

RESEARCH ARTICLE



WILEY

Analysis of mitochondrial DNA haplogroup frequencies in the population of the slab burial mortuary culture of Mongolia (ca. 1100–300 BCE)

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Funding information

Council on East Asian Studies, MacMillan Center, Yale University

Abstract

Recent research has shown evidence of ancient admixture from both eastern and western Eurasian genetics in the human populations of Mongolia going back to at least the Eneolithic Afanasievo archaeological culture (ca. 3000 BCE). Eastern mtDNA lineages found in ancient and living Mongolians in the past and present have greatest affinity with Neolithic populations from the Transbaikal region of southern Siberia, suggesting that people from this region were likely the first to colonize northern and eastern Mongolia after the last glacial maximum (ca. 24,500–17,000 BCE), while western Eurasian groups probably migrated to the steppe in association with the earliest forms of pastoralism. While some studies suggest the contribution of these ancient western lineages to the modern populations in Mongolia was minimal, this research demonstrates that western mtDNA lineages were particularly prominent among the burial populations of the Early Iron and Iron Ages in the region. This is most notable among the burial population associated with slab burials and the burial population of their successors, the people associated with the Xiongnu polity (209 BCE–91 CE). Similarities between mtDNA haplogroup frequencies of the slab burial and Xiongnu burial populations also strongly support the proposal that the builders of the slab burials were the principal ancestors of the Xiongnu people.

Objectives: The objective of this research is to increase understanding of human population change on the Mongolian steppe during the first millennium BCE and how it may be associated with cultural change and the creation of early eastern steppe empires. It examines the mtDNA haplogroup frequencies of the burial population from slab burials in Mongolia and compares it with frequencies from various other populations to determine population affinities.

Methods: This study was primarily based on Sanger sequencing the HV1 of the mtDNA of ancient individuals from Mongolia during the Early Iron Age for haplogroup determination and then comparing mtDNA haplogroup frequencies with previously published data including 110 ancient and modern populations. The 21 samples used in this study were selected based on region, dating, and availability.

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Pairwise *F*_{st}s of mtDNA haplogroup frequencies were calculated using the Arlequin population genetics program.

Results: The mtDNA hg of 20 of 21 samples are determined and added to previously published data, increasing the total sample to 35 for the particular population of interest. Using this mtDNA gene pool, it is determined that by the Late Bronze Age an east–west mixed population has already been established, which stays relatively stable into the Iron Age (Xiongnu) period, suggesting that the people practicing the slab burial tradition are the most likely biological ancestors of the Xiongnu. It also notes a distinct difference in mtDNA haplogroup frequencies between north-eastern and central populations in Mongolia during the Iron Age.

Conclusions: There was little change in mtDNA haplogroup frequencies during the first millennium BCE, which contrasts with the clear change in the first millennium CE. MtDNA hg frequencies (matrilines) seemed to be stable at around 28%; however, Y-ch frequencies have a dramatic shift towards western lineages during the Xiongnu period (300 BCE–200 CE). The mtDNA haplogroup frequencies from the population from the slab burials have close affinity with the Xiongnu population frequencies. This suggests a notable and consistent western Eurasian component in Mongolia during the first millennium BCE, established before the end of the Bronze Age and possibly associated with the introduction of the domestic horse.

