EVOLUTIONARY BIOLOGY

Genetic ancestry changes in Stone to Bronze Age transition in the East European plain

Lehti Saag[1]*, Sergey V. Vasilyev[2], Liivi Varul[3], Natalia V. Kosorukova[4], Dmitri V. Gerasimov[5], Svetlana V. Oshibkina[6], Samuel J. Griffith[1], Anu Solnik[1], Lauri Saag[1], Eugenia D'Atanasio[7], Ene Metspalu[1], Maere Reidla[1], Siiri Rootsi[1], Toomas Kivisild[1,8], Christiana Lyn Scheib[1,9], Kristiina Tambets[1], Aivar Kriiska[10]*, Mait Metspalu[1]*

Copyright © 2021 The Authors, some rights reserved; exclusive licensee American Association for the Advancement of Science. No claim to original U.S. Government Works. Distributed under a Creative Commons Attribution NonCommercial License 4.0 (CC BY-NC).

The transition from Stone to Bronze Age in Central and Western Europe was a period of major population movements originating from the Ponto-Caspian Steppe. Here, we report new genome-wide sequence data from 30 individuals north of this area, from the understudied western part of present-day Russia, including 3 Stone Age hunter-gatherers (10,800 to 4250 cal BCE) and 26 Bronze Age farmers from the Corded Ware complex Fatyanovo Culture (2900 to 2050 cal BCE). We show that Eastern hunter-gatherer ancestry was present in northwestern Russia already from around 10,000 BCE. Furthermore, we see a change in ancestry with the arrival of farming—Fatyanovo Culture individuals were genetically similar to other Corded Ware cultures, carrying a mixture of Steppe and European early farmer ancestry. Thus, they likely originate from a fast migration toward the northeast from somewhere near modern-day Ukraine—the closest area where these ancestries coexisted from around 3000 BCE.

Downloaded from http://advances.sciencemag.org/ on January 21, 2021

INTRODUCTION

The western part of the present territory of Russia has been a focal point of several prehistoric processes yet remains heavily underrepresented in ancient DNA (aDNA) studies. Some of the oldest genetically studied individuals from Europe come from this region (*1*–*3*), but overall, ancient genetic information is sparse.

The colonization of the eastern and northern European forest belt took place in two extensive waves during the end of the Paleolithic and the beginning of the Mesolithic period 13th to 9th millennium cal BCE (bordering ca. 9700 cal BCE) (*4*, *5*). In both cases, groups of peoples with similar material cultures to those spread in wide areas of Europe took part in the colonization process. In regard to the Mesolithic settlements in the area, a number of distinct archaeological cultures (Butovo, Kunda, Veretye, Suomusjärvi, etc.) have been identified (*6*–*8*). In older stages of habitation, the material culture is so similar that it has also been handled as a single cultural area. However, from the middle of the 9th millennium cal BCE, local population groups with clearly distinguished cultural differences already existed in the area (*4*). Despite a series of small changes occurring during the Mesolithic period (partly the Early Neolithic period according to the Russian periodization based on pottery production not agriculture), the cultural continuities as a general trend of those groups are observable across time until the beginning of the 5th millennium, in some areas up to the beginning of the 4th millennium cal BCE, when the so-called Pit-Comb Ware and Comb Ware cultures formed in wide areas of Europe (*9*). In the territory of the Volga-Oka interfluvial area in Russia, Lyalovo Culture with pit-comb pottery and its local variants were described (*10*). It is likely that the people from this cultural realm gave the starting boost to a series of developments in archaeological cultures specific to the 4th to 3rd millennium cal BCE, in particular to the hunting-gathering Volosovo Culture, distinguishable in large areas of Russia (*11*).

European Mesolithic hunter-gatherers (HG) can be divided into groups based on their genetic ancestry. The so-called Western group (WHG) was spread from Iberia to the Balkans and reached as far as the Late Mesolithic Eastern Baltic (*12*–*14*). The Eastern group (EHG) had genetic influences from further east (a genetic connection to modern Siberians) and so far includes six individuals from western Russia (*14*–*17*). The genomes of four of these individuals have been previously studied from Karelia in the northwest from 7500 to 5000 BCE (*14*–*16*) and two from the Samara region in the eastern part of European Russia from 9400 to 5500 BCE (*15*, *17*).

