

“More to the West”: critical comments on the new versions of the “Yamnaya expansion” hypothesis¹

Aleksey Romanchuk
Chisinau

Abstract: The article considers recent versions of the proposed by geneticists hypothesis of “Yamnaya expansion”. The author demonstrates that the data of Y-chromosome analyses, as well as the data of physical anthropology obviously does not agree with the supposed model of “population replacement” of Europe (even partial) as a result of late migrations from the area of the Yamnaya culture, already in the Bronze Age. Thus, the author suggests that the area in which the formation of the autosomal “Yamnaya component” took place was significantly wider than the area of the Sredny Stog culture, and covered very vast areas of both Eastern Europe (both its steppe and forest parts), and Central and (partly) Western.

Keywords: genetic, physical anthropology, archeology, Y-chromosome haplogroups, Yamnaya culture

New publication (“The Genetic Origin of the Indo-Europeans”) of the team led by I. Lazaridis² proposes significant changes to the hypothesis of the “Yamnaya expansion” (and the “Indo-Europeanization” of Europe as its consequence). And first of all, it shifts the original locus of the formation of the Yamnaya culture to the Azov-Lower Dnieper region (as, incidentally, did the work published synchronously with it).³

As can be seen, these changes to the basic hypothesis are primarily a response to the significant increase in data that has occurred in the last few years, which are poorly consistent with previous versions of the hypothesis (a brief review of these data in the context of criticism of the “Yamnaya Expansion” hypothesis is presented in the recently published book⁴).

This work certainly represents a huge step forward in the development of the hypothesis of the “Yamnaya expansion” and is extremely

interesting. However, it seems that even in its new versions the hypothesis of the “Yamnaya expansion” was unable to offer an adequate answer to the objections that were raised against it.⁵ Moreover, new data allow us to add new objections, and, apparently, no less significant ones. The text below tries to formulate precisely these objections.

Thus, the article⁶ tried first of all to show that the authors and supporters of the hypothesis of the “Yamnaya expansion”, relying primarily on the results of the whole genome analysis, actually ignored those contradictions in their conclusions that are revealed when using data on Y-chromosome haplogroups.

In particular, “that the branches of the R1b haplogroup of the Y-chromosome that are dominant in Western Europe today are not at all connected with the Yamnaya culture: “The ancient Yamnaya samples are located on the ‘eastern’ R-GG400 branch of haplogroup R1b-L23, showing that the paternal descendants of the Yamnaya still live in the Pontic steppe and that the ancient Yamnaya population was not an important source of paternal lineages in present-day West

¹ This paper was written within the research project “Research and valorization of the built, ethnographic, archaeological and artistic cultural heritage of the Republic of Moldova in the context of European integration” (Code: 170101), funded by the State Program (2024–2027).

² Lazaridis et al. 2024; see also: Nikitin et al. 2024.

³ Allentoft et al. 2024.

⁴ Романчук 2024, 10–12, note 1.

⁵ Романчук 2019, 56–57; 130–133; 2020.

⁶ Романчук 2020.

Europeans ... Now I would add to this that in the Corded Ware cultures, which, according to... were the result of ‘steppe migration,’ haplogroup R1a ... almost completely dominates – and not R1b at all.”⁷

The last conclusion, about the “almost complete dominance of R1a in the Corded Ware cultures” today requires significant adjustment (I am very grateful to the reviewers of the article who drew my attention to the new data). Since, as follows from the data of *Harvard University laboratory website* (https://reichdata.hms.harvard.edu/pub/datasets/amh_repo/curated_releases/V52/V52.2/SHARE/public.dir/v52.2_1240K_public.anno), relevant as of October 2024, the ratio of R1a and R1b Y-chromosome haplogroups among the Corded Ware cultures was almost equal – 34 samples demonstrated haplogroup R1a, and 29 – R1b.⁸

Moreover, in one case (Mala Ohrada, Czech Republic) it is precisely R1b-Z2103,⁹ a subclade characteristic of the Yamnaya culture.

That is, the picture today is significantly more complex than the one from which the conclusion cited above¹⁰ was based.

Nevertheless, as we can see, R1b in the Corded Ware cultures is still represented (with a few exceptions, which are discussed below) by a purely European¹¹ and is practically absent (with four exceptions, which are also discussed below) in the Yamnaya culture by the R1b-L51 subclade (primarily its R1b-L151 branch – its origin is now usually localized in Central Europe,

possibly Bohemia¹²). Or, on the contrary, it is the more ancient R-M269.¹³

And the only manifestation of the R1b-Z2103 subclade is noted on the extreme southwestern periphery of the Corded Ware cultures in the Czech Republic.

Therefore, I believe that the conclusion formulated in¹⁴ can still be considered correct: if we consider that the Corded Ware cultures arose as a result of the “Yamnaya expansion”, it is completely unclear how the Yamnaya people could bring to them something that they themselves did not possess.

In fact, in recent years this circumstance has been noted by an increasing number of researchers. For example: “Although it has been proposed that CW formed from a male-biased westward migration of genetically Yamnaya-like people, no overlap in Y-chromosomal lineages (with the exception of a few nondiagnostic I2) has been found between the predominantly R1a-carrying CW and mainly R1b-Z2103-carrying Yamnaya males. Steppe ancestry is also present in BB individuals; however, they predominantly carry R1b-P312, a Y-lineage not yet found among CW or Yamnaya males”;¹⁵ “The paternal lineages found in the BAC/CWC individuals remain enigmatic. The majority of individuals from CWC contexts that have been genetically investigated this far for the Y-chromosome belong to Y-haplogroup R1a, while the majority of sequenced individuals of the presumed source population of Yamnaya steppe herders belong to R1b”;¹⁶ “published Yamnaya Y-chromosomal haplogroups do not match those found in

⁷ Романчук 2020, 246.

⁸ It should be noted, however, that some of the data provided in the *Harvard University laboratory website* database are either not confirmed upon verification (as in the case of the alleged R1b1a1b1a from *Kunila 1*, which, according to the reference data, is characterized by R1a-Z645; Saag et al. 2017, 2187, tab. 1), or, there is duplication of information, as in the case of R1b1a1b1b3 (R1b-Z2103) from Malá Ohrada (references are given as: “PapacScienceAdvances2021”; “PattersonNature2021”). Since there is neither time nor need to verify all the source data at the moment, I will limit myself to this remark. But even if we only use the data presented in Papac et al. 2021; Linderholm et al. 2020, there are still 15 cases of R1b in the Corded Ware cultures. So the increase is quite significant.

⁹ Papac et al. 2021, 7, fig. 4A.

¹⁰ Романчук 2020.

¹¹ Myres et al. 2011, 97, 98, fig. 1: e. f. g.

¹² See also Papac et al. 2021, 6–7.

¹³ It should also be noted that R1b finds are concentrated on the southwestern and western periphery of the Corded Ware cultures, primarily in the Czech Republic and southeastern Poland (Linderholm et al. 2020, 7) even notes that “The Y chromosome haplogroup lineage R1b-M269 or R-L11 are characteristic of Yamnaya and Bell Beaker individuals ... Curiously, the haplogroup is uncommon among other published Corded Ware Complex individuals from Europe (Germany, Poland, Bohemia, Estonia, Lithuania) and is associated with the later Bell Beaker communities”, as well as in Germany. And they are represented by finds from a limited number of sites.

¹⁴ Романчук 2020, 246.

¹⁵ Papac et al. 2021, 2.

¹⁶ Malmström et al. 2019, 6.

Europeans after 5,000 bp, and the origin of this patrilineal lineage is also unresolved.”¹⁷

One could even say that this is already generally recognized, but, however, it still does not entail changes in the key provisions of the position of the supporters of the idea of the “Yamnaya expansion”.¹⁸

Based on the recently published works, we can add some more significant facts on this account. In particular, we will pay attention to the fact that “Sporadic instances of the steppe-associated Y chromosome haplogroup R-V1636 in West Asia occurred at Arslantepe in Eastern Anatolia and Kalavan in Armenia in the Early Bronze Age (~3300–2500 576 BCE) among individuals without detectible steppe ancestry and these could be remnants of the dilution process. This haplogroup was found in the male individual from Remontnoye, both individuals from Progress-25 and two of three males from Berezhnovka, in addition to its occurrence in eleven individuals of the Volga Cline and thus was a prominent lineage of the pre-Yamnaya steppe. Isolated instances have also been found beyond the steppe in Corded Ware individuals from Esperstedt in Germany and Gjerrild in Denmark. The expansive distribution of R-V1636 on the steppe and beyond contrasts with its disappearance on the steppe after the Yamnaya arrived on the scene:

¹⁷ Allentoft et al. 2024, 302. Unfortunately, I must also note that most of these works do not refer to the work of the discoverers, the work of Balanovsky / Chukhryaeva et al. 2017. Moreover, some of them (like Allentoft et al. 2024, 302) refer to other authors in this matter (whose works, with all due respect to them, appeared much later than the work of Balanovsky / Chukhryaeva et al. 2017). It seems to me that this is not a good way. The normal development of science is possible only if we respect and value each other's work. And, namely Balanovsky / Chukhryaeva et al. 2017 were the first to establish and demonstrate the fact that “the ancient Yamnaya population was not an important source of paternal lineages in present-day West Europeans”.

¹⁸ At the same time, opponents of this hypothesis emphasize precisely the above fact, which prompts them to a characteristic conclusion: “...the absence of Y-chromosomal sharing between early CW and Yamnaya males, suggests a limited or indirect role of known Yamnaya in the origin and spread of CW to central Europe” (Papac et al. 2021, 6); “...the Y chromosome record of both groups indicates that Corded Ware cannot be derived directly from the Yamnaya...” (Kristiansen et al. 2023, 71).

a single individual (SA6010; 2886–2671 BCE) from Sharakhalsun has it, with a genetic profile consistent with CLV ancestry (Fig. 2), the last detected holdout of this once pervasive population (Fig. 3).”¹⁹

In other words, even the R1b subclade (R-V1636) that appeared (albeit sporadically) in the Corded Ware cultures dominated the steppe zone in the pre-Yamnaya period. But by the time when the Yamnaya culture itself emerged, it had almost completely disappeared from the steppe.

It is worth to note also that the R-V1636 finds from Transcaucasia “among individuals without detectible steppe ancestry and these could be remnants of the dilution process.”²⁰

The model of “dilution” of the autosomal component was proposed earlier to explain cases where a certain population in Western Europe (Neolithic-Bronze Age) is characterized by a high presence of haplogroup R (or Q) – but the absence of the autosomal component ANE: “even in those cases where we see how modern or ancient carriers of the R haplogroup of the Y-chromosome in Western Eurasia are characterized by the absence of the autosomal component ANE ... – there is no doubt that initially their ancestors, having come to Europe, were characterized by a more or less significant level of the autosomal component ANE. They lost it in the process of crossbreeding with the aboriginal populations of Europe (in the case of the Basques – the Neolithic early farmers of the Atapuerca type).”²¹

It is encouraging that, albeit gradually (in the earlier published work its authors still considered the “dilution” model only as a possible “alternative scenario” that requires discussion): “an alternative scenario in which male migrants from the steppe introduced it into Southern Arc populations during the Chalcolithic, but their autosomal genetic legacy was diluted by the much more numerous locals”,²² the supporters of the “Yamnaya Expansion” hypothesis agreed with this explanatory model.

Be that as it may, another important theoretical consequence follows from the above, which was previously formulated as follows: “another

¹⁹ Lazaridis et al. 2024, 20–21.

²⁰ Ibid., 20.

²¹ Романчук 2020, 248.

²² Lazaridis / Alpaslan-Roodenberg et al. 2022, 10.

important theoretical conclusion with regard to the data of the autosomal genome analysis in general is, apparently, that in comparison with the haplogroup of the Y-chromosome (or mitochondrial DNA) – the autosomal component is ‘unstable’. And, accordingly, less suitable for the reconstruction of historical processes. Namely, in the course of the processes of crossbreeding, the autosomal genome can change quite quickly (over the course of several generations?) – up to the complete loss of the original picture.”²³

It seems important, and even necessary, to emphasize this once again. Since today geneticists in their historical interpretations tend to put the results of whole-genome analysis at the forefront. And not only geneticists but also representatives of other disciplines (primarily archaeologists and anthropologists) relying on their conclusions. For example, A. G. Kozintsev, who proposed his version of the East Eurasian hypothesis of the Dene-Caucasian ancestral homeland, emphasized that part of the conclusions,²⁴ which are based on the analysis of the ANE component (“A possible connection between the spread of the ANE component from Siberia to the west and the expansion of the languages of the Dene-Caucasian macrofamily was pointed out by A. A. Romanchuk”;²⁵ “Romanchuk’s observation that the westward migration from Siberia, marked by the ANE (Ancient North Eurasian) autosomal component ... deserves greater attention. Genome-wide components are more informative for tracing migrations than are haplogroups”²⁶). And in fact, he completely ignored the results related to the analysis of Y-chromosome haplogroups.

