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Paleogenetic Studies of Migration Processes in Eurasia

Migration processes played a key role in shaping the cultural and genetic landscapes in Eurasia. Significant progress in the field of migration studies in recent years is associated with the development of methods for studying ancient DNA, making it possible to reach a new level of understanding the population-genetic aspects of ancient migrations and significantly supplementing the evidence of paleoanthropology and genetics of modern populations, but not replacing these areas. A key challenge is the correct comparison of processes accompanying migrations at the population genetic level and at the level of material culture. The article highlights current methods used in studying ancient DNA, from the traditional analysis of individual genetic markers to the genome-wide analysis by high-throughput sequencing. Approaches to the study of ancient migrations and to the objective reconstruction of the genetic profile of populations and its dynamics in time and space are assessed. Special attention is paid to the problem of representative sampling in the study of migration processes using paleogenetic methods, and possible strategies for selecting the materials most adequate to the tasks of the study. Ways of enhancing the efficiency of the diachronic approach in reconstructing the genetic history of populations are discussed. Possible prospects of paleogenetic studies are evaluated, including the transition to more detailed reconstructions of local migration processes.

Keywords: *Paleogenetics, migrations, mitochondrial DNA, Y-chromosome, nuclear genome*

Introduction

Migrations have played the most important role in the history of humanity. The key migration events that have shaped the genetic landscape of a substantial part of the modern world population were taking place in Eurasia: from the original out-of-Africa dispersal of *Homo sapiens* to the mass movement of numerous groups of early nomads. The study of the genetic structure of modern populations by ethnogenomic techniques was essential for reconstruction of the main stages and routes of peopling of Eurasia and for evaluating the role of isolation and consequent migrations in shaping the gene pools of populations from various regions (Jobling, Tyler-Smith, 2003; Torroni et al., 2006; Underhill, Kivisild, 2007). Reconstructions of past events based on their results (i.e. the genetic structure of modern populations) usually take into account several possible alternative scenarios of every event. The same processes can be studied independently by archaeologists and biological anthropologists employing ancient artifacts and remains *per se*. But the development of paleogenetics provided for the spread of ethnogenomic techniques for studying ancient populations, thus for combining all these disciplines into a single complex approach and reaching a new level in reconstructing ancient migrations.

The role of paleogenetics is often to test the hypotheses based on the results of archaeological, anthropological, and ethnogenetic studies. Studying a minimal number of specimens for reconstructing the most large-scale migrations has long been the main strategy of paleogeneticists. Successful examples of such an approach are the series of papers devoted to the contacts of anatomically modern humans (AMH) colonizing Eurasia with other late hominins (Reich et al., 2010; Pääbo, 2015; Krause, Pääbo, 2016; Vernot, Pääbo, 2018), dynamic of the European genetic landscape during the Last Glacial Maximum (LGM) and the "Neolithic Revolution" (Haak et al., 2010; Pinhasi et al., 2012; Lazaridis, 2018; Liu et al., 2021), large-scale Eurasian migrations in the Bronze (Haak et al., 2015; Allentoft et al., 2015) and Early Iron (Unterländer et al., 2017; Krzewińska et al., 2018) ages. The outcomes of those works can be mainly viewed as preliminary reconstructions. Unfortunately, such reconstructions do not always grow up into a series of more localized and detailed studies. But the modern level of the development of paleogenetic techniques makes obtaining large amounts of data on the genomics of ancient populations unprecedentedly accessible. In this study, we set out to discuss the necessity of the transition to systematic studies of the genetic structure of local populations of different areas of Eurasia, employing existing paleogenetic tools. The main attention is paid to the principals of forming representative samples that take into account the archaeological and anthropological context of the studied data, as well as the strategies of genotyping and interpretation of the results, including perspective approaches of the field.

