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Mitochondrial DNA Diversity in the Gene Pool of the Neolithic and Early Bronze Age Cisbaikalian Human Population

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Abstract—This paper presents the results of a study of a mitochondrial DNA sample ($N = 15$) from the remains of representatives of the Neolithic and Early Bronze Age (VI–III millennia BC) Cisbaikalian human population. It was found that the mitochondrial gene pool of the ancient population under study contains lineages of East Eurasian haplogroups D, G2a C, Z, and F1b. The results of the comparative analysis of the group under study with ancient and modern Eurasian populations suggest that the development of autochtonous East Eurasian genetic components was the main mechanism of the formation of the population of the Baikal region. Genetic contacts with populations of neighboring regions of Central Asia also contributed to the formation of the gene pool of the Cisbaikalian population.

Keywords: East Siberia, Cisbaikalia, Neolithic Age, Early Bronze Age, human mitochondrial DNA, ancient DNA, paleogenetics, ethnogenetic processes

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INTRODUCTION

Formation of the indigenous population of the Baikal region has been studied for a long time by archaeological methods, physical anthropology, and ethnogenomics. The modern indigenous population of the region is represented by numerous Mongol- and Turkic-speaking groups. The gene pool of mitochondrial DNA (mtDNA) of these populations is characterized by a dominance of components of the Eastern Eurasian origin (Derenko et al., 2003, 2007; Starikovskaya et al., 2005). According to the craniometric data, modern indigenous populations of the region were attributed to different subtypes of the Central Asian and Baikal types of the Mongoloid race (Alekseev, 1974).

The archaeological materials suggest that anatomically modern humans have inhabited the southern regions of Eastern Siberia (including the Cisbaikalian region) since the final Upper Paleolithic period (not less than 20 thousand years ago) (Okladnikov, 1950, 1955; Raghavan et al., 2014). The data of physical anthropology and archaeology demonstrate the Eastern Eurasian origin of major groups of the early population (Alekseev, 1961). At the same time, analysis of the particular Upper Paleolithic archaeological and odontological materials of the Baikal region reveals signs of their West Eurasian origin. In particular, these characteristics were revealed on the materials of the Upper Paleolithic sites near the villages Mal'ta and Buret', which distinguishes them from the other Paleolithic sites of southern East Siberia (Okladnikov, 1941; Gerasimov, 1958; Zubov and Gokhman, 2003; Turner and Scott, 2007). The results of the paleogenetic analysis of single human remains from these sites confirmed the presence of West Eurasian components in their nuclear and mitochondrial genomes (Raghavan et al., 2014).

The earliest serial paleoanthropological material from the territory of the Cisbaikalian region was obtained by archaeologists for the Neolithic and Early Bronze Age (VI–III millennia BC) (Okladnikov, 1950, 1955). It is shown that the Neolithic cultures in the region were formed on the local Paleolithic basis; that is, they are autochthonous to the south of Eastern Siberia. The material culture of the population of this period has no elements of West Eurasian origin. The results of the anthropological study of Neolithic and Early Bronze Age skulls from the territory of the Cisbaikalian region indicate that these population groups are characterized by Eastern Eurasian craniometrical characteristics (Debetz, 1948, 1951; Alekseev, 1961).

The ancient ethno-cultural groups that inhabited the Cisbaikalian region from the Neolithic period to the late Middle Ages have been characterized to date. In particular, a well-founded classification of the archaeological cultures of the region of the Neolithic and Early Bronze Age has been developed and its detailed description has been given. The population of the region in this period was represented by carriers of the Kitoi (Neolithic Age, the end of VI–the middle of

V millennia BC), Serovo (Neolithic Age, the end of V–the middle of IV millennia BC), and Glazkovo (Early Bronze Age, IV–the end of III millennia BC) archaeological cultures.

The presence of the serial paleoanthropological material from representatives of the Neolithic and Early Bronze Age population of the Cisbaikalian region, suitable for research by paleogenetic methods, makes it possible to reconstruct the early stages of ethno-genetic processes in the region based on studies of the gene pool structure of the ancient population.