Meanwhile, it seems that the only correct approach will be the one that implies equal consideration (and mutual verification) of both the data of the whole genome analysis and the data of the analysis of Y-chromosome haplogroups (as well as mtDNA).²⁷ And the emphasis (at least at this

stage of development of genetic research) is preferably, I believe, placed on the analysis of data on Y-chromosome haplogroups. For the early eras of human history, they are especially informative.

Turning from this position to the discussed issue, it should be noted that, in general, the authors of recent works, on the contrary, believe that the data on Y-chromosome haplogroups “is less informative for tracing the origins of the Core Yamnaya”. And at the same time, they believe that it “proves continuity of the Don Yamnaya with their Serednii Stih ancestors. Haplogroup I-L699 was an important lineage in the Dnipro area since the Neolithic hunter-gatherer period, continued to be prevalent among the Serdenii Stih, and in the Don Yamnaya was dominant (17/20 instances). The Core Yamnaya belonged primarily to haplogroup R-M269 (49/51 instances) most of which could be determined as belonging to the Z2103 sub-lineage (41/51). This lineage is unprecedented in our sampling of the steppe before the Yamnaya period; its closest relative is the L51 lineage which dominated the Beaker group and mainland Europe outside the steppe (Fig. 3), with a slightly more distant relative in the R-PF7563 lineage found in Pylos in Mycenaean Greece. With an estimated time of formation of ~4450 BCE (<https://www.yfull.com/tree/R668L23/>; v11.04.00), the R-L23 lineage unifies Beaker, Yamnaya, and Mycenaean Y-chromosomes within an Eneolithic timeframe, which is consistent with the ancestors of these three groups being part of a single population in the Yamnaya period itself since population divergences are always lower than the genetic divergences of specific haplotypes. It is a challenge for future ancient DNA studies to find the population in which the Eneolithic R-L23 founder lived and to trace his R-Z2103 descendants. Their absence from the Eneolithic record, together with the evidence (discussed below) for isolation in the formative period of the Yamnaya suggest that he might have been part of a small group not yet sampled.”²⁸

Commenting on this quote, let’s start with the fact that, as one can see, the new data generally confirms the conclusions of O. P. Balanovsky’s team.²⁹ That is, the R1b subclades

²³ Романчук 2020, 248, note 11.

²⁴ Романчук 2019; 2020.

²⁵ Козинцев 2023, 69; 2023a, 55.

²⁶ Kozintsev 2023, 142.

²⁷ It is interesting to point out here: “Our results suggest that despite the discontinuity observed between British Mesolithic and Neolithic samples at the autosomal and mitochondrial level, Y-chromosome lineage composition remained stable at the time of the appearance of agriculture in the region” (Brace et al. 2019, Suppl. 15).

²⁸ Lazaridis et al. 2024, 23.

²⁹ Balanovsky / Chukhryaeva et al. 2017.

that characterize (and characterize precisely with their complete dominance – “41/51”, more than 80%) the Yamnaya culture (more precisely, the so-called “Core Yamnaya”) are radically different from those that characterize Western Europe (including the Bell Beaker culture, and not to mention the Corded Ware cultures).

Despite the fact that, according to these new data,³⁰ among the representatives of the Yamnaya culture (and related groups) the subclade R-L51 was found (four cases: one among the Yamnaya people of Kalmykia, another in the Volga region, the third on the Don, and the fourth in the territory of Romania (Smeeni-Movila Mare)), it does not change the situation in any fundamental way. And even more so does the discovery of three cases of haplogroup R1a in the Neolithic materials on the Middle Don (Golubaya Krinitisa (Rossoshansky district, Voronezh region), dated to around the middle of the 6th millennium BC).

These facts do not change the situation since all the above-mentioned finds of R-L51 in the steppe zone do not tell us anything about where exactly the split of the original lineage, R-L23, occurred.

Which (R-L23), it is worth emphasizing, is absent or almost absent in most Western European populations, but is quite noticeably represented in some modern populations of the Balkans and the Mediterranean – including Greece (8%), Kosovar Albanians (11%), southern (4.8%) and northern Italy (6.5%), southern France (2.6%), Crete (4%), Slovenia (3.9%) and Romania (4.5%).³¹ And it also reaches extremely high values (27%) in the Upper Rhone Valley in the Swiss Alps.

Such territorial distribution hardly could be interpreted as the result of “Yamnaya expansion”.

And even more so, since the frequencies of R-L51 itself (that is, once again, a younger subclade derived from R-L23), including R-L151, in the Balkans (in all the populations mentioned above, and others considered in the cited study) are equal to zero.³² In Crete, the overall frequency of R-L51 is 0.6%.

That is, R-L23 (as well as the even more ancient R-M269 (xL23), which is again completely

absent in the absolute majority of the Western and Central European populations (examined by N. Myres et al. in the cited paper), but in the Balkans, on the contrary, is quite noticeable (as in Serbia (4.4%), Macedonia (5.1%), Kosovo (7.9%), Romania (2.9%)³³), penetrated the Balkans independently of R-L51, as part of completely different populations.

And, obviously, such a scenario is possible only with a very early penetration of both R-L23 and R-M269 (xL23) into the Balkans (and in the case of R-L23, into Central Europe) that occurred long before the emergence of R-L51, and certainly long before the emergence of the Yamnaya culture. It is even possible that this penetration should be dated to pre-Neolithic times, most likely the Mesolithic. As, in fact, was proposed earlier.³⁴

That’s why, even on the contrary: the fact that in the Yamnaya culture, despite the already significant array of analyzed data, the “L51 lineage” of the R1b haplogroup is almost absent, serves as a weighty argument against assuming the penetration of R-L51 into Western Europe from the area of the Yamnaya culture.³⁵

³³ Ibid., Suppl., Tab. S4.

³⁴ Романчук 2015; 2019; 2020.

³⁵ As for the statement that “with an estimated time of formation of ~4450 BCE (<https://www.yfull.com/tree/R668L23/>; v11.04.00), the R-L23 lineage unifies Beaker, Yamnaya, and Mycenaean Y-chromosomes within an Eneolithic timeframe, which is consistent with the ancestors of these three groups being part of a single population in the Yamnaya period itself since population divergences are always lower than the genetic divergences of specific haplotypes” (Lazaridis et al. 2024, 23), then, first of all, I would not consider the dating of “estimated time of formation of ~4450 BCE” as some kind of unconditional chronological reference point. We have very vivid examples of how actual datings obtained by genetic methods diverge extremely from the historical and archaeological data, and how geneticists ultimately come to the recognition of the need for a radical increase in the age of their datings in such situations (Романчук 2024, 55–64; 2024a).

The above data on the distribution of R-L23 and R-M269 (xL23) in the Balkans and Western Europe just encourage us to think that modern datings of the origin of R-L23 are considerably rejuvenated. But this, of course, should be the topic of a separate conversation.

However, even based on this dating of this event, the assertion that “which is consistent with the ancestors of these three groups being part of a single population in the Yamnaya period itself since population divergences are always lower than the genetic divergences of specific haplotypes” – obviously absolutizes as the only possible scenario. Meanwhile, there is no reason to assume that the separation of

³⁰ Lazaridis et al. 2024, Suppl., Tab. 1.

³¹ Myres et al. 2011, 96, 97, 98, fig. 1e, Suppl., Tab. S4.

³² Ibid., 97, fig. 1: f. g. h, Suppl., Tab. S4.

The logic of such a conclusion seems quite clear, but below it will be explained in more detail, by involving another haplogroup (I-L699) significant for the Yamnaya culture in the analysis of the situation.

Indeed, another important fact, and also not at all in favor of the hypothesis of “Yamnaya expansion,” is the situation with the sharp dominance of the I-L699 haplogroup in the Yamnaya culture of the Don (and, what is even more significant, in the population that was the source for the formation of the Yamnaya culture): “Haplogroup I-L699 was an important lineage in the Dnipro area since the Neolithic hunter-gatherer period, continued to be prevalent among the Serdenii Stih, and in the Don Yamnaya was dominant (17/20 instances).”³⁶ That is, since the formation of the so-called “Core Yamnaya” is associated by the I. Lazaridis’ team with the area of the Sredny Stog culture (“the population of the Serednii Stih culture from which the direct ancestors of the Yamnaya themselves were formed”;³⁷ “The Yamnaya themselves were thus the product of admixture between the Caucasus-Lower Volga easterners (for which Remontnoye is a genetic stand-in) with the Ukraine_N-admixed Serednii Stih westerners...”;³⁸ “Therefore it is parsimonious to assume that the Core Yamnaya are descended from an unsampled Serednii Stih population...”³⁹), we must conclude that it was I-L699 (according to its modern designation, I2a1b1a2a2a (generalizing: I2a1~); in 2019 it was still designated as I2a2~) that was initially the most important Y-chromosome haplogroup in the emerging Yamnaya culture. And, theoretically, along with R1b-Z2103, it was I-L699 that

a new haplogroup must necessarily precede the division of the original population. In fact, it is obvious that both options are equally probable, and the division of the original population could have occurred in ancient times – while the formation of a new haplogroup occurred much later, in one of the separated populations. Therefore, on the contrary, the presence of R-L51 in the Yamnaya culture, taking into account the overall picture of the set of haplogroups characterizing its patrilineal gene pool (and, we emphasize once again, even based on the supposed dating of the separation of R-L51 today, “~4450 BCE”), can rather be regarded as substrate (or adstrate). Or, in general, simply the result of contacts.

³⁶ Lazaridis et al. 2024, 23.

³⁷ *Ibid.*, 1.

³⁸ *Ibid.*, SI 2, 183.

³⁹ *Ibid.*, SI 2, 182.

should have characterized the “Yamnaya expansion” into Central and Western Europe – reflected in its corresponding high popularity in the Corded Ware and Bell Beaker cultures.

Meanwhile, this is again not observed at all. And although haplogroup I-L699, albeit rarely, is still represented in modern Western and Central Europe, this is obviously due to the fact that it actually originates in this region at the end of the Upper Paleolithic-Mesolithic. From where it penetrates (also in the Mesolithic) into the Lower Dnieper region.⁴⁰

In the Corded Ware cultures, as well as in the Bell Beaker culture, according to data,⁴¹ I2a (especially its branch L699), and in general haplogroup I, is very poorly represented.⁴² However (including according to the same data), I2a1 (in various subclades) is extremely widely represented in the earlier (and substrate for a number of Corded Ware cultures) Globular Amphora culture of Ukraine and Poland.⁴³ And one of the two (along with R1b1a1a; Q1a2 is also represented in it) dominant haplogroups of the Y-chromosome in Zvejnieki (Mesolithic-Neolithic of Latvia, 6th millennium BC) was also I2a and its subclades.⁴⁴ I2a~ was also very popular in the Iron Gates Mesolithic on the Danube.⁴⁵ And also in the Mesolithic-Neolithic of Britain, where it characterized “the vast majority of Mesolithic and Neolithic individuals analysed.”⁴⁶ Finally, I2a1b1a2a2a is also noticeable in the Trypillian

⁴⁰ A capacious generalization of the data accumulated to date from archeology, anthropology and genetics on the migration flows of the Mesolithic era from the northern part of Eastern Europe to the Lower Dnieper region, which served as the basis for the formation of the Neolithic Dnieper Napdorozhye, is contained in Lillie et al. 2012; Потехіна 2020; see also: Mattila et al. 2023; Гаскевич 2020; some considerations were exposed in Романчук 2013, 269–270.

⁴¹ Mathieson et al. 2018, Suppl., Tab. 1; Narasimhan et al. 2019, Suppl., Tab. 1.

⁴² Thus, I2a is still noted for individuals from Pikutkowo belonging to the Corded Ware culture in Poland; Fernandes et al. 2018, Suppl. Tab. 1. But, as is clear, this does not change the essence of the matter. This is a different, more ancient, and obviously substrate subclade, derived from local Neolithic cultures. Just as I2a is substrate in the Bell Beaker culture sites in the Iberian Peninsula and Britain; Olalde et al. 2019, 3, Suppl., Tab. S1, Tab. S4.

⁴³ Allentoft et al. 2024, Suppl. Data VII.

⁴⁴ Narasimhan et al. 2019, Suppl., Tab. 1.

⁴⁵ *Ibid.*

⁴⁶ Brace et al. 2019, Suppl., 15.

culture⁴⁷ (which, as we will see below, is quite interesting).

