin in the space of the first two principal components (PCs) based on skull measurements. Shape and color of symbols designate the respective clades according to the phylogenetic *Cytb* analysis: blue diamonds - *psammophilus*; green triangles - *meridianus*; red circles - *penicilliger*. Specimens with incongruent morphological (by Mclust) and genetic classification are marked with an asterisk (*).

How to cite this article: Nanova OG, Lebedev VS, Matrosova VA, et al. Phylogeography, phylogeny, and taxonomical revision of the Midday jird (*Meriones meridianus*) species complex from Dzungaria. *J Zool Syst Evol Res.* 2020;58:1335–1358. <https://doi.org/10.1111/jzs.12372>

APPENDIX 1

Primers used for polymerase chain reaction (PCR) amplification and sequencing.

Marker	Primer	Sequence (5' to 3')	Reference
<i>Cytb</i>	L14723(L7)	CCAATGACATGAAAAATCATCGTT	Montgelard et al. (2002)
	H15915(H6)	TCTCCATTTCTGGTTTACAAGAC	
<i>BRCA1</i>	F697	CACAAGAACAGCCCTTCACAAATAAAT	Present study
	R1722a	GAGTATCCAGTTCACTCCCTTCCATTTC	
<i>IRBP</i>	F40	GCCATGAAGAGCCATGAGATTCTGA	Present study
	R1151	CAGCACGGATACCTGAAACACAGAGC	

APPENDIX 2

List of used specimens. Specimen No: country (K - Kazakhstan, C - China, M - Mongolia) – field number – collection year.

Loc No	Region	Cytb			BRCA1 haplotypes			IRBP haplotypes			
		Specimen No	Accession No	Cytb haplotypes	Cytb clade No	Accession No	Accession No	Accession No	Accession No		
1	Southern (S) Balkhash	K-3-2015	MN204228	pen8	3	MN204314	3	24	MN204393	36	43
1	S Balkhash	K-6-2015	MN204229	pen9	3	MN204315	3	30	MN204394	41	42
2	S Balkhash	K-13-2015	MN204230	pen10	3	MN204316	2	5	MN204395	39	43
2	S Balkhash	K-17-2015	MN204231	pen11	3	MN204317	3	29	MN204396	51	38
3	S Balkhash	K-23-2015	MN204232	pen12	3	MN204318	25	25	MN204397	42	44
3	S Balkhash	K-25-2015	MN204233	pen13	3	MN204319	25	25	MN204398	38	43
4	Eastern (E) Balkhash	K-28-2015	MN204234	mer10	2	MN204320	17	17	MN204399	22	22
4	E Balkhash	K-30-2015	MN204235	mer11	2	MN204321	16	17	MN204400	13	22
5	E Balkhash	K-33-2015	MN204236	mer12	2	MN204322	16	18	MN204401	13	21
5	E Balkhash	K-34-2015	MN204237	mer13	2	MN204323	15	17	MN204402	13	26
6	E Balkhash	K-230-2007	MN204238	mer2	2	-	-	-	MN204403	13	16
6	E Balkhash	K-236-2007	MN204239	mer2	2	MN204324	17	19	MN204404	19	24
7	Zaisan depression	K-71-2007	MN204240	mer1	2	MN204325	15	16	MN204405	13	16
7	Zaisan depression	K-72-2007	MN204241	mer2	2	MN204326	13	13	MN204406	13	16
7	Zaisan depression	K-73-2007	MN204242	mer3	2	MN204327	13	16	MN204407	13	13
7	Zaisan depression	K-74-2007	MN204243	short fragment	2	MN204328	5	16	MN204408	13	13
8	Dzungar basin	C-1-2012	MN204244	pen1	3	-	-	-	-	-	-
9	Dzungar basin	C-2-2012	MN204245	pen2	3	MN204329	25	26	MN204409	39	42
10	Dzungar basin	C-4-2012	MN204246	pen4	3	MN204330	1	3	MN204410	34	35
10	Dzungar basin	C-3-2012	MN204247	pen3	3	MN204331	4	28	MN204411	38	50
11	Dzungar basin	C-6-2012	MN204248	pen6	3	MN204332	23	25	MN204412	42	42
11	Dzungar basin	C-7-2012	MN204249	pen7	3	MN204333	3	22	MN204413	39	43
12	Dzungar basin	C-5-2012	MN204250	pen5	3	MN204334	3	3	MN204414	36	39
13	Mongolian Dzungaria	M-181-2011	MN204251	mer2	2	MN204335	16	16	-	-	-
13	Mongolian Dzungaria	M-182-2011	MN204252	mer2	2	MN204336	13	16	MN204415	14	19
13	Mongolian Dzungaria	M-183-2011	MN204253	mer2	2	MN204337	16	16	MN204416	16	16
13	Mongolian Dzungaria	M-184-2011	MN204254	mer2	2	MN204338	16	16	MN204417	2	25
13	Mongolian Dzungaria	M-180-2011	MN204255	mer2	2	MN204339	13	16	-	-	-
14	Mongolian Dzungaria	M-160-2011	MN204256	mer6	2	MN204340	16	16	MN204418	16	22
14	Mongolian Dzungaria	M-161-2011	MN204257	mer2	2	MN204341	16	16	MN204419	16	22