This work is devoted to the analysis of mtDNA diversity in the gene pool of the Neolithic and Early Bronze Age population of the Cisbaikalian region and the reconstruction of some aspects of the formation of the genetic structure of regional populations.

MATERIALS AND METHODS

As the material for this study we used fragments of the postcranial bones and teeth of 17 representatives of the Neolithic and Early Bronze Age Cisbaikalian population of the following archaeological cultures from several burial grounds: Kitoi (burial Borki-1, one individual), Serovo (Huzhir-Olkhon, six individuals; Ust-Anga, one individual; Manzurok, one individual), and Glazkovo (Obkhoi, five individuals; Khataruk, one individual; Eduganka, one individual; Makarovo, one individual). Paleoanthropological samples were represented by the teeth for ten individuals and by the postcranial skeleton fragments for seven individuals. The study included samples from skeletons of high macroscopic preservation with reliable attribution and cultural identity.

Preprocessing of the paleoanthropological material and DNA extraction was carried out by the methods described previously (Pilipenko et al., 2010; Pilipenko et al., 2011). After the mechanical and chemical decontamination of the paleoanthropological samples, they were grinded to fine powder, which was incubated in a 5M guanidine thiocyanate buffer (pH 8.0) (for the postcranial skeleton fragments) or decalcified in 0.5 M EDTA and incubated in a buffer with proteinase K (for teeth). Extraction of DNA was carried out by the phenol/chloroform method.

Amplification of the mtDNA HVR I fragments was carried out using two PCR variants: (1) amplification of mtDNA HVR I fragment in position 16074–16366 (according to the numeration of the revised Cambridge reference sequence (Andrews et al., 1999)) in the form of one amplicon by the nested PCR method (Pilipenko et al., 2008); (2) amplification of mtDNA HVR I fragment in position 15997–16409 in the form of four overlapping amplicons by the method of single-round PCR (Haak et al., 2005).

For some samples of ancient mtDNA, PCR products were cloned in the bacterial vector using the pGEM-T® Easy Vector System kit (Promega, United States), followed by the sequencing of multiple clones.

The sequencing reaction was carried out using ABI Prism BigDye Terminator Cycle Sequencing Ready Reaction Kit v. 1.1 and v. 3.1 (Applied Biosystems, United States). The results were analyzed on an automated capillary sequencer ABI Prism 3130XL Genetic Analyzer and ABI 3730XL Genetic Analyzer (Applied Biosistems, United States) in the Genomics Core Facility, Siberian Branch, Russian Academy of Sciences (SB RAS) (http://sequest.niboch.nsc.ru, Novosibirsk).

Analysis of the obtained mtDNA sequences was carried out using the program DNA Baser v. 3.5.4.2. (Heracle BioSoft S.R.L., Romania). To determine the structure of mtDNA HVR I haplotypes , sequences of ancient DNA were compared to the revised Cambridge reference sequence of mtDNA (Andrews et al., 1999). MtDNA samples were attributed to haplogroups and haplotypes using the software tool HaploGrep (http://haplogrep.uibk.ac.at/) (Kloss-Brandstatter et al., 2011) based on the modern classification of mtDNA (http://www.phylotree.org/, version 16 dated February 19, 2014) (van Oven and Kayser, 2009).

To carry out phylogeographic analysis, we used the database on the structure of mtDNA HVR I from published sources, which included more than 25 000 samples from modern populations of Eurasia.

Interpopulation differences of the studied ancient population with other ancient and modern populations of Eurasia in terms of the haplogroup pattern in the mtDNA gene pool were estimated by distance Fst (Slatkin, 1994) using the program Arlequin v.3.5.1.2 (Excoffier et al., 2005). The significance level of Fst distances was assessed using the Monte Carlo method, the number of interchanges was 100, and the level of significance of $P = 0.05$. Multidimensional scaling, based on a matrix of pairwise Fst differences, was carried out using the XLStat program (www.addinsoft.com).