Human migrations, and how they are studied

At present, *Homo sapiens* is a cosmopolitan species populating almost all inhabitable areas of the Earth. This means an important role the human migrations have played in acquiring those huge spaces with variable natural and climatic conditions. Importantly, the history of our species presents many cases of repopulation of some regions, for instance, the peopling of Central and northern Europe, which followed the retreat of glaciers after the LGM.

After the initial settling of a geographic area, population migrations remain active. As a result, widening of the inhabited area is replaced with contacts between groups from its various parts, the populations previously isolated due to geographic and other factors. At least two groups take part in such processes: migrants, i.e. the group changing its location, and the autochthonous population of the receiving territory. In such cases, a robust genetic study must not only postulate the fact of migration but also reconstruct the nature of the ethnocultural interplay between migrants and autochthons. The population genetic pattern of this contact determines the effect that the migration has had on the genetic history of the region.

The design of the studies addressing migrations should be based on an account of the archaeological knowledge about the area of interest, including the stages of regional development and possible migratory events. From the archaeological point of view, such events are typically marked by the appearance of innovations (in a broad sense) in the material culture. This always raises the question of if the spread of the innovation was or was not associated with human migration (Meiggs, Freiwald, 2018).

As any migratory event evinces a relocation of a population, being thus a population-demographic process, it can only be directly assessed via studying the biological remains of the respective migrating group. Comprehensive study of human remains by numerous methods and approaches delimits the field of bioarchaeology (Ibid.). The main bioarchaeological disciplines addressing human migrations are physical anthropology, paleogenetics, stable isotope and microelement analyses; the two former are the most effective at the population level. Notably, these disciplines employ systems of variables (markers) not directly connected with each other, thus providing independent views on the migratory events and their reconstruction.

The effectiveness of the use of paleogenetic methods for reconstructing ancient migratory processes at the population level will depend on two main factors: correct selection of study specimens (forming representative samples); choice of informative genetic markers, genotyping method, and an appropriate strategy of interpretation of the results.

Forming representative samples of specimens for studying migrations via paleogenetic techniques

A full-scale reconstruction of the population-genetic aspect of a migratory event, using paleogenetic methods, implies solving several interrelated tasks: 1) fixation of changes in the genetic composition of a population potentially connected to an influx of migrants; 2) localization of the source of the gene flow; 3) determination of the scale of the flow, sex composition of the immigrant group, pattern and intensity of the genetic contacts between the migrant and aboriginal groups during the period of migration; 4) evaluation of the genetic legacy of the migrants in the region at later chronological stages. All these tasks together can be solved only seldom, mainly owing to the absence of the necessary number of skeletal specimens suitable for an analysis by paleogenetic methods. A comprehensive historical reconstruction requires information on the genetic structure of a series of groups of ancient populations, including those inhabiting the region before the hypothetical migratory event (in order to detect the change in the gene pool due to the migration), samples of the migration period (might include both migrants and aborigines), and the groups that emerged after the active phase of the migration had ended. Such a diachronic series of samples from a particular region makes possible the most informative analysis, leading to a reconstruction of the genetic history of the region, including the history of migrations.

In order to determine the source of migration, the genetic components associated with the immigrants should be compared with some specific fragments of the gene pool of the population potentially ancestral to the migrants. The circle of such source groups and regions can be substantially restricted based on the archaeological and anthropological knowledge regarding the direction of the ethnical and cultural contacts of studied populations. As paleogenetic data for many regions of Eurasia are scarce, such a comparative analysis employing the groups suggested by archaeologists or anthropologists requires a special study. Thus, a preliminary step is to compare new genetic data with samples and populations studied earlier. Such a "compelled" approach to sampling reference specimens, available but not necessarily relevant, often provokes skepticism of archaeologists and anthropologists towards the results obtained by paleogeneticists. These preliminary results, thus, imply verification and substantial refinement through consequent targeted additional research. As an example, the conclusion suggesting that some groups of the Yamnaya culture were the source of the genetic influence from the steppe nomads of Eastern Europe on the populations of the neighboring regions during the Early Bronze Age (Allentoft et al., 2015; Haak et al., 2015) can only be viewed as evidence of the impact from those nomads in a broader sense. This means that in fact other populations from the same area, genetically close to the Yamnaya people but not yet studied, might be the source population. A similar situation has arisen with the use of the Altaian Pazyryk culture and "classic" Scythians from the Northern Black Sea region as an "etalon" for the evaluation of the migratory influence of the early nomads from the eastern and western parts of the Eurasian Steppe Belt, respectively (Unterländer et al., 2017; Krzewińska et al., 2018). The problem with such an approach is that the early nomads from this area were extremely diverse.

