ORIGINAL ARTICLE

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

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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
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 gerbilles 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, Dubrovsyky, Rossolimo, & Potapova, 1990). Despite intensive study (Heptner, 1968; Huang & Zhou, 2012; Ito et al., 2010, 2011; 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 Meriones 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 Meriones meridianus species complex: Meriones meridianus (Pallas, 1773), Meriones penicilliger (Heptner, 1933), and Meriones 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), Meriones 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; Meriones 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 Meriones 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 chengii Wang, 1964, is probably a junior synonym of Meriones 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 Meriones 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 Kara-Irtysy 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 Irtysy 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 Meriones 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 Meriones 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 Meriones 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. ibycus* 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 allele 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 Steppan (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 Steppan, 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 = 3.15–6.10 × 10⁻³) and 5.83 × 10⁻³ (95% HPD interval = 4.04–8.02 × 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
| No | Locality                                                                 | Lat     | Long     | n  | Source | Species          |
|----|--------------------------------------------------------------------------|---------|----------|----|--------|------------------|
| 1  | Kazakhstan, southern Balkhash, Topar                                     | 44.7711 | 75.2486  | 2  | a      | M. pencilliger   |
| 2  | Kazakhstan, southern Balkhash, Boztobe                                    | 45.2572 | 75.4254  | 2  | a      | M. pencilliger   |
| 3  | Kazakhstan, southern Balkhash, Ushkara                                    | 45.9083 | 77.7647  | 2  | a      | M. pencilliger   |
| 4  | Kazakhstan, eastern Balkhash, Sarykurak                                  | 46.3813 | 78.9566  | 2  | a      | M. meridianus    |
| 5  | Kazakhstan, eastern Balkhash, Karabanai                                   | 45.8869 | 80.5558  | 2  | a      | M. meridianus    |
| 6  | eastern Kazakhstan, eastern Balkhash, right bank of Emily river           | 46.3704 | 82.2203  | 2  | a      | M. meridianus    |
| 7  | eastern Kazakhstan, Zaysan depression, Chernyi Irtysh river, Buran        | 47.9502 | 85.1271  | 4  | a      | M. meridianus    |
| 8  | China, Dzungar basin, Xinjiang, Musowan Field Station                    | 45.1256 | 86.0278  | 1  | a      | M. pencilliger   |
| 9  | China, Dzungar basin, Xinjiang, Baytag-Bogdo southern slope, 23 km to   | 44.9141 | 91.2474  | 1  | a      | M. pencilliger   |
|    | the northeast from Turunghy-khuduk                                       |         |          |    |        |                  |
| 10 | China, Dzungar basin, Xinjiang, Baytag-Bogdo southern slope, 29 km to   | 44.8564 | 91.3297  | 2  | a      | M. pencilliger   |
|    | the East from Turunghy-khuduk                                            |         |          |    |        |                  |
| 11 | China, Dzungar basin, Xinjiang, Uzunlag Mt., 10 km to the southeast      | 44.4636 | 91.3218  | 2  | a      | M. pencilliger   |
| 12 | China, Dzungar basin, Xinjiang, Zhifan, 18 km to the northwest           | 44.5476 | 91.6312  | 1  | a      | M. pencilliger   |
| 13 | Mongolia, Mongolian Dzungaria, right bank of Bulgan river                | 46.1166 | 91.1164  | 5  | a      | M. meridianus    |
| 14 | Mongolia, Mongolian Dzungaria, Elhon                                     | 45.6167 | 92.2653  | 3  | a      | M. meridianus    |
| 15 | Mongolia, Mongolian Dzungaria, northern slope of the Huh-Unduriyn-Nurru | 45.1493 | 92.8185  | 1  | a      | M. meridianus    |
| 16 | Mongolia, Mongolian Dzungaria, Gun-Tamga-Bulak spring                    | 45.2569 | 93.6731  | 5  | a      | M. meridianus    |
| 17 | Mongolia, northwestern Transalai Gobi, Govi-Altaim, Nogon-dovon         | 44.8926 | 94.1919  | 2  | a      | M. psammophilus  |
| 18 | Mongolia, northwestern Transalai Gobi, 55 km to the northwest from Altai| 44.8003 | 94.2359  | 5  | a      | M. psammophilus, M. meridianus |
| 19 | Mongolia, northwestern Transalai Gobi, Alag-Nuur                         | 45.1677 | 94.5488  | 1  | a      | M. psammophilus  |
| 20 | Mongolia, northwestern Transalai Gobi, Alag-Nuur                         | 45.1677 | 94.6032  | 1  | a      | M. psammophilus  |
| 21 | Mongolia, northwestern Transalai Gobi, Alag-Nuur                         | 45.1264 | 94.5757  | 10 | a      | M. psammophilus  |
| 22 | Mongolia, northwestern Transalai Gobi, 19 km to the southwest from Altai| 44.4838 | 94.7669  | 1  | a      | M. meridianus    |
| 23 | Mongolia, northwestern Transalai Gobi, southwestern Harmatgin-Hutag      | 44.5012 | 95.6165  | 3  | a      | M. psammophilus  |
| 24 | Mongolia, northwestern Transalai Gobi, northern Harmatgin-Hutag          | 44.5205 | 95.7039  | 3  | a      | M. psammophilus  |
| 25 | Mongolia, northwestern Transalai Gobi, Toroin-Holoi                      | 45.0023 | 95.8452  | 2  | a      | M. psammophilus  |
| 26 | Mongolia, northwestern Transalai Gobi, Harin-Anda                        | 44.6735 | 95.9578  | 10 | a      | M. psammophilus  |
| 27 | Mongolia, northwestern Transalai Gobi, Ih-Dzarmag                        | 44.7977 | 97.3199  | 1  | a      | M. psammophilus  |
| 28 | central and northwestern Mongolia, the Great lake basin, the             | 49.4832 | 90.6326  | 2  | a      | M. psammophilus  |
|    | southeastern bank of Achit-Nuur lake                                      |         |          |    |        |                  |
| 29 | central and northwestern Mongolia, the Great lake basin, the             | 49.0312 | 93.5035  | 2  | a      | M. psammophilus  |
|    | southeastern bank of Hyargas-Nuur lake                                    |         |          |    |        |                  |
| 30 | central and northwestern Mongolia, Sharga Gobi, 20 km to the southeast   | 46.1743 | 95.5174  | 2  | a      | M. psammophilus  |
|    | from Sharga                                                               |         |          |    |        |                  |
| 31 | central and northwestern Mongolia, the Lake Valley, 18 km to the East    | 45.7205 | 97.4106  | 3  | a      | M. psammophilus  |
|    | from Biger                                                                |         |          |    |        |                  |
| 32 | Central and northwestern Mongolia, the Lake Valley, northern slope of    | 44.9855 | 100.6517 | 1  | a      | M. psammophilus  |
|    | the Ih-Bogdjin-Nuur                                                      |         |          |    |        |                  |
|    | – China, Gansu, Anxi                                                     | 40.0775 | 97.1234  | 9  | b      | M. psammophilus  |
|    | – China, Gansu, Jinta                                                    | 39.9662 | 98.9547  | 9  | b      | M. psammophilus  |
|    | – China, Gansu, Gaotai                                                   | 39.4131 | 99.8356  | 10 | b      | M. psammophilus  |
|    | – China, Gansu, Dongdashan                                               | 38.4225 | 102.0295 | 6  | b      | M. psammophilus  |

