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Entwined relationships: genetic and cultural diversity in the Caucasus and the adjacent steppes in the Eneolithic–Bronze Age period

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Abstract

The paper provides an overview of the most recent results of DNA analysis of ancient populations inhabiting the Caucasus and the adjacent steppes against the background of the cultural diversity of the Eneolithic–Bronze Age (c 5000–2000 BC). It is noted that in the Caucasus, cultural diversity prevails over genetic, and genes flowed through the Caucasus in only one direction from south to north. The genetically ‘pure’ Caucasus hunter-gatherer component has not yet been found in the North Caucasus. It comes there in the first half of the 5th millennium BC as a mixed ancestry with Anatolian and Iranian farmers during the re-occupation in the mid-Holocene, following a significant depopulation of the North Caucasus in the previous cold and dry phase. This highlights that the issues relating to the cultural and historical interpretation of genetic data are caused by inconsistency between genetic and archaeological taxonomies, an underestimation of the archaeological context by geneticists, and a naïve interpretation of differences in the DNA by archaeologists as cultural attributes.

Keywords: ancient DNA, archaeological cultures, Caucasus, steppe, Eneolithic, Bronze Age

10.1 Introduction

In recent three decades the progress of paleogenetic studies (Hagelberg et al. 2015) has revolutionized the analytical capacity of archaeology and set higher requirements for the cultural and historical interpretation of the results of ancient DNA analysis (Lebrasseur et al. 2018; Kristiansen 2022). Basically, the results of ancient DNA analyses are creating an entirely new knowledge area of the genetic aspects of cultural, economic and social processes in their historical development. In other words, paleogenetics is opening up new opportunities for archaeology related to the analysis of the history of relationships between the biological nature of humans and their material culture.

The genetic revision of two hypotheses that are the most prominent in pre-historic archaeology of the Old World – regarding massive migrations during the Neolithization of Europe and the hypothesis concerning the spread of Indo-European languages – became a genuine demonstration of the power of the new tool. These hypotheses were advanced at different times independently from each other and were combined by Colin Renfrew in a powerful theory (Renfrew 1990), which the author himself planned to validate with data from genetic analyses earlier than any other scholar (Renfrew 2000). Renfrew could never have imagined that ten years later this area of research, which he called archaeogenetics, would produce data (Allentoft et al. 2015; Haak et al. 2015) that would be used to support a competing theory, i.e. the Kurgan or Steppe theory of the Indo-European homeland (Gimbutas 1970; Mallory 1989; Anthony 2007). However, the results of the paleogenetic analyses carried out in the past decade go beyond the explanatory capacity of these theories and can hardly be used to prove or reject either of them in a straightforward way. To a great extent, this is linked to the finding that the Caucasus population contributed 50% to the steppe gene pool of the Eneolithic–Bronze Age (Jones

et al. 2015: 5). This unexpected circumstance has changed not only the framework for addressing the Indo-European issue, but also provided an absolutely new context for the analysis of cultural contacts between the ancient populations of the Caucasus and the adjacent areas in prehistory.

Ideally, in order not to prejudice interpretation of paleogenetic analysis results, genetic data alone must drive the groupings of specimens before examining their associations with cultural groupings (Fu et al. 2016). In practice, this procedure is not always followed because of the low and uneven spatial and chronological density of the analysed samples, the biased archaeological attribution of some specimens, and an excessive desire to address a high-profile issue when data shortage is obvious. In the following, we will see what paleogenetic data can be used by the archaeology of the Caucasus and how these data change conceptions on its cultural development during the Eneolithic–Bronze Age.

10.2 Caucasus hunters-gatherer ancestry in the Caucasus and north of it

The determination of a distinct Caucasus hunters-gatherer ancestry (CHG) in population genetics of the Caucasus (Jones et al. 2015) has been the most important regional discovery of recent years. The first pair of sampled individuals with the CHG ancestry included a young male (30–35 years) from a burial in the Mesolithic layer A2 in the Kotias Klde rock shelter and another individual from the Late Upper Paleolithic layer in section B in the Satsurbliia cave in western Georgia (Fig. 1a–c; Table 1). Direct radiocarbon dating put the absolute archaeological age of these human remains at 7940–7599 calBC for Kotias Klde (95.4%), and 11,417–11,224 calBC for Satsurbliia (95.4%), respectively (Jones et al. 2015). Therefore, analysis of ancient DNA demonstrates the genetic continuity of the population of western Georgia for almost 5000 years, which in archaeological chronology means from the 12th to the

