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Low genetic diversity and relatively strong population genetic structure of Przewalski's Wondergecko, *Teratoscincus przewalskii* Strauch, 1887, in the Mongolian Gobi Desert

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Abstract. We examined the genetic diversity and phylogenetic relationships of 75 *Teratoscincus przewalskii* from seven different populations in the Mongolian Gobi Desert using partial sequences of the mitochondrial *ND2* gene. Our diversity estimations showed a relatively low level of genetic diversity for these samples (*H*d; 0.416, π; 0.0009), with only five polymorphic sites that defined six haplotypes. Our Bayesian Inference (BI) and Maximum Likelihood (ML) phylogenetic trees suggested monophyly of a group comprising Mongolian and non-Mongolian *T. przewalskii* populations. In addition, we found that *T. roborowskii*, a geographically close species, is the likely sister taxon of *T. przewalskii*. The approximate estimated time for *T. przewalskii*'s colonization of Mongolia was 149,000 years ago (95% highest posterior density interval: 51,900–275,000 years ago). Among studied populations, we found that the Gurvantes population was genetically distant from the six remaining populations (mean uncorrelated *p*-distance = 1.3%, pairwise distance F_{ST} = 0.57). Our hierarchical AMOVA suggested a relatively strong genetic structure of *T. przewalskii* at the population level, with 45% of total genetic variation resulting from differences between populations.

Keywords. Diversity, evolutionary divergence, geckos, phylogenetic analysis.

Introduction

Desert and semi-desert environments, collectively known as drylands, are considered to be the largest biome on Earth (Sternberg et al., 2015). This biome covers approximately 41% of the Earth's land surface and hosts relatively unique biodiversity (Sternberg et al., 2015; Tamar et al., 2021). Excluding large ungulates (hoofed mammals), much of the biodiversity in this biome, reptiles included, has received less attention than that of other biogeographic regions (Gudka et al., 2014; Yadamsuren et al., 2018). In the Mongolian Gobi Desert, this is most likely the result of a lack of research: all reptiles recorded from this vast region are understudied (Terbish et al., 2006).

As a major part of the Mongolian Plateau, the Gobi Desert is a cold desert that covers 42.7% of Mongolia's total land surface (Yembuu, 2021). Despite the harsh continental climate conditions, the Gobi Desert supports a relatively diverse reptile fauna, with 18 of 22 species known from Mongolia inhabiting this region. This herpetological hotspot was initially explored by Russian scientists (e.g., Pallas and Bannikov, 1940), followed by Mongolian scientists (see Terbish et al., 2006).

The sphaerodactylid genus *Teratoscincus* comprises nine recognized species. Among them, *T. przewalskii* is the only one found in Mongolia, where it is distributed across desert regions the country's southwestern area, from Khonin Usny Gobi, Altai Soum [District], Gobi-Altai Province (44.827°N, 94.765°E) in the east to Zag Sujyn Gobi, Bayan-Ovoo Soum, Omnogobi Province (42.397°N, 106.701°E) in the west (Macey et al., 1999;

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Terbish et al., 2006). This species was first documented for Mongolia in the 1960s (Terbish et al., 2006) and it is mostly distributed in the Gobi Desert in sandy areas with saksaúl trees (*Haloxylon ammodendron*) and areas covered with gravel. Approximately 37% of the species' range in Mongolia falls within protected areas, notably the Great Gobi and Lesser Gobi Strictly Protected Areas (Terbish et al., 2019; Munkhbayar et al., 2020). The species is listed as Least Concern on the IUCN Red List (Terbish et al., 2019), but regionally it is assessed as Near Threatened due to habitat loss primarily caused by extractive industries (mining), overgrazing (Terbish et al., 2006, 2019), and collection for the pet trade. So far, no study has investigated the ecological and biological characteristics of *T. przewalskii* in Mongolia, from where only historical records are known. We here provide an initial molecular study on the phylogeny, genetic diversity, and population genetic structure of *T. przewalskii* in Mongolia.