(Continues)
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 $\Gamma(2, 100)$ and $\Gamma(1, 100)$ were specified for the $\theta$ and $\tau$ 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 $Fs$ (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 Transsaltai 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 (Nanova, 2014). The modified Bayesian information criterion (BIC) (Lebedev & Lissovoy, 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 for different geographic regions as the 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 Transsaltai 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 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-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/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, and this raster was resampled to a 30 arc-second-resolution. Ten-day NDVI 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 interfluve 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
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 nominate subspecies M. m. meridianus and M. m. bucheni, whereas cluster 2b comprises M. m. nagaiorum 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 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.
The population of *Meriones meridianus* from Zaysan Hollow is connected only with populations from Dzungarian Basin, and it is isolated from other Kazakhstan populations. Populations of *Psammophilus 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
The contact zone between Honin-Us-Sair (localities 18 and 22) and the southern foothills of Adzh-Bogdo may act as a partial barrier to gene flow between these lineages. The Tahiyn Shar Nurru mountains may also act as a partial barrier to gene flow between Honin-Us-Sair and 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, Harmagtain-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 Ne (/1,000) | Migrant number |
|------------------|----------------------------------------|----------------|
|                  |                                        | *psam* > *mer* | *mer* > *psam* |
|                  | *psam*/*mer* | *pen*/*psam + mer* | *mer* | *psam* | *psam* | *mer* | *mer* | *psam* |
| 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 | 476.7 | 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 |
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 southeastern 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
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

