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SCIENTIFIC AND APPLIED SIGNIFICANCE OF THE ANALYSIS OF Y-CHROMOSOME VARIATION FOR CRIMINALISTICS, ETHNODEMOGRAPHIC STUDIES AND HISTORICAL RECONSTRUCTIONS



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The purpose of the paper is to briefly review the knowledge accumulated by geneticists using modern DNA technologies about the variation of the Y-chromosome in human populations and to popularize this knowledge among demographers and sociologists. The data on the spatial and temporal variability of Y-chromosome markers, theoretical (problems of human evolution, migration routes during the settlement of mankind around the globe, ethnodemographic studies, historical reconstructions of the origin of individual populations and ethnic groups) and the applied significance of these studies for

medicine and criminalistics (DNA-based identification, formation of forensic databases, establishing kinship, in particular paternity, ethno-territorial origin of an unknown person based on DNA sample). The analysis of Y-chromosome haplogroups is applicable in ethnodemographic studies, as it allows marking modern migration flows along the male line. As an example, we present the forecast developed by the authors of the frequency dynamics of Y-chromosome haplogroups in the population of Moscow under the influence of migration, suggesting an increase in the frequency of haplogroups of “southern origin”, which is consistent with data on migration flows to Moscow. This result indicates the necessity for constant updating and maintaining reference databases for DNA-based identification purposes.

Y-chromosome, human populations, megapolis, DNA-based identification, microsatellites, Y-chromosome haplogroups, migration.

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Introduction

By now, molecular technologies for studying the human genome have made it possible to describe the history of human ancestral population formation and to clearly characterize and date major migrations of ancient humans during their dispersal across continents (Rosenberg et al., 2002).

Based on the sequencing (DNA nucleotide sequencing) of the Neanderthal genome and the study of Denisovan DNA, the time of separation of these forms from *Homo sapiens* was established and the presence of small fragments of their genome in the human genome was revealed (Meyer et al., 2012; Prüfer et al., 2014). Some fragments of the Neanderthal genome play a significant role in sensitivity or resistance to COVID-19 (Zeberg and Pääbo, 2020; Zeberg and Pääbo, 2021). It should be noted that paleogeneticist Svante Pääbo was recently awarded the Nobel Prize for the sequencing of the Neanderthal genome. Thus, important problems of human origins have been solved.

DNA technologies are used for personal identification of war dead, victims of natural and man-made disasters and terrorist attacks, and for historical identifications. In some cases, these technologies make it possible to determine the place of origin of an unknown person from a DNA sample. DNA-based identification is used not only in criminalistics, but also to solve current problems arising in society,

such as establishing maternal or paternal lineage. Molecular genetic markers such as microsatellites, which are variable repeats of subunits of several nucleotides, are successfully used, in addition to DNA-based identification, to consider the genetic differentiation of populations and create population reference databases (Chakraborty et al., 1999). The latest DNA technologies stand for the institution of paternity, as they allow not only to rule out paternity, but also to establish it reliably, which is highly demanded in modern society.

Population reference databases are the basis for the interpretation of probabilistic estimates of the results of personality identification (in criminalistics, the identification of disasters victims, terrorist attacks, the remains of war victims, the establishment of kinship, etc.). During forensic examination, the reliability of the personal identification using a standard set of forensic microsatellites (STR) depends on the correct choice of the reference population.

The male Y-chromosome, the sex chromosome, is a unique genetic structure that is passed down through the male line from father to son and serves to determine the development of the male sex in offspring. The uniqueness of the Y-chromosome is that it has a non-recombining region (NRY) in which the accumulated changes in DNA are inherited as a single block from generation to generation. They constitute the molecular record of the lineage of people, carriers of a

