doi:10.17746/1563-0110.2022.50.4.137-144

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Planigraphic (Spatial) Distribution of Mitochondrial DNA Variants at the Andronovo Time Cemetery Tartas-1: Preliminary Results

The most informative funerary site documenting the Andronovo (Fedorovo) migration to the West Siberian forest-steppe is Tartas-1, where more than 600 burials of that period, associated with Late Krotovo (Cherno-Ozerye) and Andronovo (Fedorovo) cultures, have been excavated to date. On the basis of skeletal remains from these burials, we have formed and successfully analyzed 256 samples of mitochondrial DNA, uniformly covering the entire area of the cemetery. This approach is a genetic counterpart of the continuous area method, which is used to excavate Tartas-1. The article opens a series of publications addressing the analysis and interpretation of this sample. We present the findings of the first stage in the analysis of spatial distribution of mtDNA lineages over the cemetery area under a simplified model that disregards the archaeological differentiation of the Andronovo time burials other than their spatial distribution. The analysis was performed at several resolution levels: from crude (at the level of the West Eurasian and East Eurasian clusters of mtDNA haplogroups) to high-resolution (at the level of specific structural variants). The information potential of each of those levels is evaluated. Data on the pattern of individual mtDNA lineage distribution are analyzed with regard to clusters on the cemetery area, indicating a considerable role of kinship across the site. The most promising areas for revealing groups of close relatives are identified. The findings enable us to minimize the effect of close kinship on assessing the population structure of Tartas-1.

Keywords: *Paleogenetics, mitochondrial DNA, spatial (planigraphic) analysis, Bronze Age, Andronovo time.*

Archaeology, Ethnology & Anthropology of Eurasia 50/4 (2022) 137–144 E-mail: Eurasia@archaeology.nsc.ru

Introduction

Large burial sites containing hundreds of funerary complexes of one or several historic periods are the bases for comprehensive study of the ancient population of the forest-steppe zone of Western Siberia. The abundant archaeological and skeletal collections excavated at such sites can be used for complex interdisciplinary research. The Sopka-2 cemetery in the Baraba forest-steppe is one of the basic sites of this type where most of the funerary complexes are dated to various periods of the Bronze Age, mainly pre-Andronovo. The results of excavations at this site were employed by V.I. Molodin for substantial enhancing and clarifying his classification and periodization of the ethnic and cultural groups of the Neolithic and Bronze Age in the West Siberian forest-steppe (Molodin, 2010). Another multilayered site, "key" for this region, is the flat-grave burial ground of Tartas-1, located at the above-floodplain terrace on the right bank of the river of the same name, close to Sopka-2 (Vengerovsky District, Novosibirsk Region). During the 2003–2022 field seasons, the main part of the site, containing more than 800 burials of various times, has been excavated by the West Siberian team of the IAET SB RAS, led by Molodin (see, e.g., (Molodin, Durakov, Kobeleva, 2018; Molodin et al., 2020)). Most of the complexes studied at Tartas-1 are dated to the period of the Andronovo (Fedorovo) people migration to the Western Siberia in the first half of the 2nd millennium BC, including the Late Krotovo (Cherno-Ozerye) and Andronovo (Fedorovo) burials. An important feature of the necropolis is the presence of numerous syncretic burials displaying combinations of traits typical of the funerary traditions of the Andronovo migrants with those of the aboriginal (Late Krotovo or Cherno-Ozerye) population. Thus, at present, Tartas-1 is the basic site for the reconstruction of the ethnic and cultural processes accompanying the Andronovo (Fedorovo) migration to the Baraba forest-steppe. The excavations at Tartas-1, as well as at Sopka-2 earlier, were carried out using the continuous area method, which provides the most complete representation of a burial site. In addition to the overall high representativeness of the obtained materials, this approach makes it possible to comprehensively account for the spatial distribution pattern of the site when analyzing not only the objects of material culture but skeletal samples as well.

The first stage of the paleogenetic study of the samples from Tartas-1 was carried out in 2006–2011 and included an analysis of a diachronic sample from the Bronze Age Baraba consisting of approximately 30 mtDNA specimens (of both the Andronovo and Late Krotovo cultures) (Molodin et al., 2013: 27–35, 178–181; Molodin et al., 2012). Recently, the research was resumed at a new level: besides the widening of spectrum of the studied genetic markers (Y-chromosome, markers of sex and kinship of skeletal individuals), there emerged a possibility of analyzing the mtDNA variation across the whole space of the site. Together with the other research areas, sampling mtDNA specimens from the whole burial ground (a kind of a "paleogenetic continuous area method") provides the great potential of a comprehensive study of the genetic structure of the populations that were using the necropolis. This is achieved through exploring and interpreting the paleogenetic data with respect to the internal spatial distribution of the complexes, sophisticated features of the material culture and funerary rites, craniometric data, kinship, and other factors.