Materials and Methods

Sampling and laboratory protocols. We collected a total of 75 samples (tail clips of length 1.5 mm) from seven localities in the Gobi Desert of Mongolia in 2023 and 2024. We visited and searched for animals in historic locations of *T. przewalskii* (Fig. 1). During fieldwork, we searched for geckos by torchlight after dark 22:00 and 00:00 h (Table 1). All geckos were released within approximately 1 min of capture. Our surveys in 2023 included 21 days in the Trans Altay Gobi, where we collected 54 samples at the following locations: Nogoon Dovon (NDV; $n = 10$), Nogoon Tsav (NTS; $n = 11$), Ehyn Gol (EHG; $n = 9$), Gurvantes (GTS; $n = 11$), and Zulganai (ZUL; $n = 13$). In 2024, we conducted another survey in Galbyn Gobi and Borzon Gobi to close sampling gaps (Fig. 1), where we collected 21 samples, in Zag Sujyn Gobi (ZSG; $n = 16$) and Tsagan Ders Hudag (TDH; $n = 5$).

We extracted total genomic DNA from tail tip samples using a Qiagen DNeasy kit (QIAGEN Group, Hilden, Germany) according to the manufacturer's protocol. We ran extracted gDNA on a 2.0% agarose gel at a constant voltage of 150 V for 30 min in 1x TAE buffer to see gDNA bands under UV light before PCR amplification. We completed PCR amplification and direct sequencing with a designated primer for this study: TP_F 5'-GCA ACA GAA GCC GCA ACA AA-3' and TP_R 5'-TGT GCC GAG GTC AGT AAT GG-3'. We used a reference sequence (NC067620) of the dehydrogenase subunit 2 gene (*ND2*) of *T. przewalskii* for our primer design. The reaction condition for PCR amplification consisted of initial denaturation at 94°C for 3 min, followed by 33 cycles with denaturation at 94°C for 30 s, annealing at 60°C for 30 s, extension for 1 min at 72°C, and final extension at 72°C for 5 min, with a total volume of 20 µl. We sequenced purified 543 bp PCR products directly using Sanger DNA sequencing on an ABI PISM 3730XL Analyzer. We deposited all haplotype sequences ($n = 6$) in the GenBank public database under accession numbers PQ671883–PQ671888.

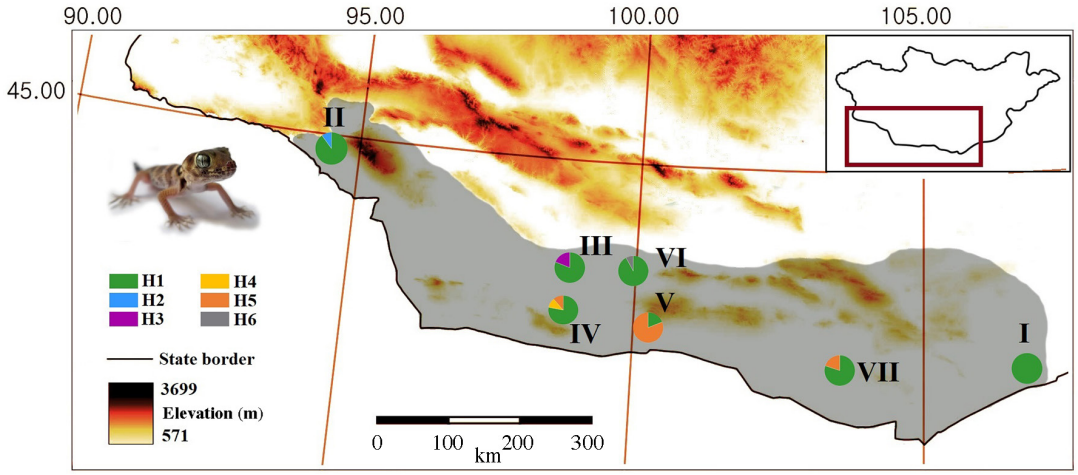

Figure 1. Seven sampling locations of *Teratoscincus przewalskii* in the Mongolian Gobi Desert, indicated by colour-coded haplotype pie charts showing the proportion of haplotypes (H1–H6). The potential range of *T. przewalskii* in Mongolia is shown as the grey shaded area. Roman numerals on the map refer to our seven sampled populations, including Zag Sujyn Gobi (I), Nogoon Dovon (II), Nogoon Tsav (III), Ehyn Gol (IV), Gurvantes (V), Zulganai (VI), and Tsagan Ders Hudag (VII).