particular Y-chromosome. Information analysis concentrated in Y-chromosome markers combined with information about the specifics of geographical distribution of Y-chromosome variants allows us to obtain unique information about the ancient history of human populations, assess the level of populations genetic diversity, describe their origins and reconstruct past migrations, providing often more accurate and reliable information compared to ancient artifacts discovered during excavations (Mitchel, Hammer, 1996; Mendez et al., 2013). Microsatellite markers of the Y-chromosome from the non-recombining region and the haplogroup Y-chromosome, which represent a set of specific single-nucleotide substitutions with the main substitution determining the belonging to a specific haplogroup, are most in demand. For example, belonging to haplogroup *R1b* is defined by the basic substitution in position M343. Modern tools for the study of Y-chromosome markers, including statistical analysis along with molecular genetic analysis, allow us to determine the time of some important events in human history, such as the origin of modern human populations, and to date ancient migrations (Rosenberg et al., 2002; Mendez et al., 2013). Undoubtedly, the synthesis of classical historical data and the results of scientific research using modern molecular genetic methods will provide a significant expansion of knowledge about the history of mankind.

Specific geographical features of the Y-chromosome haplogroups distribution help to efficiently mark migration flows, which are particularly in demand when studying migration to megalopolises in the Russian Federation, and to consider the contribution of certain gene flows to the gene pool of the megalopolis population. The specificity of the Y-chromosome as a unique genetic marker allows us to predict changes in the Y-chromosome haplogroup frequency profile of the megalopolis population as a result of the influx of migrants from the North Caucasus, Transcaucasus and Central Asia. This is important not only for the development of forensic DNA marker reference databases for criminalistics purposes, but also,

in part, for ensuring the genetic safety of the megalopolis population, given the association of some diseases with Y-chromosome markers (Quintana-Murci et al., 2001; de Kniff, 2022). In order to assess the probability of a random match of genotypes by Y-chromosome markers in members of the same population, the creation of population databases on these markers is necessary. In addition to applications in forensic medicine, DNA databases are also required for solving population genetic problems and studying male lineage migrations.

In this article we will review the main achievements in the study of the Y-chromosome markers in the historical time and geographical space, which have the access to the historical and social problems of the modern world. The aim of the publication is to briefly review and popularize the main accumulated knowledge on human populations using modern DNA technologies, primarily obtained by studying the Y-chromosome, in order to make them available for demographers and sociologists. Human beings are a cross-section of the biological and the social, and a synthesis of these two components is necessary to solve the problems of modern society.

Establishing paternity using DNA-based identification methods

Paternity identification is now a well-established DNA-based identification procedure using analysis of a set of autosomal microsatellites (i.e., microsatellite markers that are not localized in the human sex chromosomes) against putative fathers, the child, and the mother (Jobling et al., 1997). Microsatellites are a reliable tool for this procedure. These DNA markers are highly polymorphic and therefore have a high resolving power, which is ensured by the high rate of occurrence of mutations, i.e., derived variants. In some cases, it is possible to attract markers directly from the Y-chromosome. In any case, when performing DNA-based identification, it is desirable to determine the frequency in the population of the attracted markers in order to assess the reliability of the personal identification as part of evaluating the

reliability of this procedure. It is clear that rarer markers, as compared to those that are widely distributed in the population, may give a higher reliability of the result.

Analysis of Y-chromosome markers for criminalistics, male lineage and historical reconstructions

One example of the establishment of a male lineage is the case of historical personal identification. A member of the antifascist resistance in a Scandinavian country, a certain Peter Hoffer, was shot at the age of 23 by members of the Danish resistance on suspicion of collaborationism. Many years later it was determined that he was not an accomplice to the Nazis. While searching for the burial of Peter's remains, a DNA-based identification procedure was carried out using the DNA of his male relative, isolated from the biological traces on the envelope of Peter's 1947 tracing letter addressed to the Red Cross. The remains were identified and reburied with honors (van Kooten et al., 2013). Similarly, using DNA analysis of the descendants' Y-chromosome, the prisoner's burial on the grounds of the Peter and Paul Fortress was identified.

The most striking example of the application of Y-chromosome markers for criminalistics is the identification of the suicide bomber who carried out the explosion at Domodedovo airport. Determination of the haplogroup of the Y-chromosome in a biological sample obtained at the airport made it possible to establish the geographic region of the individual's origin and subsequently identify the terrorist (Borinskaya et al., 2020).

