

GENETIC HISTORY OF EURASIA BEFORE THE COMMON ERA

L.R. Gabidullina^{1*}, *M.A. Dzhaubermezov*^{1,2}, *N.V. Ekomasova*^{1,2},
*Z.R. Sufyanova*¹, *E.K. Khusnutdinova*^{1,2}

¹ Federal State Educational Institution of Higher Education “Ufa University of Science and Technology”, 32 Zaki Validi St., Ufa, 450076, Russia;

² Institute of Biochemistry and Genetics, Ufa Federal Research Center of the Russian Academy of Sciences, 71 Prospekt Oktyabrya St., Ufa, 450054, Russia.

* Corresponding author: liliya.gab@gmail.com

Abstract. In 2010, the first scientific study was published on genome-wide data on ancient DNA belonging to a male of the Paleo-Eskimo culture, who lived about 4000 years ago. Since then, advances in DNA techniques have made it possible to sequence hundreds and thousands of ancient genomes. Today, 13 years later, scientists have obtained genome data from more than 10,000 ancient humans, and data accumulation continues at an exponential rate. The vast majority of the studied ancient genomes were obtained from various places in the territory of Eurasia, which is distinguished by the huge diversity of its genes, cultures, and languages. Here we give an overview of the migration, mixing and continuity of the human population across the territory of Eurasia, starting from the period of its settlement by modern people and ending with the most mobile period in the history of mankind – the Iron Age.

Keywords: ancient DNA, human populations, admixture, migration, human origins, adaptation.

List of Abbreviations

ANA – Ancient Northeast Asian
ANE – Ancient North Eurasians
APS – Ancient Paleo-Siberians
BCE – Before the common era
CHG – Caucasus hunter-gatherers
EEF – Early European farmers
EHG – Eastern hunter-gatherers
HG – hunter-gatherers
ky – kilo (thousand) years
kya – kilo (thousand) years ago
LGM – Last Glacial Maximum
MH – modern humans
mtDNA – mitochondrial DNA
SHG – Scandinavian hunter-gatherers
SNPs – single nuclear polymorphisms
WHG – Western hunter-gatherers
Y chr – Y chromosome

Introduction

The analysis of ancient DNA has found wide application in the scientific field, has become a tool in solving key issues of archeology, evolution, and ecology. Today, geneticists can find out the general patterns of relationships between populations, but also provide detailed answers to historical questions about human populations. When, where, and how did different ethnic groups arise? Who mixed with whom,

and when did the admixing occur? How do archaeological finds reflect populations shifts or cultural developments? Did ancient archaeological cultures have genetic descendants? We will discuss how the analysis of ancient DNA allows us to successfully elucidate some of these issues, but nevertheless, how it has brought new challenges to our understanding of the history of human populations.

Our knowledge of the events that led to the development and distribution of anatomically modern humans was formed by archaeological and paleontological evidence. However, essentially, this data cannot be used to identify the genetic connections between various individuals or groups of individuals. Even while archaeological study has been quite successful in showing how cultures spread, it is frequently difficult to tell whether cultures spread through the movement of people or ideas. It is made easier to directly identify ancestry between individuals, as well as to understand migration patterns, diversification processes, and genetic admixture between various groups, by include genomic study of contemporary or historical populations.

In this review, we present a summary of the most important findings on the history of human evolution during the Paleolithic and Neo-

lithic before the Common Era, made possible by the sequencing of hundreds of human genomes dating back tens of thousands of years. Some traditional assumptions, previously supported by paleontological and archaeological data, have received additional support from the study of genetic data. On the other hand, sometimes completely different points of view arise, which were unexpected, but provide a new opportunity to discover the history of mankind.

Archaic people

The first reconstructed and studied genomes of ancient people were the genomes of Neanderthal and Denisovan in 2010 (Green *et al.*, 2010; Reich *et al.*, 2010). According to the results of the analysis, the relationship between these groups was revealed, which shows a closer connection with each other than with anatomically modern human (MH). Comparing the investigated ancient genetic variations with modern ones estimated the time of separation of human lines branches: split of archaic people was ~550-765 thousand years ago (kya), as well as ~445-473 kya for Denisovans and Neanderthals (Prüfer *et al.*, 2014).

MH overlapped in time and space with other hominins and were accompanied by processes of admixture, that evidenced by certain archaic hominin sequences that survives in modern genomes (Vattathil & Akey, 2015). The ability to identify the archaic hominin sequences in MH genomes allows us to conclude about the functional, evolutionary, and phenotypic significance of the archaic admixture. Thus, established presence of gene flow between the above-mentioned archaic Neanderthals and Denisovans with the ancestors of modern people gave us an understanding of adaptive introgression across geographically diverse human populations (Green *et al.*, 2010; Martin & Jiggins, 2017; Meyer *et al.*, 2012; Prüfer *et al.*, 2014).

The hypothesis about the crossing of Neanderthals and early MH, suggested by paleontologists more than 30 years ago, has now been convincingly confirmed (Green *et al.*, 2010; Prüfer *et al.*, 2014). The term «early modern humans» refers to people who are anatomically

and physiologically similar to the modern population, this group refers to the Middle and Early Upper Paleolithic – transition started ~47 kya. Analyses of the genomes of Neanderthals and modern humans have shown that gene flow occurred between the two hominin groups ~60–50 kya, probably in southwestern Asia (Fu *et al.*, 2014; Green *et al.*, 2010; Prüfer *et al.*, 2014).

Derived from the closest extinct related Neanderthal hominid, parts of the genome, even in it small number, played an important role in adapting to the environment, such as an unusual cold weather, new viruses and pathogens and solar radiation level (Hajdinjak *et al.*, 2021; Prüfer *et al.*, 2014, 2021; Reilly *et al.*, 2022). Depending on the region of residence, modern non-African populations carry approximately 2% of Neanderthal genes in their genomes (Green *et al.*, 2010; Meyer *et al.*, 2012; Prüfer *et al.*, 2014; Sankararaman *et al.*, 2016; Vernot *et al.*, 2016), at the same time this number is 20% higher among the inhabitants of Oceania, which is associated with genetic drift from another archaic group - the Denisovan (Browning *et al.*, 2018; Mallick *et al.*, 2016; Sankararaman *et al.*, 2016; Vernot *et al.*, 2016). Using the IBDmix application it was found that African people carry a stronger signal of Neanderthal ancestry than previously thought (Chen *et al.*, 2020). This can be explained by the actual origin of Neanderthal traces due to migrations back to Africa, mainly from the ancestors of Europeans, as well as by the flow of genes to Neanderthals from an older archaic lineage that settled from Africa and preceded the split of Neanderthals and MH (Chen *et al.*, 2020). In addition, it has been hypothesized that some African populations carry ancestry from an even older archaic lineage that predates the divergence of Neanderthals and MH (Durvasula & Sankararaman, 2020; Liu *et al.*, 2021).

