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Ancient Paleo-DNA of Pre-Copper Age North-Eastern Europe: Establishing the Migration Traces of R1a1 Y-DNA Haplogroup

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Abstract

The work considers the problems of paleogenetics and anthropology connected with problem of pre-Copper Age after-Glacial repopulation process of the North-Eastern Europe. The unified data, obtained in various laboratories in 2010-2016, collects a certain amount of the ancient mt-DNA and Y-DNA haplogroup samples of the considered period, what allows establishing the connection between some of them, comparing them with the data of neighboring regions, and attributing them to certain migration flows traceable in archeology. The paper makes an attempt to build a picture of the population of North-Eastern Europe in pre-Copper Age time and to systemize the paleo DNA genotyping results into clusters corresponding to different migration waves. The paper can be of use for biomedical purposes also, as some correlations between diseases and haplogroups were noticed in various medical works.

Keywords: Y-DNA haplogroup, R1a1, J2b, mtDNA haplogroups U4 and U5a1, paleogenetics.

1. Introduction

The interest in the origin and early localization of carriers of Y-DNA haplogroup R1a1 is serious, since this Y-DNA subclade is inherent to the significant percentage of the population of Central and Eastern Europe, India, Middle East. It is widely recognized and already proven in terms of archeology and paleogenetics that a significant concentration of R1a1 Y-DNA haplogroup was inherent to the population of European Corded Ware culture (authors note that there also existed less famous East Asian Corded Ware culture group [1]). However, the location of R1a1 bearers of Pre-Corded Ware horizons causes debates due to a lack of experimental data. Nevertheless, over the last year such data emerged, allowing formulating a data-based hypothesis.

The domain of palogenetics is still young but rapidly developing. Much data from different archaeological cultures are obtained from different research groups. Among very profound and deep works the authors can mention [2-7] which give the wide picture of dispersion of mitochondrial and Y-chromosome haplogroups in prehistoric and early historical layers. This works offer a certain profound conclusions of some archaeological group origins (for example,

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a connection between Corded Ware and Yamnaya) but the conclusions deal with Copper Age and Bronze Age Cultures.

The main aim of the work is to make a certain conjecture based on available data on the distribution of Y-DNA haplogroup R1a1 in Pre-Copper Age Europe. In spite of the scarcity of findings, the rigor archaeological attribution of the findings allows tom make a certain conclusion which reconstructs the areal. The main data contains in works [5,6, 8, 9] Namely, the bearers of Neolithic R1a1 may have been concentrated in the area of Comb Ware Pottery, which precedes the Corded Ware cultures what are proven to be the areal of R1a1 dominance, and which comes from the East, as the Comb Ware pottery centers are situated in Easter European plain.

The serious importance of ancient haplogroup distribution knowledge is connected with possible correlations between haplogroups and different hereditary diseases. The ancient locations of haplogroups for which the correlations are established can point where the probability of a certain genetic illness is higher, and so the inhabitants of these areas should make genotyping more actively. For example in [10] the correlation between mtDNA haplogroups B5 and possibly V20 and Alzheimer disease probability was mentioned. This approach could also work for positive characteristics as longevity. For example, in popular and scientific literature the peoples of Hunza-Burushaski and Abkhazians considered to contain higher percentage of long-living people that most other populations. Though this information is disputable and should be verified, it should be mentioned, that both peoples belong to Sino-Caucasian language macrofamily and according to [11] the spread of the languages of that kind is associated with Y-DNA haplogroups Q and R. In [12] is pointed that the representatives of old subclades of R1a were find in Iran, Eastern Turkey and Caucasus. Also, Y-DNA haplogroup R2 (~14%), related to old R1 Y-haplogroup parental to R1a1 and a high percentage of R1a1 (~25%) are inherent to Burushaski [13]. According to [14] high percentage of R1a1 (~33%) is found among Abkhazians. So the hypothesis of corresponding of the higher longevity within the bearers of the old subclades of R and R1a compared to the newer (to which many European peoples belong) could be rigorously tested and if the hypothesis is true, the factors which yield such situations should be studied.

Also the paper can be useful for popular genetic specialists themselves as they can use it to decide which new archaeological sites to study to verify the outlined hypothesis, if they are interested in Y-DNA haplogroups R and J, mtDNA haplogroups U4 and U5.

2. Material and Methods

The main materials for the research are data from paleogenetic samples of Y-DNA haplogroups, described in other research works, namely [7, 10, 9, 12] grouped in Table 1.

All these results were obtained by the defining haplogroups of the ancient genomes by the genotyping procedure.

In [5] the insolution hybridization capture was used to enrich next generation sequencing libraries for a target set of 394,577 single nucleotide polymorphisms (SNPs) ("390k capture"), 354,212 of which were autosomal SNPs that have also been genotyped using the Affymetrix Human Origins array in 2,345 humans from 203 population.

In [8] the DNA was extracted by the CTAB method. To avoid the effects of degradation, the amplification of HVS1 mtDNA was conducted with the help of single round PCR represented by four overlapping amplicons.