KEYWORDS

ancient DNA, bronze age, Mongolia, slab burial, Xiongnu

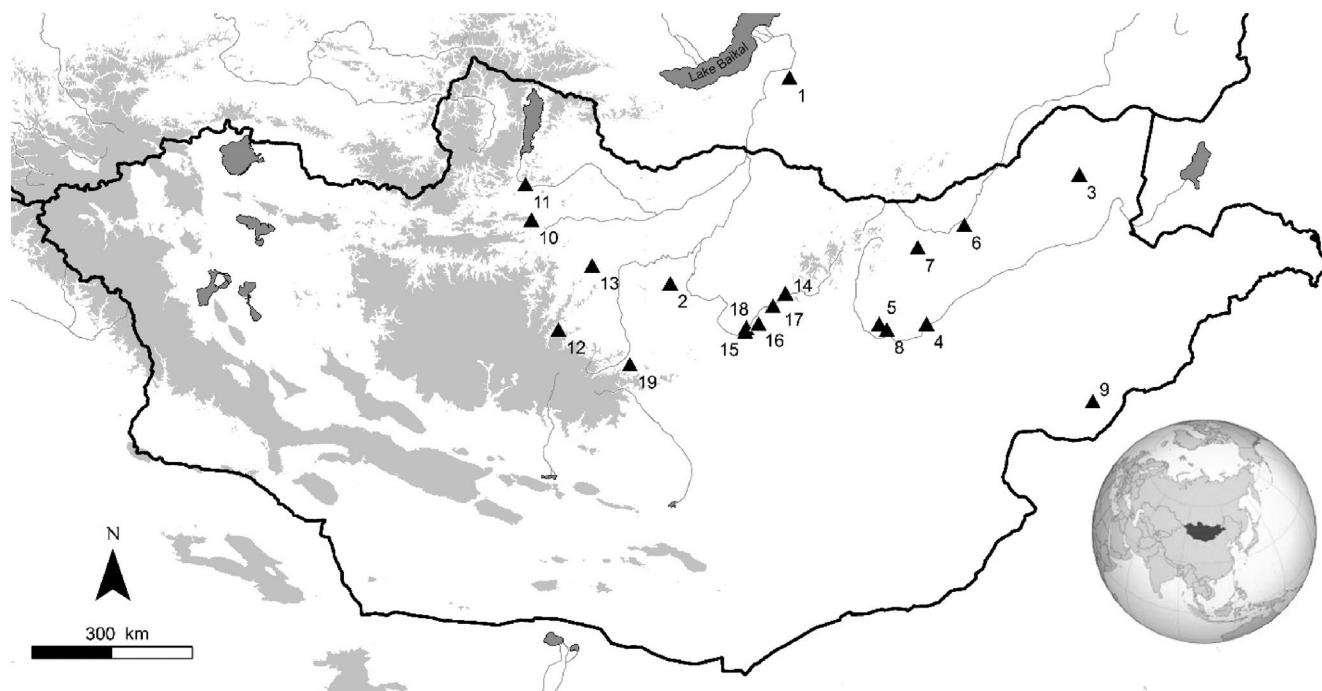
1 | INTRODUCTION

This study examines the mitochondrial DNA (mtDNA) haplotypes and their frequencies for the population associated with the slab burial archaeological culture of Mongolia (ca. 1100–300 BCE) comprising the mtDNA haplotypes obtained from 19 individuals from this study in addition to published data (Jeong et al., 2020; Shinoda, 2016; Wang et al., 2020). The slab burial mortuary tradition, its material culture, and associated settlement sites constitute the primary archaeological culture found on the Mongol central and eastern steppes by the sixth century BCE. The slab burial tradition was partially contemporaneous with the neighboring Pazyryk archaeological culture of the Altai Mountains and the Western and Eastern Zhou Dynasties of China. This period of slab burial construction precedes the archaeological culture based on the Noin Uul and Derestui type sites (ca. 300 BCE–200 CE) (Rudenko 1962).

The Xiongnu polity (historically dated to 209 BCE–91 CE) is recognized as the first documented state society on the Mongol steppe and the primary competitor of the Han Dynasty (202 BCE–220 CE) (Atwood, 2004; Twitchett & Loewe, 1987); however, the sources of the people of the Xiongnu state have long been a mystery. Recently ancient DNA research has been a leading contributor to furthering our understanding of the origins of the Xiongnu people and population dynamics on the Mongol steppe during the Bronze and Iron Ages. Archaeologists and historians have argued that the Early Iron Age peoples of Mongolia

most likely contributed to the population of the Xiongnu state, although these earlier groups are thought of as dispersed, variable, and politically disaggregated. The results of this study are consistent with hypotheses suggesting that the people who built slab burials shared a common mortuary tradition yet were themselves diverse and descendants of long-standing local communities in situ from the Bronze Age or earlier (Burentogtokh et al., 2019; Honeychurch et al., 2009; Houle, 2009). These communities would be expected to be locally differentiated while sharing genetic ancestry from both eastern and western populations derived from migrations and interaction events dating from centuries or millennia prior. Furthermore, this study also strongly supports the hypothesis that the people associated with slab burials were the primary population of origin for the matrilines of the subsequent Xiongnu burial population (Honeychurch et al., 2009; Tumen, 2004).

The slab burial archaeological culture first emerged on the south-east Mongol steppe, eventually replacing other local Late Bronze Age archaeological cultures, including the Khirigsuur tradition (ca. 1400–700 BCE), a widespread and monumental “kurgan” tradition of western and central Mongolia (Taylor, 2017). Currently, some archaeologists argue that the practice of building slab burials emerged from an earlier Bronze Age practice of constructing what is now referred to as “prone burials.” The prone burial tradition¹ has many structural similarities to later slab burials with the primary difference being a prone instead of a supine position for the interred individual (Honeychurch, 2015, pp. 122–126; Wright et al., 2019). Slab burial



MAP 1 Slab burial sites considered in this study. The following are the site names to their corresponding numbers (site names in italics are ones sequenced in this study): 1. Pesterevo 82; 2. *Zaraa Tolgoi*; 3. Khadan Khuv; 4. Bus Khaikhan; 5. Khanan Uul; 6. Shuusyn Boom; 7. Tugsiin Uvdug; 8. Rashaant Tolgoi; 9. Baraan Khavtsal; 10. Uushigiin Uvur; 11. Ulaan Tolgoi; 12. *Altan Sandal*; 13. *Delen Tolgoi*; 14. Dartsagt; 15. Morin Tolgoi; 16. Erdenekhairkhan; 17. *Bayankhairkhan*; 18. *Tariat Brigad*; 19. *Shunkhlai Uul*

funerary practices are thought to have diffused westward based on exchange networks and political alliances but were predominantly accepted from neighboring groups by in situ local communities (Burentogtokh et al., 2019). In other words, while the practice of the burial practices expanded, this does not seem to be accompanied by an expansion of a specific population.

The slab burial archaeological culture consists of individual burials, about 1.8 m in depth, and fenced by a rectangular wall of moderate to large vertical stone slabs that may extend as much as two meters above the surface. The grave structures range from 2 to 7 m in length and 3 to 4 m in width with an east–west orientation that are often found constructed in parallel rows running north–south. The environs of slab burials are diverse, including valley mouths, the base of mountain slopes, near waterways, and are often in association with earlier monumental sites due to diachronic site re-use (Erdenebaatar, 2002; Honeychurch et al., 2009; Turbat, 2006). The geographic distribution of slab burials in Mongolia shows a clear pattern of high densities in the eastern and central region, where most of the earliest sites have been located, with gradual decline westward into the mountainous areas of Mongolia (Honeychurch & Amartuvshin, 2011; Map 1).