Table 1. Estimated genetic diversity parameters for partial sequences of the mitochondrial *ND2* gene of seven *T. przewalskii* populations in Mongolia. Values include the number of individuals in each sample (*n*) the number of haplotypes present in the population (*h*), haplotype diversity (H_d), nucleotide diversity (π), the number of polymorphic sites (S), and the average number of nucleotide differences (K).

Population	*n*	*h*	H_d	π	S	K
Zag Sujyn Gobi	16	1 (H1)	-	-	-	-
Nogoon Dovon	10	2 (H1, H2)	0.201	0.0004	1	0.200
Nogoon Tsav	11	2 (H1, H3)	0.327	0.0007	1	0.327
Ehyn Gol	9	3 (H1, H4, H5)	0.416	0.0009	2	0.444
Gurvantes	11	2 (H1, H5)	0.327	0.0007	1	0.327
Zulganai	13	2 (H1, H6)	0.153	0.0003	1	0.158
Tsagan Ders Hudag	5	2 (H1, H5)	0.400	0.0008	1	0.400
Totals	**75**	**6 (H1–H6)**	**0.367**	**0.0008**	**5**	**-**

Sequence editing, genetic diversity. We initially edited 75 *ND2* sequences using Chromas v2.6.6 (Technelysium, South Brisbane, Queensland, Australia; technelysium.com.au), and we aligned positions with BioEdit v7.2.5 (Clustal W tool; Thompson et al., 1994) together with other reference sequences. For more comprehensive phylogenetic analysis, we downloaded *ND2* gene fragments from Genbank ($n = 7$), including those of three additional samples of *T. przewalskii* (MW491837, NC067620, OL471044) and four other species of *Teratoscincus* as outgroups, namely *T. keyserlingii* (AY753545, $n = 1$), *T. roborowskii* (MT107158, $n = 1$), *T. scincus* (MT977329, $n = 1$), and *T. microlepis* (AB612275, $n = 1$). Our dataset therefore consisted of 83 sequences for phylogenetic analysis. We used DNA Sequence Polymorphism v6.12.03 (DnaSP; Rozas et al., 2017) to calculate genetic diversity parameters for *T. przewalskii*, including number of haplotypes (*h*), haplotype diversity (H_d), number of segregating sites (S), nucleotide diversity (π), and average number of nucleotide difference (K) (Table 1).

Time-calibrated phylogenetic analysis. We reconstructed two main types of phylogenetic trees, including a Bayesian Inference (BI) tree and a Maximum Likelihood (ML) tree. Prior to reconstructing trees, we determined the best fit substitution models for ML and BI trees using the Akaike Information Criterion (Kumar et al., 2018). We determined that HKY + Γ model with a site-specific gamma distribution was the best fit substitution model (-InL = 1475.52; AIC = 3286.48) for our phylogeny analyses (Hasegawa et al., 1985). For phylogenetic trees, we used all 83 *ND2* sequences to reconstruct a 50% majority-rule consensus tree but only 12 taxa comprising six haplotypes were used for reconstruction of the time-calibrated tree.

We used MEGA v10.2.2 (Kumar et al., 2018) to reconstruct an ML tree with 1000 bootstrap replicates. Among the total number of reconstructed trees, we used the tree with the highest log likelihood (-1485.84). Moreover, we constructed BI trees in MrBayes v3.2.7 (Ronquist et al., 2012). We computed a single BI run for four Markov Chain Monte Carlo (MCMC) chains over 10 million generations, with a sampled interval of 1000 generations and a 'burn-in' command to discard the first 15% of the constructed tree. Then, we viewed the trace plots of clade posterior probabilities on Tracer v1.7.1 (Drummond et al., 2012) and constructed a 50% majority-rule consensus tree in Figtree v1.4.4 with posterior probabilities of nodes.