Currently, Y-chromosome markers are being studied in criminalistics for particularly serious crimes. Biological traces are recovered from crime scenes or from the bodies of victims, such as rape victims. Molecular genetic techniques are tools that help in solving crimes. Interestingly, even animal footprints at crime scenes are often the key to solving a crime, because DNA analysis can identify a specific animal. For example, the hair of a dog found at a crime scene can lead to the discovery of its owner, who is related to the crime committed.

Using historical DNA-based identification methods, the remains of the royal family have been identified. With the help of short fragments containing microsatellites, historical identifications of the remains of famous personalities, such as Mozart, Schiller, and Haydn, have been carried out. In the former Yugoslavia the DNA-based identification of the victims of the recent war has been carried out.

In the 21st century the analysis of Y-chromosome haplogroups has taken mass character – millions of people, interested in ethno-territorial origin of their ancestors, the establishment of possible affinity with their namesakes, have submitted their biological samples to commercial laboratories and as a result have enriched the knowledge about their genealogy. This method can be designated as a method of genetic genealogy.

It is evident that male namesakes in the prevailing number of cases are the carriers of the same Y-chromosome, except for the carriers of the most widespread surnames, which may have occurred repeatedly in the history of mankind (for example, Kuznetsov in Russia or Smith in Western Europe and USA).

Thus, modern DNA-based technologies for the study of the human genome, including the Y-chromosome, make it possible to solve important social problems demanded by society.

Analysis of the distribution of Y-chromosome haplogroups in different regions of the world

Due to the fact that the molecular genetic markers in the non-recombining region of the Y-chromosome, the mutations that occur in it (spontaneously occurring substitutions in DNA) – single-nucleotide polymorphisms are inherited as a single unit, there is a classification of haplogroups of the Y-chromosome – a set of diverse variants. Specific haplogroups arose in certain geographic regions, and from there they spread and continue to spread to other regions. The peculiarities of the geographical distribution of Y-chromosome variants in the global space have been well studied (Hammer et al., 1997). *Figure 1* shows the distribution of haplogroups in the geographical space of Europe.

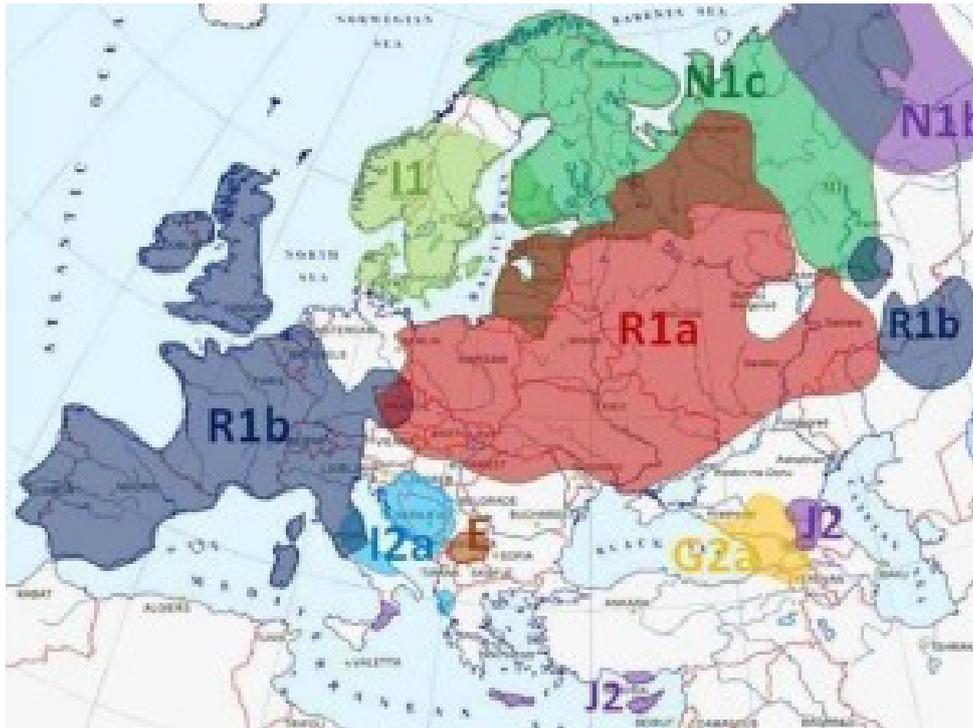


Fig. 1. Peculiarities of the distribution of major Y-chromosome haplogroups in Europe

Source: (Balanovskii, 2015).