In [6] in-solution hybridization was also used with synthesized oligonucleotide probes to enrich promising libraries for more than 1.2 million SNPs ("1240k capture"). The targeted sites included nearly all SNPs on the Affymetrix Human Origins and Illumina 610-Quad arrays, 49,711 SNPs on chromosome X and 32,681 on chromosome Y, and 47,384 SNPs with evidence of functional importance. To learn about the history of archaeological cultures for which genomewide data was reported for the first time, were studied either 1,055,209 autosomal SNPs when analyzing 230 ancient individuals alone, or 592,169 SNPs when co-analyzing them with 2,345 present-day individuals genotyped on the Human Origins array.

In [9] to reduce the effects of post-indexing contamination, raw reads were retained if the Hamming distance for the observed index was within 1 base of the expected index. Adapter sequences were trimmed from the 3' ends of reads using cutadapt version 1.3 (ref. 35), requiring an overlap of 1 bp between the adapter and the read. As ancient DNA damage is more apparent at the ends of sequences, the first and last two bp of all reads from the deep sequencing phase of analysis

were removed using SeqTK. A minimum read length of 30 bp was imposed. Sequences were aligned using Burrows-Wheeler Aligner (BWA) version 0.7, with the seed region disabled, to the GRCh37 build of the human genome with the mitochondrial sequence replaced by the revised Cambridge reference sequence (NCBI accession number NC_012920.1). Sequences from the same sample were merged using Picard MergeSamFiles and duplicate reads were removed using SAMtools version 0.1.19. Average depth of coverage was calculated using genome analysis toolkit (GATK) Depth of Coverage and indels were realigned using RealignerTargetCreator and IndelRealigner from the same suite of tools. Only data from the deep sequencing phase of the project (100 bp single-end sequencing on a HiSeq,000) were used in the subsequent analyses.

The main research method of this paper is the interpretation of recently obtained genetic data, which is compared with archaeological cultures distribution. To support some conclusions, data on mtDNA haplogroups was also used as supplementary instrument.

Table 1. The main results of paleoDNA genotyping from the Eastern Europe archaeological sites

Sample	Y-DNA	MtDNA	Source
R1a1			
Yuzniy Oleni Ostrov	R1a1	C1g (formerly C1f)	[5, p. 25]
burial № 125, 5500- 5000 BCE.	M459+, M198-		
Serteya archeological	R1a1	H2	[8, p. 294]
site, middle of V-IV mill. BCE			
Khvalynsk-II burial	R1a1, preliminary	U5a1i	[6]
5200-4000 BCE.	classification was		
	determined as R1a1 M459+, M198-[15]		
J			
Yuzniy Oleni Ostrov	J	U4a	[6]
burial № 40, 5500-			
5000 BCE.			
Satsurblia burial	J	К3	[9]
(Georgia), Upper			
Paleolithic			
Kotias burial	J2a	Н13с	[9]
(Georgia), Mesolithic			

3. Results and Discussions

R1a1*, M459+, M198- on Yuzhniy Oleni Ostrov burial (North-Western Russia)

One of the most well studied Eastern European archeological sites is the Yuzhniy Oleni Ostrov burial on the shores of Lake Onega (Karelia, Russia) and it is dated back to the developed and late Mesolithic period of VII-V millennium BC. Three individuals from the Yuzhniy Oleni Ostrov, who lived 7500 years ago (UZOO-7, 8 and UZOO-UZOO-74), possessed a non-existing now in Europe mitochondrial haplogroup C1f [2]. Also among the burials of Yuzhniy Oleni Ostrov were found mitochondrial haplogroups U4, U2e, U5a [3], J and H [4, p. 36]. The Mesolithic inhabitant of Yuzhniy Oleni Ostrov (burial Nº Ioo61) possessed Y-chromosome haplogroup R1a1 (SRY10831.2, M198- subclade) [5] and mitochondrial haplogroup C1g (formerly C1f) [5]. The other Mesolithic inhabitant of Yuzhniy Oleni Ostrov (Io221 / UZOO40) possessed Y-chromosome haplogroup J, and mitochondrial haplogroup U4 [6].

The author of one the most detailed publication on Yuzhniy Oleni Ostrov antropology V.P. Yakimov adhered to the Eurocentric point of view on the formation of the Mesolithic Onega inhabitants. He suggested that their origins are linked to the Paleolithic population of Eastern Europe, who moved along the glacier to the northern and northeastern directions [16]. But some

cross-breeding with Eastern population was also confirmed: *«Later, it was concluded that it belonged to the described in the southern edge of the region so-called «flint» Mesolithic culture associated by origin with cultures of the Volga-Oka area, and (since the appearance in the VIII millennium BCE) coexisted with an earlier (since the X millennium BCE) local «quartz-slate» culture created by people from the North Urals and Trans-Urals and related to Finnish Askola – Suomusyarvi» [17]. But as we see further, ultimate western origins of that culture is probable also as we see a wide migration towards east in early Mesolithic. Currently, researchers emphasize that <i>«Yuzhniy Oleni Ostrov burial site is as an archaeological source extremely multifaced»* (ibid) and represents a particular genetic type, different from the classical Mongoloid and Caucasoid (ibid). A very heterogeneous composition of the population is now well proven by the presence of Y-chromosome haplogroup J, which indicates the influence of the southern areas and communication of Yuzhniy Oleni Ostrov people with populations of the Black and Caspian Sea.