Subsequently, we estimated evolutionary divergence times between identified haplotypes of *T. przewalskii* through a time-calibrated phylogenetic tree using BEAST v10.5.1 (Bouckaert et al., 2014). For this contribution, we used the same substitution models described above. We used a default Strict Molecular Clock model to estimate rates of evolution pattern on each node of our time-calibrated tree. We obtained a Calibrated Yule tree prior model as the best tree prior (Gernhard, 2008). We used one calibration point for our time-calibrated tree, using data from Tamar et al. (2021) that showed the possible split between *T. scincus* and *T. keyserlingii* at approximately 4.1 Mya. This previous work used two calibration points, mostly based on biogeographical events, such as the split between *T. microlepis* and the other *Teratoscincus* species, which resulted from the rise of the Hindu Kush approximately 20 Mya. We then performed a run of 20 million MCMC chain lengths, sampling every 10,000 generations. We discarded 10% of total constructed trees and summarized a maximum clade credibility tree

with TreeAnnotator v2.6.3 (Bouckaert et al., 2014). Finally, we constructed a maximum clade credibility tree in Figtree, with node a median age (mya) and 95% highest posterior density (HPD).

Population structure analysis. We used ARLEQUIN v3.5.2.2 (Excoffier and Lischer, 2010) to estimate pairwise F_{ST} genetic differences between populations of *T. przewalskii*, which we accepted as significant at $p < 0.05$. Additionally, we calculated mean uncorrected *p*-distances (sequence divergence by %) between studied populations using MEGA v10.2.2 (Kumar et al., 2018). An Analysis of Molecular Variance (AMOVA) was used to evaluate population genetic structure of *T. przewalskii* in ARLEQUIN. We ran hierarchical AMOVAs at two levels to clarify how much variation was partitioned (1) within populations and (2) among populations.

Results

mtDNA variation of *T. przewalskii*. Analysis of 75 *ND2* gene sequences revealed low genetic polymorphism in *T. przewalskii*. A total of six haplotypes defined by five polymorphic sites over the 543-bp fragments (two parsimony informative sites and three singleton sites) was observed. We obtained low levels of overall haplotype and nucleotide diversity for studies populations (H_d; 0.367 ± 0.004, $\pi = 0.0008$; Table 1). Among *T. przewalskii* populations, EHG accounted for the highest genetic diversity values ($H_d = 0.416 \pm 0.02$, $\pi = 0.0009$) while there were no polymorphic sites observed in the ZSG population (Table 1).

Phylogenetic status of *T. przewalskii*. Initially, we drew a median-joining haplotype network for *T. przewalskii* populations in Mongolia, using partial mtDNA-*ND2* gene haplotypes ($n = 6$) (Fig. 2A). Haplotype 1 (H1) is shared by geckos from all seven populations, followed by Haplotype 5 (H5) which is shared by geckos from three populations. Four of the identified haplotypes were population specific (H2–H4, H6), but with one to two animals each. Unlike other populations, the majority of geckos from GTS presented with H5, shared with one gecko from each of ZUL and TDH (Fig. 2A).

In our phylogenetic analysis, we obtained a monophyletic clade for *T. przewalskii* that contained haplotypes from Mongolia and China. We estimated the earliest split between any of six haplotypes of *T. przewalskii* in Mongolia, approximately 149,000 years ago (95% HPD; 51,900–275,000 years ago; H4 and H6 diverged first; Fig. 2B). More specifically, the most frequently observed haplotype (H1) was observed as the most recently formed haplotype, nearly 33,000 years ago (Fig. 2B). Finally, the earliest divergence between *T. przewalskii* (Mongolian haplotypes and reference sequences) was observed around 181,000 years ago, which occurred between Mongolian and Chinese populations (Fig. 2B).