Genetic studies have shown that the people associated with the Yamnaya cultural complex spread out of the Steppe region of the East European Plain and contributed substantially to the ancestry of the European populations (*15*, *18*) that started to produce Corded Ware around 2900 to 2800 cal BCE (*19*). For brevity, we will use culture names when talking about individuals whose archaeological context—funerary practices and/or time period—has been associated with a certain culture. It is important to stress that, in reality, the link between culture and genetic ancestry is not to be assumed. The migration of the Yamnaya population has been estimated to have been two times faster than the Anatolian early farmer (EF) migration into Europe a few thousand years earlier and coincided with a decrease in broad-leaf forests and increase in grasslands/pastures in Western Europe (*20*). The Corded Ware cultural complex (CWC) was spread on a wide area, reaching Tatarstan in the East; the southern parts of Finland, Sweden, and Norway in the North; Belgium and The Netherlands in the West; and Switzerland and Ukraine in

[1]Estonian Biocentre, Institute of Genomics, University of Tartu, Tartu 51010, Estonia. [2]Institute of Ethnology and Anthropology, Russian Academy of Sciences, Moscow 119991, Russia. [3]Archaeological Research Collection, School of Humanities, Tallinn University, Tallinn 10130, Estonia. [4]Cherepovets State University and Cherepovets Museum Association, Cherepovets 162600, Russia. [5]Peter the Great Museum of Anthropology and Ethnography (Kunstkamera), Russian Academy of Sciences, St. Petersburg 199034, Russia. [6]Institute of Archaeology, Russian Academy of Sciences, Moscow 117292, Russia. [7]Institute of Molecular Biology and Pathology, National Research Council, Rome 00185, Italy. [8]Department of Human Genetics, KU Leuven, Leuven 3000, Belgium. [9]St. John's College, University of Cambridge, Cambridge CB2 1TP, UK. [10]Department of Archaeology, Institute of History and Archaeology, University of Tartu, Tartu 51014, Estonia.
*Corresponding author. Email: lehti.saag@ut.ee (Lehti Saag); aivar.kriiska@ut.ee (A.K.); mait.metspalu@ut.ee (M.M.)

the South (*21*, *22*). Its easternmost extension—Fatyanovo Culture—is a prominent Eastern European CWC branch that was spread over a large area in European Russia and introduced animal husbandry and probably crop cultivation into the forest belt (*23*, *24*). So far, only 14 radiocarbon dates have been published for Fatyanovo Culture, placing it to 2750 to 2500 (2300) cal BCE (*24*). The burial customs characteristic of the culture included the placement of the dead in flat earth graves (less often in barrows), mostly flexed and on their side—men mostly on the right and women on the left side—with shaft-hole stone axes, flint tools, ceramic vessels, etc., as grave goods (*23*, *25*).

The Yamnaya complex pastoralists shared ancestry with EHG and Caucasus HGs (CHG) (*26*). Genetic studies have revealed that CWC individuals, with predominantly Yamnaya ancestry, showed some admixture with European EF of Anatolian ancestry and were most similar to modern populations from Eastern and Northern Europe (*14*–*16*, *18*, *27*). Lactase persistence, frequent in contemporary Central and Northern Europe, was still at low frequency in the CWC individuals (*14*, *16*, *18*, *28*) but underwent a fast frequency increase soon after (*14*, *28*, *29*). It has also been shown that the Yamnaya expansion was male-biased (*30*), while the Anatolian EF ancestry in the CWC individuals was acquired more through the female lineage (*27*) [see discussion in (*31*, *32*)].