(Continues)

APPENDIX 2 (Continued)

Loc No	Region	Specimen No	Cytb		Cytb haplotypes		Cytb clade No		BRCA1 haplotypes		IRBP haplotypes		
			Accession No	Cytb	Accession No	Cytb	Accession No	Cytb	Accession No	Cytb	Accession No	Cytb	
14	Mongolian Dzungaria	M-164-2011	MN204258	mer2	2	2	2	MN204342	16	21	MN204420	16	28
15	Mongolian Dzungaria	M-220-2011	MN204259	mer7	2	2	2	MN204343	5	16	MN204421	5	32
16	Mongolian Dzungaria	M-115-2011	MN204260	mer4	2	2	2	MN204344	13	14	MN204422	4	7
16	Mongolian Dzungaria	M-116-2011	MN204261	mer5	2	2	2	MN204345	9	16	MN204423	18	29
16	Mongolian Dzungaria	M-117-2011	MN204262	mer5	2	2	2	MN204346	6	21	-	-	-
16	Mongolian Dzungaria	M-118-2011	MN204263	mer5	2	2	2	MN204347	6	16	MN204424	16	29
16	Mongolian Dzungaria	M-119-2011	MN204264	mer5	2	2	2	MN204348	9	16	MN204425	16	33
17	northwestern (NW) Transaltai Gobi	M-86-2012	MN204265	ps23	1	1	1	MN204349	5	5	MN204426	4	31
17	NW Transaltai Gobi	M-88-2012	MN204266	ps31	1	1	1	MN204350	6	14	MN204427	1	4
18	NW Transaltai Gobi	M-91-2012	MN204267	ps16	1	1	1	MN204351	5	8	MN204428	4	4
18	NW Transaltai Gobi	M-92-2012	MN204268	ps32	1	1	1	MN204352	5	5	MN204429	3	48
18	NW Transaltai Gobi	M-221-2011	MN204269	mer8	2	2	2	MN204353	16	17	MN204430	20	20
18	NW Transaltai Gobi	M-223-2011	MN204270	mer2	2	2	2	MN204354	5	15	MN204431	16	22
18	NW Transaltai Gobi	M-222-2011	MN204271	ps2	1	1	1	MN204355	14	21	MN204432	4	29
19	NW Transaltai Gobi	M-80-2012	MN204272	ps3	1	1	1	MN204356	5	27	MN204433	4	45
20	NW Transaltai Gobi	M-74-2012	MN204273	ps28	1	1	1	MN204357	5	6	MN204434	4	12
21	NW Transaltai Gobi	M-41-2012	MN204274	ps25	1	1	1	MN204358	6	11	MN204435	2	46
21	NW Transaltai Gobi	M-70-2012	MN204275	ps20	1	1	1	MN204359	8	8	MN204436	4	46
21	NW Transaltai Gobi	M-71-2012	MN204276	ps26	1	1	1	MN204360	6	7	MN204437	4	47
21	NW Transaltai Gobi	M-72-2012	MN204277	ps14	1	1	1	MN204361	5	6	MN204438	4	4
21	NW Transaltai Gobi	M-73-2012	MN204278	ps27	1	1	1	MN204362	5	6	MN204439	8	46
21	NW Transaltai Gobi	M-75-2012	MN204279	ps21	1	1	1	-	-	-	MN204440	1	4
21	NW Transaltai Gobi	M-76-2012	MN204280	ps22	1	1	1	-	-	-	MN204441	4	9
21	NW Transaltai Gobi	M-77-2012	MN204281	ps21	1	1	1	-	-	-	MN204442	1	4
21	NW Transaltai Gobi	M-78-2012	MN204282	ps29	1	1	1	MN204363	5	5	MN204443	4	4
21	NW Transaltai Gobi	M-79-2012	MN204283	ps30	1	1	1	MN204364	5	8	MN204444	2	4
22	NW Transaltai Gobi	M-235-2011	MN204284	mer9	2	2	2	MN204365	16	17	MN204445	16	16
23	NW Transaltai Gobi	M-94-2012	MN204285	ps24	1	1	1	MN204366	5	5	-	-	-
23	NW Transaltai Gobi	M-100-2012	MN204286	ps10	1	1	1	MN204367	6	8	MN204446	27	46
23	NW Transaltai Gobi	M-101-2012	MN204287	ps11	1	1	1	MN204368	6	21	MN204447	4	7
24	NW Transaltai Gobi	M-115-2012	MN204288	ps34	1	1	1	MN204369	6	20	MN204448	4	4