All stages of the work with the ancient material prior to DNA amplification were carried out in an isolated rooms specially equipped for working with ancient DNA using clothing for cleanrooms, face masks, eye-glasses, and sterile gloves. All work surfaces in the rooms were regularly treated with 5% sodium hypochlorite solution and irradiated with ultraviolet light. Only sterile reagents and plastic utensils were used for the work. Blanc control tubes (without the addition of the paleo material) passed through the full procedure of extraction and amplification in parallel with the ancient samples to detect possible contamination of the used reagents and equipment. The nucleotide sequence of mtDNA HVR I was determined for all the stuff working with ancient DNA.

RESULTS

After pretreatment of the paleoanthropological material, DNA extraction, and its quality assessment, 15 samples of DNA suitable for the study by molecular and genetic methods were obtained. For them, nucleotide sequences of mtDNA HVR I were determined

Results of genotyping of mtDNA of representatives of the Neolithic and Early Bronze Age (IV–III millennia BC) Cisbaikalian human population

No.	Nucleotide substitutions in mtDNA HVR I*	mtDNA haplogroup	Burial ground	Archaeological culture
1	223-362	D	Khuzhir-Olkhon	Serovo
2	223-362	D	Obkhoi	Glazkovo
3	223-362	D	Borki-1	Kitoi
4	223-362	D	Eduganka	Glazkovo
5	223-260-362	D	Khuzhir-Olkhon	Serovo
6	223-260-362	D	Khuzhir-Olkhon	Serovo
7	223-319-362	D	Makarovo	Glazkovo
8	223-227-278-362	G2a	Manzurok	Serovo
9	223-227-278-362	G2a	Obkhoi	Glazkovo
10	223-227-262-278-362	G2a	Obkhoi	Glazkovo
11	223-298-327	C	Khuzhir-Olkhon	Serovo
12	223-298-327	C	Obkhoi	Glazkovo
13	185-189-223-260-298	Z	Khuzhir-Olkhon	Serovo
14	129-185-223-224-260-298	Z	Khuzhir-Olkhon	Serovo
15	189-232CA-249-304-311	F1b	Ust'-Anga	Serovo

Positions of variable nucleotides (–16000) are presented in accordance with the revised Cambridge reference sequence of human mtDNA (rCRS) (Andrews et al., 1999).

(fragment 15997–16409). By comparing the structure of HVR I in mtDNA samples from the Neolithic and Early Bronze Age Cisbaikalian population with the revised Cambridge reference sequence of mtDNA, specific nucleotide substitutions were identified and mtDNA haplotypes of the investigated individuals were defined (table).

Among the investigated mtDNA samples, nine HVR I haplotypes (mitotypes) were found. The structure of the haplotypes allows to unambiguously attribute the studied lineages to specific mtDNA haplogroups. The studied sample includes five haplogroups belongs to the East Eurasian mtDNA cluster: D, G2a, C, Z (derivatives of macrohaplogroup M), and F1b (derivative of macrohaplogroup R).