In this study, we aim to shed light on the demographic processes accompanying the change from fishing-hunting-gathering to productive livelihoods in the forest belt of northeast Europe and to look into the genetic changes involved in the transition from the Stone to the Bronze Age in the western part of present-day Russia. We add 28 new radiocarbon dates from western Russia and characterize the genetic affinities of the HG and Fatyanovo Culture farmers. As part of the study, we set out to examine whether and how the major population movements seen in other parts of Europe during the Holocene have affected this area—what was the ancestry of the settlers of northwestern Russia and was the Fatyanovo Culture population the result of a direct migration from the East European Steppe or is European EF ancestry involved similarly to more western CWC groups. In addition, our aim is to shed light on local processes like the potential admixture between Volosovo and Fatyanovo Culture people suggested by archaeological evidence (*21*).

RESULTS

Samples and archaeological background

In this study, we have extracted DNA from the apical tooth roots of 48 individuals from 18 archaeological sites in modern-day western Russia and Estonia (Fig. 1, data S1, table S1, and text S1). The 30 individuals with the highest preservation yielded 10 to 78% endogenous DNA and <3% contamination (table S1). We have shotgun-sequenced these individuals to an average genomic coverage of >0.01× (n = 2), >0.1× (n = 18), >1× (n = 9), and 5× (PES001) (Table 1 and table S1). The presented genome-wide data are derived from 3 Stone Age HGs (WeRuHG; 10,800 to 4250 cal BCE) and 26 Bronze Age Fatyanovo Culture farmers from western Russia (Fatyanovo; 2900 to 2050 cal BCE) and 1 Corded Ware Culture individual from Estonia (EstCWC; 2850 to 2500 cal BCE) (Fig. 1, data S1, table S1, and text S1). We analyzed the data in the context of published ancient and modern populations (tables S3 and S4).

In the case of radiocarbon dating, it is possible that fish from rivers and lakes consumed by Stone Age fisher-hunter-gatherers may cause a notable reservoir effect. This means that the radiocarbon dates obtained from the human bones and teeth can be hundreds but not thousands of years older than the actual time these people lived (*33*). Unfortunately, we do not yet have data to estimate the size of the reservoir effect for each specific case. However, this does not change the overall picture regarding the Stone Age individuals of this study.

Affinities of Western Russian HGs

First, we assessed the mitochondrial DNA (mtDNA) and Y chromosome (chrY) variation of the three Stone Age HGs from western Russia. The oldest individual PES001 belongs to mtDNA haplogroup (hg) U4 (Table 1 and table S1), which has been found before in EHG and Scandinavian HG individuals (*13*–*15*, *27*, *34*). The other two represent mtDNA hgs T2 and K1 (Table 1, fig. S1, and table S1), which is noteworthy because hg U was, by far, the most frequent in European HG before the spread of farming. However, hgs H11 and T2 have also been found previously in HG individuals (*13*, *14*), and the estimated ages of the lineages determined for the Western Russian individuals (T2a1b1 and K1) are ~11,000 ± 2800 and ~22,000 ± 3300 years, respectively (*35*), likely predating the ages of the individuals (~8500 to 8300 and ~6500 to 6300 years). The chrY lineages carried by PES001 and BER001 are R1a5-YP1272 and Q1-L54, respectively (Table 1 and tables S1 and S2); both hgs have also been found previously in EHG individuals (*13*–*16*, *27*).

Next, we compared the WeRuHG individuals to a set of available ancient and modern populations (tables S3 and S4) using autosomal data. We performed principal components analysis (PCA), by projecting ancient individuals onto components calculated on Western Eurasian individuals from the Human Origins (HO) dataset (https://reich.hms.harvard.edu/downloadable-genotypes-present-day-and-ancient-dna-data-compiled-published-papers) (tables S3 and S4). The PCA revealed that all three WeRuHG individuals cluster together with individuals positioned at the EHG end of the European HG cline (Fig. 2A). We then projected ancient individuals onto a worldwide modern sample set from the HO dataset (tables S3 and S4) using ADMIXTURE analysis. We ran the calculations on $K = 3$ to $K = 18$ (fig. S2, C and D) but discuss $K = 9$ (Fig. 2B and fig. S2, A and B). This K level had the largest number of inferred genetic clusters for which >10% of the runs that reached the highest log likelihood values yielded very similar results. The analysis again shows that WeRuHG individuals are most similar to EHG, being made up of mostly the component maximized in WHG (blue) and considerable proportions of the components most frequent in modern Russian Far East and ancient Caucasus/Iran (orange and olive, respectively) (Fig. 2B and fig. S2, A and B).