MH appeared in Europe at least 45 kya and coexisted with Neanderthals, who disappeared ~40 kya, an admixture of these hominids was occurred ~40 kya in Europe (Benazzi *et al.*, 2011; Fu *et al.*, 2014). There are a number of studied haplotype candidates of adaptive introgression from Neanderthals to modern human

genome (Racimo *et al.*, 2017). Occurring with a high frequency in MH populations (60–70%) introgressed haplotypes cover some genes associated with skin and hair pigmentation: BNC2 encodes a zinc finger protein that is expressed in keratinocytes and provides variation in skin pigmentation (Jacobs 2013), POU2F3 gene encodes a transcription factor expressed in the epidermis and is responsible for the proliferation and differentiation of keratinocytes (Takemoto *et al.*, 2010). Data on metabolic candidate genes have also emerged: TSHR gene encodes the thyroid stimulating hormone receptor that binds thyrotropin, the pituitary hormone involved in a number of physiological function of thyroid gland and thyroid-mediated energy metabolism in most tissues (Kopp, 2001; Setter *et al.*, 2020).

Different populations of MH have inherited different regions of the Neanderthal genome, so the frequencies of occurrence in Europeans and East Asians differ (Dannemann, 2021; Vernot *et al.*, 2016). But the Neanderthal ancestry was not distributed randomly – the frequency of Neanderthal alleles was significantly decreased due to negative selection (Fu *et al.*, 2016a; Petr *et al.*, 2019; Sankararaman *et al.*, 2014). In this context, a recent study of COVID-19 (Coronavirus disease 2019) host genomics identified Neanderthal variants contributing to protection against COVID-19 in Eurasian populations (Zeberg & Pääbo, 2020, 2021). Incidentally, the COVID-19 protection haplotype which was passed on to modern humans ~50-60 kya lie near to OAS1 gene cluster, which is strong candidate for Neanderthal adaptive introgression (Mendez *et al.*, 2013; Reilly *et al.*, 2022; Zeberg & Pääbo, 2020; Zhou *et al.*, 2021).

Thus, fragments of Neanderthal genomes can be said to survive in every studied MH population and admixture between MH and archaic people was found in both directions. It is noteworthy that Neanderthals were carriers of the mitochondrial and Y-chromosomal genome of early MH as a result of an introgression of ~270 kya (Meyer *et al.*, 2016; Posth *et al.*, 2017). This hypothesis conforms contradictions in data on phylogeny and dating of the human lineages split according to nuclear and mito-

chondrial DNA (mtDNA) and suggests that Denisovan mtDNA type was shared among early Neanderthals in Eurasia and was then substituted by introgression from African mtDNA that later has become the Late Pleistocene Neanderthal mtDNA type (Posth *et al.*, 2017). The same phenomenon was found in a second uniparental marker, the late Neanderthal Y-chromosome (Y chr) was introgressed into Neanderthals between ~370 and ~100 kya (Petr *et al.*, 2020). These processes are probably explained explained by the low effective size of the Neanderthal population and the increased genetic load in them compared to MH.

Modern humans in Paleolithic

Anatomically modern humans appeared in Europe around 45 kya (Benazzi *et al.*, 2011; Fu *et al.*, 2014; Hublin *et al.*, 2020). The final stage in The Last Glacial Period was the point of The Last Glacial Maximum (LGM) 25-19 kya, at that time most of Northern Eurasia was still covered with ice, which affected the settlement of people and wildlife, limited to certain refugia (Gamble *et al.*, 2004; Mangerud *et al.*, 2004). The first people who settled Europe were hunter-gatherers until 7,5 kya when agriculture spread here from the Middle East, which led to significant changes in the social structure of human. The number of human remains found and analyzed from this period stays low, especially in the East of Eurasia, but nevertheless, the available data made it possible to study the genetic structure of Paleolithic hunter-gatherers during the period LGM 45-25 kya and after LGM 19,5 -14,5 kya and in the transition to the Holocene ~17.5 kya to the present (Gamble *et al.*, 2004).

Genomic data has been obtained from early anatomically modern humans that lived in Eurasia ~50 kya, but interestingly some studied lines of the MH ancestors are genetically related to MH populations, while others didn't show a noticeable genetic continuity with later populations. Three gained genomes of early MH that lived in Eurasia as early as ~45 kya are Zlatý kůň from Czechia, Oase from Romania and Ust'-Ishim from Central Siberia of Russia, they represent the most basal and oldest modern

human genomes to date (Fu *et al.*, 2014, 2015; Prüfer *et al.*, 2021). The oldest of the specimens is the ~45 ky old Ust'-Ishim individual shares more alleles with present-day East Asians than with present-day Europeans, he is equally closely related to ancient Europeans and to present-day East Asians, suggesting he is from a population that did not contribute to any present-day Eurasian populations (Fu *et al.*, 2014). Zlatý kůň is of approximately the same age as the Ust'-Ishim individual or up to a few hundred years older and she was part of a population that formed before the populations that gave rise to present-day Europeans and Asians split from one another (Prüfer *et al.*, 2021). The ~42-37 ky old Oase1 individual shares a similar number of alleles with both Europeans older than 14 ky and present-day East Asians and Native Americans, suggesting that he also belonged to a distinct population that did not contribute substantially to later Eurasians, also in the genome was indicates a Neanderthal trace 6–9%, that means Neanderthal ancestor as recently as four to six generations back (Fu *et al.*, 2014).