Some scholars have suggested that the people who built the slab burials have more East Asian cranial-facial characteristics than those of the Bronze Age archaeological populations in Mongolia, and thus it has been argued that perhaps the slab burial practitioners were “eastern” migrants (Lee & Zhang, 2013; Tumen, 2004; Turbat, 2006). However, data from this study show that a large component of the mtDNA lineages are “western” in origin, more so than any of the

Bronze Age populations from central and eastern Mongolia compared in this study. The earliest evidence of these western lineages in the region is with the arrival of people associated with the appearance of the Afanasievo archaeological culture (ca. 3100–2500 BCE), who introduced pastoralism and copper metallurgy to the region (Honeychurch, 2017; Rogers et al., 2019). The large western component in the mtDNA gene pool of the slab burial population and its affinities to contemporaneous west Eurasian steppe populations suggest that the number of people with western Eurasian mtDNA haplotypes on the Mongol Steppe was substantial by at least the middle of the second millennium BCE. The frequencies of mtDNA haplogroups (hg) of these burial populations support the proposal that this intermixed east–west population represented in the slab burials were the primary contributors to the succeeding population of the Xiongnu period.

2 | MATERIALS AND METHODS

This study consists of genetic analysis of the mtDNA HV1 (np16056–16356) haplotypes from 21 individuals excavated from slab burial archaeological contexts located in the central Mongolian steppe region, including additional published data from other slab burials (Jeong et al., 2020; Shinoda, 2016; Wang et al., 2020). Geographical criteria for sample selection specified that the samples were to be from sites in central Mongolia, defined as ranging within ~200 km from Kharkhorin township in Uvurkhangai province, and are from

Khairkhan *sum* in Arkhangai province, Büregkhangai township in Bulgan province, and Altan Bulag township in Töv province (see Map 1, for archaeological sites). This region was chosen due to the relatively large number of excavated multi-phase sites available to better understand regional population differences through time. It is also the central political region for multiple historical polities, including the Xiongnu state, and the Türkic and Mongol empires.

2.1 | Contamination control

Contamination with exogenous DNA is a serious issue to consider when working with ancient samples and thorough measures must be taken to reduce the probability of contamination as much as possible and to detect contamination should it occur (Kaestle and Horsburgh 2002; Pääbo et al. 2004; Gilbert et al. 2005; Kemp & Smith, 2005; Raff et al., 2006; Kemp et al., 2007; Raff et al., 2011; Ballantyne et al., 2015). Samples used in this study were processed in the dedicated limited-access aDNA laboratory, with continuous positive pressure and HEPA filter, of Dr. Frederika Kaestle at Indiana University Bloomington. Established protocols for reducing contamination were strictly followed and all PCR amplification and post-PCR analyses occurred in a laboratory in a different building (Tamariz et al. 2006; Ballantyne et al., 2015). Negative (no sample) controls were processed in parallel during each DNA extraction with each set of five samples extracted, and all PCRs also included two negative (no sample) controls for every set, in addition to the extraction control, to detect any contamination that may have occurred in the laboratory. Results for samples were confirmed with a minimum of two identical sequences from three separate extractions. To guarantee removal of previously amplified products that could result in carry-over contamination, a dNTP mix containing uracil instead of thymine was used in all PCR amplifications, and each amplification was pre-digested with AmpErase uracil N-glycosylase (Thermo Fisher Scientific) (Longo et al. 1990). After selection from the skeletal archives, the only researcher that handled the samples and was present in the aDNA laboratory during extractions and amplifications belongs to a different Z mtDNA haplotype than all Z haplotypes identified.

2.2 | Ancient DNA extraction

DNA extraction from the ancient skeletal samples was conducted in Dr. Kaestle's aDNA laboratory located in the Institute for Molecular Biology at Indiana University, Bloomington, with established protocols using the Thermo Fisher Scientific Geneclean for Ancient DNA™ kit (Ballantyne et al., 2015; Kemp et al., 2007; Kemp & Smith, 2005; Raff et al., 2006, 2010). All samples used in this study were from long bones, predominantly ribs, carpals, and tarsals. The protocol used 0.4–0.5 g of a sample for each extraction (0.2–0.4 g was used in secondary and tertiary extractions when sample amounts were limited). One negative (no sample) control was added for every sample set. After protein digestion in the ProK solution, the 15-ml tubes were

centrifuged for 10 min at 14,000 rpm and the supernatant was transferred to a new 15-ml tube. Any remaining samples were then stored at -80°C . Then 300 μl glass milk (silica) solution from the Geneclean for Ancient DNA™ kit and 800 μl of 5 M guanidine thiocyanate solution were added to the supernatant, which was then rocked at room temperature for a minimum of 30 min to bind the DNA in solution to the glass milk. From here, the 15-ml tube was centrifuged for 10 min at 14,000 rpm to collect the glass milk at the bottom, and the supernatant was discarded. From this point resuspension and purification were done according to the protocols from the Geneclean for Ancient DNA™ kit. Each sample was extracted three separate times with several months between extractions, to confirm results. No negative controls from the extraction groups showed subsequent amplification.