Next, we used F_{ST}, outgroup $f3$, and D statistics to compare the genetic affinity of WeRuHG to those of other relevant populations (tables S3 and S4). We found that WeRuHG and EHG are similar in their genetic affinities both to other ancient and to modern populations (Fig. 3A, figs. S3 and S4A, and tables S5 to S8). On the other hand, when comparing WeRuHG to the later Fatyanovo, we found that WeRuHG shares relatively more genetic drift with EHG-like populations, West Siberian HG, ancient Iranians, and modern populations from Siberia, while Fatyanovo shares more with most of ancient European and Steppe populations and modern populations from the Near East, the Caucasus, and Europe (Fig. 3B, fig. S4B, and tables S5 to S8).

We studied the genetic affinities of the higher-coverage (5×) HG PES001 further using outgroup $f3$ statistics by comparing the affinities of three higher-coverage Russian Mesolithic HGs—PES001

Downloaded from http://advances.sciencemag.org/ on January 21, 2021

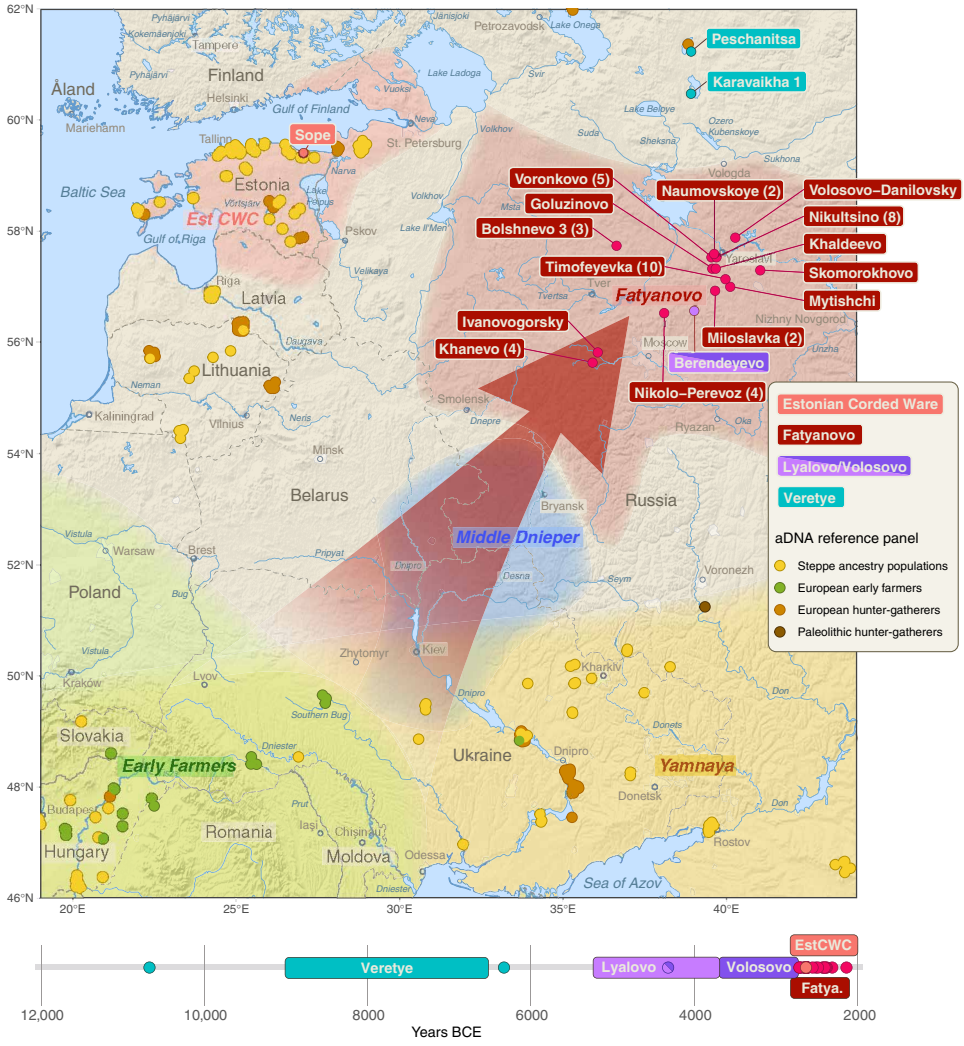

Fig. 1. Map of the geographical locations of the individuals of this study and timeline showing the dates of individuals and cultures. Numbers in parentheses beside site names indicate the number of individuals included from this site (if more than one). Shaded areas mark the spread of each cultural group indicated on the map. Arrow indicates the proposed direction of migration of the predecessors of the Fatyanovo Culture people. On the timeline, each individual of this study is marked by a dot using the midpoint of the 95% calibrated date estimate, and the periods of the associated cultures are shown in shaded bars.

(Peschanitsa; 10,785 to 10,626 cal BCE), I0061 (Yuzhnyy Oleni Ostrov; 6773 to 5886 BCE), and Sidelkino (Sidelkino; 9386 to 9231 cal BCE)—to Mesolithic and Paleolithic HGs from different areas of Europe and Siberia (Fig. 2C and table S9). All three are most similar to individuals from the European part of Russia or from Siberia who lived within 10,000 years of each other—to each other, the West Siberia Neolithic population and the Afontova Gora 3 individual. These are followed by individuals from Central