In the situation of the scarcity of studied samples of ancient populations, the data on the gene pool of modern native groups, which are well studied in most regions, can be useful for a crude localization of the source of migration. The methods of phylogeny and phylogeography can help to arrive at some correct conclusions even with a diachronic comparison and to determine the role of ancient immigrants in the later genetic history of a region.

Many Eurasian areas are poorly studied from an archaeological point of view. Another complication hampering obtaining representative samples of specimens is the poor preservation of DNA in some climatic conditions: in Eurasia, genetic material is typically better preserved at higher rather than lower latitudes (excluding highland areas), while many key migratory events were taking place in the latter. Some successful (due to the development of methods) paleogenetic studies based on samples from such "unfavorable" areas were published, but in general, the misbalance in the representation of paleogenetic data between northern (temperate) and southern parts of Eurasia is expected to persist in the future.

When selecting specimens, it is crucial to include in the sample only those individuals whose association with the ancient population of interest is doubtless. Archaeological complexes with clear cultural attribution are found alongside questionable interments lacking dating inventory, even at the same burial site. Besides correct cultural attribution, direct dating of remains is becoming a standard for large-scale paleogenetic studies, in particular dealing with multilayer or syncretic sites.

The scarcity of studied paleogenetic data available for the reconstruction of migration events might be overcome via the development of statistical methods for incomplete sequences, and building respective models (see, e.g., (Loog et al., 2017)); vie careful accounting for the results obtained by specialists of related disciplines, i.e. the use of several independent lines of evidence (Meiggs, Freiwald, 2018); and via deeper and more flexible analysis of the spectrum of genetic markers (Orlando et al., 2021).

Genetic markers for the study of migration events, strategies of genotyping and interpretation of the results

The structure of the gene pool of human populations acquires its specific features through the combined action of such factors as mutations, genetic drift, relative genetic isolation versus extensive genetic exchange with other groups, natural selection, bottlenecks (i.e. the periods of a rapid decrease followed by a rapid increase of population size), and founder effects. Immigrants bring the genetic components typical for the population of their origin to the gene pool of autochthonous groups. How difficult it is to detect a gene flow largely depends on the level of genetic differentiation between the migrant and aboriginal groups: the stronger are the differences, the easier the novel genetic components in the autochthonous population can be detected. As the pattern of genetic variation in Eurasia is mainly clinal, the following rule is generally held: the farther is the source of migration from its final point, the more genetically distinct are immigrants in respect to aboriginal groups. Another factor of a successful detection of the genetic consequences of a migration event is the quantity of migrants: the higher it is, the easier the influence of the incoming group can be detected. These two aspects are interrelated, i.e. the more genetically distinct the immigrants are in respect to the autochthons, the smaller-scale migrations might be traced via paleogenetic methods. The first examples of successful detection of ancient migrations are the advent of early agriculture in Europe from the Near East during the “Neolithic Revolution”, and the most massive Bronze Age migrations (Allentoft et al., 2015; Haak et al., 2010; Pinhasi et al., 2012; Lazaridis, 2018).