Thus, from the above, it can be concluded that the work of I. Lazaridis' team has indeed confirmed the previous and added new counter-arguments against the idea of the "Yamnaya expansion" into Europe. Of course, they are trying to resolve the outlined contradictions (to the extent that they notice and acknowledge them) by resorting to the hypothesis of a small and not yet studied population ("an unsampled Sereidii Stih population"; "a small group not yet sampled"). However, this hypothesis, initially seeming completely far-fetched (and the larger the array of accumulated and studied data became, the more far-fetched), as it logically develops taking into account new data, it finally seems to lose its plausibility.

Indeed, now we must talk about this hypothetical micropopulation (let's emphasize: precisely a micropopulation, which is important, as I will try to show below) of the Yamnaya culture as a population in which not one, but two leading, absolutely dominant in the Yamnaya culture, Y-chromosome haplogroups are missing, R1b-Z2103 and I-L699. As well as (and this also looks extremely strange) not a single other R1b subclade from the extensive series presented (albeit in small quantities) in the Yamnaya culture materials,⁴⁸ or a single subclade of G and J haplogroups.⁴⁹

⁴⁷ Nikitin et al. 2024, SI, 3, Tab. S1.

⁴⁸ Lazaridis et al. 2024, Suppl., Tab. 1.

⁴⁹ Note: as follows from the data (Lazaridis et al. 2024, Suppl., Tab. 1), many of these R1b subclades are quite evident in the Yamnaya culture monuments from the territory of Romania and the Republic of Moldova (in the origin of which, as a result of migrations from the Yamnaya culture area, none of the archaeologists ever doubted, even those who emphasized the role of local, Carpathian-Balkan, elements and roots in the emergence of these monuments ("While we assume the 'Yamnaya' being mostly covered by an intense wave of migrant people from the east, in a novel socio-economic-ideological atmosphere, it remains to be seen whether the first Pit-Graves under Kurgans at the Lower Danube from c. 3300 cal BC are also carried by steppe people related to those using the north-Pontic Nizhne-Mikhailovka and Kvityana burial traditions, or by local populations integrating new 'eastern' burial customs into their own rituals. Perhaps a combination of both is the most likely scenario"; Frînculeasa et al. 2015, 46–47).

Indeed, this is a striking contrast to the situation in the Corded Ware and Bell Beaker cultures.

Moreover, it is significant that, in relation to the supposed "Yamnaya expansion" into Central and Western Europe, we should speak not of one, but of two such "wonderful micropopulations", one of which should have become the ancestor of the Corded Ware cultures (that is, characterized by the dominance and, apparently, still a very sharp dominance, if not absolute) of the corresponding R1a subclades (still, we recall, not discovered in the Yamnaya culture despite the already very significant increase in data) and the complete absence of R1b-Z2103 and I-L699, and the other – for the Bell Beaker cultures (that is, characterized by the absolute dominance of R1b-L51 and the complete absence of R1b-Z2103 and I-L699).

The fact that we have to assume the existence of two such "miraculous populations" already reduces the mathematical probability of such a development of events not by half, but by significantly more.

A significant problem for the "non-attested micropopulation" hypothesis is that it must be precisely a micropopulation. That is, according to the logic of the supporters of this assumption, in the Early Bronze Age, two (if we are talking only about Europe) by definition small groups of people should have in the shortest possible time (in practice, we should be talking about a couple of centuries, if not less: "It has been estimated that admixture in diverse Corded Ware populations occurred in a narrow date of ~3000–2900 BCE"⁵⁰) mastered the vast spaces of Central and Western Europe (as well as the forest zone of Eastern Europe), almost completely replacing and assimilating, since the huge substrate contribution is obvious both in the Corded Ware cultures and in the Bell Beaker culture; they, it seems, can rightfully be called "substrate cultures"⁵¹ the masses of the autochthonous population that significantly outnumbered them.⁵²

⁵⁰ Lazaridis et al. 2024, Suppl., 180.

⁵¹ More details in Романчук 2020, 252–254.

⁵² Apparently, the genesis of the Afanasievo culture was also much more complex than is implied by the hypothesis of the "Yamnaya expansion" in the version of I. Lazaridis et al. In any case, although I. Lazaridis et al. for including the analyzed individuals in the so-called "Core Yamnaya" proceeded primarily from "the following criteria: (i) labeled as either Yamnaya or Afanasievo based on archaeological considerations, ..." (Lazaridis et al. 2024, Suppl., 153), the set of Y-chromosome haplogroups in the carriers of the

Really, a completely implausible scenario.⁵³

Afanasievo culture also differs significantly from that characteristic of the Yamnaya culture. Thus, according to Holard et al. 2018, 97, “most of the Afanasievo men submitted for analysis belonged to a single sub-haplogroup, R1b1a1a, which reveals the predominance of this haplogroup in these early Bronze Age populations”. The R1b1a1a branch, or R1b-M73 (another defining marker is M478), today is distributed mainly in the territories to the east of the Urals and further to Altai (Балановский 2015, 87). And it is an even more distant relative of the R1b-Z2103 subclade characteristic of the Yamnaya culture.

Let me note in passing that it is R1b1a1a (Narasimhan et al. 2019, Suppl., Tab. 1; Lazaridis et al. 2024, Suppl., Tab. 1) that is one of the two (along with I) dominant Y-chromosome haplogroups in the Zvejnieke burial ground (Mesolithic of Latvia, 6th millennium BC). In general, “Haplogroup R1b1a1a (R1b-M73) was frequent among Russian Neolithic individuals” (Allentoft et al. 2024, Suppl. Note 3b, 48).

In the Yamnaya culture, the R1b1a1a subclade is not attested (according to: Lazaridis et al. 2024, Suppl., Tab. 1), but in the Botai Eneolithic culture of Kazakhstan, it is represented by “the R1b1a1 haplogroup, restricted almost exclusively to Central Asian and Siberian populations. Neither of these Botai lineages has been observed among Yamnaya males” (de Barros Damgaard et al. 2018, 5).

According to Lazaridis et al. 2024, Suppl., Tab. 1, about 50% of the Afanasevo culture carriers analyzed by them are indeed characterized by haplogroup R1b-Z2103 (or, more precisely, R1b1a1b1b3, taking into account samples determined through other markers, but also included in R1b1a1b1b3). But the authors also note the presence of the same R-Y13200 (R1b1a1a), N-Y6503 (which is another analogy with the Botai culture), R-M269 (R1b1a1b) and Q-Y6826 (Q1b2a1a~).

According to Narasimhan et al. 2019: Suppl., Tab. 1, three cases of Q1a2 are also noted for the Afanasievo culture (obviously substrate; it later, in various subclades, completely dominates in the Okunev culture, as well as in the Shaman-ka II burial ground (South Baikal)).

The Yamnaya culture of Kazakhstan is characterized by haplogroups R-Y106006 (R1b1a2b), Q-L939 (Q1b2b1b2b~) and R-V1636 (R1b1a2); Lazaridis et al. 2024: Suppl., Tab. 1.

⁵³ In fact, Lazaridis et al. 2024 are forced to resort to the idea of “an unsampled Serednii Stih population” even to explain the emergence of “Core Yamnaya” itself. Since, if the derivation of the Yamnaya culture of the Don from the Sredny Stog culture looks relatively convincing, then for “Core Yamnaya” it turns out that the original population of the Sredny Stog culture (Lazaridis et al. 2024, Suppl., Tab. 1), characterized almost exclusively by haplogroup I (I-L699, I-Y3259), and if we add the Neolithic sites, then also R-V88, R-V2219, R-L754, R-M1214 (Deriivka), R1a (Golubaya Krinita), Q (Igren, Allentoft et al. 2024, Suppl. Data VII), suddenly turns into a population characterized almost exclusively by haplogroup R-Z2108 (R1b1a1b1b3). The same is true for Allentoft et al. 2024, 306, who try to derive the Yamnaya Culture from a population of the Golubaya Krinita type, characterized almost exclusively by R1a. Indeed, it seems more logical to me to assume that the area in which the formation of the autosomal “ancient Yamnaya

Moreover, it seems that the authors themselves apparently have some doubts about the plausibility of the scenario for the emergence of the Corded Ware cultures suggested by the hypothesis of the “Yamnaya expansion”. I believe this is evidenced by the reservations they made in the article (and repeatedly) such as “The Corded Ware population ... was formed indeed by ... or, at the very least, genetically Yamnaya ancestors that need not have been Yamnaya in the archaeological sense.”⁵⁴

Alas, but if the ancestors of the Corded Ware culture “need not have been Yamnaya in the archaeological sense” – this de facto means the destruction of the basic postulate of the “Yamnaya expansion” hypothesis.

The implausibility of the scenario for the emergence of the Corded Ware and Bell Beaker cultures suggested by the “Yamnaya expansion” hypothesis (as well as the implausibility of the “Yamnaya expansion” hypothesis in general) becomes even more obvious if we involve physical anthropology data (more precisely, craniometry) in the analysis. Indeed, the authors of the “Yamnaya expansion” hypothesis (geneticists, first of all, but also archaeologists and anthropologists), having completely focused on the data of whole-genome analysis, actually neglected to compare the conclusions and interpretations they obtained not only with the data on the Y-chromosome haplogroups – but also with the data of physical anthropology. Which, in fact, in this case should have been a mandatory stage of the research procedure. Especially since the data of physical anthropology, as it seems, poorly agree with the key theses of the hypothesis of “Yamnaya expansion” even in its new incarnation.

Here we present some results of the latest work of A. A. Kazarnitsky, devoted to the problem of possible migrations from Western to Eastern Europe in the context of the formation of the Fatyanovo and Abashevskaya cultures.

Thus, characterizing the Western European series of the Neolithic-Eneolithic times, A. A. Kazarnitsky writes: “The most ancient of them ... have long, narrow or medium-wide

component” took place was significantly wider than the area of the Sredny Stog culture, and covered very vast areas of Eastern Europe (both its steppe and forest parts).

⁵⁴ Lazaridis et al. 2024, 23–24.

dolichocranic skulls, as a rule, a narrow and low face ... Almost the same set of features, but with a greater length and width of the brain section and a greater width of the eye socket, is observed in the Neolithic and Eneolithic series ... among them, only one – from Ostorf, the Funnel Beaker culture – has an unexpectedly wide face.”⁵⁵

Speaking about the Bronze Age of Western and Central Europe, he characterizes the anthropological appearance of the bearers of the Corded Ware cultures as follows: “a combination of features that is almost never found in the materials of the Neolithic era is characteristic of most samples of the Corded Ware culture ... very long, narrow, dolichocranic, high skulls. At the same time, among them, a small zygomatic diameter and an average height of the face are observed in the western groups, while in the eastern ones the facial skeleton is noticeably wider and higher. An exception is the sample from the Złota culture sites: close to the circle of Corded Ware cultures in archaeological features, craniologically it is closer to the Neolithic population.”⁵⁶

Let us emphasize once again two key and characteristic features of the “very dolichomorphic skulls of the Corded Ware (f) and Unetice (g) cultures”:⁵⁷ a) very long and narrow skull; b) very narrow (“small zygomatic diameter”; the further west, the narrower) and medium-high face.

Meanwhile, “craniological samples of the Eneolithic Sredny Stog and Khvalynsk cultures (j), local series of the Yamnaya culture (l), as well as the Catacomb and Poltavka cultures (m), with all their regional diversity, have a number of common features... The long and very long brain sections vary greatly in absolute (and relative) width from narrow to wide (from dolichocranial to brachicranial), but the face, as a rule, is wide and medium-high with wide and low eye sockets.”⁵⁸

That is, let us formulate it once again: the key feature of the local series of the Yamnaya culture (as well as the Eneolithic Sredny Stog and Khvalynskaya, ancestral to it), and in contrast (radical difference) from the bearers of the Corded Ware cultures, is precisely the large

width of the cranium (with pronounced brachycrania, or, at least, a tendency to brachycrania, in many local series) and, especially, a wide (and even very wide in many local series) face.

At the same time, even the most dolichocranic and less wide-faced samples of these cultures (Yamnaya, Sredny Stog, Khvalynskaya) turn out to be significantly far from the characteristics of the bearers of the Corded Ware cultures.⁵⁹ And it is obviously not possible to deduce the anthropological (craniological) type of the carriers of the Corded Ware cultures from any population of the Yamnaya culture.

The bearers of the Bell Beaker culture are the most distant (even more than the steppe series) from the Corded Ware culture in their craniological appearance.⁶⁰ Which also excludes the possibility of tracing the origin of the Bell Beaker culture to the Corded Ware culture (contrary to the assumptions made in the works of some supporters – from among geneticists – of the “Yamnaya expansion” hypothesis on this matter).