The question if the culture of Yuzhniy Oleni Ostrov is non-ceramical Mesolithic or ceramical Neolithic, is still open. It should be mentioned that P.N. Tretiakov in his book «Finno-Ugrians, Balts and Slavs at the Dnieper and Volga» mentioned: «The population, which left behind the Oleni Ostrov burial ground seems to be familiar with the ware. It is proven by the bone plates with pinked edge, which must have served as ornament molds for clayware. If this statement is true, the Oleni Ostrov burial ground should be connected with the ancient culture of the Pottery Neolithic of the East Baltics – the Sperrings culture» and further: «Comb ware of Sperrings type, according to different researchers, has the closest analogs to the Neolithic cultures of the Kama Region, the Cisuralian area and Trans-Urals, and we agree with this statement. Anyhow, there is no doubt that numerous Ural and Kama analogs to Sperrings ware, which have been detected in the recent years are incomparably more convincing than the Middle Dnieper one» [18, p. 24]. This supports the version of the possible connections of Yuzhniy Oleini Ostrov people with the southern or eastern Neolithic cultures.

In addition to the local component the cultural influences on Yuzhniy Oleni Ostrov, the influences of most far-off regions have been mentioned in different works. For example, one article highlights the unexpected similarities of Yuzhniy Oleni Ostrov inhabitants and the representatives of culture Çatalhöyük [19, p. 92]: "However, the distribution observed on the charts provokes a number of questions because of the convergence of typological characteristics of the groups diametrically opposed geographically and for which the likelihood of direct biological kinship and mutual contacts excluded. The most vivid illustration of this is the convergence of characteristics a series of Mesolithic Oleni Ostrov burial ground with sample from Çatalhöyük by the values of the second factor ...". But the finding of the Y-DNA haplogroup J, which is associated with significantly more southern regions, only confirms ties of Yuzhniy Oleni Ostrov with the Southern cultures.

This way, the southern Neolithic influences on Yuzhniy Oleni Ostrov seem to be strongly probable and they could be originated from the Neolithic tribes of Comb Ware cultures.

R1a1 in Serteya Culture (Western Russian Plain)

The Usvyaty Culture or the Usvyaty level of Serteya culture is another area of finding of an R1a1 bearer of pre-Corded Ware period [8, p. 294]. According to A.N. Mazurkevich: «The first ceramic ware within Pskov area emerged no later than in the middle of the VI millennium BC. At this time the sites of Serteya culture were located in the Lovat-Dvina interfluve on the shores of lakes, running into the stream, connecting the basins.... The first clayware appeared. These are small raw clay vessels with cylinder body and conic bottom. The pots were made of the small clay 'stripes' with the beveled edge and were covered with the thin clay wash. After that the surface of the vessels was ornamented with the ornament mold, leaving the triangle, double or comb prints. The ornament was often molded in plotted manner. The similar ware emerged in forest, forest-steppe and steppe zones of the Russian Plain, as well as in the Lovat-Dvina interfluve. Other components of the material culture (stone, bone and horn artifacts) did not have the fundamental changes in time of the spread of this ware. It enables to propose the emergence of this type of ware in one center and the quick spread of the idea of the ware industry from this area. Such center was supposedly located in the Lower Volga Region and the North Caspian Sea Region in the VI millennium BC» [20].

A.M. Miklyaev also gives a detailed picture of emerging the ware industry in Serteya Region «The most ancient early Neolithic culture featuring ware development phases of the area is the Serteya Culture. This phase includes fragments of heavy-walled vessels produced through the 'overlap' method. After drying, the ribbons were jointed together and their joints were smoothed out by a comb press for a proper binding. The surface of ready vessels was covered with the thin clay wash and the ornament in a form of geometric composition, performed in a stroke-setback or (more rarely) in a stroke manner. The vessels were not burnt, but dried up. Judging by the ornament techniques (Smirnov, 1989), the idea for pottery manufacture came from Azov-Caspian Cultural province, but it cannot be proved by reliable sources of information so far. It should be noted that the Serteya Culture could have entered the Early Neolithic Community extending from the South of the Russian Plain to as far as Valday». Therefore, the first stage has links to the Caspian region.