The assessment of differences in the genetic structure of populations strongly depends on the genomic tools employed. Using modern paleogenetic techniques, both the spectrum of the molecular markers analyzed and the depth of the analysis of each of those markers can be variable. Methods of the polymerase chain reaction (PCR) make it possible to analyze the structure of only a relatively small number of markers for each sequence of ancient DNA (Pääbo et al., 2004). But the advent of the Next-Generation Sequencing (NGS), whereas a huge number of DNA fragments are read simultaneously, made the informative value of ancient DNA much closer to modern data. An analysis of a conventionally “full” genome of an ancient individual became possible (Stoneking, Krause, 2011; Veeramah, Hammer, 2014; Orlando et al., 2021). Thus, two strategies of paleogenetic research of the population gene pool can be discerned: analysis of single markers providing the highest phylogenetic and phylogeographic resolution (Underhill, Kivisild, 2007); and genotyping of numerous phylogenetically independent markers with a limited phylogenetic and phylogeographic value each, followed by a summary interpretation based on sophisticated mathematical models

Phylogenetically and phylogeographically informative loci as a tool for studying ancient human migrations

Phylogenetically informative are the markers for which a reconstruction of a complete genetic history, starting from the common ancestor and to the modern variety of structural variants, is possible. This history is typically visually represented in genetic studies in the form of phylogenetic trees. In order to be used for the reconstruction of migrations, such markers must be highly variable, and thus, phylogeographically informative. This means that the structural variants combined into a phylogenetic tree must have specific geographic distributions and differ in populations of various origin and locations.

Among the most phylogeographically and phylogenetically informative are the uniparental markers: mitochondrial DNA, passed only through the maternal line (Torroni et al., 2006), and the Non-recombining Region of Y-chromosome (NRY), which is only present in male genomes and passed through the paternal line (Underhill, Kivisild, 2007). The main features of these markers as paleogenetic tools for the reconstruction of ancient migrations, as well as advantages and disadvantages of the markers, have been outlined elsewhere (Torroni et al., 2006; Underhill, Kivisild, 2007; Kivisild, 2017). Importantly, owing to the high mutation rate and the absence of recombination, mtDNA and Y-chromosome greatly outperform single autosomal nuclear phylogenetic markers from the point of view of the phylogeographic and phylogenetic resolution (Underhill, Kivisild, 2007; Jobling, Tyler-Smith, 2017). Comprehensive global phylogenetic trees reflecting the relationships between all the currently known structural variants, as well the classification of phylogenetic clusters, were built for mtDNA and Y-chromosome (Karafet et al., 2008; Oven, van, Kayser, 2009). In addition, a great amount of data on the structure of the gene pool of uniparental markers in modern human populations has been acquired. There is much less data regarding ancient groups of most regions though.

An important advantage of mtDNA and the Y-chromosome for studying ancient migrations is the opportunity to reconstruct their sex-specific patterns, e.g. to evaluate the proportion of males and females among immigrants and their relative involvement in the gene exchange with aborigines. The list of disadvantages includes a higher (as compared to the autosomal nuclear genome) susceptibility of uniparental markers to genetic drift, and a high mutation rate in mtDNA. Taken together, these features lead to independent emergence of the same structural variants, thus hampering the reconstruction of migrations that occurred more than several dozens of thousands of years ago (Underhill, Kivisild, 2007). Also, a much larger sample is required to reliably represent the mtDNA and the Y-chromosome diversity in a population as compared to a "whole-genome" analysis of autosomal markers (Veeramah, Hammer, 2014).

MtDNA. This is the first marker used for reconstruction of the genetic past of human populations, including the justification of African origins of the AMH (Cann, Stoneking, Wilson, 1987) and establishing the routes of his dispersal in Eurasia. The diversity of mtDNA markers was explored in the very first paleogenetic studies addressing the genetic structure of ancient populations (Pult et al., 1994). The methods have been developing from assessing the status of single loci and sequencing the most informative fragments to the analysis of whole mitochondrial genomes (mitogenomes) (Torroni et al., 2006; Underhill, Kivisild, 2007). Great amounts of data on the mtDNA variation in modern human populations were acquired, and its comprehensive global phylogeny was built before the advent of NGS.

