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Potential maternal kinship among humans from the Northern Caucasus "post-dolmen" burials

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ABSTRACT

The Middle Bronze Age was an important period in the history of the Northern Caucasus. The archaeological Shushuk "post-dolmen" phenomenon, characterized by the reuse of dolmen orthostats for the construction of "stone-frame" burial structures, appeared in this region in the 3rd millennium BCE. Using Sanger sequencing, we were able to characterize the mitochondrial diversity of Shushuk individuals, whose remains were excavated from three collective burials. In this study, we provide new data for a better understanding of the genetic diversity of communities of the Northern Caucasus during the Middle Bronze Age and show a degree of potential maternal kinship among individuals from collective burials. Mitochondrial DNA analysis allots the same haplotype to the five individuals, who belong to H1a mitochondrial haplogroup. The results point to the possibility of maternal kinship among individuals from a specific collective burial (Shushuk 75, burial 2) through the maternal line.

1. Introduction

The Northern Caucasus region is defined by the Greater Caucasus mountain range and the surrounding steppe zone to its north. Both are heavily watered by ample rainfall and the multiple rivers flowing through the mountainous outcrops into the vast, steppe zones. Of these, the Kuban River with its ample basin and hinterland is most prominent. The result is dense forest cover in the foothills, effectively shielding archaeological sites from view. Characteristic amongst these are the numerous megalithic, Bronze Age complexes (dolmens) generously peppering the outcrops (Erlikh et al., 2020; Erlikh and Godizov, 2020).

A number of archaeological cultures characterize the Middle Bronze Age of the region, including the earlier Novotitorovskaya culture (named after the site near the *stanitsa* (village) of Novotitorovskaya), the Severokavkazkaya culture (also known as North Caucasus Culture), and the later Baturinskaya Catacomb culture (named after a site near the *stanitsa* (village) of Baturinskaya) (Erlikh et al., 2020; Erlikh and Godizov, 2020; Erlikh, 2018) (Fig. 1).

The Shushuk archaeological site is located in the northern Caucasus outcrops at an elevation of 830–870 m above sea level, near the village of Pobeda in the Maykop District of the Republic of Adygea (Russia). Archaeological survey and fieldwork at the site was initiated in 2015 as part of an industrial mining initiative in this particularly gypsum-rich region of the Caucasus. The site itself is located some 1.5 km away from the Shushuk dolmen cemetery of the Late Bronze Age excavated by Alexey D. Rezepkin from 2009 to 2011 (Rezepkin, 2019), with a genetic analysis (mtDNA haplogroup diversity) following in 2017 by Sharko et al (2017). The site was studied by the team of the Russian State Museum of Oriental Art (Moscow, Maykop) in consecutive seasons until 2019. During the first seasons, it was possible to identify a previously unknown

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type of burial structure, which we have designated as a "stone-frame" grave. Such structures consisted of reused stone slabs from dismantled dolmens (Erlikh, 2018).

Subsequent seasons revealed this "post-dolmen" tradition to have begun as early as the Middle Bronze Age. The majority of structures of this period comprise collective burials in "stone-frame" graves constructed of reused dolmen slabs and large stones and under a small mantle of broken stones (one of the burial structures (Shushuk-75, burial 2) may in fact be an actual dolmen). We also find non-structural burials in shallow pits (Shushuk-75, burial 1), as well as individual burials in the gypsum rills (Shushuk 57). Elevated areas – outcrops of gypsum bedrock – were selected for the burial structures. The inhumations in collective graves contained up to ten secondary burials. In all burials, the preservation of the bones was poor.

Currently, a total of 27 burial and ritual structures – some containing more than one burial – have been studied in detail by the archaeological team. Radiocarbon data was obtained from animal and human bones, together with a few rare charcoal samples, allowing us to propose a tentative chronology for the site, distinguishing three periods:

- Shushuk I – the Middle Bronze Age (3rd millennium BCE);
- Shushuk II – i.e. the Late Bronze Age 1 (first half of the 2nd millennium BCE);
- Shushuk III – i.e. the end of the Bronze Age (2nd half of the 2nd millennium BCE) (Erlikh and Godizov, 2020).