The earliest Late Pleistocene modern humans left a trace in modern populations were three individuals dated to between 45 and 42 kya from Bacho Kiro Cave, Bulgaria, they were found in association with an Initial Upper Palaeolithic artefact assemblage (Hajdinjak *et al.*, 2021). Bacho Kiro are likely related to the contemporary expansion and transition of Initial Upper Paleolithic cultures, such as the spread of the Aurignacian complex (Hublin *et al.*, 2020). Bacho Kiro Cave individuals were associated to populations that contributed ancestry to the ~40 ky old Tianyuan individual in China as well as, to a lesser extent, to the ~35 ky old GoyetQ116-1 from present-day Belgium and Ust'-Ishim individuals, this resolves the previously unclear relationship between the GoyetQ116-1 and Tianyuan individuals (Fu *et al.*, 2016b; Hajdinjak *et al.*, 2021; Yang *et al.*, 2017). The Tianyuan individual from outside Beijing was shown to be more similar to present-day East Asians and Native Americans than to present-day or ancient Europeans (Fu *et al.*, 2013; Yang *et al.*, 2017). Tianyuan-related ancestry later

was widespread geographically and temporally in northern East Asia before the Last Glacial Maximum (Mao *et al.*, 2021).

Only two pre-Ice Age genomes are available from East Asia: the approximately 40 ky old individual from Tianyuan Cave in northern China and the around 35 ky old Salkhit individual from Mongolia (Massilani *et al.*, 2020; Yang *et al.*, 2017). Salkhit individual carried more West Eurasian ancestry than the Tianyuan individual, indicating that after the major West/East Eurasia split, gene flow from West Eurasia to East Asia occurred earlier than 34 kya, probably mediated by populations related to the Siberian Yana individuals (Massilani *et al.*, 2020). Tianyuan-related lineage with a northern geographical distribution contributed 98% of the ancestry of Neolithic people from Mongolia and 90% to Neolithic farmers from the Upper Yellow River (Wang *et al.*, 2021).

One more Late Pleistocene individual from before the LGM with widespread ancestry is ~35-33 ky old AR33K represents Amur region. Despite the high genetic similarity between AR33K and Tianyuan, it was found that AR33K sample compared to Tianyuan individual didn't relate to GoyetQ116-1. Instead, AR33K presents a profile similar to other ancient East Asians, showing a trend of elevated GoyetQ116-1 ancestry compared with other ancient western Eurasians, but just at or below the cutoff for statistical significance (Mao *et al.*, 2021).

Therefore, in that time «genetically» European populations existed in Europe and «genetically» Asian populations existed in Asia, it means that the Asian–European separation likely happened about 40 kya, consistent with inferences using de novo mutation rates that have pushed back the estimated date of separation from ~40-20 kya to ~80-40 kya (Scally, 2016; Scally & Durbin, 2012; Yang *et al.*, 2017).

Despite current limited knowledge of these earlier periods, can be assumed increasing population structure, population contacts, and higher migration occurred across Eurasia (Yang & Fu, 2018). Other early MH lineages

~24-40 kya are genetically connected to present-day populations. Only from around ~37-35 kya do all analyzed the European individuals share ancestry with present-day Europeans. The ~36 ky old Kostenki-14 individual from western Siberia and the ~35 ky old Goyet Q116-1 from Belgium are more closely related to Europeans than to other Eurasians. Unlike present-day Europeans, ancient Europeans from 35-45 kya do not have Basal Eurasian ancestry (Fu *et al.*, 2016; Seguin-Orlando *et al.*, 2014). In period of 37-14 kya from the time of Kostenki-14 until the time of the Villabruna Cluster, all individuals seem to derive from a single ancestral population with no evidence of substantial genetic influx from elsewhere (Fu *et al.*, 2016).

In the work of Lazaridis *et al.* comparing ancient genomes from the territory of Europe with modern European genomes showed a special ancestral component that was not observed in early Europeans. It has been suggested that this component is descended from a population that diverged from other non-Africans at an early stage of non-African origin, this component has been called “Basal Eurasian” (Lazaridis *et al.*, 2014). In subsequent work, it was found that this component occurs in high proportions in the inhabitants of the Middle East of 12-2 kya, seemingly this population separated from other non-Africans before the appearance of archaic admixture (Lazaridis *et al.*, 2016). However, no ancient specimen or present-day population sampled thus far shows evidence of being from a Basal Eurasian population. The earliest evidence of individuals with this ancestry are from the Caucasus region ~13 kya who also possess European ancestry and from the Levant region ~12 kya (Yang & Fu, 2018).

Among the Asian specimens there is a sample of Siberian individuals approximately 24-17 kya, this is a 24,000-year-old individual (MA-1) from Mal'ta northwest of Lake Baikal and Afontova Gora-3 south- dating to approximately 17-18 kya from central Siberia near the city of Krasnoyarsk, they show a stronger connection with Europeans than with Asians, and they also have the strongest connection with Native Americans (Fu *et al.*, 2016b; Raghavan

et al., 2013). This emphasizes that Native Americans are a mixture of East Asian and North Eurasian origin, represented by these people living in Siberia.

Represented by the Malta-Buriel (MA-1) and Afontova Gora samples, the «Ancient North Eurasian» (ANE) formed as a genetic population component which contain ancient West-Eurasian (Paleolithic European) and East-Eurasian (Ancient Eastern Siberian) components. ANE was once widespread in parts of northern Eurasia, mostly in Western Siberia and Eastern Europe, until it got nearly completely replaced by East Asian-related Paleo-Siberians which themselves again got largely replaced by East Asian Neo-Siberians (Raghavan *et al.*, 2013; Sikora *et al.*, 2018).

Scientists have used the term «Ancient North Siberian» ANS to describe the earlier sample which can be considered ancestral to the later ANE sample. Between 20 and 11 kya, the ANS population was largely replaced by whose lineages are modern East Asians, which gave rise to the ancestors of the Native Americans and the «Ancient Paleo-Siberians» (APS), represented by a skeleton of 9,8 kya from mouth of the Kolyma River, Beringia in Russia. The APS were formed from a combination of ancient East Asians and ANEs and extended from northeastern Siberia to south of Lake Baikal. In addition, APS are closely related to the Siberian ancestors of the Native Americans and the ancestors of modern people such as the Koryaks and Itelmens (Liu *et al.*, 2021; Sikora *et al.*, 2018).

These ancient North Eurasians have Asian influences as well, but the low representation by ancient genomes of this period in the region rejects a direct assessment of the structure and population turnover, however the available data on an individual from Tianyuan suggest that there must also was a population structure dating back to the period of the above samples from 45-35 kya (Lipson *et al.*, 2017; Yang & Fu, 2018). Some South American populations show links to Oceanians, Andamanese Onge (from Andaman island) and Tianyuan individual, but not to modern East Asian populations, suggesting that the ancestral Native American

populations before migration to America were structured with different types of Asian influences (Skoglund *et al.*, 2015; Yang *et al.*, 2017). Existence of this connection means that as early as ~40 kya, its ancestry are found in some subpopulations of Eastern Eurasia and must have persisted in some form until the colonization of America (Yang & Fu, 2018).