At the same time, the situation with the craniological portrait of the Bell Beaker culture bearers differs from the situation of the Corded Ware cultures. Since, “the skulls of the Bell Beaker culture bearers both in Central Europe and on the Iberian Peninsula (e) have different [different from other Western European ones of both the Neolithic-Eneolithic and the Bronze Age – A. R.] proportions: they are of medium length, wide, brachycranial, the face in these samples is also narrow, but higher than in the Neolithic.”⁶¹

However, despite their characteristic brachycrany (which brings them closer to the skulls of both the Yamnaya culture and the Eastern European Neolithic-Eneolithic cultures in general), the bearers of the Bell Beaker culture, based on the totality of the studied craniometric features, are almost as far (of the populations examined by A. A. Kazarnitsky) from both the Yamnaya culture (as well as the Khvalynsk and Sredny Stog) and the Eastern European Neolithic. And they are located in opposite corners of the graph.⁶² Which, it seems, excludes for the bearers of the Bell Beaker culture the possibility of deriving their craniological type from

⁵⁵ Казарницкий 2024, 28.

⁵⁶ Ibid., 29.

⁵⁷ Ibid., 31.

⁵⁸ Ibid., 30.

⁵⁹ Ibid., 29, рис. 2: 6.

⁶⁰ Ibid., 29, рис. 2: 2. 5. 6.

⁶¹ Ibid., 28.

⁶² Ibid., 29, рис. 2: 5. 6.

the Yamnaya culture (as well as Sredny Stog and Khvalynskaya).

Moreover, craniological data allow us to outline a local Western European late Neolithic prototype (or analogue) of the craniological portrait of the bearers of the Bell Beaker culture. A. A. Kazarnitsky specifically draws attention in this regard to the Seine-Oise-Marne culture: “in the late Neolithic and Eneolithic of Western Europe, new craniological features appear that are characteristic only of the bearers of the Seine-Oise-Marne culture (c): shorter and wider mesocranial skulls of medium height with even smaller eye sockets than in the previous era.”⁶³ And he emphasizes that “the closest, albeit incomplete, morphological analogies to them [the skulls of the bearers of the Bell Beaker culture – A. R.] are in the materials of the Seine-Oise-Marne culture.”⁶⁴

It seems that it is impossible to directly trace the craniological type of the Bell Beaker culture bearers to the type of the Seine-Oise-Marne culture bearers. But the brachycrany of the Bell Beaker culture bearers, as well as the mesocrany of the Seine-Oise-Marne culture bearers (which sharply distinguishes them from other Neolithic-Bronze Age populations of Western and Central Europe and brings them closer to the characteristic circle of populations of Eastern Europe) obviously correlates with the genetic portrait of the Bell Beaker culture bearers. And serves as confirmation of their Eastern European, ultimately, origin.⁶⁵

However, it is also obvious that the genesis of these populations is connected with an impulse from Eastern Europe not in the Early Bronze Age (and not from the Yamnaya culture) but in times much earlier. At least in the Neolithic era. Or rather, as was suggested⁶⁶, even in the Mesolithic.

Let me remind you that it was previously suggested that “large-scale early Neolithic migrations from the Middle East (from Anatolia, according to modern ideas) to Europe and their result (the formation of powerful Neolithic and Eneolithic cultures of Europe) hid an earlier

genetic landscape and, due to the above-mentioned reasons, made it invisible to us (or rather, almost invisible) until the beginning of the Bronze Age, when a kind of “renaissance” of this earlier genetic landscape took place.”⁶⁷ At the same time, attention was paid both to ethnographic evidence of the possibility of such a model (the ritual, and custom, recorded among some Indo-European peoples of the defeat of the defeated refusing to be buried in the ground in favor of the victors), and to the observations of geneticists themselves in connection with the so-called “resurgence of WHG ancestry during the European Middle Neolithic.”⁶⁸

It is worth to note in this regard that the data of craniology for Eastern Europe also testify to the implementation of precisely this model. A. A. Kazarnitsky drew attention to this: “A similar model of the formation of ancient populations was proposed by us for an even earlier time [Казарницкий, 2014]: ‘The features of the Mesolithic population of Eastern Europe are not noticeable among the inhabitants of this territory in the Neolithic, but the features of the populations of both eras of the Stone Age are recorded in different local groups of the Early Bronze Age.’”⁶⁹

In fact, the very recognition of the fact that different (or even the same) subclades of haplogroups R1a and R1b (and partly Q) are associated (dominating in the corresponding populations) already in the Bronze Age (and even in the Mesolithic-Neolithic) of Europe with different, and even very different from each other,

⁶⁷ Романчук 2020, 245.

⁶⁸ Recent research shows that in Poland and Romania this “Mesolithic renaissance” manifested itself to an even greater extent than in Western Europe: “In comparison with the early Neolithic LBK individual from Germany, a significant increase in allele sharing with the local hunter-gatherers were detected in 16 out of 30 investigated Neolithic/Eneolithic individuals from Poland and Romania” (Mattila et al. 2023, 7).

Moreover, it was established that in the Prut-Dniester interfluvium the influence of the “Mesolithic hunters” reappears even much later – in the Mnogorollikova Ceramics Culture (Babino) of the Middle Bronze Age: “3.5. Hunter-gatherer genetic ancestry resurgence in Babyne/Multi-Cordoned Ware. Modeling shows that both the Yamna of Ukraine of the EBA and the later Multi-Cordoned Ware of the MBA were largely descended from the Core Yamna but the latter experienced gene flow from a population that seems to have had more hunter-gatherer ancestry”; Nikitin et al. 2024, SI, 32.

⁶⁹ Казарницкий 2021, 133.

⁶³ Ibid., 28.

⁶⁴ Ibid., 29.

⁶⁵ See also in connection with this correlation: Романчук 2013; 2015; 2019; Романчук / Семенов 2014.

⁶⁶ starting from Романчук 2012; 2013; Романчук / Семенов 2014.

craniological types, which (craniological types) are recorded in the corresponding regions over the course of two to three millennia, requires us to also recognize that this connection between a certain craniological type and certain haplogroups could not have arisen in the blink of an eye and already at a late (or even sufficiently developed) stage of the evolution of these craniological types.⁷⁰

No, this could only be the result of long-term processes of crossbreeding of various populations, which began very early, at the dawn of the formation of the corresponding craniological types (that is, back in the Mesolithic era), and which occurred (with different results, depending on the difference in the initial components and the conditions of their interaction) in different parts of Europe.

And this picture obviously does not agree with the supposed hypothesis of the “Yamnaya expansion” model of “population replacement” of Europe (even partial, in the newest versions of this hypothesis) as a result of late migrations from the area of the Yamnaya culture, already in the Bronze Age.

Moreover, the ideas of I. Lazaridis et al. on this account do not even agree with the picture of the development of the Yamnaya culture itself according to physical anthropology data. If I. Lazaridis et al. suggest that “the expansion of people of the Yamnaya culture ... totally displaced previous groups on the Volga and further east”,⁷¹ then the data of craniology paint a different picture. Namely, “the greater morphological variability of the Yamnaya groups than the Eneolithic ones does not allow us to consider the bearers of the Khvalynskaya-Sredny Stog burial traditions as a substrate component for the entire steppe population of the Early Bronze Age The noticeable Khvalynskaya-Sredny Stog population influence is traced mainly in the western part of the Yamnaya area. The population of other origin prevails in the composition of the remaining Yamnaya groups, in which at least three regional communities are distinguished: the Don-Volga

⁷⁰ Meanwhile, this is precisely what the supporters of the “Yamnaya expansion” are actually proposing: “It has been estimated that admixture in diverse Corded Ware populations occurred in a narrow date of ~3000-2900BCE”; Lazaridis et al. 2024, Suppl., 180.

⁷¹ Ibid., 1.

(including the Ural left-bank), the Caspian and the Ural right-bank.”⁷²

Let me emphasize once again an important point: if according to the data of the whole genome analysis the Yamnaya culture looks extremely homogeneous (“The Core Yamnaya homogeneity is remarkable given that this cluster includes individuals sampled across 5,000 km from Hungary to southern Siberia, a vast slice of Eurasia”⁷³), which is precisely what distinguishes it significantly from the preceding Eneolithic population of the steppe zone (“The genetic heterogeneity of the Srednii Stih contrasts with the homogeneity of the Core Yamnaya”⁷⁴), then the data of physical anthropology also paint a directly opposite picture of “greater morphological variability of the Yamnaya groups than the Eneolithic ones”.

This obvious fact makes us think that the results of the whole-genome analysis used by supporters of the “ancient Yamnaya expansion” hypothesis to justify it (which depict, among other things, an “extremely homogeneous” Yamnaya culture from the Danube to the Altai) clearly require further understanding both at the level of the methodology used and the interpretation of the results obtained.⁷⁵

⁷² Казарницкий 2021, 130.

⁷³ Lazaridis et al. 2024, 12.

⁷⁴ Ibid.

⁷⁵ In fact, the need for further understanding of the use of whole-genome analysis in historical reconstructions is also evidenced by the dynamics of changes in the “Yamnaya expansion” hypothesis itself over the past ten years. These changes, as is obvious, were caused not only (and not even so much) by the increase in data, but also by changes in both the method itself and the approach to interpreting the results of whole-genome analysis.

Without trying to outline all the twists and turns of these changes here, I will limit myself to reminding that almost simultaneously with Lazaridis et al. 2024 another work suggests the emergence of the Yamnaya culture in a significantly different way: “Although the broader effects of the steppe migrations around 5,000 cal. bp are well known, the origin of this ancestry has remained a mystery. Here we show that the steppe ancestry composition (Steppe_5000BP_4300BP) can be modelled as a mixture of around 65% ancestry related to herein-reported HG genomes from the Middle Don River region (MiddleDon_7500BP) and around 35% ancestry related to HGs from Caucasus (Caucasus_13000BP_10000BP) (Extended Data Fig. 6 and Supplementary Data 9). Thus, Middle Don HGs, who already carried ancestry related to Caucasus HGs (Extended Data Fig. 4a), serve as a hitherto-unknown proximal source for the majority ancestry contribution into Yamnaya-related genomes.

In the context of the prerequisites for such an understanding, it is worth to draw attention to some key points.

First of all, if we raise the question of what is the key innovation in the hypothesis of “Yamnaya expansion” by the work by I. Lazaridis et al., then it seems that this is their conclusion about the decisive significance of the contribution of the gene pool of the carriers of the Neolithic traditions of the Dnieper-Don interfluvium (through the population of the already Eneolithic Sredny Stog culture) to the genesis of the Yamnaya culture: “We have traced the origins of the Yamnaya to the Dnipro Cline and the populations of the Serechnii Stih culture: the Yamnaya were formed as people of the CLV cline admixed with people of the Dnipro-Don area having UNHG ancestry.”⁷⁶

However, what does this mean in a more general sense?

In fact, this means, first of all, the recognition of a sharp increase in the role of the gene pool of the so-called “Western Hunter-Gatherers”, WHG, in the genesis of the Yamnaya culture population.

Since the Neolithic population of the Lower Dnieper region, “UNHG”, obviously had a very complex genesis within which two factors constituting this population are particularly distinguished, associated with migrations to the Dnieper Nadporozhye region in the Mesolithic era of population groups from the northwest and southwest. That is, exactly WHG, but two quite different groups.

The first of these migrations, mentioned above, is the Mesolithic migration from the more northern areas of Eastern Europe, adjacent to the Baltic Sea coast. It has long been noted by archaeologists, anthropologists, and later by geneticists.⁷⁷ The second migration, from the southwest, was outlined relatively recently by D. L. Gaskevich,⁷⁸ and its original region was designated the Iron Gates area on the Danube.

It was these migrants (both from the northwest and the southwest) who brought with

them the anthropological types characteristic of the Mesolithic-Neolithic of the Dnieper Nadporozhye region, and haplogroup I of the Y chromosome (and also, apparently, R1-V88; which, in particular, dominates (along with I2a) in Dereivka on the Dnieper⁷⁹ and is widely represented in the Mesolithic of the Iron Gate region).