Populations differentiation and genetic structure. We used two main approaches to evaluate genetic distances between *T. przewalskii* populations in Mongolia, namely Wright's pairwise F_{ST} genetic differences and uncorrected *p*-distances (as sequence divergences percentage; Table 2). Consistent with Fig. 2B that showed dissimilarity between GTS and other populations, we obtained the highest values of both genetic distances between GTS and other *T. przewalskii* populations in Mongolia (Table 2). The mean uncorrected *p*-distance between GTS and other populations was 1.3% with a mean pairwise F_{ST} genetic distance of 0.57. The highest value of uncorrected *p*-distances, 2.0% was observed between the GTS and NTS populations (Table 2).

Table 2. Estimated Pairwise F_{ST} genetic differences (above the diagonal), and uncorrelated *p*-distances (below the diagonal) for seven populations of *T. przewalskii* in Mongolia. Populations are abbreviated using numbered localities as Zag Sujyn Gobi (1), Nogoon Dovon (2), Nogoon Tsav (3), Ehyn Gol (4), Gurvantes (5), Zulganai (6), and Tsagan Ders Hudag (7). Significant *p*-distances ($p < 0.05$) are printed in bold.

Population	1	2	3	4	5	6	7
1	-	0.042	0.146	0.060	**0.828**	0.011	0.241
2	0.0002	-	0.061	0.004	**0.710**	0.003	0.039
3	0.0004	0.0006	-	0.487	**0.672**	0.077	0.060
4	0.0005	0.0007	0.0008	-	**0.555**	0.018	-0.121
5	0.0017	0.0019	0.0021	0.0018	-	**0.738**	**0.487**
6	0.0002	0.0004	0.0005	0.0006	0.0019	-	0.069
7	0.0004	0.0006	0.0008	0.0008	0.0015	0.0006	-