Humanity encountered the most severe environmental conditions during the LGM period in Europe, East Asia and Siberia, which affected survival and peopling. It is noteworthy that the ancestral line GoyetQ116-1 survived during this period, which did not disappear, as its descendants became widespread again after ~19 ky in the El Mirón in Iberia (Villalba-Mouco *et al.*, 2019). At the end of the LGM one important adaptive variant for East Asians is the EDAR V370A mutation associated with traits such as thicker hair shafts appeared in all ancient East Asians, except for AR33K and Tianyuan – two before LGM samples from the same region (Fujimoto *et al.*, 2008; Tan *et al.*, 2013). These observations make the hypothesis that EDAR V370A was under selection during a warm and humid environment less likely, this allele emerged as early as ~19 kya, as observed in the AR19K individual from Amur river (Liu *et al.*, 2021).

Some early Late Paleolithic Eurasian populations before LGM showed high genetic diversity and low mutational load, whereas bottlenecks associated with a reduction of diversity occurred in northern latitudes with the LGM. With the end of the LGM came a more favorable stable climate, which contributed to rapid population growth, migrations and active interactions.

Haplogroup distribution in Paleolithic

The majority of the Y chr haplogroups present in Paleolithic males in Eurasia carry C, F, I, J, K, and R haplogroups whereby the Y chr haplogroups C with sub-haplogroups C1 and CT are mostly found in ancient individuals from the Gravettian period at ~33-21 kya and/or during the before the LGM period (Fu *et al.*, 2014, 2016b; Seguin-Orlando *et al.*, 2014). The Y chr haplogroups C, I, and J are found more abundantly in ancient individuals from the ~17–12 kya Magdalenian and

~21–10 kya Epigravettian periods. One individual from Villabruna ~14 kya carrying the Y chr haplogroup R1b*, which later became common among ancient individuals arriving from the Pontic-Caspian Steppe during the Bronze Age migration events (Fu *et al.*, 2016b; Haak *et al.*, 2015). This indicates an early link between Europe and the western edge of the Steppe Belt of Eurasia.

The study of mtDNA haplogroups revealed higher diversity during the Pre-LGM period in ancient people carrying mtDNA haplogroup U with different sub-haplogroups, as well as haplogroups M and R. Haplogroup M is predominantly found in modern Asian populations and absent in modern European populations, however, it was attributed to one individual, Ostuni1, who lived about 27 thousand years ago in southern Italy, which indicates the possible path and time of the settlement of modern people in Eurasia (Kivisild, 2015; Posth *et al.*, 2016). During the PostLGM period, mtDNA haplogroup lines U2'3'4'7'8'9 are present in samples from Western Europe, but not in samples dating from the Late Glacial period (14-11 kya) or during the transition to the Holocene (Fu *et al.*, 2016b; Mathieson *et al.*, 2018; Posth *et al.*, 2016). The most common mtDNA haplogroup is U5b*, which suggests a population shift after the end of the Late Glacial (Fu *et al.*, 2016b; Posth *et al.*, 2017).

In addition to the diversity of mtDNA and Y chr haplogroups, the researchers are able to study the genetic history of Late Paleolithic European humans and identify at least 5 genetic clusters (El Miron, Malta, Sacurblija, Vestonice, and Villabruna) that are largely dependent on genetic drift (Fu *et al.*, 2016a; Villalba-Mouco *et al.*, 2019). As a result, each cluster was named after the oldest representatives of archaeological cultural complexes.

Hunter-Gatherer in Post LGM period

With the end of the Paleolithic about 15 kya, three main groups of hunter-gatherers formed on the territory of Eurasia, differing in geographical distribution and, of course, in the content of ancestral components. The Western European hunter-gatherer group (WHG), one of

the most important for modern Europeans, was first identified on the basis of individuals from Loschburg and La Brana-1 at the age of 8 ky. In general, WHG individuals belong to the Villabruna cluster, which shares the main mtDNA U5 haplogroup and is associated with the R1b1 Y chr haplogroup (Fu *et al.*, 2016b; Lazaridis *et al.*, 2014; Olalde *et al.*, 2014; Posth *et al.*, 2016).

The next group identified was the Eastern European hunter-gatherers (EHG), originally represented by two samples from Karelia ~7,5-7 kya and Samara ~7.6 kya from the territory of Russia. The representatives of the group have a high content of the ANE component, probably through EHG it manifested itself in modern Europeans (Haak *et al.*, 2015; Lazaridis *et al.*, 2014). The third group was formed as a mixture of WHG and EHG and named Scandinavian hunter-gatherers (SHG) and included specimens such as ~9,6 ky old Motala-12 from Sweden (Haak *et al.*, 2015; Lazaridis *et al.*, 2014, 2016).

A study by Günther *et al.* found significant differences between SHG and WHG and suggests two different early postglacial migrations into Scandinavia from the South and Northeastern part of Eurasia (Günther *et al.*, 2018). Further hunter-gatherers (HG) samples from Southeast Europe and the Baltic region were analyzed and showed a similar pattern of admixture between WHG and EHG depending on their geographic location, with WHG origins predominating during the Mesolithic and decreasing as the transition progressed to the Neolithic (Mathieson *et al.*, 2018; Mittnik *et al.*, 2018).

Individuals from central and western Europe ~14-7,5 kya associated with the Azilian, Epipaleolithic, Epigravettian, and Mesolithic cultures (Villabruna and Loschbour) show connections to present-day Near Easterners and/or East Asians (Fu *et al.*, 2016b; Lipson *et al.*, 2017; Yang *et al.*, 2017). In the Caucasus, ~13-10 ky old individuals from Kotias Klde rock shelter and the Satsurblia Cave sites from Georgia show a close relationship to ancient individuals in West Eurasia, but they also possess the Basal Eurasian ancestry observed in popula-

tions from Europe and the Near East (Lazaridis *et al.*, 2014, 2016). Basal Eurasian ancestry is highest in the Near East, with estimates as high as 66% in Epipaleolithic Natufian ~12-9,8 kya individuals from the Levant, and 44% in a Mesolithic ~9 kya individual from Hotu cave in Iran (Lazaridis *et al.*, 2016).