It is worth emphasizing the D. L. Gaskevich’s assumption that it was not a one-time migration, but a stable and long-term cultural continuum, within the framework of which regular contacts and population movements were realized (“long-term interaction between the inhabitants of the two regions, accompanied by multiple counterflows of population due to the exchange of marriage partners”). As he notes, “the assumption of closer ties than previously thought between the late Mesolithic populations of the Danube and Dnieper regions allows us not to contrast these two regions, but to consider them as extreme parts of a single cultural region, covering the entire steppe zone from the Azov region in the east to the Banat in the west.”⁸⁰

Thus, the work of I. Lazaridis et al. in fact fundamentally changes the ideas of the supporters of the “Yamnaya expansion” hypothesis about the number and composition of the basic initial components that participated in the process that led to the genesis of the Yamnaya culture. If initially we were talking about two such components, the so-called “Eastern Hunter-Gatherers”, EHG (that is, ultimately ANE, “Ancient North Eurasians”) and “Caucasian Hunter-Gatherers”, CHG (“population mixture, specifically EHG and CHG/Iranian ancestry, a combination that forms the so-called ‘steppe-ancestry’”⁸¹), now a third one is added to them, and added in even decisive roles – “Western Hunter-Gatherers”, WHG.⁸²

This fact, by the way, has not yet been clearly recognized by either Lazaridis et al. 2024 or their competitors Allentoft et al. 2024. Meanwhile, it is fundamentally important.

Thus, in other words, to the previously considered exclusively “eastern” and “southern” factors of the genesis of the Yamnaya culture, a new one is added – “western”. And it must be emphasized once again that in its origin, this “western”

The individuals in question derive from the burial ground Golubaya Krinitza”; Allentoft et al. 2024, 306.

And although Lazaridis et al. 2024, 14 disagree with these results, the dispute itself is more than revealing.

⁷⁶ Lazaridis et al. 2024, 21.

⁷⁷ In particular Lillie et al. 2012; Потехіна 2020.

⁷⁸ Гаскевич 2020.

⁷⁹ Lazaridis et al. 2024, Suppl., Tab. 1.

⁸⁰ Гаскевич 2020, 176.

⁸¹ Wang et al. 2019, 5, line 171.

⁸² However, compare *Ibid.*, 10, lines 442–449.

factor is associated precisely with the region where the Corded Ware and Bell Beaker cultures later emerged – the territories of Europe to the west (and northwest) of the future locus of the emergence of the Yamnaya culture.

However, it is also very important to note that from the very beginning, from the Mesolithic, the “eastern” factor⁸³ played no less a significant role in the genesis of the Neolithic of the Lower Dnieper region, “UNHG” – associated with the influence of “Eastern Hunter-Gatherers”, EHG, and, ultimately, carriers of the autosomal component of ANE and Eastern Eurasia.

Moreover, today, we note, already according to the data of the whole genome analysis, and according to the data of Y-chromosome haplogroups (as well as mtDNA), it is quite clear that impulses from Eastern Eurasia to its western part, including Europe (including Central and even Western) begin to penetrate as early as the end of the Upper Paleolithic-Mesolithic – as was previously proposed.⁸⁴ That is, they played a certain role already in the genesis of the “Western Hunter-Gatherers”, WHG.

Thus, as far as the whole genome analysis is concerned, according to the results of a recent study, “one of the most striking findings was that before the dawn of the European Neolithic, Central and Eastern Europe was inhabited by a population that descends from a gradient admixture population between genetically distinct West European and Siberian hunter-gatherer groups. Such a pattern suggests long distance population genetic connectivity, likely via a stepping-stone admixture model.”⁸⁵

Also, the presence of East Eurasian mtDNA haplogroups (C5a) is found in Mesolithic and Neolithic burial grounds of the Dnieper Nadporozhye.⁸⁶ There are already quite a lot of finds of haplogroups R1b, R1a and Q of the Y-chromosome (marking this early East Eurasian impulse) in the Mesolithic-Neolithic sites of Europe (primarily Eastern and Central).⁸⁷

⁸³ Mattila et al. 2023, 8.

⁸⁴ Романчук 2019; 2020, 249.

⁸⁵ Mattila et al. 2023, 8

⁸⁶ Потехіна 2020, 242.

⁸⁷ See, in particular Lazaridis et al. 2024, Suppl., Tab. 1; Allentoft et al. 2024, Suppl. Data VII; also, a review of these finds with the corresponding commentary: Романчук 2024, 10–12, note 1.

Thus, the genesis of the Neolithic population of the Lower Dnieper region, and the “Western Hunter-Gatherers” (WHG) in general, was also even more complex than previously thought. And the interaction of “eastern” and “western” factors, which eventually led to the formation of the Yamnaya culture, took place over vast areas of Eastern Europe starting from the Mesolithic.

On the other (or third) hand, it is also obvious that already in the Mesolithic, a powerful influence on Eastern Europe from the Caucasus (and, further, Western Asia) began to manifest itself. This influence is also recorded by I. Lazaridis et al. within the framework of the “Volga Cline” they identified – arising primarily due to the meeting of the population of the “Eastern Hunter-Gatherers”, EHG, type and groups related by origin to the Caucasus (“CHG-related source”). Let me quote: “The ‘Volga Cline’ consists of sites on waterways that drain into the Caspian Sea and is suggestive of a zone of ongoing human contact within its region ... The decrease of hunter-gatherer affinity is counterbalanced by increased affinity towards populations of the Caucasus. ... Archaeological correlates for such south-north interactions do exist, and begin with the expansion of the Seroglazovo forager culture around the Lower Volga estuary ~6200 BCE.”⁸⁸

They also believe that “The Golubaya Krinitisa individuals present an important data point for the early presence of populations of mixed Caucasus and steppe origins in the Middle Don.”⁸⁹ Golubaya Krinitisa dates back to the middle of the 6th millennium BC,⁹⁰ and, let me remind you, is characterized by the complete predominance (three samples) of the R1a haplogroup of the Y chromosome (in Allentoft et al. 2024⁹¹ two cases of R1a, one of R1, and two more cases of I2a are indicated; in the Neolithic site of Ksizovo 6, located on the Middle Don (Lipetsk region), along with R1a and I2a, one case of R1b is also noted).

In fact, the influence from Western Asia begins much earlier, and reaches territories up to and including Karelia and the Arkhangelsk region, where we observe the Western Asian haplogroup J (of the Y-chromosome) in the burial

⁸⁸ Lazaridis et al. 2024, 8.

⁸⁹ Ibid., Suppl., 171; comp.: Allentoft et al. 2024, 306.

⁹⁰ Lazaridis et al. 2024, Suppl., Tab. 1.

⁹¹ Allentoft et al. 2024, Suppl. Data VII.

ground of Yuzhny Oleniy Ostrov (along with R1a) in Karelia (6773–5886 BC) and in Popovo 2 (7500–5000 BC) in the Arkhangelsk region.⁹² These sites belong to the so-called “Sidelkino Cluster” (“Sidelkino Cluster based on its oldest representative”⁹³), and are included by I. Lazaridis et al. in the above-mentioned “Volga Cline”. In which, as you move downstream of the Volga, the proportion of genetic participation of EHG decreases and the proportion of CHG increases: “The decrease of hunter gatherer affinity is counterbalanced by increased affinity towards populations of the Caucasus.”⁹⁴

Sidelkino itself (Samara region) dates back to more than 9000 years BC.⁹⁵

The picture that emerges as a result of taking into account the above facts makes us recall once again a remark by another team of researchers regarding the role of the “Yamnaya component” in the genesis of the Estonian Corded Ware culture, which was quoted earlier:⁹⁶ “It is interesting that Yamnaya, which in turn can be seen as a combination of CHG and EHG, is not directly needed for explaining the admixture pattern in Estonian CWC.”⁹⁷ As is the case that even today “in Europe, ‘steppe’ ancestry has hitherto been identified only in admixed form, but the origin of this admixture event and the mechanism by which the ancestry subsequently spread with the CWC have remained elusive.”⁹⁸

If we turn further to the Eneolithic era, it seems critically important to pay attention to some facts related to the Sredny Stog culture. First of all, it is significant that, speaking about

the Sredny Stog culture, I. Lazaridis et al. proceed from its localization in the Dnieper-Don interfluvium. And although in principle this is true, it should be taken into account that in general we must proceed from the fact that “in the second half of the 5th millennium BC ... the Khvalynsk-Sredny Stog community was formed, stretching from the Volga basin to the Lower Danube.”⁹⁹

It is within the framework of this community that large-scale movements of metal and raw materials take place from the Balkans all the way to the Volga: “on the territory of the Northern Black Sea region and the Lower Volga region, two relatively independent centers of copper processing are formed, the functioning of which was based on imported Balkan raw materials...”¹⁰⁰

In fact, I. Lazaridis and his team also point to this, emphasizing (the key point!) that these archaeological realities are not captured in genetic data, since we are talking about a genetically related population involved in the exchange process: “Archaeological analysis has documented long-distance movement of Balkan copper to the Volga-Cline site of Khvalynsk and the Csongrád and Mayaky individuals were plausibly part of the cultural exchange that mediated this process—a process our results show has no evidence of being contributed to genetically by people with ancestry typical of the Dniipro and Don basins.”¹⁰¹

That is, as other researchers have put it, “there are no successive waves as claimed by Gimbutas ... But what we see can otherwise be best described in a long-term interaction model

⁹² Narasimhan et al. 2019, Suppl., Tab. 1. See in this regard the considerations expressed earlier: Романчук 2020, 251, notes 16–17.

⁹³ Lazaridis et al. 2024, 8.

⁹⁴ Ibid. Note that according to the genome-wide analysis (Allentoft et al. 2024, 305), “In the eastern Baltic region, Ukraine and western Russia, local HG ancestry prevailed until around 5,000 bp without a noticeable input of Anatolian-related farmer ancestry”. However, the above-mentioned presence of Near Eastern patrilineal haplogroups serves as an obvious marker of the reality of the spread of influence from Near East to Eastern Europe up to Karelia and the Arkhangelsk region already in the Mesolithic. The fact that it is not yet captured in autosomal data is explained, in all likelihood, by the action of the same “dilution” model.

⁹⁵ Narasimhan et al. 2019, Suppl., Tab.1.

⁹⁶ Романчук 2020, 251.

⁹⁷ Saag et al. 2017, 2187.

⁹⁸ Allentoft et al. 2024, 302.

⁹⁹ Манзура 2024, 195.

¹⁰⁰ Ibid., 200.

¹⁰¹ Lazaridis et al. 2024, 9–10.

The individual buried in Csongrád (“A genetically Volga Cline individual not from the Volga Basin is from Csongrád-Kettőshalom in Hungary, whose direct date is 4331–4073 cal BCE.”; Lazaridis et al. 2024, 9) is characterized by haplogroup Q1b (Q-Y6802); Lazaridis et al. 2024, Suppl., Tab. 1. We will discuss this in more detail below.

I will also mention in this regard that “The two groups from Golubaya Krinitsa (GK1 and GK2) are not cladal to each other ($p=2.5e-12$), but GK2 is cladal to a single outlier individual of the Srednii Stih culture ($p=0.997$) (Igren_o, individual I27930) according to qpWave, and also clusters with it in PCA. ... The closest neighbors of these two individuals are the Upper Volga individuals: Igren_o forms a clade with Upper Volga ($p=0.197$), however, GK2 does not” (Lazaridis et al. 2024, Suppl., 155). Igren, it is worth to note, is also characterized by haplogroup Q (Allentoft et al. 2024, Suppl. Data VII).

between populations of similar steppe environments north and west of the Black Sea. This starts already in the mid-Vth millennium BC with the Suvorovo-Novodanilovka graves, continues throughout the Ivth...¹⁰²

However (and especially taking into account the data of D. L. Gaskevich cited above), it can be said that the formation of this zone of “intensive contacts” (let’s call it that) from the Danube to the Volga began in the Mesolithic-Neolithic era. Archaeological data indicate large-scale influences from the agricultural cultures of the Balkan-Carpathian region on the Eneolithic steppe (up to the Volga and Ciscaucasia) and in other areas. They were previously considered by many researchers, among whom I would like to highlight I. V. Manzura first of all.¹⁰³

At the same time, if we talk about genetic data, I. Lazaridis et al. also note the high heterogeneity of the population of the Srednii Stog culture (“The genetic heterogeneity of the Srednii Stih contrasts with the homogeneity of the Core Yamnaya”¹⁰⁴) – and at least three genetic clusters are distinguished. The second of them, which is significant, apparently includes, in part, representatives of the Cucuteni-Trypillian people: “A female from Kopachiv (I7585), represented by a long bone found loose in a Trypillia phase BI-II settlement, is part of a second ‘SSmed’ cluster that is further along the Dnipro Cline; this group also includes three individuals from Oleksandria and three from Deriivka.”¹⁰⁵

Data from physical anthropology (especially) and genetics indicate significant heterogeneity of the population of the Trypillian culture itself.¹⁰⁶

Moreover, it is worth to emphasize that “When we attempt to model Trypillians as a mixture of two or three sources using qpAdm, we find no fitting model for them as a whole. We explored removing the Trypillian individual that is the strongest genetic outlier (I20069 from Dănceni, 3323–2935 calBCE). However, even after excluding I20069, we still were not able to model Trypillians successfully ($p < 1e-5$ even for $N=3$ models).”¹⁰⁷ Or, as A. Nikitin et al. note in

the Supplementum, “The Trypillian population is heterogeneous in PCA and cannot be modeled well with any 1, 2, 3 sources.”¹⁰⁸ The last point is of great importance, and we will dwell on it further below.