Then «The next stage features the cauldron-type vessels. This time, the ornaments included more compositions performed by a comb press and the first appeared dents and cuts. As a rule, an ornament was placed in the upper part of a vessel. This stage ware has a narrower range of analogs — The Upper Dnieper tableware (Artemenko, 1954; Kalechits, 1987) and Lithuanian territory (Rimantane, 1966 and 1973). This may indicate to a separation of local groups within the above said community. In this case, it is a group located between two rivers: the Dvina and the Lovat, the Upper Dnieper and Lithuania. The links between the Upper Volga Region and the Left-bank Ukraine are getting weaker» [21]. The Upper-Dnieper Culture located to the South of Serteya can be classified as a forest culture with comb ware traditions [22, p. 73] and could be considered as a more Western tradition than what had come from the North Caspian area and Lower Volga.

The genotyped carrier of R1a1 haplogroup belongs to Usvyaty culture group. A. M. Miklyaev indicates that Serteya culture can be divided into three phases: a, b and c, followed by phase d and e of Rudnya culture. Ceramic phase and is characterized by stroked technique, in phase b comb stamp appears, in the next phase c comb stamp becomes prevailing, holes and notches appear (A.M. Miklyaev with reference to Artemenko and Rimantene relates this last phase with Upper Dnieper Early Neolithic culture and Lithuanian Neolithic) [22, pp. 16-22]. Usvyaty culture dating from the late IV till the middle of the III millennium BC [23, p. 369] allows comparing its combstamped ceramics with a close-type comb-stamped pottery of the North European part of Russia, for example in Kargopol culture [24, p. 222]. In the A. M. Miklyaev's work is emphasized the connection of the population of the region with the Narva culture, especially during the Rudnya culture stage [21, p. 24]. In this respect, we can (of course, in the first schematic approximation) see in the history of ceramics in the region of Eastern Europe Neolithic period a certain competition between the two types of pottery: comb inherent to the North and the North -West and stroked, what came from the South and the South-East, and is most likely connected with the Lower Volga Neolithic cultures. And Usyvaty culture belongs to the time continuing the large period of comb ware domination, having undergone the influence of European Linear Band Ceramics.

So forth, the zone of Neolithic cultures of Serteya region was within the bigger zone of comb ceramics culture of Eastern Europe. During early stages, the eastern connections were prevailing, but then the west and south-west connection became defining. Usvyaty stage emerged after Comb Ware domination and moreover has definite Central European connections.

R1a1*- M459+, M198- in Khvalynsk-II burial (Steppe Volga Region)

The mentioned before connection between Serteya and the Low Volga Region lead us to the analysis of Khvalynsk-II burial, which also belongs to the pre-Corded Ware comb-stroke ornament group: «Khvalynsk culture can be characterized by flat-bottomed and sharp bottomed ware ... Ornament composed of the rows of horizontal strokes separated by horizontal wave lines, usually cowers all the ware specimen or its upper half» [25, p. 39]. I.N. Vassilieva gives the characteristics to the ornaments of ware in the Khvalynsk I and Khvalynsk II burials: «According to the opinion of I.N. Vassilieva, based on the microscopic research of the Khvalynsk ceramics technology, the ornament was made by the wicker factures... Sometimes the ornament was made by ammonite

prints, strokes, short lines or comb stamp» [26, p. 66]. The similar technique has the analogs in the b and c phases of Serteya Culture, identified by A.M. Miklyaev [20].

The analysis of the ceramics of Khvalynsk culture shows that it definitely does not belong to the Corded Ware areal, and can be referred to as belonging to the cultures of comb-and-stroked pottery.

The areal of Comb Pottery cultures. Y-haplogroup J2b as a possible companion of R1a1 on Neolithic sites

The analyzed material showed that the discovery of Y-haplogroup R1a1 bearers in pre-Corded Ware sites happens in the areas influenced by cultures of comb-stroked ceramic, and everywhere the presence of a comb ornament is noticeable. In the context of the analysis of cultural influences in the Eastern Europe, it is necessary to distinguish between stroked and comb pattern. Comb pattern is traditionally considered to be brought about from the north to the south of Eastern Europe, but D. L. Gaskevich in his long article «North Pontic Impresso: the origin of the Neolithic Pottery with Comb Decoration in the South Eastern Europe» [27] wrote the opposite. He made quite a bold assumption that runs counter to the tendency to minimize the migration, and proposed the origin of this type of pottery in the northern Black Sea coast.

«The absolute data collected over the last 15 years in Kiev Radiocarbon Laboratory, have revealed that such ware appeared in the North-Pontic region earlier than in Upper Dnieper, Volga Region, Kama basin, Trans-Urals. However, in the steppe Pontic region it appeared earlier than in forest-steppe. All these data have proved unreliability of above mentioned hypothesis. As an alternative, the author suggests considering the Pontic region Neolithic area with comb ceramic ornamentation as a part of Neolithic cultures with Impresso ware from the Mediterranean region» [27, p 246-247].