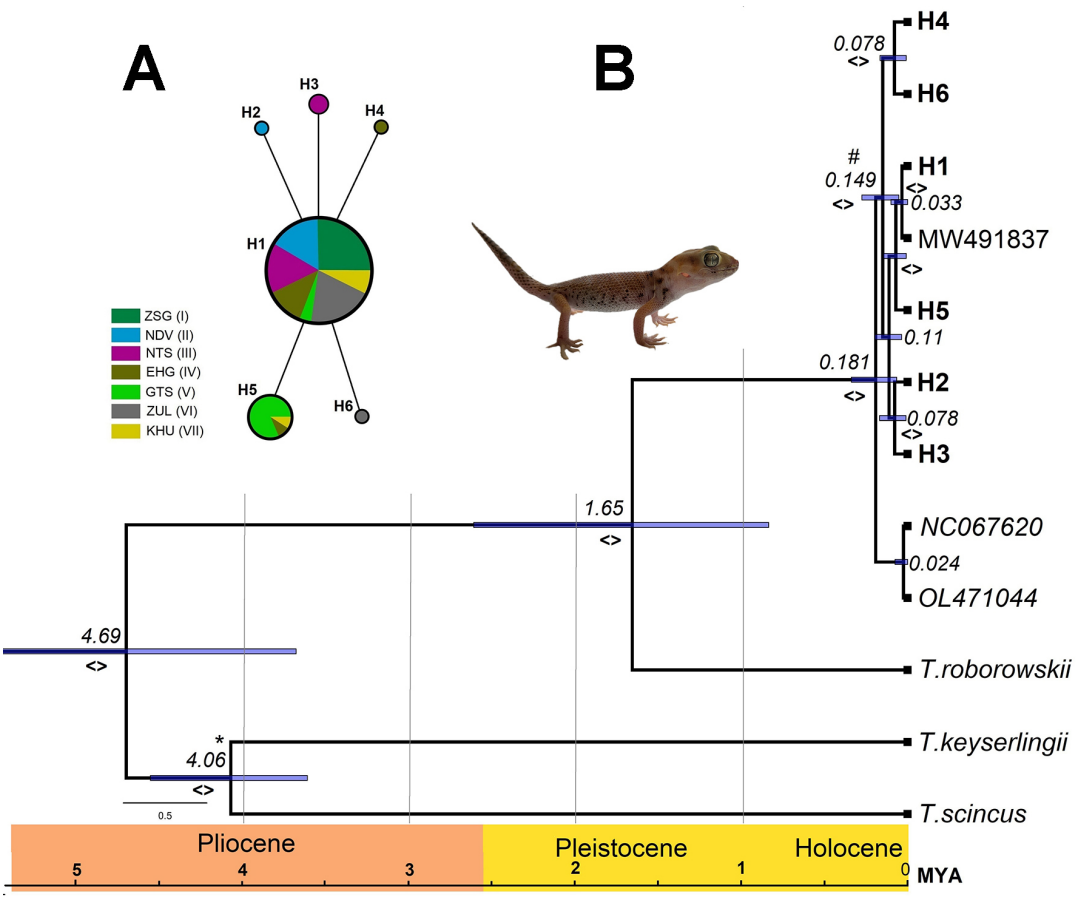

Figure 2. (A) Median-joining network analysis of six *Teratoscincus przewalskii* haplotypes from populations in the Mongolian Gobi Desert. (B) Phylogenetic tree for the same populations, with the addition of Chinese populations and three other *Teratoscincus* species, inferred from 543 base pairs of the mitochondrial *ND2* gene. The single calibration point is indicated by the asterisk. Values on nodes are posterior mean divergence estimated times. Nodes supported by posterior probability and bootstrap values > 0.60 are indicated by arrows (< >).

Interestingly, we observed relatively stronger population genetic structure among studied populations (n = 7) of *T. przewalskii*. This could be a result of the presence of four population-specific haplotypes in these populations and the dominance of H5 in GTS. According to our estimated hierarchical AMOVA for populations of *T. przewalskii*, 45.7% of total variation resulted from genetic differences between populations (Table 3), despite very limited polymorphisms observed across used sequences in this study (n = 75).

Discussion

As a Central Asian species, *T. przewalskii* has a very limited distribution in the Central Asian Desert (Terbish et al., 2019). Most of its range is in China, while the eastern and northeastern limits of its range occur in Mongolia. We sampled animals from every known historic population of *T. przewalskii* in Mongolia (only excluding Shar Hulstai) to reconstruct a better phylogenetic tree with estimates of genetic diversity that might more fully represent the entire Mongolian population.

To date, there are three previous phylogenetic studies available for *T. przewalskii*, none of which estimated levels of genetic diversity (Tamar et al., 2021; Yu et al., 2021; Li and Guo, 2023). Our results for genetic diversity parameters show that *T. przewalskii* has very low genetic diversity (against our expectation), which contrasts with some other reptiles in this desert region. For example, Ganbold et al. (2022) found relatively higher genetic diversity in the agamid *Phrynocephalus versicolor*.

Moreover, Araya-Donoso et al. (2022) emphasized that desert populations of some reptiles had higher genetic diversity than their forest populations. Therefore, we cannot conclude that *T. przewalskii* has low genetic diversity because it inhabits a desert. Instead, the lower genetic diversity in *T. przewalskii* could be a result of its population size (positive correlation between population size and genetic diversity; Avise, 1992; Frankham, 1996) or its limited regional distribution. Furthermore, the different sample sizes from each population may introduce biases in diversity estimation. Obviously, alternative genetic markers (e.g., Single Nucleotide Polymorphisms, Microsatellites) are needed to measure the level of genetic diversity more deeply (e.g., heterozygosity, inbreeding coefficient).

In terms of phylogeny, a previous study by Tamar et al. (2021) mainly focused on *T. keyserlingii* and these authors included eight *T. przewalskii* samples in their comprehensive phylogenetic study. Moreover, two recent studies (Yu et al., 2021; Li and Guo, 2023) successfully sequenced the full mitogenome of *T. przewalskii*, both using only one sample from China. Since, the majority of previous studies focused on the genus level (e.g., Macey et al. 1999; Nazarov et al., 2017), we reconstructed our initial phylogenetic tree for *T. przewalskii* using more samples from multiple regions (including Mongolian samples from this study and Chinese samples from previous studies) using a partial *ND2* gene.