Europe from the same time window. Geographically close Paleolithic Sunghir and Kostenki individuals from >30,000 cal BCE share less than temporally close HGs from Central Europe with the Russian Mesolithic individuals. We also tried modeling PES001 as a mixture of WHG and either CHG, Mal'ta, or Afontova Gora 3 using qpAdm, but all three models were rejected (P value of 1.96×10^{-85} to 7.93×10^{-13}) (table S10).

EF ancestry in Fatyanovo Culture individuals

Then, we turned to the Bronze Age Fatyanovo Culture individuals and determined that they carry maternal (subclades of mtDNA hg U5, U4, U2e, H, T, W, J, K, I, and N1a) and paternal (chrY hg R1a-M417) lineages (Table 1, fig. S1, and tables S2 to S4) that have also been found in CWC individuals elsewhere in Europe (*14–16*, *18*, *27*). In all individuals for which the chrY hg could be determined with sufficient depth (n = 6), it is R1a2-Z93 (Table 1 and tables S1 and S2), a lineage now spread in Central and South Asia, rather than the R1a1-Z283 lineage that is common in Europe (*36*). R1a2-Z93 is also not rejected for the individuals that were determined with less depth due to missing data on more apical markers (table S2).

On the PCA, the Fatyanovo individuals (and the Estonian CWC individual) group together with many European Late Neolithic/Bronze Age (LNBA) and Steppe Middle/Late Bronze Age individuals on top of modern Northern and Eastern Europeans (Fig. 2A). This ancient cluster is shifted toward Anatolian and European EF compared to Steppe Early/Middle Bronze Age populations, including the Yamnaya. The same could be seen in ADMIXTURE analysis where the Fatyanovo individuals are most similar to LNBA Steppe

Downloaded from http://advances.sciencemag.org/ on January 21, 2021

Table 1. Archaeological information, genetic sex, mtDNA and Y chromosome haplogroups, and average genomic coverage of the individuals of this study. Date (cal BCE), calibrated using OxCal v4.2.4 (*105*) and IntCal13 atmospheric curve (*106*); Morph., morphological; Gen., genetic; MT hg, mtDNA haplogroup; Y hg, Y chromosome haplogroup; Av. cov., average genomic coverage; RUS, Russia; EST, Estonia; NA, not available.