No	Site	N	Archaeological culture or period	Reference
1	Sharakhalsun 6	5	Maykop, 'Steppe Maykop', Yamnaya, Catacomb	Wang et al. 2019
2	Aygurskiy 2	2	'Steppe Maykop'	Wang et al. 2019
3	Ipatovo 3	1	Eneolithic-'Steppe Maykop'(?)	Wang et al. 2019
4	Zolotarevka 2	1	Yamnaya	Wang et al. 2019
5	Rashevatskiy 1	3	Yamnaya, North Caucasus	Wang et al. 2019
6	Rashevatskiy 4	2	Catacomb, Post-Catacomb	Wang et al. 2019
7	Nevinnomiskiy 3	1	Post-Catacomb	Wang et al. 2019
8	Sinyukha	3	Maykop	Wang et al. 2019
9	Marchenkova Gora	1	Dolmen	Wang et al. 2019
10	Klady	4	Maykop-Novosvobodnaya	Wang et al. 2019
11	Unakozovkaya	3	Darkveti-Meshoko	Wang et al. 2019
12	Lysogorskiya 6	1	North Caucasus	Wang et al. 2019
13	Goryachevodskiy 2	2	North Caucasus	Wang et al. 2019
14	Beliy Ugol 2	1	North Caucasus	Wang et al. 2019
15	Vonyuchka 1	1	Eneolithic	Wang et al. 2019
16	Marinskaya 3	1	Catacomb	Wang et al. 2019
17	Marinskaya 5	5	Maykop, North Caucasus	Wang et al. 2019
18	Kabardinka	2	Late Bronze Age	Wang et al. 2019
19	Progress 2	3	Eneolithic, North Caucasus	Wang et al. 2019
20	Baksanyonok	1	Maykop(?)	Wang et al. 2019
21	Kudakhurt	2	Middle Bronze Age	Wang et al. 2019
22	Nogir 3	1	Maykop	Wang et al. 2019
23	Velikent II	2	Kura-Araxes, Bedeni(?)	Wang et al. 2019
24	Mentesh Tepe	1	Shulaveri-Shomutepe	Skourtanioti et al. 2020
25	Kaps	2	Kura-Araxes	Wang et al. 2019

No	Site	N	Archaeological culture or period	Reference
26	Kalavan 1	2	Kura-Araxes	Lazaridis et al. 2016
27	Katnaghbyur	2	Late Bronze Age	Lazaridis et al. 2016
28	Areni1	5	Chalcolithic	Lazaridis et al. 2016
29	Polutepe	1	Shulaveri-Shomutepe	Skourtanioti et al. 2020
30	Hotu	2	Mesolithic	Lazaridis et al. 2016
31	Seh Gabi	6	Chalcolithic	Lazaridis et al. 2016
32	Ganj Dareh	5	Neolithic	Lazaridis et al. 2016
33	Satsurblia	1	Upper Paleolithic	Jones et al. 2015
34	Kotias Klde	1	Mesolithic	Jones et al. 2015
35	Talin	1	Kura-Araxes	Lazaridis et al. 2016
36	Alkhantepe	1	Leilatepe	Skourtanioti et al. 2020

Table 1. Archaeological sites of the 12th–2nd millennium BC in the Caucasus and adjacent territories – sources of anthropological samples with Caucasus Hunter-Gatherer genetic ancestry.

8th millennium BC in archaeological chronology, and in climatic and geological terms roughly from the end of the late Dryas to the early Holocene in climatic and geological terms. More importantly, this analysis implies a degree of continuity that has not been disrupted for at least the last 13,000 years, supported by the wide distribution of the same DNA in modern populations from the Caucasus (Jones et al. 2015: 5, Fig. 4).

The analysed ancient DNA of the populations from modern Armenia, Azerbaijan and northwestern Iran (Fig. 1a–c) became an important complement to the initial characteristics of the Caucasus ancestry (Lazaridis et al. 2016; Skourtanioti et al. 2020). Twenty-five samples, including the CHG ancestry in various combinations with Iranian and Anatolian Neolithic ancestry, represent the main archaeological periods stretching from the Mesolithic to the Late Bronze Age, covering the period between the 9th and 2nd millen-