Similar data were gradually obtained for ancient populations from various Eurasian regions as well. The first large-scale research of diachronic mtDNA samples was devoted to the European population (Pinhasi et al., 2012; Brandt et al., 2013) and the Bronze Age groups from the forest-steppe zone of Western Siberia (Molodin et al., 2012). The analysis of whole mitogenomes of ancient individuals has significantly simplified with the advent of the NGS techniques (Veeramah, Hammer, 2014). But the leading world laboratories have switched to the study of the nuclear genome, which has led to a decrease in the rate of targeted research of whole mitogenomes of ancient Eurasian populations. At present, the mitogenomes are commonly obtained as "byproducts" of some types of analysis of autosomal nuclear data. The number of these is typically insufficient for a comprehensive assessment of the structure of the mtDNA gene pool in a population. Thus, the great potential of exploring large-scale diachronic samples of mtDNA specimens remains unrealized for most regions of Eurasia.

Research of the interaction of *H. sapiens* with other hominins during his initial dispersal in Eurasia has clearly shown the specifics of mtDNA as a marker. The study of the Neanderthal mtDNA variation was not able to fully resolve the question of the participation of that species in the formation of the gene pool of modern humans: the high susceptibility of the haploid markers to the influence of stochastic factors, i.e. genetic drift, led to a complete absence of evidence of hybridization with Neanderthals in the modern human mitogenome. It is thus generally believed that the chronological resolution of mtDNA markers is insufficient for tracing such ancient genetic events. Based on the mtDNA data, it was only possible to suggest that if hybridization with Neanderthals even occurred, it had only a very limited effect on the modern gene pool (Serre et al., 2004). This notion was then confirmed by autosomal data. Later, a new hominin species—Denisovans—was discovered via an analysis of mtDNA (Krause et al., 2010). A new prospective trend in employing mtDNA for the reconstruction of the early stages of human history in Eurasia became the study of mitogenomes from cave sediments of the sites occupied by ancient hominins. An analysis of diachronic samples of such specimens from several caves permits tracing the periods of their occupation and the genetic turnover due to migrations, even for sites lacking skeletal material (Vernot et al., 2021).

Non-recombining region of the Y-chromosome (NRY). This region is also potentially one of the most phylogenetically informative loci in the human genome (Underhill, Kivisild, 2007; Kivisild, 2017).

The value of NRY is determined by the large length of the non-recombining region and the presence of two types of polymorphic sites: slowly evolving single nucleotide polymorphisms (SNP) and rapidly changing short tandem repeats (STR). The rich informative content of the Y-chromosome is also explained by the patrilocality of many human populations (Burton et al., 1996), which led to the long-term persistence of their phylogeographic structure according to the pattern of the male gene pool in Eurasia.

The study of the male gene pool variation in the modern human population has lagged behind as compared to mtDNA, due to the difficulties associated with the search for phylogenetically informative loci in the Y-chromosome (Karafet et al., 2008). A parallel analysis of the two types of polymorphisms permitted building a common phylogeny and a common classification of variants (based on SNPs), and assessing the diversity of the variants inside phylogenetic clusters, as well in gene pools of single populations (STR) (Ibid.; Underhill, Kivisild, 2007). The information about the diversity of structural variants in world-wide modern populations was collected, and the main routes of human dispersal in Eurasia were reconstructed. One of the factors stimulating collection of the data on the Y-chromosome is its validity for forensic science (Kayser, 2017). However, owing to the large length of NRY (unlike mtDNA), only a part of phylogenetically informative markers of the Y-chromosome were discovered before the advent of NGS. Even the researchers of modern populations have been dealing only with a part of the existing structural diversity of NRY. Only a very limited amount of data was obtained for the Y-chromosome in ancient populations of Eurasia, since its analysis by PCR-based methods is complicated and can be only carried out using specimens with relatively good DNA preservation (Kivisild, 2017). Using NGS, it is possible to substantially widen the Y-chromosome phylogeny for modern data through the detection of numerous previously unknown phylogenetically informative SNPs (Batini, Jobling, 2017; Poznik et al., 2016).