In this study, we focused on the analyses of ancient DNA of human individuals from three specific burials of the early period of the site – the Middle Bronze Age Shushuk I period of the 3rd millennium BCE – each selected for the amount and quality of archaeological and anthropological material they contained.

2. Material and methods

2.1. Samples

The anthropological material used in the study was obtained during archaeological excavations of the Shushuk archaeological site. Twelve human tooth samples from 11 individuals were taken for analysis from the three Shushuk collective burials – Shushuk 75 (burial 2), Shushuk 42 (burial 1), and Shushuk 49 (burial 1) – as well as from one of the individual burials in the gypsum rills, Shushuk 57. The distance between the objects is considerable: Shushuk 42 (burial 1) is located 284 m northwest of Shushuk 75, Shushuk 49 (burial 1) 238 m west and Shushuk 57 153 m southwest of the same. Detailed information about the specimens studied and their origins is presented in Table 1.

2.2. Genetic analysis

Mitochondrial DNA (mtDNA) haplogroup identification is one of the common methods used in ancient DNA (aDNA) studies, which have seen a surge in recent years to investigate questions of origin, ancestry and migration of the various population groups inhabiting the Caucasus in ancient times (Sharko et al., 2017; Boulygina et al., 2020; Nedoluzhko et al., 2014; Sokolov et al., 2016). In this study, we have used mtDNA testing to analyze the maternal lineages of the Shushuk tooth samples in order gain better understanding of the genetic connections of the deceased from the three Shushuk burials.

The ancient DNA extraction was carried out in the aDNA facilities of the 'National Research Center "Kurchatov Institute" (Moscow, Russia) under strict conditions in order to avoid contamination through modern DNA. Laboratory researchers wore specific protective clothing and gear required for sterile spaces. All work surfaces and instruments were decontaminated with the DNA AWAY Surface Decontaminant (Thermo Fisher Scientific, USA) and UV light. Multiple negative controls were used during the DNA extraction and mitochondrial hypervariable region (HVR) amplification. The negative controls did not contain DNA after