The present study begins a series of publications outlining the findings of the paleogentic studies of the Andronovo specimens from Tartas-1. At the moment, the sample includes 256 mtDNA specimens from Late Krotovo (Cherno-Ozerye) and Andronovo (Fedorovo) burials. The aim of this study is the spatial analysis of the distribution of mtDNA variants across the main part of the site in the frame of a simplified model not accounting for the details of the archaeological context.

Material and methods

All the studied specimens were obtained from the archaeological skeletal collection of the IAET SB RAS (Novosibirsk). The sampling was carried out by a paleogeneticist from the IC&G SB RAS (A.S. Pilipenko) together with archaeologists

and anthropologists from the IAET SB RAS (headed by V.I. Molodin). The specimens were extracted from postcranial bones and teeth of 310 individuals from the Andronovo cemetery Tartas-1. Only macroscopically well-preserved skeletal material of each of the skeletons was sampled. For preliminary processing and extracting samples of the total DNA, the methods detailed in previous works of the authors (Pilipenko et al., 2018) were employed.

The analysis of the mtDNA structure included the determination of the sequence of the first hypervariable segment of the control region of mtDNA (HVR I). Amplification of the mtDNA HVR I was performed using two different protocols: 1) four short overlapping fragments, using one-cycle PCR (Haak et al., 2005); and 2) one long fragment, using two-cycle nested PCR (Pilipenko et al., 2008).

Sequencing was carried out using ABI Prism BigDye Terminator Cycle Sequencing Ready Reaction Kit (Applied Biosystems, USA; v.1.1 – for the short fragments, v.3.1 – for the long fragment). Sequencing extracts were then analyzed on an automatic capillary ABI Prism 3130XL Genetic Analyser (Applied Biosistems, USA) at the Center for Collective Use "Genomika" of SB RAS (http://sequest.niboch.nsc.ru).

All procedures with the skeletal specimens were carried out in a specially-equipped paleogenetic lab of the inter-institutional sector of molecular paleogenetics of the IC&G SB RAS. The infrastructure and equipment used meet all the modern requirements for paleogenetic laboratories. The description of the anti-contamination measures and verification of the results can be found in our previous publication (Pilipenko et al., 2018). The conditions of the research, study protocols, and the obtained findings unequivocally confirm the high reliability of our paleogenetic data.

Results and discussion

Forming the model sample of mtDNA specimens. The informative value of large necropolises for reconstructing population history of ancient groups via a multidisciplinary approach is without doubt. But studying large amounts of data, including vast skeletal collections, is associated with numerous difficulties. For a paleogenomic study, such difficulties are the high costs and laboriousness of an analysis of a large sample of DNA specimens necessary to get a representative overview of the features of genetic structure of the population buried at a cemetery and/or its parts. Therefore, in most cases, only a limited sample of specimens selected on the basis of a "vivid" archaeological context (and the degree of preservation sufficient for a genetic analysis) is studied. The authors were following this approach at the earlier stage of studying the Andronovo specimens from Tartas-1 included in the diachronic mtDNA sample of the Bronze Age population of the Baraba forest-steppe (Molodin et al., 2013: 27–35, 178–181; Molodin et al., 2012). The new stage implies the formation of a large sample of DNA specimens covering all the parts of the burial ground. We consider this sample as the model that will show if studying large or limited samples from vast cemeteries is efficient for various research purposes. Thus, the formation of the model sample from Tartas-1 is a necessary step for carrying out a number of studies aimed at the analysis and interpretation of the paleogenetic data in different contexts in the near future.

The following requirements were respected when forming the sample: 1) materials from funerary complexes of the Late Krotovo (Cherno-Ozerye) and Andronovo (Fedorovo) cultures (according to the cultural attribution made by Molodin so far for all the burials studied between 2003 and 2022) were employed; 2) specimens of a fairly good degree of macroscopic preservation (i.e. where a descent preservation of ancient DNA might be expected) were selected; 3) in order to fully cover the area of the necropolis, specimens from all the parts of the burial ground, as well as from all of the spatially observed groups of the Andronovo burials (rows, etc.), were selected; 4) the number of selected specimens was related to the spatial concentration of funerary complexes (inhumations); burials with cremated remains were disregarded, because bones from such burials are in most cases unsuitable for a molecular genetic analysis; 5) both adult and sub-adult individuals were sampled; no preference was given to male versus female remains (the selection criteria

followed the general sexual composition of the skeletal sample); 6) for double and collective burials, specimens from all the individuals were collected when possible.