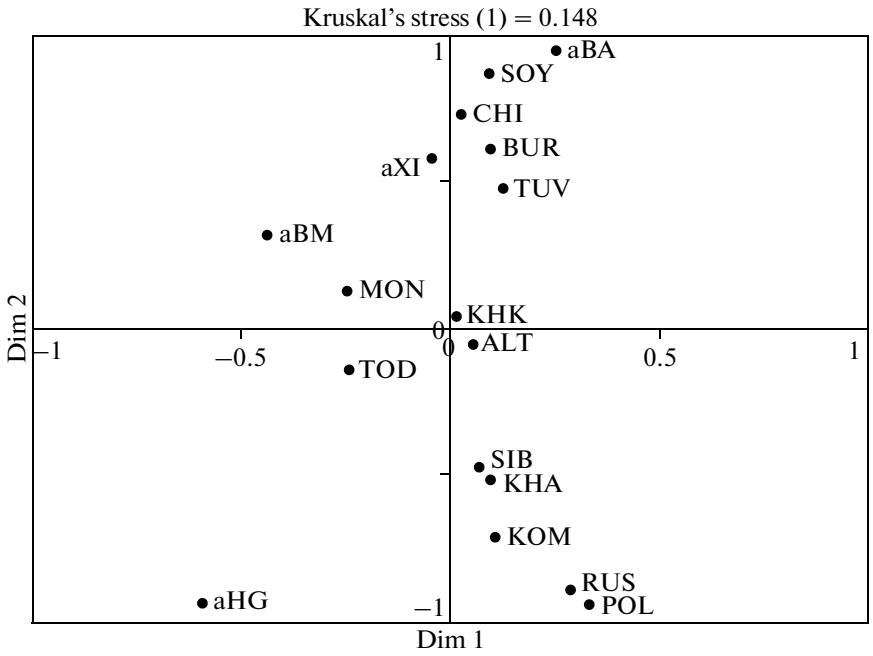
Haplogroup D (seven samples) has the highest frequency in the sample. The investigated series includes both the root variant of haplogroup D (sample nos. 1, 2, 3, and 4) and its derivatives (two haplotypes, sample nos. 5, 6, and 7). Two lineages of each haplogroup G2a (sample nos. 8, 9, and 10) and Z (sample nos. 13 and 14) were also revealed in the series. Each of haplogroups C (sample nos. 11 and 12) and F1b (sample no. 15) is represented by single lineage.

Analysis of the published data showed that the mtDNA gene pool of the modern Cisbaikalian populations is characterized by a high frequency and variety of D and C haplogroups (Derenko et al., 2003, 2007). The greatest variety of the lineages was identified for haplogroup D, which is correlated with our data on the mtDNA gene pool of the ancient population. The modern populations are differed from the studied ancient population of the Cisbaikalian region by the diversified state of haplogroup C.

Haplogroups G2a and F1b (including lineages identical to those that we found in the gene pool of the studied ancient population) are presented with different frequencies in the gene pool of most previously studied ancient and modern populations of the Baikal region and the adjacent territories of Central Asia (Yao et al., 2002; Derenko et al., 2003, 2007; Keyser-Tracqui et al., 2003; Mooder et al., 2006).

Haplogroup Z shows a low frequency and a variety of lineages in the modern populations of the region. Haplotype (129-185-223-224-260-298), which we identified in the ancient series, was found in the gene pool of the mtDNA of Buryats (Derenko et al., 2007). It is interesting that this lineage is present also in the gene pool of the Middle Bronze Age population from the Kola Peninsula (Sarkissian et al., 2013).

Comparison of our data with the results of the study by Mooder et al. (2006), which is also dedicated to the analysis of the mtDNA of the Neolithic Cisbaikalian population, revealed both similarities and differences between the two series of ancient mtDNA samples. Lineages of haplogroups D, C, G2a, and F1b are present in both the series and are identical, apparently, at the level of the haplotype structure. The series studied by Mooder et al. (2006) included West Eurasian components (lineages of haplogroup U5a) and lineages of East Eurasian haplogroup A, which were not found in the our series. The presence of haplogroup Z lineages



Position of the studied Neolithic and Early Bronze Age Cisbaikalian population and some other ancient and modern Eurasian populations on the graph showing the results of multidimensional scaling based on a matrix of population differences Fst (according to the frequencies of mtDNA haplogroups in the population).

Populations: ALT, Altaians (Derenko et al., 2003); BUR, Buryats (Derenko et al., 2007); aHG, Paleolithic and Mesolithic hunter-gatherers of Central and Eastern Europe (Bramanti et al., 2009); aBM, Neolithic population of the Cisbaikalian region (Mooder et al., 2006); aBA, Neolithic and Early Bronze Age Cisbaikalian population (this study); aXI, Xiongnu population (the beginning of the I millennium AD) of Northern Mongolia (Keyser-Tracqui et al., 2003); CHI, Chinese (Yao et al, 2002); KOM, Komi (Gubina et al., 2005); MON, Mongols (Derenko et al., 2004); POL, Poles (Malyarchuk et al., 2002); RUS, Russians (Malyarchuk et al., 2002); SOY, Soyots (Derenko et al., 2003); SIB, Siberian Tatars (Naumov et al., 2008); TOD, Todjins (Derenko et al., 2003); TUV, Tuvinians (Derenko et al., 2003); KHK, Khakasses (Derenko et al., 2003); KHA, Khanty (Gubina et al., 2005).

rather was found only in our series of the ancient Cisbaikalian population.