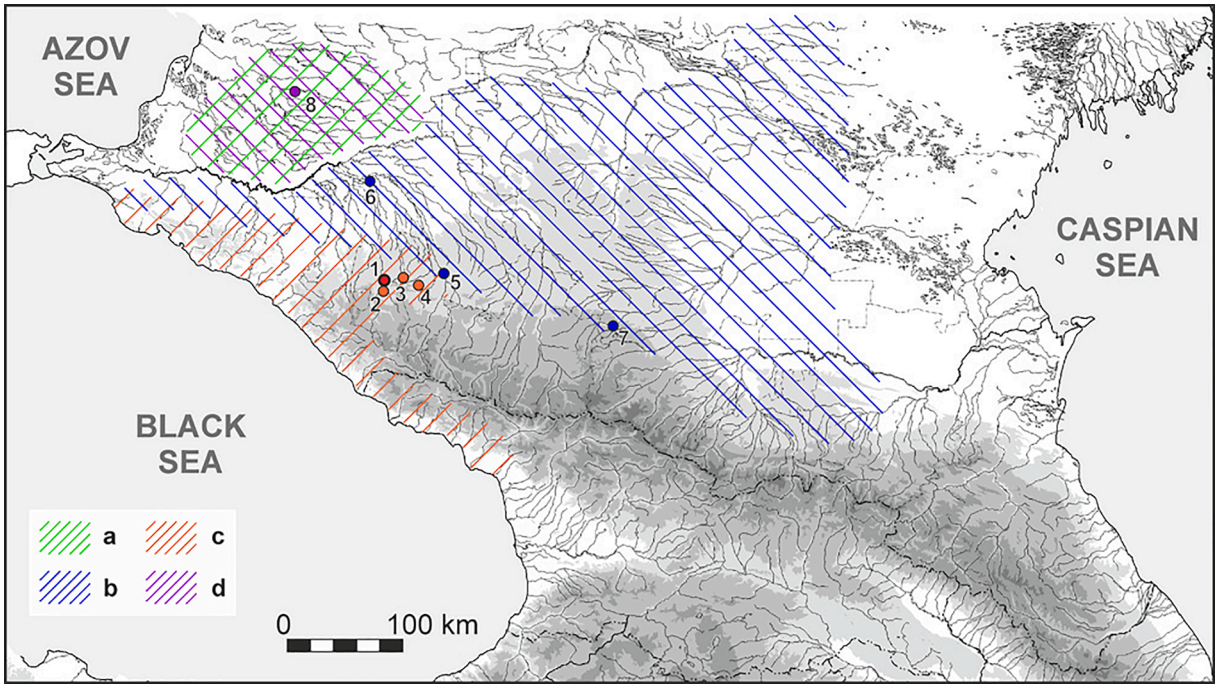

Fig. 1. The North Caucasus during the Middle Bronze Age. Archaeological cultures: a – Novotitorovskaya culture (first quarter of the 3rd millennium BCE); b – North Caucasus culture (first half of the 3rd millennium BCE); c – Dolmen culture (1st – 3rd quarters of the 3rd millennium BCE); d – Baturinskaya culture (3rd quarter of the 3rd millennium BCE); Archaeological sites: 1 – Shushuk; 2 – Deguakskaya Polyana and Deguako-Dakhovskoye settlement; 3 – Starchiki settlement; 4 – Kizinka; 5 – Ippodromny; 6 – Ulyap; 7 – Nezhinsky II; 8 – Baturinskaya.

Table 1
Anthropological material from the Shushuk archaeological site and mitochondrial haplogroups for ancient individuals studied.

Individual ID	Source	Sample number	Mitochondrial haplogroup
#1	Shushuk 75, burial 2, tooth from the jaw of skull no. 1. Sample belongs to same individual as Sh05.	Sh01	H1a
#1	Shushuk 75, burial 2, 2 teeth from the jaw of skull no. 1. Sample belongs to same individual as Sh01.	Sh05	H1a
#2	Shushuk 75, burial 2, tooth from the jaw of skull no. 2	Sh04	H1a
#3	Shushuk 75, burial 2, tooth from the vicinity of skull no. 3	Sh02	H1a
#4	Shushuk 75, burial 2, tooth from unidentified skull	Sh03	H1a
#5	Shushuk 75, burial 2, tooth from unidentified skull.	Sh06	H1a
#6	Shushuk 42, burial 1, layer 2, skull and teeth no. 9.	Sh07	H2a2a1
#7	Shushuk 42, burial 1, layer 2, skull and teeth no. 10.	Sh08	HV21
#8	Shushuk 42, burial 1, layer 2, skull and teeth no. 14.	Sh09	H5
#9	Shushuk 49, burial 1, layer 4, teeth near skull no. 3.	Sh10	could not be determined
#10	Shushuk 49, burial 1, layer 4, tooth near skull no. 4.	Sh11	could not be determined
#11	Shushuk 49, burial 1, layer 4, tooth near skull no. 6.	Sh12	H1aj1

the DNA extraction. Finally, the DNA of all researchers involved in the mtDNA haplogroup identification at the aDNA facilities was taken to analyze contamination from researchers to DNA extracts. The results showed that the mtDNA haplogroups identified for the Shushuk individuals clearly did not match those of the researchers.

The DNA was extracted from the tooth samples in accordance with standard established methodology (Orlando et al., 2011) with some modifications, including twice reaction volume reduction during proteinase K digestion and silica bead ethanol washes. It was possible to extract ancient DNA from ten of the samples (Table 1).