Individual	Site	Location	Group	Date (cal BCE)	Morph. sex	Gen. sex	MT hg	Y hg	Av. cov.
BER001	Berendeyevo	Yaroslavl, RUS	WeRuHG	4447–4259	Male	XY	K1	Q1	0.13
KAR001	Karavaikha 1	Vologda, RUS	WeRuHG	6457–6258	Female?	XX	T2a1	–	0.19
PES001	Peschanitsa	Arkhangelsk, RUS	WeRuHG	10785–10626	Male	XY	U4a1	R1a5	5.03
BOL001	Bolshnevo 3	Tver, RUS	Fatyanovo	2829–2460	Male	XY	H1b	R1a	0.11
BOL002	Bolshnevo 3	Tver, RUS	Fatyanovo	2468–2211	Female	XX	J1c1	–	0.12
BOL003	Bolshnevo 3	Tver, RUS	Fatyanovo	2571–2345	Male	XY	H41a	R1a2	1.13
GOL001	Goluzinovo	Yaroslavl, RUS	Fatyanovo	2575–2349	Male	XY	T2b	R1a	0.12
HAL001	Khaldeevo	Yaroslavl, RUS	Fatyanovo	2832–2473	Male	XY	N1a1	R1a2	1.35
HAN002	Khanevo	Moscow, RUS	Fatyanovo	2859–2495	Male	XY	U5a1	R1a2	1.28
HAN004	Khanevo	Moscow, RUS	Fatyanovo	2835–2471	Male	XY	H6a1	R1a2	1.25
IVA001	Ivanovogorsky	Moscow, RUS	Fatyanovo	2864–2496	Female	XX	U4a1	–	1.29
MIL001	Miloslavka	Ivanovo, RUS	Fatyanovo	2624–2474	Female	XX	U5b2	–	0.17
MIL002	Miloslavka	Ivanovo, RUS	Fatyanovo	2287–2047	Female	XX	H	–	0.11
NAU001	Naumovskoye	Yaroslavl, RUS	Fatyanovo	2836–2573	Male	XY	T2a1	R1a2	1.58
NAU002	Naumovskoye	Yaroslavl, RUS	Fatyanovo	2836–2469	Male	XY	U5b2	R1a2	1.14
NIK002	Nikultsino	Yaroslavl, RUS	Fatyanovo	2865–2500	Male	XY	U5a1	R1a	0.12
NIK003	Nikultsino	Yaroslavl, RUS	Fatyanovo	2522–2298	Male	XY	H15a1	R1a	0.12
NIK004	Nikultsino	Yaroslavl, RUS	Fatyanovo	2876–2620	Male	XX	T2a1	–	0.18
NIK005	Nikultsino	Yaroslavl, RUS	Fatyanovo	2881–2581	Female	XX	J1c1	–	0.12
NIK007	Nikultsino	Yaroslavl, RUS	Fatyanovo	2862–2466	Female	XX	U5a1	–	0.12
NIK008AB	Nikultsino	Yaroslavl, RUS	Fatyanovo	2834–2472	Male	XY	H5b	R1a	1.34
RDT002	Nikolo-Perevoz	Moscow, RUS	Fatyanovo	2562–2299	NA	XX	T2b	–	0.02
TIM001	Timofeyevka	Ivanovo, RUS	Fatyanovo	NA	Male	XY	K1b1	R1a	0.02
TIM006	Timofeyevka	Ivanovo, RUS	Fatyanovo	2833–2470	Female	XX	W6	–	0.12
TIM008	Timofeyevka	Ivanovo, RUS	Fatyanovo	2832–2473	Male	XY	K1c1	R1a	0.12
VOD001	Volosovo-Danilovsky	Yaroslavl, RUS	Fatyanovo	2570–2299	Female	XX	J1c1	–	0.24
VOR003	Voronkovo	Yaroslavl, RUS	Fatyanovo	2573–2466	Male	XY	H6a1	R1a	0.12
VOR004	Voronkovo	Yaroslavl, RUS	Fatyanovo	2878–2627	Female	XX	W6	–	1.38
VOR005	Voronkovo	Yaroslavl, RUS	Fatyanovo	2840–2343	Male	XY	K2a5	R1a	0.12
SOP002	Sope	Ida-Viru, EST	EstCWC	2864–2495	Female	XX	R1b1	–	0.12