2.3 | Ancient DNA amplification

Sanger PCR amplification of the extracts was conducted using three sets of primers covering most of the HV1 region of the mtDNA (see Table 1 for primers and amplicon). Presumably due to excellent preservation conditions in Mongolia (cold, dry, and saline), extractions were consistently amplified, and thus it was possible to compile high-quality sequences spanning np16038–16356 from the mtDNA of 20 out of the 21 samples. An additional section was sequenced for np16266–16422 to clarify a few samples for haplogroups when necessary. Amplification was performed with PCR_x Enhancer (Thermo Fisher Scientific), 10 \times Invitrogen PCR buffer (Thermo Fisher Scientific), Invitrogen 25 mM MgCl₂ (Thermo Fisher Scientific), 20 mg/ml bovine serum albumin (BSA; Thermo Fisher Scientific), 10 mM dNTPs, 20 μM primers, Invitrogen Hot-Start Platinum Taq (Thermo Fisher Scientific), Applied Biosystems AmpErase™ uracil N-glycosylase (Thermo Fisher Scientific), and nuclease-free H₂O. Each PCR was performed with 3- μl of extracted sample as template in a 25- μl -volume, 0.2-ml thin-walled tube. At least one negative (no extract) amplification control was included with every six sample extractions, including the extraction negative control. After PCR set-up the sample tubes were sealed and transferred from the aDNA laboratory to the modern DNA laboratory for the amplification reaction in either an MJ Research PTC-200 or Bio-Rad C1000 thermal cycler. For each sample 13.13 μl DNA-free H₂O, 2.5 μl PCR Enhancer, 2.5 μl 10 \times PCR buffer, 1.5 μl MgCl₂, 0.4 μl dNTPs, 0.52 μl BSA, 0.4 μl of each primer, 0.4 μl Platinum Taq, 0.25 μl AmpErase™ uracil N-glycosylase, and 3 μl of extracted aDNA template were added for a 25- μl reaction volume per 0.2-ml tube. The following cycling parameters were used for amplification reactions: initial soak at 95 $^{\circ}\text{C}$ for 2 min; followed by 40 cycles of denature at 94 $^{\circ}\text{C}$ for 30 s, anneal at 50 $^{\circ}\text{C}$ (for np16038–16213 and np16266–16422) or 57 $^{\circ}\text{C}$ (for np16209–16356) for 30 s, extend at 72 $^{\circ}\text{C}$ for 30 s; followed by a final extension at 72 $^{\circ}\text{C}$ for 5 min. This was followed by a hold at 4 $^{\circ}\text{C}$ until sample was moved to a -20°C freezer to await gel electrophoresis. Amplification success was assessed through ultraviolet visualization after agarose gel electrophoresis with ethidium bromide stain before sequencing.

2.4 | Sequencing

Following electrophoretic detection of amplification, each fragment was sequenced in both directions using ABI Big Dye v3.1 chemistry (Thermo Fisher Scientific) on an Applied Biosystems 3730 automated sequencing system at the Indiana Molecular Biology Institute. Amplicons were purified using the manufacturer's protocol for the QIAquick PCR Purification Kit™ (Qiagen); then sequenced using the manufacturer's protocol for ABI Big Dye v3.1. Each extraction, amplification, and sequencing reaction were repeated at least twice following at least a 1-month interval so that different batches of reagents were used. Resulting electropherograms were assessed using Geneious 6.1.8 software (Biomatters Ltd.) and aligned against the revised Cambridge Reference Sequence (rCRS) (Genbank Accession Number NC_012920; Anderson et al. 1981, Andrews et al., 1999). A consensus sequence was generated from at least two identical sequences from three extractions per individual using Geneious 6.1.8. SNP differences between the consensus sequences and the rCRS were used to determine mtDNA haplogroup and haplotype. In a few ambiguous sequences, restriction fragment length polymorphisms (RFLP) were checked for the R (np12705) and H (np7028) hg diagnostic SNPs. After the mtDNA haplotypes were determined through sequences from multiple extractions using the Haplogrep2 algorithm (Kloss-Brandstätter et al., 2011; Weissensteiner et al., 2016) based on PhyloTree17 and back traced for accuracy (van Oven, 2015), the frequencies of mtDNA haplogroups were calculated and compared to those from 110 ancient and modern populations from published studies (see ST3 in Data S1) using the Arlequin 3.5.2.2 population genetics software to generate conventional F-statistics for computing pairwise distances (Excoffier and Lischer 2010; for full Fst results for these populations, see ST1 in Data S1).

3 | RESULTS

The first hypervariable regions of 20 out of the 21 individuals were successfully sequenced with multiple extractions and had haplotypes assigned (ST2 in Data S1). Of these 19 different haplotypes within 12 hgs were identified (3A, B, 2C, D, G, 4H, HV, J, K, 3 M, R, and Z). The H2a5b2 haplotype appears in one individual at each of two different sites, the Altan Sandal site in Arkhangai province, and the Tariat Brigad site in Tuv province, which are 403 km apart. In addition to these 20 samples, previously published mtDNA hg data for

15 additional slab burial samples were included (Jeong et al., 2020; Shinoda, 2016; Wang et al., 2020). This resulted in a 35 individual total sample size for a slab burial aggregate (SBA) population in Mongolia.

The SBA population was compared with 45 ancient Eurasian populations and 65 modern Eurasian populations for population affinity using conventional F-statistics (Fst) to evaluate population mtDNA gene frequencies. The ancient populations statistically indistinguishable from the SBA gene pool (negative Fst values) include the Bronze Age Mongolia aggregated (BAMA) population ($n = 71$), the Bronze Age population of western Mongolia (BAMW) from Bayan-Ulgii, Khovd, Uvs and Zavkhan provinces ($n = 12$), the Bronze Age population of central and eastern Mongolia (BAMCE) from Bulgan, Bayankhongor, Khentii, and Sukhbaatar provinces ($n = 27$), the aggregate burial population of the Xiongnu ($n = 116$), the Xiongnu of central Mongolia (CMX) ($n = 48$), the Xiongnu period site at Oginuur ($n = 17$), the Xiongnu period site at Battengel ($n = 14$), the Mongol Empire (MEA) period (1206–1368 CE, $n = 128$), which includes a cemetery ($n = 21$) at Shangdu (Upper Capital) in northeast Inner Mongolia, and the central Mongol Empire period population (CME) ($n = 48$) (see ST1 in Data S1 for Fst values). The next most similar was the “Xianbi” period Lamadong site population ($n = 17$; Fst 0.00369; Wang et al., 2007). The only other ancient populations with which the SBA has similar mtDNA hg frequencies (Fst scores under 0.01) is the aggregate population of the Bronze Age prone burial population of Mongolia ($n = 19$) (Fst 0.00419) (Figure 1: PCoA). The SBA population mtDNA gene pool also has a relatively close affinity with the gene pool of the female population of the Xiongnu period Egiin Gol cemetery site ($n = 16$; Fst 0.01503), but quite different from the males ($n = 22$; Fst 0.08069) (Keyser-Tracqui et al., 2003). While the two and a half millennia that have passed since the Early Iron Age makes the similarities of mtDNA hg frequencies with modern populations of less interest than those with ancient ones, the following modern populations have notable similarities (conventional Fst scores less than 0.01): Altaian Kazakh, Khamnigan, Kirghiz, Mongol, Telengit, Teleut, Uyghur, Uzbek, and a composite Central Asian population. While these Fst scores are of interest, it should be noted that the p -values for the majority of these extremely small Fst scores are high; this is most likely due to the population sizes (n) and means that it is quite possible that much of the extreme affinities may be due to chance (see ST4 in Data S1 for p -values).