This way, according to D. Gaskevich we see in the Eastern Europe only a small episode of a big process, which took place from Sahara to Trans-Urals and from Marocco to the Levant. Probably, the early appearance of ceramics in Samara region and in the Mideterranian area are two faces of one wave of the spread of the Neolithic technologies. The ancient subclades of Y-DNA R1b haplogroup can be detected both in the Volga-Ural region and in the Northern Africa, and the Neolithic findings of R1b are attributed to the Elshanskaya (Lebyazhinka IV) and Els Trocs cave (Spain). At the moment of writing the paper the opinion about the spread of R1b Y-haplogroup carriers from the Eastern Eurasia is dominating, and in moving westward the R1b (and may be R1a) bearers of ceramic Neolithic technologies could obviously merge with the carriers of other haplogroups, J among others.

As D.L. Gaskevich refers to the initial spread of the Neolithic within the Eastern Europe, we should consider the issue of the genetic reflection of this process and specify the genetic map of the North Black Sea Region and the adjust territories in the period, preceding the Mediterranean ware adoption (though, there is another possible address of this initial spread, namely Elshanskaya culture and its derivates up to the Crimea). In VIII-VII millennia BC the North Black Sea Region was inhabited by the bearers of the Kukrek and Zimnikovskaya cultures [28, p. 44-45], the final Paleolithic includes Osokorovskaya culture, considered with the Caucasian Imereti one as a group of «Epi-Gravettian traditions» (ibid, [29, p. 43]) (Figure 1).

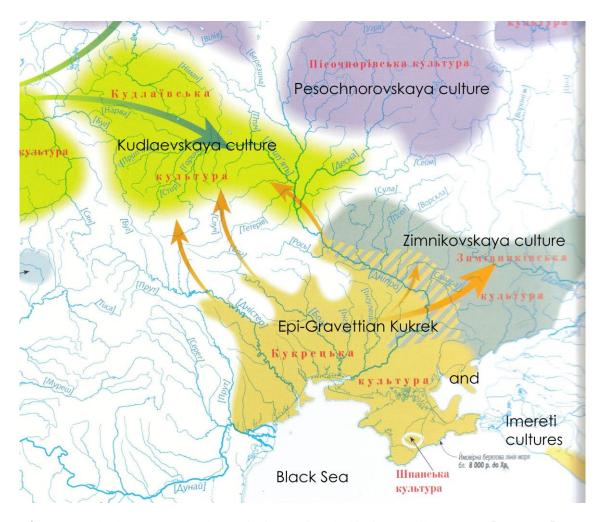


Figure 1. Black Sea area in the end of IX – first half of VII milleina BCE [29, p. 14].

Pre-Neolithic Bug-Dniester culture developed on the basis of the Kukrek one. As the above mentioned Satsurblia and Kotias burial grounds, genetics of which contains the male haplogroup J refer to the habitat of Imereti culture, we can make the conclusion that one of the subclades of the haplogroup J could have been spread across the North Black Sea Region in the pre-Neolithic period (common epi-Gravettian tradition). The mentioned migration by D.L. Gaskevich is supported by genetic data, if we consider that its representatives were the bearers of subclade J2b Y-haplogroup J. Nowadays subclade J2b is widely spread within the zone of ancient migrations of cardial tribes (Fig. 2).

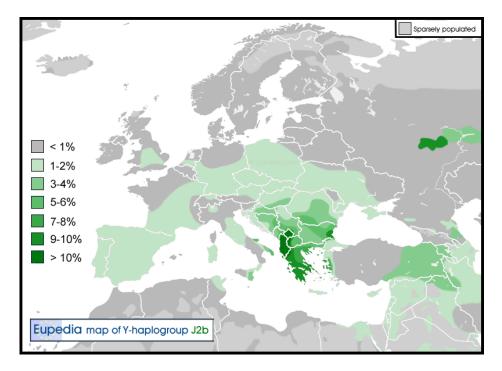


Figure 2. Distribution of haplogroup J2b (M102) in Europe, the Middle East & North Africa. http://www.eupedia.com/europe/Haplogroup_J2_Y-DNA.shtml

Those cardial tribes that could have given rise to the comb ceramics culture, may have been centered around Black Sea and Adriatic shores, and they could contain Y-DNA subclade which could be different with those of Georgia but related to them. The regions of the highest concentration of the haplogroup J2b bearers, namely Albania, the South-East of Bulgaria, Greece and some coastal regions of Italy (from 10 to 26 % of population) up to the Black Sea are represented on the above mentioned map.

This view is strongly supported by the spread of J2b in populations, which can be considered theoretically connected with the cultures of comb ware and were least of all Indo-Europeanized among all the East of Europe (nowadays they speak Uralic languages with some pre-Uralic substrate [30]). So, the presence of J2b in these populations may not reflect the Indo-European migrations, but earlier waves of Neolithic spread.