In general, owing to the absence of systematic research on the NRY variation in ancient samples because of the marker's features mentioned above, the accumulation of paleogenetic data for the Y-chromosome using NGS is progressing very slowly. The paleogenetic approaches widely employed at present—low-coverage sequencing of whole nuclear genomes, and the SNP-based whole-genome analysis of ancient individuals—provide only limited phylogenetic information regarding the Y-chromosome structure, and only for some specimens. The number of the latter is too low to obtain a representative population picture for the male gene pool. In this light, targeted research of the NRY variation, employing available PCR- and NGS-based methods, seems necessary. The development of deep sequencing of ancient Y-chromosomes is also important from the point of view of refining the phylogeny of clusters, which may not be presented in modern human populations. Thus, the potential of the study of NRY from ancient specimens for reconstructing migrations remains poorly realized at present.

Autosomal nuclear markers. Every individual has two copies of the autosomal part of the nuclear genome received from both parents, and contains the main part of the whole genetic information of an organism. Owing to recombination, autosomes are not a single phylogenetic marker but rather a system of such markers, each with its own independent evolutionary history. A phylogenetic tree can thus only be built for relatively short fragments of autosomal nuclear DNA, with a low probability of recombination that would have disrupted a continuous phylogeny. The structural diversity of single nuclear loci is much lower as compared to mt DNA and NRY (Veeramah, Hammer, 2014), which decreases their phylogenetic and phylogeographic resolution.

The autosomal nuclear genome, as a huge set of relatively independently evolving markers with their own share of phylogenetic information, is less susceptible to the influence of such factors as genetic drift. This means that even genetic events from the distant past have more chance of leaving traces in a population than mtDNA and the Y-chromosome (Ibid.). The signs of new genetic components received from migrants can persist in the nuclear genome of the descendants for a long time. While the structure of mtDNA and the Y-chromosome of an individual reflect his maternal and paternal genetic history only, the composition of the components of the autosomal nuclear genome represents the population genetic processes of multiple intersecting ancestral lineages. Therefore, even an individual nuclear genome is, to some extent, a reflection of the population history of the group to which the individual belongs. A consequence of this is that fewer specimens are required for evaluating the gene pool of a group as compared to studying mtDNA or NRY. The genetic heterogeneity of any human population must be taken into account as well. In order to obtain a full representation of the genome, an analysis of a solid sample of genomes is essential. As a flux of immigrants leads to an increase in genetic diversity of a population, whereas individuals of different origins become members of the same group, the analysis of samples, rather than single specimens, is even more important at the genomic level when studying migrations.

Thus, numerous markers of the autosomal genome should be analyzed for reconstructing migration events. It was not possible via the PCR-based techniques even for modern DNA specimens. The development of NGS made a massive parallel analysis of a substantial number of autosomal markers, including whole-genome sequencing, possible for the first time (Ibid.). Unlike mtDNA and NRY, the autosomal markers from ancient specimens have been studied via NGS almost simultaneously with modern genomes. Parallel analyses of ancient and modern data have been carried out to compare the former with the population of various regions of Eurasia. While the employment of NGS had solved the problem of obtaining raw data, the analytic tools and interpretation of those massive results became an issue. Algorithms and software for assessing numerous parameters of the gene pool of a population have been developed (Sousa, Hey, 2013; Orlando et al., 2021). The tools suitable for comparing the genomic patterns between individuals and for discerning genetic components of various origins are particularly important for studying migrations (Patterson et al., 2012). Importantly, with a representative reference database at hand, such components can be detected both in a series of genomes from a population and in an individual genome.