For example, during the settlement of the American continent from Siberia, only a few haplogroups of the Y-chromosome with the prevalence of C and Q haplogroups (Zegura et al., 2004) penetrated there, which suggests a limited range of ancient people who came to new territories.

Analysis of Y-chromosome marker variability to study migration, population mixing, and event dating in the settlement history of human populations in selected geographic regions

Against the background of nucleotide substitutions at specific positions on the Y-chromosome, there is a gradual accumulation of microsatellite variants. Knowing the rate of spontaneous mutations, which approximately corresponds to 10^{-3} per site per generation (slightly different for microsatellites with different subunits), it is possible to calculate the time of occurrence of a single nucleotide substitution coupled with the corresponding pattern of microsatellite variability, which can be characterized by molecular-genetic

methods. For example, using this approach, the time of population migration to America was estimated: approximately from 10,100 to 17,200 years ago (Fig. 2).

Similarly, the timing of the emergence of specific Y-chromosome haplogroups, both large and smaller haplogroups derived from them, has been determined in other regions of the world (Semino et al., 2004).

The study of Y-chromosome haplogroups makes it possible to assess the degree of mixing between populations of different origins. For example, the level of intermingling between the main population groups in the United States, represented by African, European, Spanish (Spanish-speaking), Asian groups (mostly Chinese and Koreans) and the Native American population, the American Indians, has been studied (Hammer et al., 2006).

We should note that the study of Y-chromosome markers is very effective for establishing ancestry when mixing different population streams, for example, in Argentina (Caputo et al., 2019), which is partly similar to the situation in metropolitan gene pools.