More than one third of the 600 Late Krotovo (Cherno-Ozerye) and Andronovo (Fedorovo) burials from Tartas-1 was unsuitable for sampling for the following reasons: cremation (more than 100 burials), absence of human remains, or their very poor preservation (typically in sub-adult or supposedly secondary burials). Form the rest of the burials, a sample of more than 300 specimens was acquired. From these, DNA was extracted, its preservation was evaluated, and an analysis of the mtDNA structure was performed, resulting in 256 individuals with reliable data on the structure of mtDNA. Thus, more than 80 % of the specimens included in the sample were suitable for the analysis, which once again confirms the high degree of DNA preservation in the Andronovo skeletal specimens at Tartas-1 (though, the degree of preservation was varying across different spatial parts of the cemetery). For all of the sampled specimens, the haplotypes of the mtDNA HVR I were determined, and the phylogenetic affinity of each of the variants was identified. Thus, a highly representative sample of mtDNA specimens was obtained for the large burial ground of Tartas-1 (more precisely, for its main part dating to the Andronovo time). To our knowledge, this is one of the largest samples from contemporaneous complexes of a single necropolis published to date. The availability of such a representative sample provides great opportunities of studying it via the methods of phylogenetics, phylogeoraphy, and with statistical tools of population genetics. This research can be carried out at both intra- and interpopulation levels, with account for the archaeological and anthropological contexts of the studied materials.

Spatial distribution of mtDNA variants across the burial ground. At present, we do not take into account the data on the detailed cultural attribution of the funerary complexes (only their association with the period of the Andronovo migration to the south of Siberia) or various nuances of the funerary rites detected by archaeologists (this is the aim of the prospective studies). Thus, the space of the burial ground is conventionally considered as culturally (archaeologically) homogeneous.

Specimens from all of the main spatial groups of the necropolis were included in the sample. Notably, the specimens from the southern part of the cemetery substantially outnumber those from the northern part, which is explained by the decrease in the density of the burials from the south to the north of the necropolis. Another reason is a higher proportion of cremated burials in the northern part (where the cremations are prevalent in some areas) as compared to the southern part (where the percentage of cremations is negligible). So, if the number of successfully studied mtDNA is adjusted for the number (density) of the burials containing human remains suitable for the analysis, then the samples for the northern and southern parts of the necropolis are equally representative.

Though a full-scale analysis of the phylogenetic and phylogeoraphic features of the described mtDNA variants was not among the aims of the present stage of the study (these will the subject of another publication), we evaluated the informative potential of the spatial analysis of phylogenetic components of different levels. The following categories were employed: the groups of variants of the West and East Eurasian clusters of mtDNA haplogroups; single haplogroups and particular structural mtDNA variants (determined from the structure of the HVR I haplotype).

Our model sample exhibits similar representation of variants of both West and East Eurasian mtDNA clusters. Such a mixed composition is typical of other populations of the Baraba forest-steppe of the preceding and subsequent chronological periods as well. Notably, at the present stage of the study, we do not consider the composition and proportion of particular haplogroups in samples, which is expected to provide much more information. The spatial distribution of the West and East Eurasian mtDNA variants shows that both are widely represented in all the main parts of the burial ground, i.e. if it is crudely divided into northern and southern areas. Such a result was expectable based on the admixed structure of the mtDNA pool in the region and our earlier hypothesis (Molodin et al., 2012; Molodin et al., 2013: 27–35, 178–

181) stating that the genetic composition of the population inhabiting the site had been formed in the process of active interaction between the autochthonous groups and Andronovo migrants. But such a coarse approach cannot reveal the mechanisms and patterns of the formation of the burial ground. It is of note, however, that at the level of small spatial groups (i.e. rows or other separated aggregations of burials), a substantial variation in the proportion between the West and East Eurasian mtDNA variants is observed: in some groups either West or East variants are prevalent, while in other groups the proportion is equal. This is the first evidence supporting the idea of the difference between the mtDNA genetic composition between various spatial groups.