All West Eurasians sampled from the post LGM period showed some Middle Eastern or Asian ancestry or both regardless of the time of gene flow between East and West Eurasia. Connections with East Asia and the Middle East differ, while Western Eurasians of this time period partially show a connection with East Asians, while all of them show a connection with the Middle East (Fu *et al.*, 2016b). Some ancient individuals of European origin, such as the Karelian specimen of about 8,5 ky old from Russia and the Motala-12 specimen of ~7,5 ky old from Sweden, show a ancestry associated with the ancient inhabitants of Northern Eurasia (Yang *et al.*, 2017). Other Western European specimens from ~14-7,5 kya (Bichon, Loschbour, La Brana-1, Koryosh-1) show an ancestry potentially related to East Asians, although all individuals except the Bichon, are also related to the population associated with the admixture of the Karelian individual (Lazaridis *et al.*, 2016). These results suggest rich and complex history of gene flow between Western and Eastern Eurasia.

In the East Asian mainland and archipelagos, diverse genetic lineages were present during the Neolithic, including populations that carried northern East Asian ancestry, ancient hunter-gatherer ancestry from Southeast Asia associated with the Hòabìnhian culture, at least two distinct southern East Asian lineages, and ancestry lineage best presented by individuals associated with the Jomon culture present in the Japanese archipelago (Wang *et al.*, 2021; Yang *et al.*, 2020; Yang & Fu, 2018). Genetic differentiation between northern and southern East Asians, the earliest branches of present-day East Asians, traces back as early as ~19 ka (Mao *et al.*, 2021; Yang *et al.*, 2020). After the Neolithic, northern East Asian ancestry spread across southern East Asia, with increased genetic affinity to northern East Asians occurring

in southern East Asians over time. South-to-north gene flow can be seen from southern East Asian ancestry identified in northern Han populations and some northern East Asians (Ning *et al.*, 2020; Yang *et al.*, 2020; Yang & Fu, 2018). In northern East Asia, an ~14 ky old individual found in the Amur River Basin is most closely related to the East Asian source found to date that contributed to APS in Siberia; a genetic continuum is maintained in the Amur River Basin to the present day ((Mao *et al.*, 2021)).

Individuals from ~7,7 kyr ago, selected from Chertovy Vorota from the Primorsky region of Russia, show the closest relationship to the Ulchi population in the same region today, which suggests the continuity of populations in this area (Siska *et al.*, 2017). Present-day East Asian populations show remarkable homogeneity relative to ancient samples, both when used as a potential source population for Asian gene flow into Europe and when treated as the admixed population with gene flow from Europe (Yang *et al.*, 2017; Yang & Fu, 2018). East Asians today are more genetically homogeneous than Neolithic East Asians (Yang *et al.*, 2020).

Since ~14 kya, association with present-day Near Easterners can be observed, which remarkable interspersed with the appearance of a HERC2-derived allele (HECT and RLD domain-containing E3 ubiquitin protein ligase-2), that is the primary driver of light eye colour in Europeans appears nearly simultaneously in specimens from Italy and the Caucasus ~14-13 kya (Fu *et al.*, 2016).

Archaeological evidence shows that agriculture spread across the European continent during the Neolithic period, starting from ~8,5 kya, however, it has been argued whether the spread of agriculture came about through human migration, or rather through the lateral transfer of ideas and culture. Ancient DNA analysis has shown that the Neolithic agricultural population of Anatolia largely spread throughout Europe and intermingled with Mesolithic hunter-gatherers in subsequent millennia, demonstrating that the spread of agriculture was moderated by the migration of people, not ideas (Skoglund & Mathieson, 2018).

Neolithic Hunter-Gatherer and Farmers in Europe

The transition from hunter-gatherers to early farmers occurred gradually with the entry of the Early European Farmers (EEF) component from the Eastern Mediterranean Basin (Lazaridis *et al.*, 2014). Undoubtedly, with the adoption of a new culture, there was an admixture with local European HGs with the exception of some regions that did not adopt the EEF component. During the Neolithic, HGs lifestyles in Europe still persisted in northern regions, such as Scandinavia and the Eastern Baltic, although the use of ceramics was already common. HG of Scandinavia of the Pitted Ware culture were similar to Mesolithic SHG and very different from the contemporary Neolithic farmers of the same region, here the spread of farming was blocked for a millennium. In the Eastern Baltic the Comb Ceramic culture individuals were most similar to Mesolithic EHG individuals (Mittnik *et al.*, 2018; Pinhasi *et al.*, 2017; Skoglund *et al.*, 2012, 2014). The introduction of farming reached a 1 ky standstill at the doorstep to Southern Scandinavia before finally progressing into Denmark around 6 kya. Interestingly, in Britain, the story is different, Present-day people from England and Wales have more ancestry derived from EEF than did people of the Early Bronze, the ancestral components were almost completely replaced during the Early Neolithic period with the later arrival of the Neolithic transition in the British Isles (Brace *et al.*, 2019; Patterson *et al.*, 2021).

The transition from HG to farming represents one of the most dramatic shifts in lifestyle and diet in human evolution with lasting effects on the modern world. For millions of years our ancestors relied on hunting and foraging for survival but 12 kya in the Fertile Crescent of the Near East, plant cultivation and animal husbandry were developed (Allentoft *et al.*, 2022). EEF-derived populations dispersed throughout Europe via two major routes: one along the Mediterranean and the other through Central Europe along the Danube river and into Northern Europe (Brace *et al.*, 2019).

The EEF component spread over various regions over 3 thousand years, starting with the

very first penetrations into the Balkans (Lepenski Vir) at about 8,7 kya and ending with 5 kya in Denmark, where the component made its way through Scandinavia for a millennium (Gron *et al.*, 2015; Mathieson *et al.*, 2018). In Eastern Europe maintaining HG lifestyle prevails until about 5 kya without a noticeable contribution of EEF origin, which is consistent with archaeological evidence and a delay in the introduction of agriculture by several thousand years (Allentoft *et al.*, 2022; Saag *et al.*, 2017). In Eastern and Central Europe, the Neolithic period is still characterized by the use of stone culture and/or the presence of ceramics (Mittnik *et al.*, 2018).