Firstly, the spot of the noticeable spread of J2b (10-15% of population) is Mordovia (central Russia) (particularly, Moksha environment [31]). V.V. Stavitsky in his thesis work on the theme «Neolithic, Eneolithic and the Early Bronze Age of Sura-Oka Interfluve and the Upper Prikhoper'e: Dynamics of North and South Cultures' Interrelations in the Forest-steppe Zone», shows that the local population continued the development of the Upper-Volga comb-stroked traditions at the late stage of this culture existence without leaving the region. «The ornamentation of the ware of Ozimenki 2 site widely uses the broad-toothed prints of the long stamp with the rare rows of deep patches on top, having the complete analogs in the late Upper-Volga ware» [32]. V.A. Yurchenkov in his book, which is the review of academic research, says about the prevailing comb nature of Moksha river area ware: «There are 20 memorials with the so-called comb-stroke ware in the Moksha basin. The prints of comb stamp prevailed in the ware decoration; the share of stroke ornament is low» [33, p. 113]. Thus, the penetration of J2b into Mordovia territory can be explained by the migration from the south, and the Mordovian J2b peak can be explained by the fact that the population of comb-stroke ware had not left the territory.

Secondly, Saami J2b phenomenon. The Saami have the reputation of the relict, some kind «reserve» of the ancient genes of Europe (and the bearers of the considerable pre-Uralic language substrate), that is why it is not surprising that one of the first Neolithic migrations to the European continent could be preserved in the genes of this isolated northern people, unaffected by «Indo-Europeanization» [34]. The population of the Saami within Kola Peninsula contains about 14% of haplogroup J2b [35]. As the Comb Ware cultures in pure form were displaced to the north of the

Eastern Europe in early Bronze Age, it is quite possible that their creators could have played an important role in the Saami formation.

New findings of 2016 year in Germany

Thus, we can suppose that haplogroup R1a1 could be found in the wide range of comb-stroke cultures, especially comb ware cultures often accompanied by J2b (at the north-west area – in Karelia and Mordovia exactly comb cultures exist in the considered period) in the Neolithic horizons. Besides, it is also possible that the epicenter of the spread and divergence of modern most widespread subclades R1a1 (M198+, M417+) was located to the west of Serteya, which is indicated by the relations of Serteya culture with the funnel beaker (developed on the basis of Ertebelle) and Narva cultures (Fig. 3).

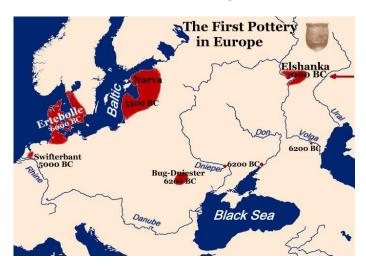


Figure 3. Main Ceramic Neolithic Cultures of Europe

But the issue of R1a1 bearers' Upper Paleolithic origin is debatable. Firstly, the variant of the Black Sea Region origin is still possible, as this haplogroup can be present in Bug-Dniester culture and further southward. This fact is supported by the detection of basal haplogroup in the population of the Middle East Region: «... more basal (R1a-M420*) Y-chromosomes have been detected in Iran and eastern Turkey. Overall, our detection of haplogroup R1a1 in a northwest Russian hunter-gatherer establishes the early presence of this lineage in eastern Europe, and is consistent with a later migration from eastern Europe into central Europe which contributed such haplogroups to the Corded Ware population» [5].

In [36] we discussed two possibilities. The first is that Y-DNA R1a1 could be ultimately a Zarzian marker which denotes the representatives of mesolithic cultures who came to Karelia from the South-East from the Caspian seashores (possibly via the Black sea region). The second is that R1a1 could come from the East or Central Asia in paleolithic time. The newest archaeological findings allow us to support the Zarzian point of view.

In the Northern Germany, where "Mesolithic in different forms continued along with the existing agrarian societies of the Central Europe" [37, p. 151], very interesting burial ground were found in recent years, which can be compared both with the Southern Scandinavia and Yuzniy Oleiny Ostrov burial (standing burials) (ibid). There is the theory that such unusual type of burial is the result of oriental influence (ibid), and this influence needs feasible explanation. Micro-blade techniques, which appeared in the Atlantic period and some forms of ware of the early V millennium BC also point at the oriental influence in the region (ibid). The priority of the oriental center of the mentioned influences in comparison with the west regions (Northern Germany) is determined by dating of the Yuzniy Oleiny Ostrov burial grounds (most of the burial grounds date back to the middle VI millennium BC [38, p. 307-464]).

Analogies of North German post-Mesolithic cultures and Yuzniy Oleiny Ostrov are found in such technology, as ware organic additives (fluff chamotte), which is rare for the early European Neolithic. Such types of ware are found within Karelia area in the beginning of V millennium BC