And at the same time, in general, the population of the Trypillian culture is obviously closest to the Neolithic farmers of Asia Minor, the Balkans, and Europe in general.¹⁰⁹ Demonstrating simultaneously (at the level of intergroup analysis) its intermediate position between the above-mentioned Neolithic populations and the population of the Mariupol culture of the late Neolithic-early Eneolithic of the Dnieper-Don interfluvium.¹¹⁰ According to the results of modeling the data from whole genome analysis, “For the 23 Trypillia individuals modeled in our framework, we estimate that their genetic ancestry is, on average, 81% Balkan Eneolithic (such as in YUN_CA), 14% BHG, and the remaining 5% comes from the CLV cline.”¹¹¹ By “BHG” here is meant the Mesolithic inhabitants of the Iron Gate region on the Danube.

The results of the cited work¹¹² are extremely noteworthy here.

And it seems appropriate to pay special attention to the data on the Usatovo culture, as well as the late Eneolithic burial ground of Giurgiulesti on the Lower Prut (and the above-mentioned Csongrad in Pötisye).

Namely, according to the mtDNA data we see that “Usatove mitochondrial haplogroup composition consisted of lineages of predominantly ANF/EEF origin (H*, K1b*, T2*, W1, X2d), as well as steppe and European hunter-gatherer-derived U4* and U5a1* lineages.”¹¹³ Going into more detail, it turns out that even the last two lineages actually refer us to the Mesolithic Iron Gates on the Danube.

Thus, “the Mesolithic distribution of U5a1 lineages is primarily confined to the Iron Gates area, as well as Norway and the Baltic region. In

¹⁰² Frînculeasa et al. 2015, 84.

¹⁰³ Манзура 2000; 2006; 2024.

¹⁰⁴ Lazaridis et al. 2024, 12.

¹⁰⁵ Ibid.

¹⁰⁶ Потехіна 2020, 243–244; Nikitin et al. 2024, SI, 26–30.

¹⁰⁷ Nikitin et al. 2024, 8.

¹⁰⁸ Ibid., SI, 123.

¹⁰⁹ Of significant importance in the question of the genesis of the population of the Trypillian culture are also the data of odontology, to which, with reference to the results of A. V. Zubova (Зубова 2010, 94), attention was drawn earlier; Романчук 2020, 252.

¹¹⁰ Потехіна 2020, 245.

¹¹¹ Nikitin et al. 2024, 8.

¹¹² Namely Ibid., SI, 26–30.

¹¹³ Ibid., SI, 26.

the Neolithic, U5a1 lineage distribution extends to the North Pontic, likely accompanying the migration of carriers of WHG ancestry to the Dnipro Valley.¹¹⁴ Likewise, “Phylogeographic distribution of the U4 node and its derivatives in pre-Eneolithic Europe includes the Iron Gates area of the Danube, the Baltic region, and the Middle Dnipro Valley.”¹¹⁵

And “The chronologically earliest individual I12615 from the Mayaky archaeological site shared mtDNA lineage U4b1b2 with the individual of Serechnii Stih ancestry (SSmed) from Kolomyitsiv Yar Tract (KYT). It has been suggested that the U4b1b1~ lineage represents the pre-Neolithic mitochondrial lineage diversity, expanding from the Mesolithic Balkans and not being directly influenced by the steppe.”¹¹⁶ Which leads the authors of the cited work to the fair conclusion: “The presence of a Balkan-derived mitochondrial lineage in an individual of steppe ancestry supports the existence of mating interactions between the steppe and their trade allies from the eastern Balkans.”¹¹⁷ A conclusion, we note, that is quite consistent with the hypothesis of D. L. Gaskevich.

According to patrilineal data, representatives of the Usatovskaya culture are characterized¹¹⁸ by haplogroups E1b1b1a1 and J1 (J-FT265222) – ultimately, of Middle Eastern origin, as well as the “forest” R1a – dominant already in the Mesolithic-Neolithic forest belt of Eastern Europe. But not represented, let us recall once again, in the steppe zone, either in the Yamnaya culture, or in the pre-Yamnaya period (as well as absent in the Neolithic of the Dnieper Nadporozhye).

That is, neither according to mtDNA data, nor according to Y-chromosome data, we can in no way deduce the representatives of the Usatovo culture from the steppe zone of the pre-Yamnaya period (as well as the Yamnaya), be it the Volga region or more western territories. On the contrary, everything points to their local, Carpathian-Danubian, origin, with the participation of the population from the forest belt of

Eastern Europe (which, naturally, is close to CLV in its autosomal genome).¹¹⁹

It should be noted that the individual from the late Eneolithic burial site of Durankulak in Bulgaria (3500–3000 BC) is also characterized by the “forest” R1a1a1 (R-M417).¹²⁰ And the approximately synchronous representative of the so-called “Zhivotilovsky horizon” from the Bursuceni burial ground in the Republic of Moldova is again of the Middle Eastern “J2b2b2~ (J-Z42942).”¹²¹

No less interesting is the situation with the Giurgiulesti burial ground. In which one of the mtDNA haplogroups is K1b2b (<2X) (that is, “ANF/EEF origin”, referring us to the “Neolithic farmers of the Balkans”, in fact, to the Cucuteni-Trypillia culture), the second is haplogroup H13.

Turning to the discussion of the second of these mtDNA haplogroups, H13, we see that “MtDNA lineage H13 of the Giurgiulesti individual I20072 matches that of the Mesolithic Iron Gate individuals from Lepenski Vir and Ostrovul Corbului, suggesting potential genetic admixture between the Serechnii Stih II/Skelya/Novodanylivka migrants from the Dnipro Valley and local populations of the Lower Danube. On the other hand, H13 could have arrived at the Dnipro Valley as part of the WHG Iron Gates ancestry in the Neolithic, thus becoming part of the Dnipro Cline ancestry from which Serechnii Stih was 1/5th derived. An H13-derived lineage H13a1 was recorded in a Lower Volga individual I22199 from Berezhnovka II, as well as in a Yamna individual from Ishkinovka in pre-Ural steppe.”¹²²

That is, the second of the discussed mtDNA haplogroups of the Giurgiulesti group also

¹¹⁴ Ibid., SI, 27.

¹¹⁵ Ibid.

¹¹⁶ Ibid.

¹¹⁷ Ibid.

¹¹⁸ Ibid., SI, 4, 29.

¹¹⁹ Doesn't this mean that there is something to think about in relation to conclusions based on autosomal data? In any case (and what is clearly not in doubt), according to the autosomal genome data, the carriers of the Usatovo culture “are genetically varied”; Nikitin et al. 2024, 9. The authors of the cited study further believe that “CLV ancestry in Usatovo was not from the lower Volga-centered BPgroup, but had a significant proportion of southern Caucasus Neolithic-related ancestry”; Ibid. However, wouldn't this conclusion change if we assume that the “Caucasus Neolithic-related ancestry” of the Usatovo culture carriers is not at all related to the “CLV ancestry”, but represents a contribution from some third source?

¹²⁰ Nikitin et al. 2024, SI, 6.

¹²¹ Ibid., SI, 5.

¹²² Ibid., SI, 28.

directs us to the west, to the Mesolithic of the Iron Gates on the Danube, and not to the east.

In addition, it is significant that the mtDNA haplogroups characteristic of the Iron Gates on the Danube region are already found in the pre-Yamnaya time in the Volga region (and, further, even in the Urals, albeit a little later). This serves as a clear refutation of the thesis of I. Lazaridis et al. about the “elusiveness” of the genetic correlate of those ethnocultural interactions (and impulses from the Danube region to the east) within the Khvalynsk-Sredny Stog community, which are obvious from archaeological data.

Turning further to the patrilineal data, we see that one individual from Giurgiulesti is characterized by a very archaic haplogroup CF, which there is no reason to associate with the steppe (rather, with the Middle East). The second is represented by the Q1a2 haplogroup of the Y chromosome,¹²³ which is indeed quite noticeable¹²⁴ in the Khvalynsk 2 cemetery (Saratov region, forest-steppe, late 6th – mid-5th millennium BC).

However, does the presence of Q1a2 in the Khvalynsk 2 cemetery mean that it appears in Giurgiulesti as a result of an impulse from the Khvalynsk-Sredny Stog area?

There seem to be significant doubts about this. Since Q1a2 is not found in the burial grounds of the Khvalynsk-Sredny Stog community located to the south and west (including the Sredny Stog culture proper), as well as in the Yamnaya culture sites of the Volga-Urals, Don, or Ciscaucasia.¹²⁵ It is also not found in the Neolithic of the Dnieper Nadporozhye region.

However, we note that Q1a2 appears very close to Giurgiulesti (in the Targșorul Vechi burial ground, Prahova County, Romania, approximately three hundred kilometers west of Giurgiulesti), but already in the Yamnaya period.

At the same time, it seems clear that Q1a2 penetrates into the forest-steppe Volga region from the north, from the forest belt of Eastern Europe, where it is already represented in the Mesolithic-Neolithic in the Zvejnieki burial ground.¹²⁶ And all the buried men from the Eneolithic burial ground Murzikha 2 (the Kama

River at its confluence with the Volga, 5th millennium BC) were characterized exclusively by haplogroup Q1a.¹²⁷

Taking into account these facts, as well as those stated above in relation to the Usatovo culture and the Durankulak burial in Bulgaria (in both places, let us recall, it is precisely the “forest” R1a that manifests itself; moreover, for Durankulak, according to the autosomal genome, modeling indicates an admixture from the Globular Amphora culture: “For this individual (I1456 / 3500–3000 BCE) from Durankulak only a single 2-way feasible model exists that involves a fairly even mix of Core Yamna (~45%) and Globular Amphora (~55%) ancestries”¹²⁸) – which also refers us specifically to the forest belt of Eastern Europe; we will dwell on this below), it seems more correct to consider the appearance of Q1a2 in Giurgiulesti as an influence from the north, from the forest belt of Eastern Europe.¹²⁹

I would venture to suggest, however, that it is unlikely that this influence from the forest belt of Eastern Europe manifested itself precisely at the time of the formation of the Giurgiulesti group. Rather, it should be attributed to an earlier time. And the genome of the representatives of the Giurgiulesti group, accordingly, should be interpreted as its more distant in time, and manifested significantly later, consequence.

Actually, the situation is similar with the haplogroup Q1b of the burial in Csongrad. Found in the early Eneolithic burial ground of Yekaterinovskiy Mys (Samara region (that is, much further north than Saratov), the second half of the 6th millennium BC), to the south and west (and later), in the monuments of the Khvalynsk culture and Sredny Stog, as well as Yamnaya, Q1b is not found. At the same time, it is also obvious that in this case the source of Q1b is the forest belt of Eastern Europe, where it is also well represented from the Mesolithic-Neolithic (in the Neolithic Lyalovskaya and Volosovskaya cultures on the Volga; in the Neolithic of Denmark; in the Mesolithic of Sweden).

¹²³ Ibid., SI, 3–8, Tab. S1.

¹²⁴ Lazaridis et al. 2024, Suppl., Tab. 1.

¹²⁵ Ibid.

¹²⁶ Ibid.

¹²⁷ Ibid., Suppl., 10.

¹²⁸ Nikitin et al. 2024, SI, 113.

¹²⁹ For the autosomal genome of Zvejnieki and the Iron Gates Mesolithic, see also: Nikitin et al. 2024, SI, 113.

True, Q1b was also found¹³⁰ in the Neolithic of the Dnieper Nadporozhye (Igren, Yasinovatka), along with Q (Yasinovatka). However, one can hardly ignore the cultural and chronological gap between the Neolithic of the Dnieper Nadporozhye and the burial in Csongrad (last third of the 5th millennium BC). Rather, the fact of the presence of Q1b in the Neolithic of the Dnieper Nadporozhye allows us to assume that Q1b, again, gets to the Carpathian-Danubian region as part of the interactions between the Iron Gate region and the Dnieper-Azov region that occurred in the Mesolithic-Neolithic.

Moreover, in archaeological terms, according to the kind message of I. V. Manzura, the burial in Csongrad is characterized by a purely local, Carpathian-Balkan, archaeological complex, without any traces of eastern influences.