The new avenues opened by the whole-genome analysis of autosomal markers are most evident in the case of reconstruction of the earliest stages of the dispersal of AMH: the use of whole-genome data led to a paradigm shift from the theory of a recent African origin of *H. sapiens* to the scenario including the hybridization of the African immigrants with late hominin species in Eurasia, at least with Neanderthals and Denisovans. These taxa, thus, are now believed to have participated in the formation of the gene pool of the modern population (Reich et al., 2010; Pääbo, 2015; Krause, Pääbo, 2016; Vernot, Pääbo, 2018). Recently, later migration events and their role in the history of the Eurasian (mainly European) population have been actively studied. Clearly, more or less representative whole-genome diachronic models of the gene pool of various regions of Europe have gradually emerged. The analysis of such models is, undoubtedly, the best tool for objective reconstruction of the genetic past of populations and the role which migrations have played in it (Aneli et al., 2021). The data for regions outside Europe begin to accumulate with some delay (Allentoft et al., 2015; Wang et al., 2021), though the representativeness of those samples in most studies leaves a lot to be desired and the detailization of reconstructions is limited. The issues related to the preservation of ancient nuclear DNA are still pressing: most of the results are based not on full genomes of a good quality but either on genomes of a very low coverage (Allentoft et al., 2015) or on large sets of SNPs spread throughout the nuclear genome. The tools for the statistical analysis and modeling the huge amounts of whole-genome data need further improvement. The full potential of this approach is yet to be explored.

Conclusions

Despite the rapid development of paleogenomic methods employed for the reconstruction of ancient migrations, we are now still at one of the earliest stages of the full exploration of the potential of these methods. This review shows that the advent of NGS triggered revolutionary progress of the technological facilities of paleogenetics. This changed the roles of different approaches to the reconstruction of both ancient migrations and the genetic history of human populations as a whole. No doubt, the tools of the whole-genome analysis of autosomal markers will hold the central position among the paleogenomic techniques, as those tools provide access to the main value of genomic data (Orlando et al., 2021). Besides this, comprehensive targeted research of the mtDNA and, especially, the Y-chromosome gene pools of ancient populations are promising, as the potential of these markers is still to be realized. Rapid accumulation of paleogenetic data for various Eurasian regions providing paleoanthropological material suitable for genetic analysis is to be expected. This, in turn, will lead to the formation of a kind of system of detailed population genetic coordinates reflecting the phylogeographic patterns not only of the modern population of the continent but of different ancient groups as well.

The most prospective way seems to be the study of non-contemporaneous groups combined in diachronic models reflecting the dynamics of the gene pool of a local population. The reconstruction of migrations based on such models would be the most objective.

A rapidly growing reference database of paleogenetic data from various Eurasian areas will be helpful in detailing the sources of migratory flows and their routes. Eliminating the disproportion between the amount of data available for Europe and other continents is also an important task. In this way, a full-scale transition from analyzing separate groups of paleogenetic samples for testing stand-alone hypotheses about the genetic past of populations to large-scale and systematic research of the genetic structure of ancient populations will occur. The most prospective approach in the field of the reconstruction of migrations would be the transition from approximate models of the most large-scale migration events to the refinement of such models, which will require much more detailed research of the local and territorial patterning of the gene pool in its temporal dynamics.

A substantial part of the skeletal data potentially available for the reconstruction of migrations and other aspects of the genetic history of the Eurasian population comes from non-contemporaneous archaeological sites in Russia. Russian specialists can make a significant contribution in the further study of the genetic past of the northern areas of Eurasia. This will be possible if the existing Russian centers of competence in the fields of paleogenetics and paleogenomics are being intensively developed, and if facilities for employing the whole cycle of paleogenetic research are created. To this end, the creation of depositories of archaeological skeletal collections studied by the methods of physical anthropology, archaeology, and molecular genetics must be intensified, and this will become a serious competitive advantage in the future.

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