ancestry populations from Central Europe, Scandinavia, and the Eastern Baltic (Fig. 2B and fig. S2). These populations are composed of the "WHG" (blue) and "ancient Caucasus/Iran" (olive) component and small amounts of the "Russian Far East" (orange) component, similarly to Yamnaya populations. However, the European LNBA populations (including Fatyanovo) also display a component most frequent in Anatolian and European EF populations (light green), which is not present in the Yamnaya from Russia.

We studied the affinities of the Fatyanovo individuals by comparing F_{ST}, outgroup *f*3, and *D* statistics' results of different populations and found that Fatyanovo shares more with European EF populations and modern Near Easterners than Yamnaya Samara does (Fig. 3C; figs. S3, S4C, and S5C; and tables S5 to S8). This signal can also be seen when using either autosomal or X chromosome (chrX) positions from the 1240K dataset (https://reich.hms.harvard.edu/downloadable-genotypes-present-day-and-ancient-dna-data-compiled-published-papers) instead of the autosomal positions of the HO dataset with less single-nucleotide polymorphisms (SNPs) (fig. S5, A and B, and tables S11 and S12). We also compared the affinities of Yamnaya Samara and Fatyanovo directly with *D* statistics and saw that Fatyanovo is significantly more similar ($Z > 3$) to most EF populations than to Yamnaya Samara, and the latter, in turn, is significantly more similar to most Steppe populations than to Fatyanovo (table S13). We studied the apparent EF input in Fatyanovo further using admixture *f*3 statistics and got significant results ($Z < -3$) for admixture between different Yamnaya groups and a wide variety of EF populations (table S14). Furthermore, when comparing outgroup *f*3 and *D* statistics' results for Fatyanovo