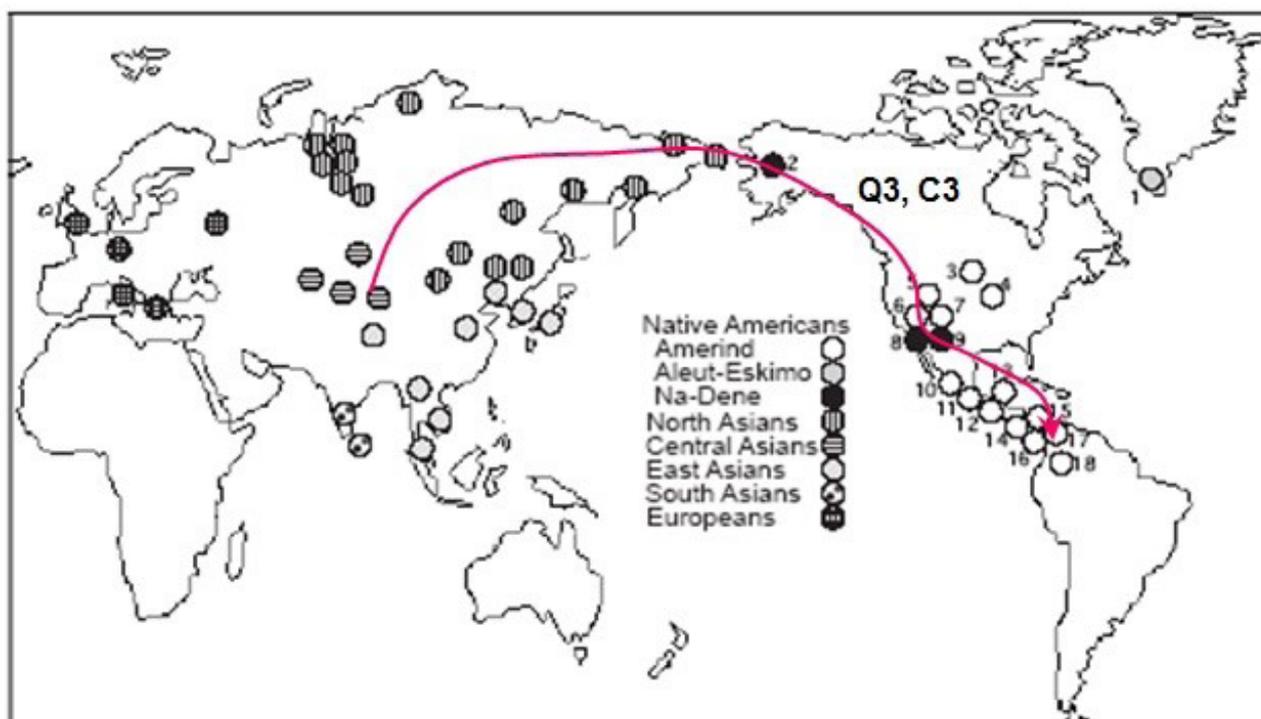


Figure 2. The settlement of America. C3 and Q3 haplogroups of Y-chromosome entered America from Siberia.

Indications (from top to bottom): Native American populations – American Indians, Aleut-Eskimos, Na-Dene, Natives of North, Central and East Asia, Europeans. The arrow indicates the direction of migration. C3 and Q3 are haplogroups of the Y-chromosome.

Source: (Zegura et al., 2004).

Based on molecular markers, the global diversity of the human Y-chromosome is now fairly well understood (Hammer et al., 2001), and Y-chromosome variants are represented in databases (Purps et al., 2014; de Kniff, 2022).

Of significant interest is the study of the Y-chromosome, which expands the possibilities of analyzing events over a vast temporal depth of human history. In particular, it has been shown that a sharp decline in Y-chromosome diversity, a “bottle neck”, about 10,000 years ago was accompanied by global cultural changes (Karmin et al., 2015). Using Y-chromosome analysis, the history of population formation was clarified and ancient migration routes were reconstructed in Iran (Grugni et al., 2012).

Thus, the application of mass Y-chromosome analysis not only allows us to go deeper into time, but also to expand the ability of science to synthesize knowledge from different fields and to build deep causal relationships.

Analysis of the distribution of Y-chromosome haplogroups in megalopolises’ population in connection with migration

Let us consider this point in connection with the peculiarities of the distribution of Y-chromosome haplogroups in the Moscow population. All megalopolises are characterized by a large population size, a high level of migration from outside, and a multi-ethnic composition of residents. Population reproduction in a megalopolis is mainly due to migration (Kurbatova, Yankovskii, 2016).

External (centripetal) migration leads to an increase in the genetic diversity of megalopolis inhabitants, especially if migrants come from distant regions with populations very different from the main megalopolis population. Genetic and demographic parameters of migration to Moscow have been characterized in the studies conducted by Doctor of Sciences (Biology) O.L. Kurbatova over a period of more than a century and a half,

involving analysis of census materials, civil registry archives, and questionnaire data (Kurbatova et al., 2013; Kurbatova et al., 2021a).

We studied the frequencies of Y-chromosome haplogroups in three generations of Moscow residents using modern molecular methods. Y-chromosome haplogroups were determined using an Internet predictor based on the study of 18 microsatellite loci from the non-recombining region of the Y-chromosome. Haplogroups of Y-chromosome *R1a*, *R1b*, *E1b1b*, *N*, *T*, *I1*, *I2*, *J1*, and *J2* were detected in the Moscow population (Udina et al., 2022), which corresponds to the distribution of these haplogroups among the Russian population (Balanovskaya, Balanovskii, 2007). Statistical analysis and literature data analysis on the geographical distribution of Y-chromosome haplogroups in the population of Russia and neighboring countries allowed us to establish the spectrum of Y-chromosome haplogroups that enter the megalopolis with migrant flows. It was revealed that haplogroups that are not characteristic of the original population (*C3*, *G2a*, *G2c*, *J1*, *J2*, *L*, *O2*, *O3*, *Q*, *R2*, and *T*) are present with higher frequency in the younger generation and are spread with maximum frequency in the regions of migrants' origin (Udina et al., 2022). Thus, the peculiarities of the spectrum dynamics and frequency profile of Y-chromosome haplogroups in the generations of Moscow residents are consistent with the ethnodemographic processes characteristic of the Moscow population. For example, the carriers of haplogroup *G2a* originate from the regions of the Caucasus, where it predominates and reaches a frequency threshold of 70% in some peoples of Dagestan.