The next level of the study is the analysis of spatial distribution of mtDNA haplogroups (not considering their structural variants). Such an analysis must be based on the spatial distribution of the haplogroups represented in the sample by numerous specimens and at least several structural variants. Otherwise, the low number of specimens can produce a stochastic pattern of spatial distribution (the "small sample effect"), while the analysis of the haplogroups represented by only one structural variant is equivalent to a spatial analysis of this particular haplotype (see below). Such prevalent haplogroups in the sample are the East Eurasian C and the West Eurasian U2e and U5a. Each of these haplogroups is among the main components of the total sample, and is represented by dozens of specimens and by several structural variants. Notably, some of the haplogroups are unevenly distributed across the burial ground: the variants of the East Eurasian haplogroup C (in total) are more prevalent in the southern and central parts of the area, as well as in its eastern outskirt, as compared to the western part. Most of the individuals carrying haplogroup U5a (in total) are concentrated in the central part of the cemetery. The interpretation of these patterns of spatial distribution from the point of view of the formation of different areas of the burial ground will require the detailed consideration of the archaeological context of the burials from those areas, as well as the information regarding presence or absence of the respective haplogroups in the gene pools of the pre-Andronovo population and Andronovo migrants. Such an analysis is the aim of the next stages of research. So far, it is evident that the main (i.e. the most prevalent) haplogroups of the gene pool of the Tartas-1 population are unequally represented in different parts of the necropolis.

The next level of the analysis is the estimation of the spatial distribution of the individuals carrying identical (in terms of the HVR I sequence) mtDNA variants, which is also informative only for the variants detected in more than one specimen. Only 20 out of 256 individuals from Tartas-1 were carrying mtDNA haplotypes unique for our model. An analysis of such haplotypes is also of some value. Their concentration in a particular discrete part of the burial ground can suggest that this spatial group had been formed by multiple various population groups during a short period of time and without long-term interaction between them. Under this scenario, the individuals were buried close to each other accidentally, not due to kin relationship between them. However, the spatial analysis of the 20 unique mtDNA sequences has shown their relatively even distribution across the area of the necropolis; thus, this analysis was of low informative value for the aims of the present study.

The bulk of the sample (more than 90 %) includes series of specimens with identical mtDNA haplotypes, each represented by 2–3 to 20 skeletal individuals. Under our simplified model (not accounting for fine aspects of archaeological context), a spatial analysis of distribution of mtDNA variants (haplotypes) across the burial ground is expected to be the most informative approach. This analysis includes the following steps: 1) mapping the burials with a particular mtDNA variant; 2) detecting accumulations of individuals carrying a particular mtDNA variant; by accumulation we mean the presence of identical mtDNA variants in three or more individuals (two for rarer variants) forming spatial groups relatively isolated from other similar groups (e.g. rows of burials clearly present in many parts of the Tartas-1 cemetery); 3) analysis of the position of the accumulations (for each variant) with respect to each other, combining small accumulations according to their spatial

distribution; 4) comparing the spatial patterns for different mtDNA haplotypes for detecting cases of overlapping accumulations.

The potential informative value of such an analysis is that the presence of identical mtDNA variants in individuals buried in one collective or in neighboring graves is indicative of their maternal kinship. Thus, the concentration of a particular mtDNA variant in a spatially restricted group of burials suggests a possible (but not necessary) role of kinship in the emergence of the group (burial of potential relatives). If accumulations of two or more mtDNA variants overlap in a particular area of a burial ground, a family cluster might be potentially detected. The relatives of such a cluster can be connected through both maternal and paternal lineages, and the presence of several sub-clusters of various maternal origins is possible as well. The overlap of the accumulations can also lead to extending the area of a cluster of genetically related individuals. Thus, the analysis provides an opportunity of detecting spatial clusters of burials most perspective in terms of further molecular genetic research, for the assessment of the degree of kinship and evidential determination of groups of relatives. Such a laboratory analysis is both costly and time-consuming, and will only be carried out for the most informative specimens.

It is well known that the representativeness of a sample for a population genetic study can be biased if it comprises closely related individuals. This is another application of the analytical approach described above. The influence of kinship on compiling a population sample can be avoided if, first, representatives of various groups of potential relatives are proportionately included in the sample and, second, evidently unrelated individuals from different parts of the burial ground are sampled.