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**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 log10 of the population size (Ne*τ*) (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.
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

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

|                   | *Psammophilus* | *Meridianus* | *Penicilliger* |
|-------------------|---------------|--------------|---------------|
| **Sample size**   | 45            | 26           | 13            |
| **Tajima's D**    | -1.99887      | -1.84669     | -1.09158      |
| **Tajima's D p-value** | **.0057**     | **.0157**    | .1877         |
| **FS of Fu**      | -25.16184     | -6.03427     | -6.77658      |
| **FS p-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 Transsaltai 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

|                  | *Psammophilus N* | *Psammophilus SW* | *Meridianus Kaz* | *Meridianus Dzungaria* | *Penicilliger Kaz* | *Penicilliger Dzungaria* |
|------------------|------------------|-------------------|------------------|----------------------|-------------------|--------------------------|
| **Sample size**  | 10               | 35                | 9                | 17                   | 6                 | 7                        |
| **Tajima's D**   | -0.20468         | -1.66858          | -0.39329         | -1.86628             | -1.71499          | -1.31438                 |
| **Tajima's D p-value** | .433             | **.029**          | .37              | **.011**             | .13               | .093                     |
| **FS of Fu**     | -1.95214         | -18.37424         | -1.54367         | -3.52566             | -2.32822          | -3.1805                  |
| **FS p-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.
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 Transaltai 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 |
|-------------|--------|--------|----------------------|-----------------|----------------------------|-------------------------------------------------------------|
| 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)
The distribution of *meridianus* and *penicilliger* suggests a complex scenario of range shifts or colonization, the details of which remain to be elucidated. 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 psammophile 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 psammophyly 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
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 Cyb 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.

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**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.
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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.