Amplification of mitochondrial hypervariable region (HVR) of the D-loop mitochondrial DNA (mtDNA) was carried out using established primer pairs (Sampietro et al., 2005). PCR fragments (138–210 base pairs in length) covering the HVR region were sequenced using the ABI 3730xl platform (Thermo Fisher Scientific, USA). BioEdit software was used for primary analysis of the DNA sequences, which includes their alignment to the *D-loop* region of the Cambridge Reference Sequence (NC_012920.1, rCRS). The mtDNA profiler tool was used to obtain a list of single nucleotide polymorphisms (SNPs), which was then processed using HaploGrep2 (Weissensteiner et al., 2016) to determine the mitochondrial haplotypes of the individuals interred at the Shushuk site).

Table 2
Haplogroup-specific SNPs (mtDNA) with diagnostic potential. Range (D-loop): 16,099–16,421 bp.

Sample number	Haplogroup-specific mutations
Sh01	16162G
Sh02	16162G; 16279T; 16289T
Sh03	16162G; 16221T; 16233T
Sh04	16162G; 16239T
Sh05	16162G
Sh06	16162G; 16193T; 16304C
Sh07	16255T; 16334C
Sh08	16169T; 16318C
Sh09	16304C; 16375A
Sh12	16192T; 16223T

Haplogroup-specific SNPs (mtDNA) with diagnostic potential are presented in Table 2. All DNA sequences were uploaded to the NCBI database (BioProject ID: PRJNA643377); sample IDs are specified in Table 1.

3. Results

The results obtained revealed mitochondrial haplogroup H in all of the Shushuk individuals. Five of the interred come from burial 2 of Shushuk 75 and belong to a single mitochondrial haplotype H1a, and are thus maternally related. Haplotypes H2a2a1, HV21 and H5 were determined for three of the deceased from the Shushuk 42 stone-frame burial 1. The mitochondrial haplotype H1aj1 was determined for one individual from Shushuk 49 (burial 1) – the only one from which DNA could be successfully extracted.

Similar analyses were carried out on sample material from the neighboring Shushuk dolmen cemetery studied by Sharko and colleagues (Sharko et al., 2017), who identified mitochondrial haplogroups J1b1a1, U5a1b1, M8/N, G1b, R7a'b amongst the ten individuals examined. Mitochondrial haplogroup R7a'b was ascertained for six of the individuals in their study. Haplogroup H, however, was not identified, even though the quantity of mitochondrial DNA extracted from the human remains was equal to that extracted from the sample material discussed here.

4. Discussion

Mitochondrial haplogroup H is one of the most widespread and varied maternal lines in Europe, a greater part of the Near East and the Caucasus. In the central Northern Caucasus, it is found in a series of burials beginning in the Eneolithic/Early Bronze Ages. In the Northwest Caucasus, it is found in a deceased individual from dolmen 13 of the Marchenkova Gora burial (Fig. 2A), which belongs to the Late Bronze Age (cal. 1410-1210 BCE) (Wang et al., 2019). Amongst burial sites contemporary with the Shushuk Middle Bronze Age burials and comparable material culture we find the site of Lysogorskaya 6, a rich burial of the Severokavkazkaya culture in the central Northern Caucasus dating to the second quarter of the 3rd millennium BCE. (cal. 2863-2581 BCE, MAMS-29825) (Fig. 2A) (Wang et al., 2019; Korenevskiy et al., 2018).

H and HV haplogroups are also often observed in other archeological sites of the Northern Caucasus and the adjacent steppe during the Bronze and Iron Ages. Mitochondrial haplogroup H, in particular, has been found in ancient individuals of the Eneolithic steppe and Maykop culture (Wang et al., 2019), while the HV mitochondrial haplogroup has been identified in individuals belonging to the Maykop culture (Wang et al., 2019) as well as the medieval Koban and Alan cultures (Boulygina et al., 2020; Wang et al., 2019). At the same time, H and HV haplogroups were widespread across Europe from the Early Neolithic period on (Allentoft et al., 2015; Brandt et al., 2013; Brotherton et al., 2013). Against this background, it is all the more noteworthy that the study conducted by Sharko and his colleagues in 2017 of the individuals excavated in the nearby Shushuk dolmen cemetery revealed these to contain mitochondrial haplogroups R7 and J1, which are more closely related to the mtDNA ancestry of modern Adygeans (Sharko et al., 2017).