Early contact and admixture between 6,9-5,8 kya farming groups from southeastern Europe and Eneolithic groups from the steppe zone determined in today's southern Ukraine, possibly starting in the middle of the fifth millennium Before Common Era (BCE) when settlement densities shifted further north, connecting the lower Danube region with the coastal steppe and Cucuteni–Trypillia groups of the forest-steppe (Penske *et al.*, 2023). Closer to 5 kya, a new component associated with Yamnaya Steppe pastoralists culture appears in Central Eurasia which represents a mixture of at least two HGs ancestries from present-day Russia (Eastern HGs - EHG) and the Caucasus (Caucasus HGs - CHG), Yamnaya cultural complex was spread across the entire Pontic-Caspian-Ural steppe region and expanded westward and eastward (Haak *et al.*, 2015). This step component has become widespread from the steppe throughout Europe thanks to the expansion of the Corded Ware (hallmarked by cord-decorated ceramics) culture during the Late Neolithic and migration was probably linked to conquests and technological innovations such as horseback riding (Allentoft *et al.*, 2015; Haak *et al.*, 2015; Nielsen *et al.*, 2017).

Second wave Neolithic migration just like farming one were followed by resurgences of the previous HG populations: first, during the Middle Neolithic, when HG ancestry rose again after its Early Neolithic decline, and then between the Late Neolithic and the present, when farmer and HG ancestry rose after its Late Ne-

olithic decline. This second resurgence must have started during the Late Neolithic/Bronze Age period itself, as the Bell Beaker and Unetice groups had reduced Yamnaya ancestry compared to the earlier Corded Ware, and comparable levels to that in some present-day Europeans (Haak *et al.*, 2015; Mathieson *et al.*, 2015). Provided evidence for sex-biased admixture between HG and farmers in Europe showed that the Middle Neolithic resurgence of HG-related ancestry in central Europe and Iberia was driven more by males than by females (Brandt *et al.*, 2013; Haak *et al.*, 2015; Mathieson *et al.*, 2015).

Most present-day Europeans can be modelled as a mixture of three ancient populations related to Western hunter-gatherers (WHG), early European farmers (EEF) and steppe pastoralists (Yamnaya EHG + CHG). There are two theories according to which the Indo-European languages came to Europe and the analysis of ancient DNA helps to reveal this issue, as it makes it possible to compare representatives of ancient archaeological sites to assess migrations and mixtures of peoples. The first Anatolian hypothesis speaks of the introduction of Indo-European languages from the territory of Anatolia ~8.5 kya during the period of major Neolithic migrations that changed the structure of European populations (Renfrew, 1987; Bellwood, 2004; Bouckaert *et al.*, 2012).

However, Haak *et al.* it was found that the flow of the steppe component had sufficient power to change the ancestry of central Europeans. It is an alternative theory name 'steppe hypothesis', which proposes that early Indo-European speakers were pastoralists of the grasslands north of the Black and Caspian Seas, and that their languages spread into Europe after the invention of wheeled vehicles (Anthony, 2007). The steppe component provide at least some of the Indo-European languages in Europe by documenting a massive migration ~4,5 kya associated with the Yamnaya and Corded Ware cultures, which are identified by proponents of the steppe hypothesis as vectors for the spread of Indo-European languages into Europe (Mallory, 1991; Haak *et al.*, 2015). The steppe ancestry in South Asia, which contributed up to

30% of the ancestries of present-day groups in the region, provides additional evidence for the spread of Proto-Indo-European languages through the steppe expansion (Narasimhan *et al.*, 2019).

The Yamnaya expansion also crossed the Caucasus, and by ~4 kya, Armenia had become an enclave of low but pervasive steppe ancestry in West Asia, where the patrilineal descendants of Yamnaya men, virtually extinct on the steppe, persisted. The Armenian language was born there, related to Indo-European languages of Europe such as Greek by their shared Yamnaya heritage (Haak *et al.*, 2015). Neolithic Anatolians were descended from both local HG and Eastern populations of the Caucasus, Mesopotamia, and the Levant. By ~6 kya Anatolians became more genetically homogeneous, a process driven by the flow of Eastern ancestry across the peninsula. All ancient Indo-European speakers can be traced back to the Yamnaya culture, whose southward expansions into the Southern Arc left a trace in the DNA of the Bronze Age people of the region. However, the link connecting the Proto-Indo-European-speaking Yamnaya with the speakers of Anatolian languages was in the highlands of West Asia, the ancestral region shared by both (Haak *et al.*, 2015; Lazaridis *et al.*, 2022).

As extensive as the Yamnaya culture, there was a Bell Beaker Complex on the territory of Western Europe. The oldest radiocarbon dates associated with goblet pottery date back to ~4,7 kya in Atlantic Iberia, which is interpreted as evidence that the complex originated in this region (Olalde *et al.*, 2018). Representatives of the steppe component ~4,6 kya reached the British Isles at the period of spreading of the Bell Beaker Complex defined by assemblages of stylized bell-shaped grave goods, replacing within a few hundred years majority (90%) of the local gene pool (Olalde *et al.*, 2018). The genetic evidence suggests that this process was mostly driven by male individuals because in both the British Isles and Iberia, almost all Late Neolithic Y chromosomes were replaced by Eastern European steppe-related Y chromosomes (Goldberg *et al.*, 2017; Olalde *et al.*, 2018).

The strongest signal of selection is at the SNP (rs4988235) responsible for lactase persistence in Europe (Bersaglieri *et al.*, 2004). The earlier reliable lactase persistence individual is a Ukrainian Eneolithic individual ~6 kya, as previously noted, which presents a mixture of Anatolian farmers and steppe ancestry (Mathieson *et al.*, 2018). T allele detected in a central European Bell Beaker sample individual I0112 dated to ~4,5 kya (Allentoft *et al.*, 2015; Gamba *et al.*, 2014). It is difficult to infer whether lactase persistence originated in Yamnaya-associated cultures or in European farmers but it quickly spread across Eurasia during the late Bronze Age, which is concomitant with the expansion of Yamnaya-associated cultures. This suggests that steppe populations might have contributed to the spread of the T allele across and outside Europe (Segurel *et al.*, 2020).