Following these tests, a population consisting of slab burial samples only from central Mongolia (CSB) was compiled ($n = 25$) and

Name	np	Sequence	Amplicon length
16038 forward	16038–16055	5'-AGCAGATTTGGGTACCAC-3'	175
16213 reverse	16192–16213	5'-CTGTACTTGCTTGAAGCATGG-3'	
16190 forward	16190–16209	5'-CCCCATGCTTACAAGCAAGT-3'	185
16375 reverse	16356–16375	5'-GTCATCCATGGGGACGAGAA-3'	
16266 forward	16266–16288	5'-CCCACTAGGATACCAACAAACC-3'	157
16423 reverse	16403–16423	5'-ATTGATTTACCGGAGGATGG-3'	

TABLE 1 PCR primers

compared. The central slab burial population was different from the SBA in two notable respects; the CSB population mtDNA frequencies bear less resemblance to Mongolia's Bronze Age populations, while having notably more affinity with more western Eurasian populations. CSB comparative F_{st} scores had negative values with only the BAMW, the Xiongnu, CMX, Oginuur and Batstengel Xiongnu sites, and the CME populations, and the only ancient population with a positive F_{st} score below 0.01 was the Mongol Empire aggregated (MEA) population (F_{st} 0.00929; See SF2 in Data S1).

Additionally, since the sample population of the slab burials of the Shunkhlai Uul site, Uvurkhangaï province, consisted of 10 individuals, this subset was analyzed as a separate population as well as a part of the other slab burial populations (see SF4 in Data S1). The Shunkhlai Uul burial population is virtually identical (negative F_{st} value) with the BAMW population, CME population and the Lajia site population ($n = 14$; ca. 2000–1800 BCE) from Qinghai in China (Gao et al., 2007). It also showed close affinity with the central Mongolia

Xiongnu (CMX) population (F_{st} 0.00611) and was found to be similar with a Zhou dynasty population (F_{st} 0.00673) from a cemetery near Heng Bei (ca. 1000–800 BCE), Jiang County, Shanxi province (Zhao et al., 2015), and the Sampul site (ca. 250 BCE) (F_{st} 0.00511) from Lop County in Xinjiang (Xie et al., 2007).

The mtDNA hgs: A, B, C, D, F, G, M, Y, and Z, are generally considered “eastern” Eurasian, and are currently found in high frequencies in the populations of East Asia, Central Asia and Siberia. The mtDNA hgs: H, HV, I, J, K, N, R, T, U, V, W, and X, are commonly considered to be “western” Eurasian, as they are currently found in highest frequency in the populations throughout Europe and southwest Asia (Derbeneva, 2009; Derenko et al., 2007; Gonzalez-Ruiz et al., 2012; Gubina et al., 2016; Keyser-Tracqui et al., 2006; Schurr & Pipes, 2011; Zhao et al., 2015). Twelve of the 20 samples sequenced in this study were eastern haplotypes (60%) and eight were western haplotypes (40%). The SBA ($n = 35$) had 25 eastern haplotypes (71.43%) and 10 were western



FIGURE 1 PCoA. (a) Is a PCoA of regional specific populations while (b) shows distances between aggregated populations. BAMA, Bronze Age Mongolia aggregate; BAMCE, Bronze Age Mongolia central eastern; BAMW, Bronze Age Mongolia Western; CSB, central slab burials; Danish-IA, Danish iron age; LBK, linear beaker culture; MEA, Mongol empire aggregate; NeoRom, Neolithic Romania; SBA, slab burial aggregate. Populations in blue are modern populations for scale

haplotypes (28.57%). The central slab burials ($n = 25$) had 16 eastern haplotypes (64%) and 9 were western haplotypes (36%). The Shunkhlai Uul population had seven eastern haplotypes (70%) and three were western haplotypes (30%). All confirmed genetic sequences generated in this study have been uploaded onto Genbank (Benson et al., 2013).

4 | DISCUSSION

A sample size of 20 may be an issue in population studies, particularly with nonrecombining markers such as mtDNA, because variation can be reduced notably from unrepresentative sampling due to genetic drift. However, an aggregated sample size of 35 compiled from diverse sites should provide a reasonable representation of the larger population ($\sim 16.55\%$ margin of error: where $E = \text{Sqrt}[(N-n)x/n(N-1)]$). The central slab burial (CSB) sample size of 25 is not ideal, but it is still relatively useful and is substantially larger than sample sizes used for population comparisons in many previous studies (Fu et al., 2007; Haak et al., 2015; Keyser et al., 2009; Lee et al., 2014; Xie et al., 2007). While the Shunkhlai Uul sample consists of only 10 individuals, it represents only one site; thus, it is reasonable to consider its hg frequencies as relatively representative for a site population.