Thus, the outlined facts hardly allow us to agree with the assessment of these facts proposed by A. Nikitin et al. as evidence of “waves rolling in from the east” (“Our analysis suggests a history of three partially overlapping waves of CLV migrations into the NPR in the Eneolithic”;¹³¹ completely in the spirit of the long-standing idea of M. Gimbutas). Before us is a picture of clearly much more complex and multifaceted interactions within Eastern Europe as a whole, and which started much earlier, back in the Mesolithic-Neolithic.

Moreover, what is significant is that the share of the “eastern component” (first “CLV”, later – “ancient Yamnaya”) gradually increases in the Balkan-Carpathian region of the Eneolithic era.¹³² This is a kind of gradient, but not in space, but in time.

¹³⁰ Allentoft et al. 2024, Suppl. Data VII; Nikitin et al. 2024, SI, 3, tab. S1.

¹³¹ Nikitin et al. 2024, 17.

¹³² It is interesting to mention in this regard the research of A. Bulatovic (Bulatovic 2014), who showed the gradual, beginning with the early Eneolithic, spread of corded ceramic ornamentation in the Balkans. However, contrary to his intention to connect this with the idea of M. Gimbutas’s “three waves”, it seems obvious from his data that the idea of corded ornamentation, initially penetrating the Balkans from the steppe zone, quickly breaks away from its original carriers, and then spreads further in the Balkans and in Europe in general as a result of local ethnocultural processes.

¹³³ is significant that the manifestations of the first (according to A. Bulatovic), early Eneolithic, horizon of Corded Ware in the central and southern Balkans cover the territory mainly of the mountainous and foothill regions of the

In connection with the interpretation of the data of the whole genome analysis, it seems that special attention should once again be paid to the above-mentioned burial from Durankulak (by the way, it refers¹³³ to the “first Pit-Grave phase” (that is, arising in the pre-Pit-Grave period) on the Lower Danube identified by these researchers).

First of all, because, according to the assessment of the authors of the cited work, the analysis of the genome of the individual from Durankulak leads them to a conclusion that goes far beyond the private: “Thus, the Corded Ware represents a mixture of similar components as the Bulgarian ‘Proto-Yamna’ individual, albeit in different proportions.”¹³⁴

At the same time, let us recall, they believe that “For this individual (I1456 / 3500–3000

Eastern Balkans, and as far as Northern Greece (Bulatovic 2014, 107, map 1). A similar tendency characterizes the second horizon of the spread of corded ornamentation in the central and southern Balkans (Ibid., 117, map 2) – which, in addition, is firmly associated with influences from local, Carpathian-Balkan, cultures of the Kotsofeni-Kostolak circle. Finally, the third horizon of A. Bulatovic (Ibid., 123, map 3) can be considered the culmination, when the bulk of manifestations of corded ornamentation of ceramics in the Balkans is generally concentrated in the mountainous regions adjacent to the Adriatic Sea (that is, in the Dinaric Alps) and further on the territory of Greece (up to the Peloponnese).

Actually, A. Bulatovich himself notes this: “Significant is the fact that the sites with steppe elements of the 3rd millennium BC in the Balkans are concentrated mostly in the highland regions or in the mountainous massifs of Dinara, Stara planina, Suva planina, Rodopi, Pind...” (Ibid., 129). Likewise, he notes that “...do not necessarily imply the presence of a steppe population, especially keeping in mind the fact that pottery ornamented with cord is mainly on indigenous pottery characteristic for Balkan Eneolithic cultural complexes” (Ibid., 130).

¹³⁴ Central Europe, the spread of corded ornamentation on ceramics occurred within the framework of the Globular Amphora culture (Ibid., 133). Which, we recall, does not reveal any “steppe impulse” either according to the data of whole-genome analysis or according to the data of patrilineal and matrilineal markers.

¹³³ Frinculeasa et al. 2015, 80.

¹³⁴ Nikitin et al. 2024, SI, 113.

BCE) from Durankulak only a single 2-way feasible model exists that involves a fairly even mix of Core Yamna (~45%) and Globular Amphora (~55%) ancestries.”¹³⁵

However, if this is so, then in this case we have an obvious anachronism for the hypothesis of the “Yamnaya expansion”, which has already been noted.¹³⁶

Moreover, now the anachronism is double, not only in relation to the time of the emergence of the Yamnaya culture, but also to no lesser extent, in relation to the culture of the Globular Amphora. Indeed, the proposed appeal to the culture of the Globular Amphora, among other things, encounters obstacles of a chronological nature. Modern ideas on this account allow us to date the emergence of the culture of the Globular Amphora to the very end of the 4th millennium BC at the latest.

Accordingly, even if we proceed from the above-cited dating of the individual from Durankulak (“3500–3000 BCE”), this already does not agree well with the dating of the Globular Amphora culture. But the chronological gap is even more obvious if we proceed from the dating of the individual from Durankulak (“DUR1, Kurgan F, Burial 15 (main burial), male, adult, 3700–3300 BCE”) given in Nikitin et al. 2024¹³⁷ and, apparently, closer to the truth.

Apparently, the emergence of the genome of the individual from Durankulak requires a search for another explanation. And it is worth thinking that finding this explanation will significantly shed light on the formation of both the Yamnaya culture and the Corded Ware and Bell Beaker cultures.

And, in conclusion, I would like to draw attention to another circumstance, significantly ignored by the supporters of the “Yamnaya expansion”. It is extremely important precisely in connection with the fact that I. Lazaridis et al. deny the Trypillian culture the possibility of serving as a source (or even one of the sources) “Caucasus Neolithic-related ancestry”: “Trypillia is not resilient to the presence of a Caucasus Neolithic population.”¹³⁸ Although, other data¹³⁹

allow us to assume that the role of the “Caucasus Neolithic-related ancestry” in Cucuteni-Trypillia was quite significant.

In this regard, it is worth emphasizing the above-presented fact of the extreme heterogeneity of the gene pool of Cucuteni-Trypillia carriers. Heterogeneity is of such a degree that it practically does not even allow them to be modeled as a single whole: “When we attempt to model Trypillians as a mixture of two or three sources using qpAdm, we find no fitting model for them as a whole.”¹⁴⁰

Moreover, the conclusion about the extreme heterogeneity of Cucuteni-Trypillia based on autosomal data was de facto obtained based on the analysis of materials from only one site, the Verteba cave.¹⁴¹

And, accordingly, the question arises: to what extent does the sample of Cucuteni-Trypillia representatives used today reflect the genetic portrait of this population as a whole (given that the Cucuteni-Trypillia culture, let me remind you, occupied the territory from the Carpathians and the Danube to the Dnieper (and, in time, about two millennia)? Will the heterogeneity of Cucuteni-Trypillia turn out to be even higher if there is a proportional (including territorial) increase in this sample?

The question is, in principle, rhetorical.

Therefore, it seems that the Trypillian culture is a large-scale and critically important factor that the supporters of the “Yamnaya expansion” hypothesis (both geneticists and archaeologists) practically do not take into account in their reasoning. And in particular, they do not ask themselves the question: what happened to the huge demographic mass of the Trypillian culture population after its disappearance?

It is absolutely improbable that the disappearance of this culture in the archaeological sense would also mean the complete annihilation of the demographic potential it had accumulated. No, even if it is not captured by archaeology, this population obviously had to take part in further demographic processes in Eastern Europe.

Therefore, it can be assumed that it is the participation of the Trypillian population in subsequent demographic processes in Eastern Europe

¹³⁵ Ibid.

¹³⁶ Романчук 2020, 252.

¹³⁷ Nikitin et al. 2024, SI, 38.

¹³⁸ Ibid., SI, 146.

¹³⁹ Романчук 2020, 252.

¹⁴⁰ Nikitin et al. 2024, 8; SI, 123.

¹⁴¹ Ibid., SI, 5, Tab. S1.

that represents a critically important unaccounted factor for the hypothesis of the “Yamnaya expansion”.

Thus, the fact that, according to the genome-wide analysis, “the Corded Ware population ... had a balance of ancestral components from the Caucasus and eastern Europe indistinguishable from the Yamnaya”¹⁴² may have, as was suggested earlier,¹⁴³ a fundamentally different explanation. Repeating what was said above, it seems more logical to assume that the area in which the formation of the autosomal “Yamnaya component” took place was significantly wider than the area of the Sredny Stog culture, and covered very vast areas of both Eastern Europe (both its steppe and forest parts), and Central and (partly) Western.

In any case, it seems clear that this whole story began long before the emergence of the Yamnaya culture.

Rezime

“Više prema zapadu”: kritički komentari na nove verzije hipoteze o “Yamnaya ekspanziji”

Članak razmatra nedavne verzije hipoteze o “Yamnaya ekspanziji” koju su predložili genetičari. Nova publikacija “Genetsko porijeklo Indo-Evropljana” tima pod vodstvom I. Lazaridis donosi značajne promjene u hipotezi o “Yamnaya ekspanziji” (i “Indoeuropeizaciji” Evrope kao njenoj posljedici). Prvo i osnovno, ona pomiče originalni lokus formiranja Yamnaya kulture na području Azovskog mora i Donjeg Dnjepra (što je, usput, isto učinio rad Allentoft et al. 2024 objavljen istovremeno s njom).

Kao što se može vidjeti, ove promjene osnovne hipoteze prvenstveno su odgovor na značajan porast podataka koji su iznešeni u posljednjih nekoliko godina, a koji se slabo slažu s prethodnim verzijama hipoteze.

Međutim, čini se da čak ni u svojim novim verzijama hipoteza o “Yamnaya ekspanziji” nije uspjela ponuditi adekvatan odgovor na prigovore koji su postavljeni protiv nje. Štaviše, novi podaci omogućavaju

dodavanje novih prigovora, i to očigledno, ne manje značajnih.

Stoga, članak pokušava prvenstveno pokazati da su autori i zagovornici hipoteze o “Yamnaya ekspanziji”, oslanjajući se prvenstveno na rezultate analize cijelog genoma, zapravo ignorirali te kontradikcije u svojim zaključcima koje se otkrivaju kada se koriste podaci o Y-hromosomskim haplogrupama.

Slijedeći logiku hipoteze o “Yamnaya ekspanziji”, sada moramo govoriti o hipotetičkoj mikropopulaciji Yamnaya kulture kao populaciji u kojoj nedostaju ne jedna, već dvije vodeće, apsolutno dominantne Y-hromosomske haplogrupe u Yamnaya kulturi, R1b-Z2103 i I-L699.

Štaviše, značajno je da, u odnosu na pretpostavljenu “Yamnaya ekspanziju” u Srednju i Zapadnu Europu, trebamo govoriti ne o jednoj, već o dvije takve “čudne mikropopulacije”, od kojih bi jedna trebala postati predek Kulture Šnur-Keramike (to jest, karakterizirana dominacijom i, očigledno, još uvijek vrlo oštrom, ako ne i apsolutnom dominacijom odgovarajućih podgrupa R1a (koje, ponovo podsjećamo, nisu otkrivene u Yamnaya kulturi uprkos već vrlo značajnom porastu podataka) i potpunom odsutnošću R1b-Z2103 i I-L699, dok bi druga bila predek Kultura zvonastih pehara (to jest, karakterizirana apsolutnom dominacijom R1b-L51 i potpunom odsutnošću R1b-Z2103 i I-L699).

Činjenica da moramo pretpostaviti postojanje dvije takve “čudne populacije” već smanjuje matematičku vjerovatnost takvog razvoja događaja ne za polovinu, već za značajno više.

Značajan problem za hipotezu o “nepriznatoj mikropopulaciji” je to što ona mora biti upravo mikropopulacija. To znači da, prema logici zagovornika ove pretpostavke, u ranom bronzanom dobu, dvije (ako govorimo samo o Evropi) po definiciji male grupe ljudi trebale su u najkraćem mogućem vremenu (u praksi, trebali bismo govoriti o nekoliko stoljeća, ako ne manje) gotovo potpuno zamijeniti i asimilirati, budući da je ogroman doprinos substrata očigledan i u kulturama Šnur keramike i Zvonastih pehara.

Nevjerojatnost scenarija za nastanak Šnur keramike i Zvonastih pehara prema hipotezi o “Yamnaya ekspanziji” (kao i nevjerojatnost same hipoteze o “Yamnaya ekspanziji”) postaje još očiglednija ako uključimo podatke iz fizičke antropologije (preciznije, kranimetriju) u analizu.

U stvari, samo priznanje činjenice da su različite (ili čak iste) podgrupe haplogrupa R1a i R1b (i dijelom Q) povezane (dominirajuće u odgovarajućim populacijama) već u bronzanom dobu (pa čak i u mezolitu-neolitu) Evrope s različitim, a čak i vrlo različitim kraniološkim tipovima, koji su zabilježeni u odgovarajućim regijama tokom dva do tri milenija, zahtijeva da također priznamo da ova povezanost

¹⁴² Lazaridis et al. 2024, 23.