APPENDIX 1

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

| Marker | Primer | Sequence (5′ to 3′) | Reference |
|--------|--------|---------------------|-----------|
| Cytb   | L14723(L7) | CCAATGACATGAAAAATCATCGTT | Montgelard et al. (2002) |
|        | H15915(H6) | TCTCCATTCTGTTTACAGAC |           |
| BRCA1  | F697   | CACAAGCAGCCCTTCACAAATATT | Present study |
|        | R1722a | GAGTATCCAGTTCACTCCCTTCCATTTC |           |
| IRBP   | F40    | GCCATGAAGAGCCATGAGATTCGGA | Present study |
|        | R1151  | CAGCACGGATAACCTGAAACACAGAC |           |
| Loc No | Region | Specimen No | Accession No | IRBP haplotypes | Accession No | Cytb haplotypes | Accession No | Cytb clade No | Specimen No |
|--------|--------|-------------|--------------|-----------------|--------------|-----------------|--------------|---------------|-------------|
| 1      | Southern (S) Balkhash | K-3-2015 | MN204234 | 24 | MN204293 | 36 | K-3-2015 |
| 2      | S Balkhash | K-6-2015 | MN204235 | 30 | MN204394 | 41 | K-6-2015 |
| 3      | S Balkhash | K-13-2015 | MN204236 | 5 | MN204395 | 39 | K-13-2015 |
| 4      | S Balkhash | K-17-2015 | MN204237 | 29 | MN204396 | 51 | K-17-2015 |
| 5      | S Balkhash | K-23-2015 | MN204238 | 25 | MN204397 | 42 | K-23-2015 |
| 6      | Eastern (E) Balkhash | K-28-2015 | MN204239 | 17 | MN204398 | 38 | K-28-2015 |
| 7      | E Balkhash | K-30-2015 | MN204240 | 16 | MN204399 | 22 | K-30-2015 |
| 8      | E Balkhash | K-33-2015 | MN204241 | 13 | MN204400 | 16 | K-33-2015 |
| 9      | Zaisan depression | K-23-2015 | MN204242 | 25 | MN204401 | 38 | K-23-2015 |
| 10     | Zaisan depression | K-26-2015 | MN204243 | 17 | MN204402 | 16 | K-26-2015 |
| 11     | Zaisan depression | K-29-2015 | MN204244 | 13 | MN204403 | 16 | K-29-2015 |
| 12     | Zaisan depression | K-32-2015 | MN204245 | 22 | MN204404 | 38 | K-32-2015 |
| 13     | Zaisan depression | K-34-2015 | MN204246 | 13 | MN204405 | 38 | K-34-2015 |
| 14     | Zaisan depression | K-37-2015 | MN204247 | 13 | MN204406 | 16 | K-37-2015 |
| 15     | Zaisan depression | K-39-2015 | MN204248 | 13 | MN204407 | 38 | K-39-2015 |
| 16     | Zaisan depression | K-41-2015 | MN204249 | 13 | MN204408 | 16 | K-41-2015 |
| 17     | Zaisan depression | K-43-2015 | MN204250 | 13 | MN204409 | 38 | K-43-2015 |
| 18     | Zaisan depression | K-45-2015 | MN204251 | 13 | MN204410 | 38 | K-45-2015 |
| 19     | Zaisan depression | K-47-2015 | MN204252 | 13 | MN204411 | 38 | K-47-2015 |
| 20     | Zaisan depression | K-49-2015 | MN204253 | 13 | MN204412 | 38 | K-49-2015 |
| 21     | Zaisan depression | K-51-2015 | MN204254 | 13 | MN204413 | 38 | K-51-2015 |
| 22     | Zaisan depression | K-53-2015 | MN204255 | 13 | MN204414 | 38 | K-53-2015 |
| 23     | Zaisan depression | K-55-2015 | MN204256 | 13 | MN204415 | 38 | K-55-2015 |
| 24     | Zaisan depression | K-57-2015 | MN204257 | 13 | MN204416 | 38 | K-57-2015 |
| 25     | Zaisan depression | K-59-2015 | MN204258 | 13 | MN204417 | 38 | K-59-2015 |
| 26     | Zaisan depression | K-61-2015 | MN204259 | 13 | MN204418 | 38 | K-61-2015 |
| Loc No | Region                      | Specimen No | Accession No | Cytb haplotypes | IRBP haplotypes |
|--------|-----------------------------|-------------|--------------|-----------------|-----------------|
| 14     | Mongolian Dzungaria         | M-164-2011  | MN204238     | mer2            |                |
| 15     | Mongolian Dzungaria         | M-165-2011  | MN204239     | mer7            |                |
| 16     | Mongolian Dzungaria         | M-155-2011  | MN204240     | mer4            |                |
| 16     | Mongolian Dzungaria         | M-166-2011  | MN204241     | mer5            |                |
| 16     | Mongolian Dzungaria         | M-167-2011  | MN204242     | mer5            |                |
| 16     | Mongolian Dzungaria         | M-168-2011  | MN204243     | mer5            |                |
| 16     | Mongolian Dzungaria         | M-169-2011  | MN204244     | mer5            |                |
| 16     | Mongolian Dzungaria         | M-191-2012  | MN204246     | p23             |                |
| 17     | NW Transaltai Gobi         | M-88-2012   | MN204247     | p23             |                |
| 17     | NW Transaltai Gobi         | M-91-2012   | MN204248     | p23             |                |
| 18     | NW Transaltai Gobi         | M-93-2012   | MN204249     | p23             |                |
| 18     | NW Transaltai Gobi         | M-96-2012   | MN204250     | p23             |                |
| 18     | NW Transaltai Gobi         | M-223-2011  | MN204251     | p23             |                |
| 18     | NW Transaltai Gobi         | M-224-2011  | MN204252     | p23             |                |
| 19     | NW Transaltai Gobi         | M-225-2011  | MN204253     | p23             |                |
| 20     | NW Transaltai Gobi         | M-74-2012   | MN204254     | p23             |                |
| 21     | NW Transaltai Gobi         | M-75-2012   | MN204255     | p23             |                |
| 21     | NW Transaltai Gobi         | M-76-2012   | MN204256     | p23             |                |
| 21     | NW Transaltai Gobi         | M-77-2012   | MN204257     | p23             |                |
| 22     | NW Transaltai Gobi         | M-78-2012   | MN204258     | p23             |                |
| 22     | NW Transaltai Gobi         | M-79-2012   | MN204259     | p23             |                |
| 22     | NW Transaltai Gobi         | M-96-2012   | MN204260     | p23             |                |
| 23     | NW Transaltai Gobi         | M-100-2012  | MN204261     | p23             |                |
| 23     | NW Transaltai Gobi         | M-102-2012  | MN204262     | p23             |                |
| 23     | NW Transaltai Gobi         | M-115-2012  | MN204263     | p23             |                |
| 24     | NW Transaltai Gobi         | M-117-2012  | MN204264     | p23             |                |

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