The presence of eastern haplotypes (A, B, C, D, F, G, M, and Z) among the slab burial sample is not particularly surprising, since these have been common in northeast Asia since the last glacial maximum (LGM) which lasted from circa 24,500–17,000 BCE (Clark et al., 2009). A, B, C, and D hgs predate the LGM and contribute, along with X hg, to the founding lineages of the indigenous people of the Americas (Raff et al., 2011). While in highest frequency in northeast Asia, the C hg has been identified in samples dating to circa 5450 BCE in the Ukraine (Nikitin et al., 2012); the specific haplotype found among this slab burial sample is most similar with C4b8a, currently prevalent in Nganasan populations in northern Siberia (Volodko et al., 2008). The F hg is strongly associated with East Asia. The two particular F haplotypes found among the slab burial populations are of the F1b sub-haplogroup, with a coalescence date of 9809.5 ± 4468.5 BCE and is currently found in living populations across the Eurasian steppe (Behar et al., 2012; Tolk et al., 2001). Sample AT233 was determined to be of the haplotype G2b2 (Jeong et al., 2020; Wang et al., 2020),² which has an early coalescence date ($18,526 \pm 5481.6$ BCE). The Z hg is relatively rare and originates from the Amur River region with an estimated coalescence date for the basal Z of $19,711.6 \pm 8380.8$ BCE (Behar et al., 2012); several of the eastern rivers of the Mongol Steppe, including the Kherlen River, are eventual tributaries of the Amur River. Samples AT323 and AT326 were assigned to M31a2 by Haplogrep2, but according to mtDNAMANAGER the M3 haplotype is just as likely (Lee et al., 2008). Although the SNPs at np16093, 16126, and 16223 compared with the revised Cambridge Reference Sequence (rCRS; Andrews et al., 1999) place this individual's mtDNA haplotype within the M hg, this combination of SNPs has not been found within an M haplotype in previously published

studies. However, this combination was identified in a Bronze Age prone burial from central Mongolia (Rogers, 2016), suggesting recent ancestry between the two samples. Both M31 and M3 hgs are currently prevalent in the region of northern India and Nepal and may have arrived via migration from the southeast along the Central Asian Mountain Corridor (Endicott et al., 2007; Frachetti, 2015; Metspalu et al., 2004).

The western matriline in the samples extracted in this study are represented by three H haplotypes, one HV0a1, one J1c8a, one basal K, and one R7 haplotype. Two H haplotypes have SNPs that differ from all recorded samples in GenBank (accessed March 1, 2021), although restriction fragment length polymorphism testing at np7028 of the mtDNA indicated that they were indeed H haplotypes, while the third (AT253) was an exact match for H5. Haplogrep2 assigned H1/H7/H13 as likely haplotypes (73.86% quality for each) for sample AT321, with SNPs differing from rCRS at 16111, 16222, and 16261 within the sequenced interval (np16058–16356). Samples AT324 and AT484 were assigned H2a5b2 (89.58% quality) with SNPs np16182, 16183, and 16189. According to Behar et al. (2012) H2a5b has a coalescence date of 304.6 ± 1609.6 CE, which would place this individual close to the first appearance of this haplotype. H5 has a coalescence date of 7927.6 ± 1401.7 BCE; it is currently most common in the western Caucuses region and has been identified in the Neolithic site of Tell Halula (Syria, ca. 6800 BCE) (Fernández et al., 2008; Roostalu et al., 2007).

Sample AT276 was an exact match with the J1c8a haplotype, which has a coalescence date of 706.8 ± 5174.5 CE (Behar et al., 2012). The J1 hg has been linked to early Neolithic Middle Eastern agriculturalist expansion into Europe (Haak et al., 2010) and, while it is rare in East Asia, it appears in small numbers throughout central Eurasian steppe populations, which suggests a possible earlier presence (Isern et al., 2017). J1c haplotypes have been found regularly in ancient Carpathian and Pontic-Caspian populations (Derenko et al., 2019; Juras et al., 2018; Malyarchuk et al., 2018; Modi et al., 2019; Rusu et al., 2019). Sample AT179 was a (100% quality) match for the basal K haplotype (SNPs at np16224 and 16311). Ötzi, the frozen Tyrolean mummy from the Alps (3350–3100 BCE), has the K1 haplotype (Ermini et al., 2008), and several samples from Theopetra, Greece (7000–5000 BCE), carry the K1c haplotype (Hofmanová et al., 2016). The basal K hg, which is carried by AT179, has a coalescence date of $24,731.5 \pm 4339.3$ BCE (Behar et al., 2012). The K hg has been argued to be closely associated with early Neolithic agriculturalist expansion out of the Fertile Crescent into Europe as it has not been found among any early European forager populations (Isern et al. 2017).