The mtDNA analyses of the Shushuk bone samples indicates possible kinship through the maternal line on the basis of haplogroup H and suggests the Shushuk burials to have been collective family burials. However, unrelated individuals can share identical mtDNA haplotypes. Therefore, all indications of potential kinship presented here are but preliminary and require more detailed and complex analyses involving the SNPs of the nuclear genome (Vai et al., 2020).

In terms of the Northern Caucasus, this study demonstrates the mitochondrial haplogroup H and its continuity amongst the Bronze and Iron Age archaeological cultures in the region (Fig. 2B) (Boulygina et al., 2020; Wang et al., 2019).

The archaeological data suggests the Shushuk burials to be family

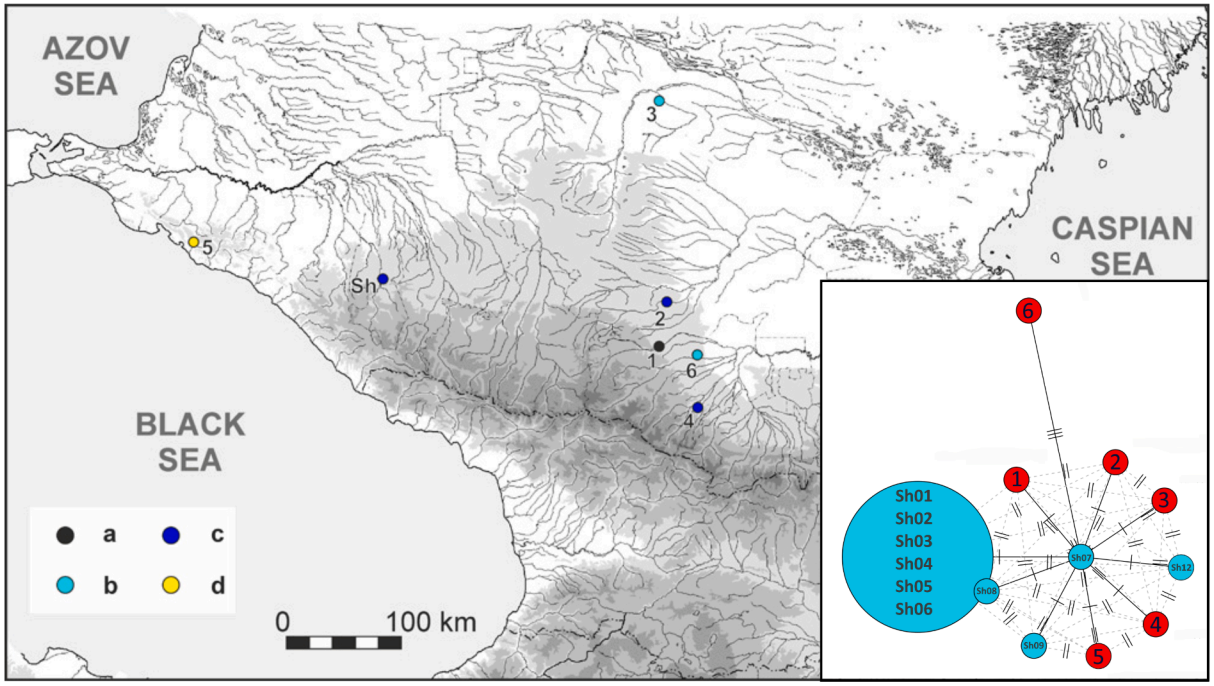

Fig. 2. Mitochondrial H haplogroup continuity amongst the Bronze and Iron Age archaeological cultures. Sites: Sh – Shushuk; 1 – (Pg2004) – Progress 2, kurgan 1, grave 37; 2 – (LYG001) – Lysogorskaya 6, kurgan 3, grave 4; 3 – (Ay2003) – Aygurskiy 2, kurgan 22, grave 9, Steppe Maykop; 4 – (KDC002) – Kudachurt, kurgan 14, grave 50; 5 – (I2051) – Marchenkova Gora, Dolmen 13; 6 – (I1720) – Baksanenok, kurgan 2, grave 5, Maykop culture. (A) Archaeogenetic material: a – Steppe Eneolithic period (5th millennium BCE), b – Early Bronze Age (4th millennium BCE), c – Middle Bronze Age (3rd millennium BCE), d – Late Bronze Age (2nd millennium BCE). (B) The mitochondrial DNA D-loop haplotype network of haplogroup H in the Bronze Age population of the Northern Caucasus. Dashed lines indicate a number of distinguishing substitutions between the subhaplotypes. Sh = Samples from the Shushuk site (see Table 1). Samples from sites in the Northern Caucasus with mtDNA haplotype H (red circles; see Wang et al., 2019 (2019).

tombs (Erlikh et al., 2020; Erlikh and Godizov, 2020; Erlikh, 2018). At the same time, we have no conclusive data on family types, sizes or kinship systems within post-dolmen societies or dolmen cultures. We lack data on the sizes of dwellings (which may indirectly have answered these questions), for while settlements of this period are known, they remain practically uninvestigated. At present, we have identified both individual and collective burials for the early period of the Shushuk complex (Shushuk I), but none belonging to a small nuclear family. With respect to kinship, we can only *suggest* matrilineal kinship, which can only be confirmed through analysis of the nuclear genome of the interred.