Prediction of frequency dynamics of individual Y-chromosome haplogroups under the influence of migration processes in megalopolises

As we have shown, the frequencies of Y-chromosome haplogroups in megalopolises change over time. The task of predicting population gene pool dynamics under the influence of migration and other ethnodemographic processes is relevant to ensure demographic and

genetic security of the population, especially inhabitants of megalopolises. The concept of genetic and demographic security includes sustainable reproduction of the population in generations and preservation of the optimal level of the population's genetic diversity. To ensure genetic security, it is necessary to monitor the threats posed not only by the introduction of new pathogens into the population, but also by an increase in the genetic load of the population as a result of weakening of natural selection and the introduction of previously uncharacteristic gene variants which may cause pathologies. Migration flows in megalopolises of the Russian Federation are so intense, the ethnic composition of migrants is so diverse that the gene pool of the population is almost completely renewed during 6–8 generations (Kurbatova, Yankovskii, 2016). The spectrum and frequencies of DNA-based identification markers in populations may change over time as a result of the uneven migration and natural increase of ethnic groups. The nature of the dynamics should be taken into account in criminalistics examinations, in particular, when creating population reference databases, which are needed to assess the reliability of DNA-based identification (Tsybovskii et al., 2017). In this regard, in the formation of databases on Y-chromosome markers, genetic and demographic methods, including questionnaires for megalopolis residents, should be applied in addition to molecular genetic analysis. Such a database has been created for the Moscow population (Kurbatova et al., 2021b).

We developed an original methodology for predicting population gene pool dynamics under the influence of migration processes (Kurbatova, Pobedonostseva, 2004). In population genetics, migration is considered as one of the main factors of population dynamics that change the level of genetic diversity of populations. Since male and female migrations to a megalopolis may differ in intensity and ethnoregional composition of migrants, it is necessary to take into account the gender specifics of migration flows – to predict the dynamics of the frequency of markers located on the Y-chromosome, data on male

migration (number of arrivals and their ethnic composition) are analyzed. A separate prediction is calculated for each megalopolis (recipient population) and each selected genetic marker.

In general terms, the dynamics of gene frequency in generations of the migrant-receiving population is described by the formula:

$$q_t = (1 - m)^t (q_0 - Q) + Q$$

where:

- q_t – frequency of the gene after t generations;
- q_0 – initial frequency of the gene in the population;
- Q – gene frequency in migrants;
- m – male migration rate (proportion of male migrants in the population).

To calculate migration parameters, demographic statistics or population questionnaire data are used, and information on marker frequencies in the metropolitan population and in ethnic groups, which make the main contribution to the flow of migrants into the metropolis, is found in the corresponding genetic databases. The forecast obtained as a result of applying this algorithm belongs to the category of long-term genetic-and-demographic forecasts, where, in contrast to a demographic forecast, a generation is considered as the unit of time (the generation

length for the modern Russian population is taken to be 25 years).

The forecast can be given in several scenarios, assuming different intensity of migration processes and different ethno-territorial composition of migrants arriving in a particular megalopolis.

As an example, we present our calculated forecast of the frequency dynamics of the *R1a* and *J2* haplogroups of the Y-chromosome in the generations of residents of Moscow.

The *R1a* haplogroup prevails among the Eastern Slavs, particularly among the Russians. The haplogroup *J2* is frequently found among the peoples of the North Caucasus.