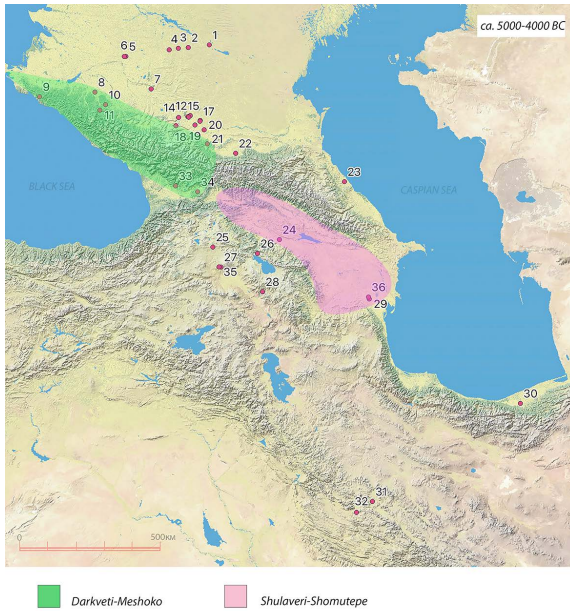


Figure 1A. Map of ancient DNA samples showing Caucasus Hunter-Gatherer genetic ancestry from 12th–2nd millennium BC archaeological sites in the Caucasus and adjacent territories (numbers correspond to numbers in Table 1) and the core areas of the main archaeological cultures mentioned in the text.

nium BC. The genetically ‘pure’ CHG component has not yet been found in the North Caucasus. It comes here in the first half of the 5th millennium BC as a mixed ancestry of the Caucasus Hunter-Gatherers and Chalcolithic populations from Anatolia and Iran. This was probably the process of a re-occupation of the North Caucasus in the mid-Holocene after its significant depopulation during the previous cold and dry phase (Trifonov 2009; Varoutskos et al. 2017: 238). Genetically, samples from the northern and southern Caucasus (Eneolithic c 5000–3500 BC, Maykop c 3700–2900 BC, Dolmen c 2900–1300? BC, and Kura-Araxes c 3500–2600? BC cultures) are almost indistinguishable (Wang et al. 2019: 6, Fig. 4b) and are in agreement with ancestry typical of Chalcolithic Armenia and Chalcolithic Iran (Lazaridis et al. 2016).

The contribution of the Caucasus to the genetic profile of the Eneolithic–Bronze Age steppe populations is of special interest to archaeology in the areas



Figure 1B. Map of ancient DNA samples showing Caucasus Hunter-Gatherer genetic ancestry from 12th–2nd millennium BC archaeological sites in the Caucasus and adjacent territories (numbers correspond to numbers in Table 1) and the core areas of the main archaeological cultures mentioned in the text.

north of the Caucasus. The Eneolithic population of the Lower Volga and the Caucasus piedmont steppe has been found to harbour the CHG ancestry and the Eastern Hunter-Gatherer ancestry as early as the 5th millennium BC, but with no signs of additional Anatolian or Iranian farmer ancestry (Mathieson et al. 2015; Wang et al. 2019). In the middle–second half of the 4th millennium BC, a small group of the Eneolithic Caucasus piedmont steppe individuals (the so-called ‘Steppe Maykop’) had the Caucasus ancestry of almost the same ‘steppe’ mixture (Wang et al. 2019), but according to archaeological criteria, they represent the indigenous steppe population influenced by the Maykop culture, and not vice versa. A mixture of the CHG ancestry with combined genetic ancestry of the Anatolian and Iranian farmers has also been detected in the genetic profile of the later Caucasus piedmont steppe populations attributed to the Yamnaya, northern Caucasus and Catacomb cultures (Wang et al. 2019: 6, Fig. 4a).



Figure 1C. Map of ancient DNA samples showing Caucasus Hunter-Gatherer genetic ancestry from 12th–2nd millennium BC archaeological sites in the Caucasus and adjacent territories (numbers correspond to numbers in Table 1) and the core areas of the main archaeological cultures mentioned in the text.

10.3 Some issues with the cultural and historical interpretation of the Caucasian genetic ancestry

A high Caucasus ancestry proportion detected in the Eneolithic–Bronze Age steppe genetic profile led to an audacious attempt to align the Steppe theory with the Anatolian theory of the Indo-European homeland. In this hypothesis, the role of the Caucasus is characterized as a conduit for the gene-flow from south to north – and then further to east and west – of the Caucasus and Near East ancestry-related populations, who spoke proto-Indo-European languages. However, this hypothesis does not clarify why in this case the Caucasus remained predominantly non-Indo-European. Furthermore, it remains unclear through which cultural and mating network the Caucasus, Anatolian and Iranian genetic ancestry was adopted by the Yamnaya people in the

steppe. In addition, neither the steppe migration to Anatolia via the Balkans (Mathieson et al. 2018: 7), nor the steppe route of Iranian language spread is genetically confirmed (Broushaki et al. 2016). In other words, the Steppe theory of the Indo-European homeland regarding its migration components has not yet been genetically confirmed.