[39, p. 249] in Sperrings [40, p. 87], [41, p. 241-251]. As we mentioned above, Yuzniy Oleni Ostrov itself can be a ceramic culture. The Middle Volga is the earlier source of the 'fluff' technique. From places, where Elshanskaya archeological culture existed 6500 BC, this techniques spread from up the Volga to the Baltic Sea and further to the west to the location of the Ertebølle culture: «Pottery was manufactured from native clays tempered with sand, crushed stone and organic material. The EBK [Ertebølle culture] pot was made by coil technique, being fired on the open bed of hot coals. It was not like the neighbouring Neolithic Linearbandkeramik and appears related instead to a pottery type that first appears in Europe in the Samara region of Russia c. 7000 cal BC, and spread up the Volga to the Eastern Baltic and then westward along the shore» (Fredrik Hallgren, The Introduction of Ceramic Technology Around the Baltic Sea in the 6th millennium, in Helena Knutsson, (ed.), Coast to Coast - Arrival, Coast to Coast book 10 (2004), pp. 123-142; Detlef Gronenborn, Beyond the models: Neolithisation in Central Europe, Proceedings of the British Academy, vol. 144 (2007), p.87; Jutta Paulina de Roever, The Pottery of Hunter-Gatherers in Transition to Agriculture, Illustrated by the Swifterbant Culture, the Netherlands in Dragos Gheorghiu (ed.), Early Farmers, Late Foragers, and Ceramic Traditions: On the Beginning of Pottery in the Near East and Europe (2009), pp. 150-166» [42, pp. 123-142]; [43, p.87]; [44, pp. 150–166]. The origin of the Elshanskaya archeological culture is connected with large migration flow of the so-called 'Zarzian' cultures of the Middle East [45, p. 154] and possibly the spread of Dene-caucasian linguistic family [46]. Y-DNA haplogroup J [6], which is mainly spread within the Middle East also points at the southern nature of the population, as well as presence of mt DNA haplogroups J and H [2].

As we mentioned in our earlier work [47] the presence of eastern mtDNA C (which was attested in Yuzniy Oleniy Ostrov) is also attestable in southern regions (Dnieper-Donetsk culture). The Elshanskaya culture male sample was genotyped and Y-DNA haplogroup was R1b1-L278 [5]. In latter Khvalynsk culture we see both R1b1-M415 and R1a1-M459 [6] (and possibly M198-[15]), so the same picture could be possibly extrapolated to Elshanskaya (presence of R1a1-M459, M198-). The appearance of Karelia-type burials in the Ertebølle period and the spread of Elshanskaya-type ceramics with organic component allows to propose a hypothesis that the bearers of the new influences were the Zarzian migrants who moved west via North-Eastern Europe.

Another argument for Zarzian or related influence is that two other waves of Yuzhniy Oleni Ostrov populating are profoundly connected with Northern Europe and were already present near the Northern Germany region to the time of new burial style arrival.

In our previous work [46] we showed that besides Zarzian, the culture of Yuzhniy Oleni Ostrov burial can have other sources: Veret'e, Askoula-Suomusyarvi, Swiderian-Butovo cultures. The bearers of mitochondrial DNA U4 and U5a in the burial grounds point at the migrants from the regions of Europe. The emergence of U4 within Lake Onega has analogs in the Kunda culture in Lithuania (aged 6350 BC) [48], although Gotland island can also be the intermediate point (as mesolithic U4 were found there). MtDNA bearers of U4 in Germany also found in Bad Dürrenberg (aged 6850 BC) (ibid), in Sweden – Stora Förvar cave, Stora Karlsö Island [49]. Generally, subclade U4 was not still found in Paleolithic Western Europe [7], but exists in Central Europe eastward, for example, in Veret'e culture [3] (Popovo burial ground). Thus, its starting dispersal point could be connected with East-European final Paleolithic, even possibly Swiderian culture or its substrate, as Veret'e is similar to post-Swiderian cultures – Butovskaya and Kunda ones.

«Veret'e culture (Oshibkina, 1983, 1989, 1997; Oshibkina, 1989) is spread within the East Prionezhe, mainly in the basin of the Lacha River. Three settlements of the Boreal time are well-studied, Veret'e 1 is concerned with the first and the Low Veret'e – with the second part of the Boreal. The lower layer of Sukhoe settlement and the poor Pogostishche site don't have natural-science dates. Besides, there is Peschanitsa burial ground, dated by the radiocarbon method 9890+-120 (GIN-4858) and Popovo burial ground. Burial grounds 9, 3 and 1 of the latter one date back 9730+-110 (GIN-4856), 9520+-130 (GIN-4442) and 9430+-150 (GIN-4447), in other words they date to the first half-middle Preborial and the burial ground in Peschanitsa – to its beginning. Burial grounds 6 and 8 date back 7510+-150 (GIN-3887) and 7150+-160 (GIN-4857) accordingly, in other words the Atlantic time. According to C.V. Oshibkina, the mentioned burial grounds belong to Veret'e culture. If it is true and the dates are correct, the excavated settlements characterize only the middle stage of this culture existence, which complicates the issue of its origin and historic fates. The similarity of the stone and bone goods and the synchronous

memorials of Kunda and Butovo cultures enables to consider the similar development of Veret'e culture in Preborial, but this issue is still open, as well as the problem of its further development. Goods of Andozer M distinguish from the bone goods of Veret'e 1, which makes it impossible to refer the sites of this type to Veret'e culture. This site has more similarities with the late Mesolithic of the Sheksna basin of the type Ust-Anogi 1 (Kosorukova, 1997). At the same time, some similar features of goods enable to agree with the opinion of S.V. Oshibkina that the bearers of Veret'e culture were the ancestors of the population, which left the burial ground of Yuzhniy Oleni Ostrov. To solve the mentioned problems the search and excavation of new memorials is necessary. Meanwhile, we can note that the Boreal settlements of Veret'e culture, having a great number of different goods of bone and horn are one of the most impressing memorials of Mesolithic of the forest zone in the East Europe» [50].