Haplogroup distribution in Neolithic

Initial studies focused on the mtDNA haplogroup diversity from various geographical locations in Eurasia and found a higher genetic diversity mainly in the haplogroup lineages H, HV, J, K, N1a, U, V, W, and X (Bramanti *et al.*, 2009; Brandt *et al.*, 2013; Brotherton *et al.*, 2013; Hervella *et al.*, 2015; Lacan *et al.*, 2011; Malmström *et al.*, 2009; Rivollat *et al.*, 2016; Sampietro *et al.*, 2007; Szécsényi-Nagy *et al.*, 2015; Wolfgang Haak *et al.*, 2005). Interestingly, based on the first mtDNA haplogroup studies, the admixture events between local hunter-gatherers and the Early European farmers were rejected because of the high differences between the assigned haplogroups to the local hunter-gatherers and the local farmers (Bramanti *et al.*, 2009). However, mtDNA is a small part of the human genome inherited by the maternal line and lacks recombination, which restricts the generalisation to a population scale.

The most frequent Y chr haplogroups found in ancient Neolithic farmers are C, F, G, H, I, and R (Battaglia *et al.*, 2009; Haak *et al.*, 2010; Keyser *et al.*, 2009; Lacan *et al.*, 2011; Rootsi *et al.*, 2004); however, the latter is not associated with R1b (Kivisild, 2017). Among these,

haplogroup G2a~ was most common in Early European farmers suggesting homogeneity of paternal lineages among early farmers but is rarely presented in present-day Europeans (Lacan *et al.*, 2011; Szécsényi-Nagy *et al.*, 2015).

Aside from the arrival of the Steppe-related ancestry component in Western Eurasia, researchers have found an almost total replacement of the most common Y chr haplogroups from the Neolithic period by the Y chr haplogroup lineages R1b* and R1a*, the latter of which had been unknown in Western Eurasia until the Early Bronze Age period (Haak *et al.*, 2015; Underhill *et al.*, 2014). The Y chr haplogroup R1b* was found in individuals dated to the Palaeolithic and Mesolithic (Fu *et al.*, 2016b; Mathieson *et al.*, 2018). The turnover of the Y chr haplogroups was thoroughly studied in individuals dated to the Chalcolithic/Bronze Age transition from the 26 British Isles and the Iberian Peninsula (Olalde *et al.*, 2014; Villalba-Mouco *et al.*, 2021) and archaeological sites located closely together (Papac *et al.*, 2021).

Eastern Eurasian Bronze Age

The Eastern Steppe was populated by hunter-gatherers of Ancient Northeast Asian (ANA) and Ancient North Eurasian (ANE) ancestry during the mid-Holocene and then shifted to a dairy pastoralist economy during the Bronze Age. During the Bronze Age, the multi-phased introduction of pastoralism drastically changed lifeways and subsistence on the Eastern Steppe (Honeychurch, 2015; Kindstedt & Ser-Od, 2019). Bronze Age in Asia is equally dynamic and characterized by large-scale migrations and population replacements.

Migrating Yamnaya steppe herders, equipped with carts and domestic livestock, appear to have first introduced ruminant dairy pastoralism ~5 kya but surprisingly had little lasting genetic impact, unlike in Europe (Allentoft *et al.*, 2015; Haak *et al.*, 2015; Mathieson *et al.*, 2015; Wilkin *et al.*, 2020). The Early Bronze Age Afanasievo culture in the Altai-Sayan region of Russia is genetically indiscernible from Yamnaya, confirming also an eastward expansion across the steppe (Allentoft *et al.*, 2015). This steppe-related ancestry spread into

the eastern steppe in present-day central Mongolia, but not further eastward (Jeong *et al.*, 2020). In Bronze Age Central Asia, the ancestries of the Bactria-Margiana Archaeological Complex, found in present-day Uzbekistan and Turkmenistan), were derived mainly from Iranian farmers and Anatolian farmers with minor contributions from West Siberian HG (Narasimhan *et al.*, 2019).

By the Middle/Late Bronze Age, ruminant dairy pastoralism had been adopted by populations throughout the Eastern Steppe, regardless of ancestry, and this subsistence has continued, with the additions of horse milking in the LBA and camel milking in the Mongol period to the present day (Bat-Oyun *et al.*, 2015; Kindstedt & Ser-Od, 2019; Wilkin *et al.*, 2020). However, there is no evidence of selection for lactase persistence over this 5,000-year history, despite the repeated introduction of this genetic trait by subsequent migrations of groups from the west. This suggests a different trajectory of lactose adaptation in Asia that to date remains unexplained (Jeong *et al.*, 2020). But it is not clear why Central Asian populations seem to have adapted culturally and possibly by gut microbiota adaptations while North Europeans and Africans have adapted genetically. Possible explanations include the composition of the herds with cattle possibly providing larger quantities of milk, ecological differences and/or cultural preferences (Segurel *et al.*, 2020).

In South Asia, the genome of an ~5 ky old individual from the Indus Valley Civilization, one of the first extensive urban societies of the ancient world, presents a population that is the largest ancestry source for present-day South Asians (Shinde *et al.*, 2019). The individual fits as a mixture of people related to ancient Iranians in the largest component and Southeast Asian HG, a unique profile that matches ancient DNA from 11 genetic outliers from sites in Iran and Turkmenistan in cultural communication with the Indus Valley Civilization. Later, related population mixed with northwestern groups carrying steppe ancestry and southeastern groups, forming the Ancestral North Indians and Ancestral South Indians. The mixture of ANI and ASI led to the main genetic cline in

South Asia today (Narasimhan *et al.*, 2019; Shinde *et al.*, 2019).

In Mongolia, as mentioned above, major genetic turnovers are associated with the expansion and migration of steppe herders, such as the Afanasievo people, and dairy pastoralists such as the Xiongnu and Mongols (Jeong *et al.*, 2018, 2020). Particularly, Neolithic populations carried almost complete East Asian ancestry, and steppe pastoralist ancestry was introduced with a pastoralist expansion ~5 kya (Jeong *et al.*, 2020; Wang *et al.*, 2021). Later ~3,4 kya, Mongolian populations showed a mix of ancestries derived from individuals associated with the Yamnaya culture and European farmers (Wang *et al.*, 2021). Individuals associated with the Xiongnu confederate, a nomadic confederation of the eastern steppes, were established ~2 ka and carried a genetic of populations from Mongolia and the surrounding regions, whereas historical Mongols have a high level of eastern Eurasian ancestry similar to those of present-day Mongolic-speaking populations (Jeong *et al.*, 2020).