If we evaluate the role of paleogenetic analyses in addressing specific issues of Caucasus archaeology during the Eneolithic–Bronze Age, putting aside the Indo-European homeland puzzle, we should first highlight the complete absence of the Anatolian and/or Iranian farmer genetic ancestry in the representatives of the Khvalynsk culture – the earliest pastoralists with CHG ancestry in the Lower Volga steppe region (Wang et al. 2019: 4, Fig. 2). There is still an unresolved contradiction here. On the one hand, people with ‘pure’ CHG ancestry could not bring cattle-breeding to the Volga region, while on the other hand there are no genetic traces of the earliest Caucasian farmers from whom this practice was borrowed in the Volga region.

Another problem is the barely noticeable Maykop contribution to the genetic ancestry of the Eneolithic population inhabiting the adjacent steppes. In the context of the results obtained, the ‘Steppe Maykop’ appears to be a group of indigenous steppe people, whose close proximity to a highly developed culture resulted in unilateral benefits and an opportunity to enrich their material culture with some Maykop symbols, such as small decorated vessels of a quality never seen before in the steppes. This situation may lead to a revision of the model of the relationships between the technically backward Eneolithic north and the technically advanced Early Bronze Age south, suggesting that the Maykop culture never sought to colonize the fore-Caucasus steppes, which had neither attractive resources, rich partners nor dangerous enemies. For the steppe, it remained a relatively passive donor of technical innovations and its northernmost enclave in the Lower Don region (Kostantinovka culture) had been assimilated and withered away before the decline of the Maykop home region in the northern Caucasus piedmont.

The Yamnaya population of the fore-Caucasus steppe does not have the Maykop genetic ancestry either. It seems that these cultures never had direct

contact as there are no mixed assemblages with authentic Maykop and Yamnaya artefacts. Together with the stratigraphical data, all this demonstrates a replacement of cultures, while a large-scale transfer of technologies from the Maykop population to the Yamnaya population was hardly possible. Most of these technologies disappeared when the Maykop culture disappeared, whereas the Yamnaya population had its own alternative sources of influence in the south.

The chronology and geographical distribution of the North Caucasus culture provide several variants for the cultural and historical interpretation of its genetic profile. In the fore-Caucasus steppe areas and the Caucasus piedmont, this culture replaced the Early Yamnaya and Maykop cultures; for this reason, the genetic ancestry of these cultures could contribute to the ancestry of the North Caucasus population. Equally, the North Caucasus culture, which was synchronous with the Late Yamnaya and apparently had influence on it, could be the source of the Caucasian genetic ancestry.

Genetic homogeneity across the entire Caucasus, regardless of cultural and chronological associations, turned out to be the most unexpected result of the ancient DNA analysis. The cultural diversity of the Caucasus exceeds its genetic diversity, and in those areas where archaeologists draw a clear-cut line, paleogeneticists do not see any differences. In the context of the major genetic flows, there are no signs of intrusion of the Eneolithic–Bronze Age steppe pool genotypes into the southern Caucasus or adjacent areas of northwestern Iran and eastern Anatolia (Skourtanioti et al. 2020). The Caucasus thus appears to have been an asymmetric, semipermeable barrier on the migration route between the continents rather than a bridge between Europe and Asia (Yunusbayev et al. 2012).

Paleogeneticists and archaeologists grasped this cultural and genetic inconsistency at the same time and offered several variants for data reconciliation using new nomenclature systems (Eisenmann et al. 2018) or revised basic principles of traditional archaeological taxonomies and criteria for differentiating between vernacular categories (cultures, technocomplexes, groups, industries, traditions, etc.) (Riede et al. 2019). Indirectly, these attempts re-

flect the different nature of interconnected cultural and genetic processes (the model of genetic and cultural coevolution or the dual inheritance theory) (Cavalli-Sforza & Feldman 1981; Boyd & Richerson 1985). The issue is how exactly genetic and archaeological spatial-temporal continua intersect and interact with each other.