U5 is the mitochondrial group, typical to the Upper-Paleolithic cultures like Gravettian one [51] and the dispersal routes of U5a bearers across Europe are concerned with the Central Europe (U5b prevailed in the west of Europe in Paleolithic-Mesolithic), rather than with the Western one. U5a seems to mark some migration (unknown to the archeologists) of the final Palelithic or early Mesolithic from the Danube (possibly where Dolni-Vestonice site was located, although this location dates back to the XXV millennium BC) (ibid) to Central Germany, where the route of the U5a bearers divides into two subclades U5a1 and U5a2.

Haplogroup U5a1 is the most probable for the U5a bearer in Yuzhniy Oleni Ostrov. The bearers of U5a spread far beyond Scandinavia and Baltics. Bearers of this haplogroup can be found in Chekalino culture – about 7800 BC [48], Lebyazhinka IV [5] culture of the VI millennium BC (ibid) and Lokomotiv burial ground of the Kitoy culture at the Angara (6100-4900 BC) [52]. The latter enables to affirm that the Kitoy culture, which some researchers consider as the ancestral for the Altai-language nation or at least for the part of it [53], may be connected with some Mesolithic migrations from the more westward regions. The analysis of the burial grounds of Bolshoi Oleniy Island [3], Lebyazhinka IV and the later cultures shows the existence of subclade U5a1 [5]. The work [3] shows similarity of populations of Yuzhniy and Bolshoi Oleniy Ostrov. This haplogroup was also found in Mesolithic Sweden (Motala burial). The latter two arguments make the existence of U5a1 in Yuzhniy Oleniy Ostrov the most possible.

Swedish burial ground Motala contains burials with a bunch of mitochondrial DNA: U2e, U5a1, U5a2, U5a2d [54, 9]. The fixed subclade U5a2 in Les Closeaux (Rueil-Malmaison) location, dated back to 8870 BC [7] and German subclade U5a2c3 in Blätterhöhle, dated back to 8638 BC [55] could be considered as the similar for Motala subclades. It is possible to consider that Motala subclades were brought from the Western or Central Europe in the period, synchronous to Yuzhniy Oleni Ostrov burial and the center of it dispersal was continental Western-Central Europe.

The possible candidate, which could have brought U5a to Yuzhniy Oleniy Ostrov is Askola-Suomusyarvi culture, possibly originating from final Paleolithic Ahrensburg culture (influenced by Hamburg final Paleolithic culture) [56, p. 185]. Though this culture differs from Motala, its population could more possibly have mitochondrial DNA U5a1, as well as the other cultures originating from Ahrensburg culture.

The possible tracks of mtDNA lineages to Karelia (Yuzhniy Oleni Ostrov), as they are seen according to contemporary data, are outlined on Figure 4.



Figure 4. Possible ways of Mesolithic-Neolithic populating of Karelia (the territory of pre-Corded Ware R1a1* Y-DNA haplogroup presence)

4. Conclusion

We can conclude that the presence of haplogroup R1a1 is strongly probable in the cultures of Comb Stamp Ware (with J2b bearers as well) in the Neolithic context. But though the origin and the trace of R1a1 migration is still unclarified and more data are needed, the new archeological findings gives arguments for South-Eastern migration via the Baltic sea region to the Northern Europe which can be possibly accompanied with the Comb-Stroked Ware pottery with organic components.

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Древние палео-ДНК Северо-Восточной Европы: к реконструкции миграций носителей R1a1 до начала энеолита

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Аннотация. В данной работе рассмотрены основные вопросы палеогенетики, археологии и антропологии, связанные с заселением Восточной Европы в мезо- и неолите. собранных различными лабораториями и коллективами, определенное количество образцов различных мтДНК И Ү-ДНК гаплогрупп рассматриваемого периода (типированные останки), что позволяет выстроить связи между носителями культур соседних регионов. Это достигается привлечением археологических данных, что позволяет отследить и миграционные потоки. В статье делается попытка построить картину некоторых миграций эпохи раннего неолита (связанных с перемещением носителей гаплогруппы R1a1). Делается вывод, что обнаружение новых древних останков с Y-гаплогруппой R1a1 возможно в слоях культур восточно-европейской гребенчатой керамики, которая в свою очередь может быть связана с неолитом Причероморья. Статья может быть использована для биомедицинских исследований, поскольку в настоящее время уже выявленны отдельные корреляции между гаплогруппами и наследственными болезнями.

Ключевые слова: Y-ДНК гаплогруппа, R1a1, J2b, митохондриальная гаплогруппа, U4, U5a1, палеогенетика.

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