Consistent with previous studies (Macey et al., 1999; Nazarov et al., 2017; Tamar et al., 2021), we obtained sister species relationships of *T. przewalskii* and *T. roborowskii*, which diverged approximately 1.6 Mya. In contrast to all of these findings, a mitogenomic phylogeny study showed monophyly of the group containing *T. przewalskii* and *T. keyserlingii* (Yu et al., 2021), which may be a result of low sample size (n = 1). For the genus-level phylogeny, the monophyletic group of *T. microlepis* and *T. bedriagai*, appears to be phylogenetically the most separated species in genus *Teratoscincus* (Nazarov et al., 2017). For Mongolian samples of *T. przewalskii*, we obtained six haplotypes of which H1 and H5 appeared to be most frequent or geographically widespread. Haplotypes from Mongolia clustered separately from other reference sequences of China in both tree (Fig. 2A, B). This intraspecific variation would suggest that the genetic dissimilarity is country-specific, but more samples from China are needed to better assess this.

Regardless of where population boundaries may occur, the intraspecific variation in *T. przewalskii* is much less than that observed in *T. microlepis* and *T. keyserlingii* (Macey et al., 1999; Nazarov et al., 2017; Tamar et al., 2021). Furthermore, geographic barriers may be responsible for producing species with high intraspecific variation (e.g., *T. microlepis*). For instance, the Indo-Eurasian and Arabian-Eurasian tectonic collisions likely played a significant role in producing the intra- or interspecific variation seen today in some species of *Teratoscincus* (Macey et al., 1999; Tamar et al., 2021). Alternatively, the lower intraspecific variation of *T. przewalskii* might be a consequence of a lack of major geographic barriers across their range in the Central Asian Desert, including Mongolia.

The genus *Teratoscincus* most likely evolved in Southwest Asia approximately 19.3 Mya (Tamar et al., 2021). Subsequently, these geckos underwent geographical extension into West and Central Asia (including the Mongolian Gobi Desert). According to this and the study by Tamar et al. (2021), *T. przewalskii* originated between 1.3–3.5 Mya in the Central Asian Desert. Even though national borders cannot affect species distributions, our time-calibrated tree shows relatively recent divergence between Mongolian haplotypes and we propose that an ancestral population of *T. przewalskii* may have moved into Mongolia from northwestern China approximately 149,000 years ago during the late Pleistocene (Fig. 2B). However, we emphasize that these divergence estimations are based on a single calibration, which may result in inaccuracies.

Table 3. Analysis of Molecular Variance (AMOVA) of seven *Teratoscincus przewalskii* populations from Mongolia. Included are values for the degrees of freedom (*df*), sum of squares (SSq), variance components (VC), and the percentage of total variation (%). For this analysis, $p = 0.001$ at $F_{ST} = 0.451$.

Source of variation	*df*	SSq	VC	%
Among populations	6	6.597	Va = 0.0944	45.2
Within populations	67	7.674	Vb = 0.1145	54.8
Total	73	14.270	0.2089	

Interestingly, we obtained relatively strong genetic population structure between studied populations of *T. przewalskii* in Mongolia (AMOVA; F_{ST} = 0.451, p = 0.001), with four of six haplotypes population-specific and H5 dominated by a single population (GTS). Such strong population structure combined with low genetic variation is probably the result of isolated, small populations (Wang et al., 2017). Unfortunately, we do not have any demographic information on our target species in Mongolia. However, we could see that there are no major geographical barriers that have led to isolation among studied populations in Mongolia (Fig. 1). Moreover, the total range of *T. przewalskii* includes the Trans Altay Gobi in Mongolia. We assume that this strong population genetic structure (resulted from isolation) of *T. przewalskii* is produced by fragmented core habitats, such as sand dunes with sparse vegetation that occur across the Mongolian Gobi Desert. In addition, we obtained non-significant pairwise F_{ST} genetic distances among studied population, only excluding the GTS population (with haplotype H5). This genetic isolation between GTS and the remaining populations most likely resulted from non-geographical barriers. Further habitat and ecological studies are needed to make certain conclusion.

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