¹⁴³ Романчук 2020, 252–253.

između određenog kраниолошког типа i određenih haplogrupa nije mogla nastati u trenutku i već na kasnoj (ili čak dovoljno razvijenoj) fazi evolucije tih kраниолошких tipova.

Ne, ovo je mogao biti samo rezultat dugoročnih procesa ukrštanja različitih populacija, koji su započeli vrlo rano, na samom početku formiranja odgovarajućih kраниолошких tipova (to jest, još u mezolitu), a koji su se događali (s različitim rezultatima, ovisno o razlici u početnim komponentama i uvjetima njihove interakcije) u različitim dijelovima Evrope.

A ova slika očigledno se ne slaže s pretpostavljenom hipotezom o “Yamnaya ekspanziji” modela “zamjene populacije” Evrope (čak i djelomične, u najnovijim verzijama ove hipoteze) kao rezultat kasnih migracija s područja Yamnaya kulture u bronzanom dobu.

Stoga, autor pokazuje da se podaci o Y-hromosomu, kao i podaci o fizičkoj antropologiji očigledno ne slažu s pretpostavljenim modelom “zamjene populacije” Evrope (čak i djelomične) kao rezultat migracija Yamnaya kulture.

Izložene činjenice također teško omogućavaju slaganje s ocjenom tih činjenica koju su predložili A. Nikitin et al. kao dokaz “valova koji dolaze s istoka”, potpuno u duhu dugotrajnog mišljenja M. Gimbutas. Pred nama je slika očigledno mnogo složenijih i višeslojnih interakcija unutar Istočne Evrope u cjelini, koje su započele mnogo ranije, još u Mezolitu-neolitu.

Autor sugerira da je područje u kojem je nastao autosomalni “Yamnaya komponent” bilo znatno šire od područja Srednj-Stog kulture i pokrivalo je veoma velika područja istočne Evrope (i njenog stepskog i šumskog dijela), te srednje i (djelomično) zapadne Evrope.

U svakom slučaju, čini se jasno da je cijela ova priča počela mnogo prije nastanka Yamnaya kulture.

Bibliography

Балановский, О. П. 2015, Генофонд Европы, Москва 2015.

Гаскевич, Д. Л. 2020, Могильник Васильевка II. Выходцы со Среднего Дуная в Надпорожье накануне неолита?, *Stratum plus* 1, 2020, 147–184.

Зубова, А. В. 2010, Население ямной культурно-исторической общности в свете одонтологических данных, *Вестник археологии, антропологии и этнографии* 13 (2), 2010, 85–95.

Казарницкий, А. А. 2021, Соотношение местного и пришлого населения восточноевропейских степей в эпоху бронзы (по краниологическим

материалам), *Археология, этнография и антропология Евразии* 49 (3), 2021, 127–135.

Казарницкий, А. А. 2024, О краниологических признаках западных миграций в Восточную Европу в эпоху бронзы (на примере материалов абашевской культуры), *Российская археология* 1, 2024, 22–39.

Козинцев, А. Г. 2023, Окуневская культура и дене-кавказская макросемья, *Археология, этнография и антропология Евразии* 51 (2), 2023, 66–73.

Козинцев, А. Г. 2023а, Дене-кавказская макросемья: лексикостатистическая классификация и прародина, *Этнография* 3, 2023, 45–67.

Манзура, И. В. 2000, Владеющие скипетрами, *Stratum plus* 2, 2000, 237–295.

Манзура, И. В. 2006, Северное Причерноморье в энеолите и в начале бронзового века: ступени колонизации, *Stratum plus* 2, 2006, 63–85.

Манзура, И. В. 2024, Топор в ритуальной практике раннего энеолита Восточной Европы: истоки традиции, *Stratum plus* 2, 2024, 193–203. DOI: <https://doi.org/10.55086/sp242193203>.

Потехина, И. Д. 2020, Антропология і археогенетика первісного населення України: координата результату, *Археологія і давня історія України* 4 (37), 2020, 240–250. DOI: 10.37445/adiu.2020.04.19.

Романчук, А. А. 2012, Восточноазиатская гипотеза сино-кавказской прародины в свете данных физической антропологии и археологии: к постановке проблемы, *Stratum plus* 1, 2012, 303–329.

Романчук, А. А. 2013, Кавкасионский антропологический тип в свете гипотезы “восточной популяции”: вопрос о древности, *Stratum plus* 2, 2013, 259–282.

Романчук, А. А. 2015, Восточноевразийская гипотеза дене-кавказской прародины: еще раз к вопросу о гаплогруппах Y-хромосомы, Кишинев 2015. DOI:10.13140/RG.2.1.4582.5120.

Романчук, А. А. 2019, Восточноевразийская гипотеза дене-кавказской прародины и данные генеогеографии, Кишинев 2019.

Романчук, А. А. 2020, “Древнеямный” генетический компонент и индоевропеизация Европы: критический анализ гипотезы, *Stratum plus* 2, 2020, 243–257.

Романчук, А. А. 2024, Проникновение гаплогруппы R1b-V88 Y-хромосомы в Африку: историко-археологический контекст, Кишиневу 2024.

Романчук, А. А. 2024а, Возникновение гаплогруппы E-M81: рубеж эр или неолит?, *Stratum plus* 2, 2024, 221–226.

Романчук, А. А. / Семенов, А. С. 2014, R и Q гаплогруппы Y-хромосомы и прасеверокавказский

- субстрат праиндоевропейцев, *Russian Journal of Biological Research* 1 (1), 2014, 46–68. DOI: 10.13187/ejbr.2014.1.46.
- Рындина, Н. В.* 1998, Древнейшее металлообрабатывающее производство Юго-Восточной Европы, Москва 1998.
- Allentoft, M. et al.* 2022, Population Genomics of Stone Age Eurasia, *bioRxiv preprint* doi: <https://doi.org/10.1101/2022.05.04.490594>; this version posted October 7, 2022. Accessed 5. 9. 2023.
- Allentoft, M. et al.* 2024, Population genomics of post-glacial western Eurasia, *Nature* 625, 1181, 301–311. DOI: 10.1038/s41586-023-06865-0.
- Balanovsky, O. / Chukhryaeva, M. et al.* 2017, Genetic differentiation between upland and lowland populations shapes the Y-chromosomal landscape of West Asia, *Human Genetics* 136 (4), 2017, 437–450. DOI: 10.1007/s00439-017-1770-2.
- Brace, S. et al.* 2019, Ancient genomes indicate population replacement in Early Neolithic Britain, *Nature Ecology&Evolution* 3 (5), 2019, 765–771. DOI: 10.1038/s41559-019-0871-9. <https://pubmed.ncbi.nlm.nih.gov/30988490/>. Accessed 15. 8. 2024.
- Bulatovic, A.* 2014, Corded Ware in the Central and Southern Balkans: A Consequence of Cultural Interaction or an Indication of Ethnic Change?, *Journal of Indo-European Studies* 42 (1–2), 2014, 101–143.
- de Barros Damgaard, P. et al.* 2018, The first horse herders and the impact of early Bronze Age steppe expansions into Asia, *Science* 360 (6396):eaar7711, 2018. DOI: 10.1126/science.aar7711.
- Fernandes, D. et al.* 2018, A genomic Neolithic time transect of hunter-farmer admixture in central Poland, *Scientific Reports* 8(1):14879, 2018. doi: 10.1038/s41598-018-33067-w. <https://www.ncbi.nlm.nih.gov/pmc/articles/PMC6173765/>. Accessed 15. 8. 2024.
- Frînculeasa, A. / Preda, B. / Heyd, V.* 2015, Yamnaya, Yamnaya, and Kurgans along the Lower Danube: Unraveling Funerary Customs, Equipment, and Chronology of the 4th and 3rd Millennia BC., *Prähistorische Zeitschrift* 90 (1–2), 2015, 45–113.
- Haak, W. et al.* 2015, Massive migration from the steppe was a source for Indo-European languages in Europe, *Nature* 522, 2015, 207–211.
- Hollard, C. et al.* 2018, New genetic evidence of affinities and discontinuities between bronze age Siberian populations, *American Journal of Physical Anthropology* 167 (1), 2018, 97–107. <https://onlinelibrary.wiley.com/doi/10.1002/ajpa.23607>. Accessed 19. 8. 2024.
- Kozintsev, A.* 2023, The Dene-Caucasian Macrofamily: Lexicostatistical Classification and Homeland, *Mother Tongue XXIV*, 2023, 133–149.
- Kristiansen, K. / Kroonen, G. / Willerslev, E.* 2023, *The Indo-European Puzzle Revisited. Integrating Archaeology, Genetics, and Linguistics*, Cambridge 2023.
- Lazaridis, I. / Alpaslan-Roodenberg, S. et al.* 2022, The genetic history of the Southern Arc: A bridge between West Asia and Europe, *Science* 377 (6609), 2022. <https://www.science.org/doi/full/10.1126/science.abm4247>. Accessed 19. 9. 2023.
- Lazaridis, I. et al.* 2024, The Genetic Origin of the Indo-Europeans, *bioRxiv preprint*, 2024. DOI: <https://doi.org/10.1101/2024.04.17.589597>.
- Lillie, M. et al.* 2012, Prehistoric populations of Ukraine: Migration at the later Mesolithic to Neolithic transition, in: Kaiser E., Burger J., and Schier W. (Eds.), *Population Dynamics in Prehistory and Early History. New Approaches by Using Stable Isotopes and Genetics*, Berlin, Boston 2012, 77–92.
- Linderholm, A. et al.* 2020, Corded Ware cultural complexity uncovered using genomic and isotopic analysis from southeastern Poland, *Scientific Reports* 10 (6885), 2020. DOI: <https://doi.org/10.1038/s41598-020-63138-w>.
- Malmström, C. et al.* 2019, The genomic ancestry of the Scandinavian Battle Axe Culture people and their relation to the broader Corded Ware horizon, *Proceedings of Royal Society, B* 286: 20191528, 2019. <http://dx.doi.org/10.1098/rspb.2019.1528>. Accessed 15. 8. 2024.
- Mathieson, I. et al.* 2017, The Genomic History of Southeastern Europe, <https://www.biorxiv.org/content/10.1101/135616v4>. Accessed 15. 9. 2019.
- Mathieson, I. et al.* 2018, The Genomic History of Southeastern Europe, *Nature* 555(7695), 2018, 197–203. DOI: 10.1038/nature25778.
- Mattila, T. et al.* 2023, Genetic continuity, isolation, and gene flow in Stone Age Central and Eastern Europe, *Communications Biology* 6(1):793, 2023. DOI: 10.1038/s42003-023-05131-3. <https://www.ncbi.nlm.nih.gov/pmc/articles/PMC10412644/>. Accessed 30. 8. 2024.
- Myres, N. et al.* 2011, A major Y-chromosome haplogroup R1b Holocene era founder effect in Central and Western Europe, *European Journal of Human Genetics* 19, 95–101.
- Narasimhan, V. et al.* 2019, The formation of human populations in South and Central Asia, *Science* 365(6457):eaat7487, 2019. doi:10.1126/science.aat7487. <https://pubmed.ncbi.nlm.nih.gov/31488661/>. Accessed 29. 8.2024.
- Nikitin, A. et al.* 2024, A genomic history of the North Pontic Region from the Neolithic to the Bronze Age, *bioRxiv preprint*. DOI: <https://doi.org/10.1101/2024.04.17.589600>; this version posted April 18, 2024. Accessed 15. 8. 2024.

Olalde, I. et al. 2019, The Beaker Phenomenon and the Genomic Transformation of Northwest Europe, *Nature* 555 (7695), 190–196. DOI: 10.1038/nature25738.

Papac, L. et al. 2021, Dynamic changes in genomic and social structures in third millennium BCE central Europe, *Science Advances* 7: eabi6941, 2021. <https://pubmed.ncbi.nlm.nih.gov/34433570/>. Accessed 15. 8. 2024.

Saag, L. et al. 2017, Extensive farming in Estonia started through a sex-biased migration from the Steppe, *Current Biology* 27, 2017, 2185–2193.

Saag, L. et al. 2021, Genetic ancestry changes in Stone to Bronze Age transition in the East European plain, *Science Advances* 7, 2021. <https://www.ncbi.nlm.nih.gov/pmc/articles/PMC7817100/>. Accessed 24. 9. 2023.

Wang, Ch.-Ch. et al. 2019, The genetic prehistory of the Greater Caucasus, bioRxiv preprint first posted online May 16, 2018. DOI: [http://dx.DOI.org/10.1101/322347](http://dx.doi.org/10.1101/322347).