The *R1a* haplogroup is predicted to have a considerable, almost two-fold decrease in the frequency within 10 generations, from 0.45 to 0.24 (Fig. 3). Especially dramatic decrease of the haplogroup frequency is accounted for by the first 6 generations, from 0.45 to 0.25. The decrease in the *R1a* haplogroup frequency under the influence of migration processes in the large megalopolis areas of Russia is expected, because, with the exception of the Belarusians and Kirghiz, all ethnic groups contributing to the gene pool of Moscow have a lower or significantly lower *R1a* frequency than in the Russian population.

According to the forecast, the frequency of *J2* haplogroup in the megalopolis will grow 7-fold in 10 generations (Fig. 4), since a significant part of the ethnic groups of migrants have a frequency of *J2* haplogroup significantly

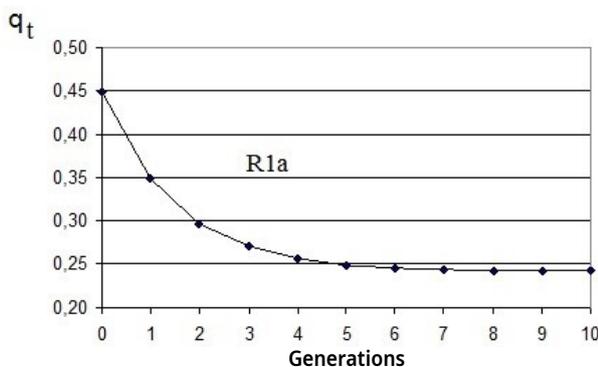


Fig. 3. Predicted dynamics of the frequency of *R1a* haplogroup of the Y-chromosome in generations of Muscovites under the influence of migration

Source: own calculation.

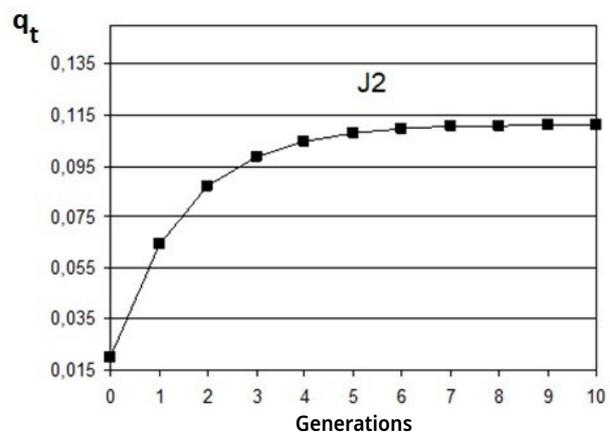


Fig. 4. Predicted dynamics of the frequency of *J2* haplogroup of the Y-chromosome in generations of Muscovites under the influence of migration

Source: own calculation.

higher than that of Russians. The highest frequency was recorded in Chechens (0.56) and Ingush (0.59).

These data convincingly demonstrate that the frequencies of Y-chromosome markers in megalopolises may change considerably over several generations and even differ appreciably among simultaneously living age groups. An increase in the frequencies of the “southern-origin” Y-chromosome haplogroups brought in by migrants from their regions of origin is characteristic of the Moscow population, which corresponds to the data on the migration flows into the capital. In this regard, in order to improve the reliability of DNA-based identification in criminalistics, the databases need to be constantly updated because of the intensive influx of migrants and the concomitant change in the ethnic composition of the metropolitan population.

Conclusion

In conclusion, we should note that the application of modern DNA technologies contributes to the solution of important issues in natural science and social science. The applied aspects of the latest DNA technologies allow us to solve the pressing needs of modern society: carrying out DNA-based identifications, historical reconstructions, and the establishment of ancestry, paternity, and kinship. The analysis of the Y-chromosome markers is very informative in solving these problems in the historical time and geographical space. The analysis of the Y-chromosome markers is effectively used to trace the flows of migrants into a megalopolis and to predict the dynamics of generations frequencies of the metropolitan population in order to create the current population reference databases.

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