(Continues)

APPENDIX 2 (Continued)

Loc No	Region	Specimen No	Cytb			Cytb haplotypes			Cytb clade No			BRCA1 haplotypes			IRBP haplotypes		
			Accession No	Cytb	Accession No	Cytb	Accession No	Cytb	Accession No	Cytb	Accession No	Cytb	Accession No	Cytb	Accession No	Cytb	Accession No
24	NW Transaltai Gobi	M-117-2012	MN204289	ps2	1	1	MN204370	5	8	-	15	MN204449	4	15			
24	NW Transaltai Gobi	M-118-2012	MN204290	ps13	1	1	MN204371	6	8	MN204450	4	6	4	6			
25	NW Transaltai Gobi	M-136-2012	MN204291	ps18	1	1	MN204372	5	12	MN204451	4	4	4	4			
25	NW Transaltai Gobi	M-137-2012	MN204292	ps19	1	1	MN204373	5	6	MN204452	4	10	4	10			
26	NW Transaltai Gobi	M-103-2012	MN204293	ps12	1	1	MN204374	5	14	MN204453	1	2	1	2			
26	NW Transaltai Gobi	M-104-2012	MN204294	ps20	1	1	MN204375	5	5	MN204454	4	7	4	7			
26	NW Transaltai Gobi	M-105-2012	MN204295	ps33	1	1	MN204376	6	20	MN204455	6	7	6	7			
26	NW Transaltai Gobi	M-106-2012	MN204296	ps33	1	1	MN204377	6	6	MN204456	4	4	4	4			
26	NW Transaltai Gobi	M-119-2012	MN204297	ps14	1	1	MN204378	5	9	MN204457	4	4	4	4			
26	NW Transaltai Gobi	M-120-2012	MN204298	ps14	1	1	MN204379	5	9	MN204458	2	2	2	2			
26	NW Transaltai Gobi	M-121-2012	MN204299	ps15	1	1	MN204380	5	10	MN204459	2	45	2	45			
26	NW Transaltai Gobi	M-122-2012	MN204300	ps16	1	1	MN204381	8	9	MN204460	4	8	4	8			
26	NW Transaltai Gobi	M-123-2012	MN204301	ps17	1	1	MN204382	6	9	MN204461	4	4	4	4			
26	NW Transaltai Gobi	M-116-2012	MN204302	short fragment	1	1	MN204383	6	6	MN204462	11	45	4	46			
27	NW Transaltai Gobi	M-75-2006	MN204303	ps3	1	1	MN204384	5	9	MN204463	4	46	4	46			
28	Central and northwestern (C & NW) Mongolia	M-197-2010	MN204304	ps7	1	1	MN204385	5	14	-	-	-	-	-			
28	C & NW Mongolia	M-198-2010	MN204305	ps7	1	1	-	-	-	-	-	-	-	-			
29	C & NW Mongolia	M-226-2010	MN204306	ps8	1	1	MN204386	6	8	MN204464	4	29	4	29			
29	C & NW Mongolia	M-227-2010	MN204307	ps8	1	1	MN204387	5	9	MN204465	4	4	4	4			
30	C & NW Mongolia	M-155-2010	MN204308	ps6	1	1	MN204388	5	5	MN204466	4	45	4	45			
30	C & NW Mongolia	M-157-2010	MN204309	ps3	1	1	MN204389	5	9	-	-	-	-	-			
31	C & NW Mongolia	M-141-2009	MN204310	ps1	1	1	MN204390	8	14	MN204467	7	28	7	28			
31	C & NW Mongolia	M-142-2009	MN204311	ps4	1	1	-	-	-	MN204468	7	49	7	49			
31	C & NW Mongolia	M-147-2009	MN204312	ps5	1	1	MN204391	5	6	MN204469	4	4	4	4			
32	NW Transaltai Gobi	M-274-2011	MN204313	ps9	1	1	MN204392	5	6	MN204470	4	7	4	7			