10.4 Archaeology and paleogenetics: awkward interaction

Archaeologists have yet to learn to use the paleogenetic analyses and avoid ‘naïve literal interpretation’ of their results (Skourtanioti et al. 2020: 1166). In turn, geneticists should not overestimate the superiority of their methods over ‘the traditional toolkit of archaeology’ (Vander Linden 2018: 657). In modern paleogenetic research, archaeologists tend to view the process and results of genetic analysis as completely independent of the cultural and historical content of the hypotheses being tested. They simplify the results of genetic analysis and prefer to use the identified haplogroups as genetic markers of a particular ethnic or cultural group. However, to determine the geographical origin of a particular genetic profile, the key is the biogeographical ancestry analysis (admixture analysis), the results of which depend on the correct choice of key genetic lineages for comparison. It is at this stage that the archaeological hypothesis is transformed into a paleogenetic one. The reliability of the result will largely depend on the genetic coordinate system in which the key objects are chosen by the archaeologists. In practice, this work is most often done by paleogenetics, while archaeologists are waiting for the final result. In fact, paleogenetic research is independent of archaeological only at the stage of ancient DNA sequencing, while at other stages it remains an area for joint formulation and testing of hypotheses. However, the cooperation between archaeologists and paleogeneticists has not been smooth. Paleogeneticists are

not planning to start to serve archaeologists, no matter how much the latter would like it, while archaeologists do not have a clear idea of the potential of genetics (Lebrasseur et al. 2018).

A much higher level of cultural diversity compared to genetic diversity, as is the case with the Caucasus Bronze Age population, is raising a blunt question: what happens to people from a specific cultural tradition who disappear from the archaeological environment with no signs of pestilence, extermination or migration? We can only suggest that having lost their cultural identity, they dissolve among other cultural populations that contribute to their genetic ancestry. In this case, the area of research that could be of interest to both archaeologists and geneticists is culture replacement and genetic recombination. This part of the fundamental issue of the relationship between cultural change and genetic change of human communities cannot be addressed unless geneticists and archaeologists work together.

If we judge a culture based on its function in forming a group identity, in the system of basic components – economic, social and cultural – the last mentioned is the key element, as it creates basic conditions for the development of the other two components (Pagel 2012). By its nature, culture appears to be a by-product of human genetic evolution, and as Edward O. Wilson (1978: 176), an evolutionary biologist, said, ‘genes hold culture on a leash’, adding that ‘the leash is very long’. Culture is an evolutionary advantage humans have over other species in maintaining genetic diversity. The continuous reproduction of cultural diversity is probably a prerequisite and part of the extra-biological mechanism for maintaining favourable conditions for preserving human genetic diversity. The boundaries between cultures serve as barriers to gene flows related to migration, aggression or epidemics that carry threats.

The instability of external living conditions poses a substantial challenge for traditional cultures with low economic adaptability. When the possibilities for economic change are exhausted, there is a period of economic decline, with demographic stress leading to a crisis in cultural identity because adherence to previous values does not guarantee prosperity any more. With no

more changes possible, the life cycle of a culture comes to its end, the culture fades away and gives way to a new culture, better adapted to new natural and cultural-historical conditions. Archaeological empirical experience demonstrates that all cultures are 'mortal', but their survival age varies. What factors the duration of their life cycle may depend on is demonstrated, for example, by applied genetic studies of two modern populations of the Shapsug, which inhabited the opposite sides of the Greater Caucasus mountain range in the western Caucasus (Pocheshkhova 2008). Both groups experienced a critical reduction of population size and suffered from the bottleneck effect at the end of the 19th century, causing a decrease in the gene pool and lower genetic diversity. In one of the groups, the tendency to reduced population size did not change over time, and this group began to face genetic problems such as a larger number of hereditary diseases, whereas the other group demonstrated a clear trend of towards restoring genetic diversity, mainly by supporting key elements of traditional culture. The prospects of studying the relationship between populations' gene pools and the stages of 'rise and fall' of the cultures associated with these stages may turn out to be equally productive for paleogeneticists and archaeologists alike. The relevance of such studies will increase because of the ease with which they can be refocused from historical to modern processes, their potential for applied research, and the predictive value of their results.

10.5 Concluding remark

It is possible that the genetic results obtained do not live up to the expectations of those archaeologists who counted on a prompt genetic solution to the issues related to origin of cultures, or at least the localization of the home regions of cultures from where these cultures spread, including the homeland of the elusive Indo-Europeans. Cultural identity is not genetically inherited. Otherwise, paleogenetics could replace archeology.

In archaeology, paleogenetics is more than a new technology. It introduces elements of a new philosophy that attempts not just to report on the nature of similarities but also to explore endlessly produced differences that form the basis of cultural and genetic diversity. This fundamental shift in focus can help traditional archaeology to become incentivised again and to better respond to public demand for relevant knowledge.

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