The results of the comparative analysis of the studied ancient population group with ancient and modern Eurasian populations with respect to the composition and frequencies of mtDNA haplogroups is shown in the figure. The studied Cisbaikalian population of the Neolithic and Early Bronze Age merged into one cluster with groups of the modern population of the Baikal region and the adjacent areas of South Siberia and Central Asia, as well as with the Xiongnu population (the beginning of I millennium AD) from Northern Mongolia (Keyser-Tracqui et al., 2003). The relative remoteness of the series of the Neolithic Cisbaikalian population (studied in the work by K.P. Mooder et al. (2006)) on the graph from other populations of the region is apparently due to the presence of the considerable West Eurasian component in it, which is not typical for most of the other ancient and modern populations from the south of Eastern Siberia.

DISCUSSION

During this study, in addition to strict following with generally accepted rules and conditions of the experiment with ancient DNA, we received direct and indirect evidence of the reliability of the experimental data: results of the DNA analysis from several independent extracts and the results of repeated PCR from each extract are identical; the obtained results demonstrate the absence in the investigated ancient series of mtDNA lineages that would be identical to the mtDNA of researchers (paleoanthropologists and paleogenetics) who contacted the paleoanthropological materials before or during their paleogenetic research or had access to clean rooms during the experiment; cloning of PCR products in the bacterial vector and sequencing of several clones for part of the mtDNA samples allowed to reveal degeneracy, characteristic for ancient DNA, which is a result of the deamination of cytosine; for the studied ancient samples, we found an inverse relationship between the size of the amplified DNA fragment and PCR efficiency, characteristic for ancient DNA; the presence of a majority of the identified mtDNA variants in the gene pool of the ancient population of the Cisbaikalian region seems logical in light of the available data on the phylogeography of the corresponding clusters of mtDNA, which were obtained in the study of the modern Eurasian population. These factors suggest that the paleogenetic data that we obtained are reliable.

The Cisbaikalian region is a zone of domination of the Eastern Eurasian influence on both the material culture of the ancient population and the genetic composition of the indigenous populations (Okladnikov, 1950, 1955; Alekseev, 1961; Derenko et al., 2003, 2007). The fact that the studied series lacks the West Eurasian component allows us to conclude that the distribution of populations with a mixed structure of the mtDNA gene pool, which within Northern Eurasia covers Western Siberia and its neighboring regions (Molodin et al., 2012; Sarkissian et al., 2013), did not extend as far east as the Cisbaikalian region. Apparently, its eastern border in the late Neolithic and Early Bronze Age was located between the rivers Ob and Yenisei. By a mixed structure of the mtDNA gene pool, we mean the presence of a well-expressed (not sporadic) West Eurasian component, along with the Eastern Eurasian one, and that mixing the genetic lines of western and eastern origin was one of the main mechanisms for the formation of the population. Obviously, the main contribution in the composition of the population of the Cisbaikalian region was made by the East Eurasian populations. However, the available paleogenetic data do not allow to deny completely the presence of sporadic West Eurasian components in the gene pool of the ancient population of the region. In particular, Mooder et al. (2006) has shown that in addition to the dominant East Eurasian mtDNA lines, the gene pool of the Neolithic Cisbaikalian population included few lineages of haplogroup U5a. Their absence in our sample suggests that the West Eurasian component was not widely distributed in the population of the region and was sporadic. In our opinion, its origin may be due to the penetration into the region of hunter-gatherers from the western regions of Northern Eurasia, whose gene pool was enriched by variants of haplogroup U. Detection of variants of haplogroup U in two representatives of the Upper Paleolithic population of the Cisbaikalian region (Raghavan et al., 2014) suggests that its presence in the gene pool of the population of the region could be a remote consequence of the ancient settlements of northwestern Eurasia by anatomically modern humans in the Paleolithic period. This relic characteristic in the gene pool of the Cisbaikalian population is apparently expressed very poorly in the Neolithic Age, due to the domination of the Eastern influence in the formation of populations in the Holocene. It is obvious that the process of rare sporadic penetration of the population from western regions of Eurasia into Eastern Siberia was not a key mechanism in the formation of the population of the region. In addition, variants of haplogroup U, which were found in the mtDNA gene pool of representatives of the Upper Paleolithic population of Eastern Siberia (Raghavan et al., 2014) and the population of the Neolithic Age (Mooder et al., 2006), may have an independent origin as a result of multitemporal genetic contacts with populations of Western Eurasia.