The mtDNA hgs of the eastern component of the slab burial population can be found in most northeast Asian populations and so can be safely assumed to be a local contribution to the slab burial gene pool. The “western” component is more difficult to source. The K hg may represent an ancient addition from early western foragers that had intermixed with early agriculturalists (Spengler, 2015), similar with the probable origins of the C hg found in the ancient Ukraine (Nikitin et al., 2012). The J1c8a haplotype might be from a regional

polymorphism that is linked to migrating populations after the expansion of agriculturalism from the Middle East, perhaps associated with the development of caprine pastoralism that reached southeast Kazakhstan by at least 2800 BCE (Hermes et al 2020). The H hg, more specifically the H2a5b* haplotype, is unlikely to have originated in Mongolia; based on coalescence times the H2a5b* most likely arrived on the Eastern Steppe near the beginning of the first millennia BCE. Besides the H2a5b haplotype, which must have arrived in a relatively recent migration, the remaining western hgs can be found already in place in Mongolia, although predominantly in the western regions, where half of the Bronze Age population ($n = 12$) carried western mtDNA haplotypes. While western mtDNA lineages are not common in early Neolithic Mongolia, the well-documented expansion of the Afanasievo archaeological culture and the populations associated with the Pontic Steppe Scythians into Central Mongolia likely introduced many of these matrilineal (Honeychurch et al., 2021; Järve et al., 2019).

Several notable patterns arise when comparing the central slab burials (CSB), the SBA and the Shunkhlai Uul burial populations with neighboring ancient populations (see SF2–4 in Data S1 for visualizations). The first pattern is that the slab burial mtDNA frequencies are extremely similar to those of the aggregated Xiongnu populations and relatively similar to those of the various Bronze Age Mongolian populations, strongly supporting a population continuity hypothesis for the region over these time periods (Honeychurch, 2013). The second pattern is that there is a moderate, but perceptible increase in western mtDNA haplotypes among the slab burial populations (SBA 28.57%: CSB 36%) compared with that of the Bronze Age of eastern Mongolia (BAMCE) (14.8%), while the western mtDNA component within the Xiongnu population remains extremely similar to that of the slab burial populations. The frequencies of western hgs within the CSB (36%) and the central Mongolian Xiongnu population (37.5%) are extremely close, while Fst scores show an increased affinity with ancient western Eurasian steppe populations during the Xiongnu period. Many of these “new” western mtDNA lineages are similar to those found in the Early Iron Age Chandmani Uul site population (Jeong et al., 2020), a north-western contemporary of the slab burial archaeological culture from Uvs province, Mongolia, but culturally associated with neighboring communities in Tuva. These “new” western mtDNA lineages are also found in the populations of the Early Iron Age Pontic Steppe Scythians and Bronze Age Sintashta archaeological culture from the Urals, both cultures being intimately linked with the use of domesticated horses (Anthony, 2007; Järve et al., 2019; Juras et al., 2017; Narasimhan et al., 2019). The mtDNA hg frequencies of the Chandmani Uul site population are indistinguishable from the Eneolithic Afanasievo burial population ($F_{st} = -0.00044$), and so could represent a remnant of the Afanasievo peoples with the addition of a limited number of new haplotypes or a recent in-migration of Afanasievo-like matrilineal into Mongolia. The third pattern is one in which the earliest mtDNA lineages in eastern and northern Mongolia have a distinct genetic signature established before the end of the Neolithic in Transbaikalia and north-eastern Mongolia. This mtDNA gene pool seems to consist primarily of A, C, and D haplotypes, with smaller amounts of B, F, and G haplotypes, and are represented by

the populations from the Fofonovo site in Buryatia, Neolithic sites in Bulgan, Bayan Ulgii, and Dornod provinces, and Bronze Age sites in Khovsgol, Khentii and Sukhbaatar provinces (Jeong et al., 2020; Mooder et al., 2005; Wang et al., 2020).

The biomes in which this Neolithic Transbaikalian population type was dominant were mixed forest-steppe, and forested mountains, with “forest” being the shared characteristic. After the Xiongnu period, the mtDNA hgs characteristic of this “Transbaikalian” population began to increase in frequency in the burials of the region so that by the Mongol Empire period these matrilineal had increased significantly in burial populations of central Mongolia, by which time 75% of the burial population carried eastern haplotypes. When the current data of the aggregate population of the entire Mongol Empire in this study is considered, the percentage of eastern hg frequencies increases to 82.81%. This Transbaikalian component is slightly larger in the population of the modern population of Mongolia (86.36%), which still has similar mtDNA hg frequencies to that of the BAMCE ($F_{st} 0.00533$), the SBA population ($F_{st} 0.00042$), and the aggregate population of all Mongol Empire (MET) samples ($F_{st} 0.00299$), demonstrating negligible change in the matrilineal in eastern Mongolia over the past four millennia if similarities are not due to chance.

It is possible that eastern haplotypes had not initially characterized the populations of the eastern steppe in large numbers and only began to increase in frequency after the emergence of mobile pastoralism. While animal husbandry of bovids originated from Western Asia *ad quem* 9000 BCE, the expansion of mobile pastoralism has been attributed to the practitioners of the Eneolithic Yamnaya archaeological culture (ca. 3400–2500 BCE) located on the Pontic-Caspian Steppe as far east as the Ural River; these people had a gene pool virtually identical to that of the Afanasievo burial population (Allentoft et al., 2015; Anthony, 2007; Bowers, 2017; Hollard et al., 2018; Jeong et al., 2020; Wang et al., 2020). The appearance of large accumulations of material culture, as well as megalithic architecture, on the eastern steppe is closely associated with the appearance of the earliest pastoralists (Janz et al., 2017; Taylor et al., 2019). While wild animal remains continue to appear in early Mongolian sites, domesticates become more common and appear in archaeological sites across Mongolia at least by circa 1600 BCE (Honeychurch et al., 2021; Janz et al., 2020; Wilkin et al., 2020).