An important aspect of an analysis of this type is accounting for the prevalence of the mtDNA of interest in both the studied sample and region as a whole: the rarer is a variant the higher is the probability that the presence of this variant in different individuals reflects their maternal kinship. Thus, the criteria for delimiting accumulations were more liberal for rarer variants: more distant (scattered) burials were considered as possibly related. Exactly such rare mtDNA variants should be first taken into account when searching for kin groups of burials.

Considering the above, we have carried out a spatial analysis of our model mtDNA sample and arrived at the following conclusions:

1. The substantially better spatial resolution of the analysis of particular haplotypes as compared to haplogroups was predictably confirmed: variants of the same mtDNA haplogoup in most cases are differently scattered across the burial ground. For instance, the areas of concentration of the three main variants of U5a (represented in our model sample as series) are located in different parts of the cemetery and almost do not overlap. A similar situation is observed for the haplotypes of haplogroups U2e and A, as well as for some haplotypes of haplogroups U4 and C.

2. The great majority of the serial mtDNA variants from our sample are found at the burial ground in one or several accumulations rather than scattered evenly across its space. This confirms the important role the kinship has played in formation of the spatial groups of burials (mainly rows).

3. For many numerous mtDNA variants, two or more accumulations can be detected. This is observed for the haplotype of haplogroup U5a, with a transition in the 16239 position, for the single variant of haplogroup G2a, for the basal haplotype of haplogroup T, as well as for most of the variants of haplogroups C and U2e. In our opinion, the individuals carrying identical mtDNA variants and belonging to the same accumulation can be close relatives through the maternal lineage. But if such individuals were buried remotely form each other (e.g. in the northern and southern parts of the necropolis), they were likely of different origins and not closely related.

4. For some mtDNA variants from our sample, only one accumulation, besides single scattered individuals, was detected; for instance, for the haplotype of haplogroup H, with a substitution in the 16311 position, for rare (in this region) variants of haplogroups Z1a and A12a, etc. Interestingly, the detection of the accumulations of rare variants in the western periphery of the burial ground suggests the presence of kin groups there, though the burials with skeletal remains suitable for a genetic analysis are not arranged in clear rows or groups in this part

of the cemetery (unlike most of the other parts). Also, many of those mtDNA variants are almost absent in other parts of the burial ground, probably suggesting some genetic specificity of the people buried at some areas of the western outskirt of the necropolis.

5. The presence of the accumulations and their overlaps made it possible to determine a number of areas of the cemetery that are potentially the most promising in the search for closely related individuals, using additional kinship markers. An objective evaluation of our hypothesis of the presence of kin groups of burials requires experimental research, which is being carried out at present as the next stage of the development of our model.

6. The distribution pattern of the accumulations suggests that a large number of the funerary complexes in the northern periphery of the necropolis was created by the populations not directly related to the groups that buried their deceased in the southern and the bulk of the central part of the burial ground.

Conclusions

An unprecedentedly large and chronologically uniform (Andronovo time) sample of DNA specimens from a single necropolis was obtained in the course of the present project. This opens avenues for a comprehensive analysis of the findings in the context of the genetic structure of the populations of the forest-steppe zone of Western Siberia, including the Baraba forest-steppe, during the period of Andronovo (Fedorovo) migration. The mechanisms of the interaction of the migrants with the autochthonous groups of the Late Krotovo (Cherno-Ozerye), and the issues related the funerary rites of that population and its family/kin structure can be explored as well. At the present stage of the analysis, employing a simplified model that does not take into account many nuances of the archaeological context of the studied funerary complexes, we were able to demonstrate the informative value of our approach and to obtain a number of important results related to the spatial distribution of the mtDNA variants across the burials of Tartas-1. Prospective research includes: sampling and analysis of the additional mtDNA specimens from the groups of burials most promising in terms of kinship, employing a wider range of genetic markers of kinship to models of various scale—from double and collective burials to spatial groups/rows; comprehensive phylogenetic and phylogeographic analysis of the findings on the mtDNA gene pool of the studied population; creating a similar model sample for the Y-chromosome for males of the population (or populations) buried in the main part of the Tartas-1 cemetery; comparing the results obtained for the Y-chromosome and mtDNA; widening the spectrum of the molecular genetic research via genotyping of phenotypically and physiologically important markers such as polymorphisms of the system of the pigmentation genes, and others. Another important direction of future work with the model will be the development of optimal tools for the visualization of our results and conclusions, using GIS technologies.

Acknowledgements

This study was performed under the Russian Science Foundation Project No. 17-78-20193 and the IC&G SB RAS Budget Project No. 0259-2019-0010-C-01.

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Received October 7, 2022.