We note the wide variety of the Eastern Eurasian cluster at the level of haplogroups in the studied ancient series. Phylogeographic analysis of the identified mtDNA lineages using the data on modern Eurasian populations shows that they are most characteristic for the gene pool of the population of southern East Siberia (including the Cisbaikalian region) and the neighboring regions of Central Asia (Mongolia and northern China) (Kolman et al., 1996; Comas et al., 1998; Derenko et al., 2003, 2007; Metspalu et al., 2004). Thus, the mtDNA genetic pool structure of the Baikal region was formed on an autochthonous basis during interaction with genetically related populations of neighboring regions of Central Asia.

The assumption that the composition of the population was formed on the autochthonous basis is consistent with localization in Central Asia (including the south of East Siberia) of secondary centers of diversification of some East Eurasian mtDNA haplogroups (Derenko et al., 2010). In particular, diversification of haplogroup D could have been occurring in the south of Siberia and the adjacent regions of Central Asia. This is confirmed by the high frequency and variety of its lineages in the mtDNA pool of modern ethnic groups of the Baikal region. Our data on the diversified state of haplogroup D in the gene pool of the Cisbaikalian population during the Late Neolithic and Early Bronze Age are also consistent with this hypothesis.

Compared to modern populations of the region, a low variety of haplogroup C, which we revealed for the Neolithic and Early Bronze Age Cisbaikalian population (as in Mooder et al. (2006)), is apparently due to the location of the diversification centers of this haplogroup outside the Baikal region.

Analysis of the available paleogenetic data shows that variants of haplogroup Z in the Neolithic and Bronze Ages were characterized by wider distribution in Northern Eurasia compared to modern populations (Molodin et al., 2012). The presence of the identical lineage of haplogroup Z (with haplotype 129-185-223-224-260-298) in the studied gene pool of the Cisbaikalian population and in the series of the mtDNA samples of the Middle Bronze Age population from the Kola Peninsula (Sarkissian et al., 2013) is especially interesting. This confirms the presence of the eastern vector of the genetic relationships of the ancient population of the North East Europe.

Thus, the composition of the investigated series of mtDNA samples from representatives of the Neolithic and Early Bronze Age Cisbaikalian population suggests that the basis of the gene pool of the Cisbaikalian population was formed by autochthonous genetic components belonged to the East Eurasian cluster of mtDNA haplogroups. An important role in shaping the mtDNA gene pool structure of the Cisbaikalian population apparently was played also by genetic components from the neighboring regions of Central Asia. Their penetration to the south of Eastern Siberia could be particularly intense after the appearance in the

Central Asian region of large associations of nomadic tribes at the turn of our era and in subsequent periods (starting with the Xiongnu Empire). This resulted in the increased mobility of the genetic material in the Central Asian region and further diversification of the mtDNA gene pool of local population groups, including the emergence of new haplogroups and increased diversity of mtDNA haplogroups previously present in the gene pool of populations (such as haplogroup C). However, many features of the mtDNA gene pool structure of the population from the south of Eastern Siberia, which were already formed by the time of the Neolithic and Early Bronze Age, are preserved in the populations of the region until the emergence of modern indigenous ethnic groups.

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