There are Y-chromosome data for only eight male slab burial individuals: four of which are from central Mongolia, two from the west central province of Khovsgol and two from the eastern regions, and all these individuals carry eastern Y-chromosome haplotypes (Jeong et al., 2020; Wang et al., 2020). While this sample is small, in comparison 28.57% of the mtDNA gene pool consisted of western hgs. By the Xiongnu period the male burial population ($n = 32$) carried 46.88% western Y-chromosome types with a total western mtDNA component of 27.59% (Jeong et al., 2020; Keyser-Tracqui et al., 2003; Wang et al., 2020). This suggests that by the beginning of the slab burial mortuary tradition, there had already been an east–west mixed population. While during the slab burial period (ca. 1100–300 BCE) eastern patrilineal seem to have been dominant, in the Xiongnu period about half of the population had western patrilineal with virtually no change to

the mtDNA gene pool in east–west terms. If sex bias migration patterns were similar with those found in Europe, this increase of western patrilineal lines would be consistent with aggressive expansion of people with western male ancestry (Batini et al., 2017); however, such a pattern could also be due to a gradual nonaggressive assimilation, such as the practice of marriage alliances associated with an expansion of trade or cultural networks that favored people with western patrilineal lines (Honeychurch, 2013). Moreover, these two hypotheses are not mutually exclusive and would require additional genetic analyses in combination with systematic archaeological research to assess their validity.

This study supports a narrative that envisions a Bronze Age population in situ in Mongolia, with prevalence of Afanasievo-like “Western Steppe” matrilineal lines in the northern and western regions and primacy of “Transbaikial” matrilineal lines in the central and eastern regions, with some intermixing on the central Mongol steppe near the southern slopes of the Khangai Mountains. An influx, likely associated with the introduction of the domestic horse from western Eurasia into Mongolia of “new” west Eurasian steppe matrilineal lines and characterized by mtDNA haplotypes with relatively recent coalescence dates, occurred during the Late Bronze Age and persisted into the Iron Age, along with a slight increase in the prevalence of western matrilineal lines. This early admixed population in Mongolia (ca. 1000–500 BCE) of Transbaikial-western steppe matrilineal lines is most associated with the slab burial tradition of building rectangular graves using vertical stone slabs, a cultural practice that expanded north and westward until perhaps by the seventh century BCE, when it encompassed the majority of the central and eastern steppe zones, including the Khentii mountains and much of the eastern foothills of the Khangai mountains. The slab burial archaeological culture remained the most prevalent practice on the eastern steppe until the third century BCE, when it was gradually superseded by the archaeological culture attributed to the Xiongnu polity. The matrilineal lines of the Xiongnu population certainly descended predominantly from this in situ population that once had practiced slab-built funerary traditions. Slab burial building communities likely originated from local earlier Bronze Age groups that had merged into larger composite group identities associated with specific territories (Burentogtokh et al., 2019). During the Xiongnu period, there seemed to have been a major increase of western patrilineal lines, mainly of R1a1 and J hgs; however, there does not seem to have been a major change in the mtDNA gene frequencies of the population overall.

The present research was limited to the sequencing of the HV1 region of the mtDNA D-Loop, with restriction fragment length polymorphism testing for hg diagnostics in the event of ambiguous sequences, and while mtDNA is generally representative of full population ancestry, it is still quite limited compared to high throughput whole genome sequencing. Understanding male lineages (Y-chromosome) and comparing them with matrilineal patterns is essential for understanding marriage patterns and extra-community relationships of local archaeological cultures. Additionally, high throughput nuclear genomic sequencing would provide important data on phenotypic traits, such as eye and hair coloration, skin pigmentation, lactase persistence and countless other genes now identified from genome wide association studies and potentially informative regarding population and culture change. Another issue concerning this sample population is the paucity of data from more

southerly examples of slab burial archaeological culture, which exist, but have not yet been adequately researched. Considering the differences between the east and west populations of slab burials it is possible that there are also significant differences between northern and southern populations, which would greatly improve our understanding of the people who practiced the slab burial culture. While some high throughput sequencing has been conducted on Bronze Age samples from Mongolia, the sample sizes are still relatively small, and no in-depth longitudinal studies on single sites have yet been completed. More research will be needed to confirm many of the currently evolving hypotheses concerning the ancient peoples of Mongolia and their spheres of cultural and biological interactions.

ACKNOWLEDGMENTS

We would first like to thank Dr. William Honeychurch for his contributions to this work. We would also like to thank Dr. Tumen Dashtseveg for allowing me access to the skeletal archives at the National University of Mongolia (export number: 12-2091038-11-E31104R), Dr. Sloan Williams at the University of Illinois at Chicago, the ERC Consolidator Grant ASIAPAST (H2020-EU.1.1/772957, P.I. C. Makarewicz) at the Institute for Prehistory and Protohistory at Kiel University and the Postdoctoral Fellowship from MacMillan Center for International and Area Studies at Yale for their generous support for further research and write up of this article.

Data Availability Statement

The new data that supports the findings of this study are available in the supplementary material of this article and all new slab burial sequences have been uploaded to Genbank (accession no. OM177196-OM177215) (Benson et al., 2013). Any other questions may be submitted to the corresponding author.

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ENDNOTES

- ¹ The prone burial tradition has been referred to as the Ulaanzuukh, Tevsh, Shaped, Figurnaia and Shorgoljiin (ant-like) burial traditions; some of these names are used for the same sites, while others show minor variation (Amartuvshin, 2020).
- ² The haplotype determined through high throughput sequencing by Jeong et al., 2020 and Wang et al., 2020 for sample AT233 differed slightly; however, they both belonged to the more basal G2b2 group, which correlates with the results from this study.

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How to cite this article: Rogers, L. L., & Kaestle, F. A. (2022). Analysis of mitochondrial DNA haplogroup frequencies in the population of the slab burial mortuary culture of Mongolia (ca. 1100–300 BCE). *American Journal of Biological Anthropology*, 177(4), 644–657. <https://doi.org/10.1002/ajpa.24478>