5. Conclusion

Our analyses have demonstrated a certain degree of kinship as well as continuity between collective burials of the Shushuk Middle Bronze Age archaeological site. All individuals studied here are related to a single mitochondrial haplogroup H.

At the same time, it should be noted that available data demonstrates the difficulty and non-linearity of ethno-cultural processes that took place in the Northwestern Caucasus foothills during the Middle to Late Bronze Ages. The ancient population that left us the Shushuk archaeological site was already practicing a post-dolmen burial rite in the early 3rd millennium BCE. The new constructions were frame-structures, perhaps emulating the timber frame-structures common to the Severokavkazkaya archaeological culture. The very phenomenon of recycling existing dolmen material, i.e. reusing dolmen slabs and orthostats for new constructions, is significant, suggesting the penetration of outsiders into this region. Archaeological and mitochondrial evidence suggests the outsiders belonged to the Severokavkazkaya peoples from the central Northern Caucasus. Meanwhile, the dolmen burial tradition continued into the Late Bronze Age (1st half of the 2nd millennium BCE) in the neighboring Shushuk dolmen cemetery. However, mitochondrial haplogroups of this megalithic culture differ substantially from those of the collective post-dolmen burials of the Middle Bronze Age at the Shushuk archaeological site, again reaffirming the clear difference between the two cultural groups (Sharko et al., 2017).

We can therefore identify a “post-dolmen” tradition of peoples crossing into the Shushuk area carrying mitochondrial H haplogroup. It is possible that they entered from the east, i.e. from the central part of the Northern Caucasus, and are related to peoples of the Severokavkazkaya culture. The main archaeological definer of this group is the construction of stone-frame structures reusing stone slabs/orthostats from older dolmens. The new stone constructions are reminiscent of the timber frame graves of the Severokavkazkaya culture – another possible indicator of their affiliation with this culture. The tradition of stone-frame constructions continued into the Late Bronze Age with some slight amendments: the new stone-frame structures were constructed of large stones instead of reused dolmen orthostats.

Declaration of competing interest

None.

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