During the Middle/Late Bronze Age the formation of a tripartite genetic structure on the Eastern Steppe characterized by the continuation of pre-Bronze Age ANA ancestry in the east and a cline of genetic variation between pre-Bronze Age ANA-ANE ancestry in the north and increasing proportions of a new Sintashta-related WSH ancestry in the west. The Sintashta, a western forest steppe culture with genetic links to the European Corded Ware cultures, were masters of bronze metallurgy and chariotry, and the appearance of this ancestry on the Eastern Steppe may be linked to the introduction of new especially horse-related technologies (Anthony, 2008; Mathieson *et al.*, 2015).

Deer Stone-Khirigsuur Complex sites in particular show widespread evidence for horse use in transport and perhaps even riding and genetic analysis has demonstrated a close link between these animals and the Sintashta chariot horses (Fages *et al.*, 2019; Timothy *et al.*, 2015). The strong east-west genetic division among Bronze Age Eastern Steppe populations at this time was maintained for more than a mil-

lennium and through the end of the EIA, when the first clear evidence for widespread horseback riding appears and the heightened mobility of some groups, notably the eastern Slab Grave culture began to disrupt this structure (Honeychurch, 2015). Eventually, the three major ancestries met and mixed, and this was contemporaneous with the emergence of the Xiongnu empire. The Xiongnu are characterized by extreme levels of genetic heterogeneity and increased diversity as new and additional ancestries from China, Central Asia, and the Western Steppe (Sarmatian-related) rapidly entered the gene pool (Jeong *et al.*, 2020).

Eurasian steppe Iron Age

Towards the end of the Bronze Age in Asia, Andronovo was replaced by the Karasuk, Mezhevskaya, and Iron Age cultures which appear multi-ethnic and show gradual admixture with East Asians corresponding with anthropological and biological research (Bendezu-Sarmiento, 2004). Ancestral component that is maximized in the north Siberian Nganasan population becomes visible from the 2nd millennium Before Common Era (BCE) onwards in the eastern steppe (Okunevo, Karasuk, Mezhevskaya). This component appears later in all Iron Age populations but with significantly higher levels in the eastern steppe zone than in the West (Unterländer *et al.*, 2017). However, Iron Age individuals from Central Asia still show higher levels of West Eurasian ancestry than contemporary populations from the same region (Allentoft *et al.*, 2015).

The early Iron Age cultures of Inner Asia occurred at a time of new technological advances, including the development of compound bows and the beginning of iron metallurgy, used to make items such as arrows and riding equipment (Honeychurch, 2015). These cultures include the widespread Slab Grave culture, prevalent in Mongolia as well as East Baikal and parts of northern China, and the Sagly/Uyuk and Pazyryk cultures in the Sayan-Altai and northwestern Mongolia. Genetic components of samples from these three groups represented by Ancient Northeast Asian and no more than one third of the time West Eurasian uniparental

components. These latter cultures were part of a broader “Scythian” cultural phenomenon that spread into eastern Kazakhstan and across the Eurasian steppes, and which was related to Saka groups of northern Iran and the Tian Shan mountains. Together with the technological advancements of the Early Iron Age came increased long-distance (Ventresca Miller & Makarewicz, 2019).

During the first millennium BCE, nomadic people spread over the Eurasian Steppe from the Altai Mountains over the northern Black Sea area as far as the Carpathian Basin across the Eurasian steppe, covering an area over 3,500 km wide (Parzinger, 2004). The classical Scythians, who had lived in the North Pontic region since the seventh century BCE, are the most famous among them due to the early reports in the Histories of Herodotus (Herodotus, 1987). The origin of the widespread Scythian culture has long been debated in Eurasian archaeology. The northern Black Sea steppe was originally considered the homeland and center of the Scythians but also formulated the hypothesis of a Central Asian origin (Bashilov, 2000).

Damgaard *et al.* observed a clear separation between two groups of Iron Age Scythians: the Hungarian Scythians and the Inner Asian Sakas that separates the three populations associated with the ‘Tagar’ culture of southern Siberia, the ‘Central Sakas’ of the central steppe, most of whom have been described as belonging to the Tasmola culture, and the ‘Tian Shan Sakas’ of the Tian Shan mountain range (De Barros Damgaard *et al.*, 2018). These differences reflect the confederal nature of the Scythian organization. Genomic inference shows that the Scythians in the east and west of the steppe zone can best be described as a mixture of Yamnya-related ancestors and an East Asian component. Demographic modelling suggests independent origins for eastern and western groups with ongoing gene-flow between them, plausibly explaining the striking uniformity of their material culture (De Barros Damgaard *et al.*, 2018; Krzewińska *et al.*, 2018; Unterländer *et al.*, 2017).

In general, gene-flow or migration over the Eurasian Steppe belt carried East Asian/North Siberian ancestry from the East to the West as far

as the Don-Volga region in southern Russia. This flow between eastern and western Eurasia seems to have been more intense during the Iron Age than in modern times, which is congruent with the view of the Iron Age populations of the Eurasian Steppe being highly mobile semi-nomadic horse-riding groups (Unterländer *et al.*, 2017).

Although distance from Altai is the main contributor to the proportion of Altaian ancestry in Scythians and Sarmatians, ancient populations preceding the Scythians (e.g., Yamnaya) exhibit less Altaian ancestry than would be predicted by this geographic correlation, indicating that Scythians have a higher eastern affinity than preceding steppe populations. This lends support to at least some degree of demic diffusion being involved in the spread of the Scythian cultural and military dominance (Järve *et al.*, 2019).

Concerning the legacy of the Iron Age nomads, modern human populations with a close genetic relationship to the Scythian groups are predominantly located in close geographic proximity to the sampled burial sites, suggesting a degree of population continuity through historical times. Contemporary descendants of western Scythian groups are found among various groups in the Caucasus and Central Asia, while similarities to eastern Scythian are found to be more widespread, but almost exclusively among Turkic language speaking (formerly) nomadic groups, particularly from the Kipchak branch of Turkic languages.

Conclusion

By providing genetic data from different time periods, ancient DNA has revealed the admixture of modern humans with previously unknown archaic populations, uncovered the emergence of key adaptive mutations, shed light on the long-running debate about our recent evolutionary past, and continually added new evidence to uncover the genetic history of past and present human populations on over the past few tens of thousands of years.

Genetic and archaeological evidence suggests that humans explored, survived, and populated various environments, including extremely harsh arctic conditions. Detailed recon-

struction of the past, especially for challenging conditions such as those encountered during the LGM, will aid in revealing human adaptation to the extreme environment.

Acknowledgments

This work has been supported by the grants of the Russian Science Foundation, RSF 22-24-00681.

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