Downloaded from http://advances.sciencemag.org/ on January 21, 2021

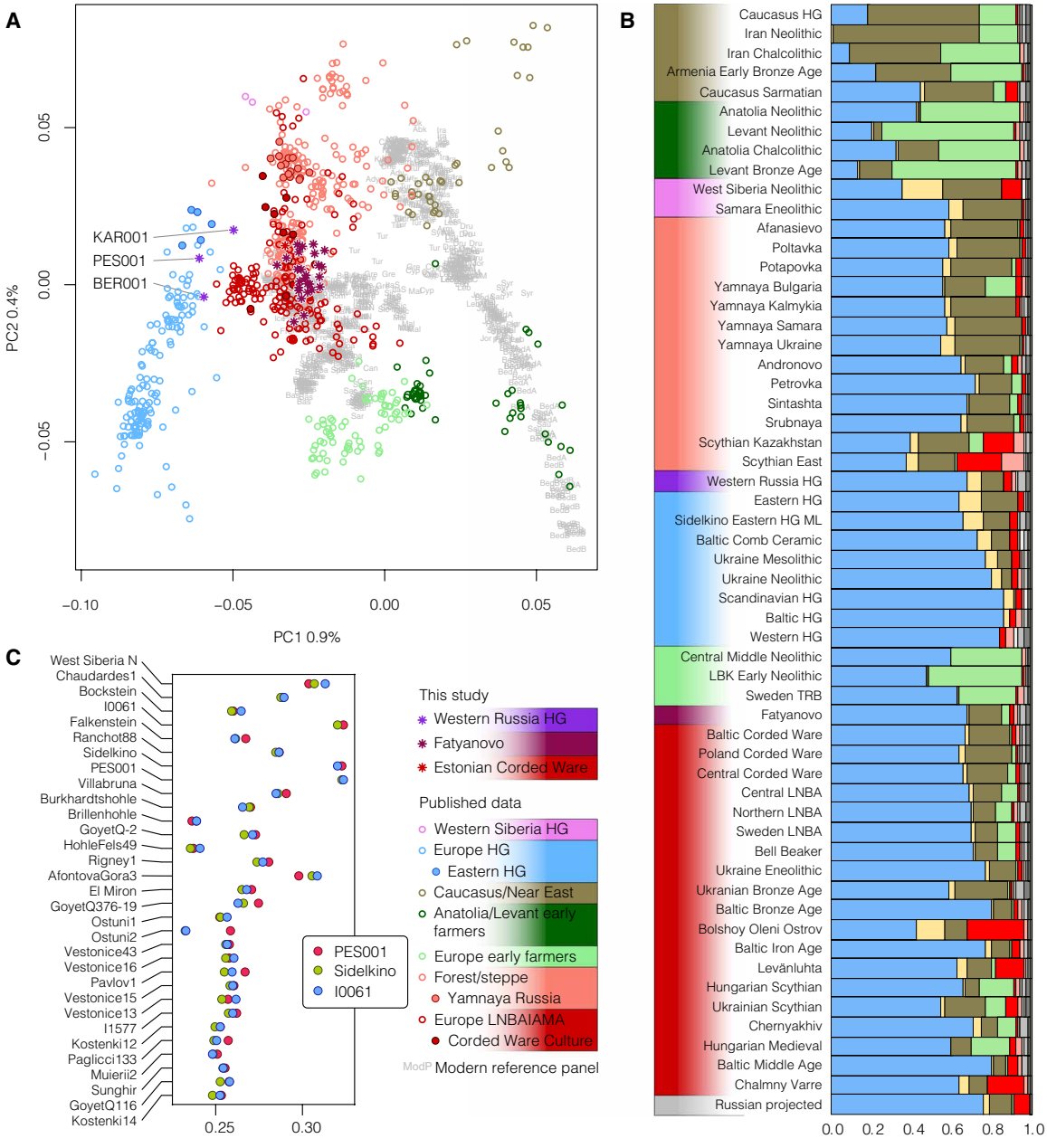

Fig. 2. Principal component, ADMIXTURE analyses', and HG outgroup *f*3 statistics' results. (**A**) PCA results of modern West Eurasians with ancient individuals projected onto the first two components (PC1 and PC2). (**B**) ADMIXTURE analysis results for a selection of ancient population averages at K9 with ancient individuals projected onto the modern genetic structure. (**C**) Outgroup *f*3 results comparing Russian Mesolithic HGs PES001, Sidelkino, and I0061 to European and Siberian Paleolithic and Mesolithic HGs (listed from youngest to oldest on the plot). LNBAIAMA, Late Neolithic/Bronze Age/Iron Age/Middle Ages; ML, Mesolithic; LBK, Linearbandkeramik, Linear Pottery Culture; TRB, Trichter(-rand-)becherkultur, Funnel(-neck-)beaker Culture.

and Central CWC, there are no clear differences in their affinities to different ancient or modern population groups (Fig. 3D, fig. S3D, and tables S5 to S8).

Because the previous analyses suggested that the genetic makeup of the Fatyanovo Culture individuals was a result of admixture between migrating Yamnaya individuals and contemporary European populations, we used two complementary methods (qpAdm and ChromoPainter/NNLS) to determine suitable proxies for the admixing populations and the mixing proportions (Fig. 4 and tables S15 to S17). We tested qpAdm models including Yamnaya from Samara or Kalmykia and a variety of EF populations one at a time and found that the two EF populations, with the highest *P* values with both Yamnaya populations, are Globular Amphora and Trypillia (*P* values of 0.02/0.16 and 0.06/0.26, respectively) (table S15). The admixture proportions are 65.5%/66.9% Yamnaya Samara/Kalmykia + 34.5%/33.1% Globular Amphora and 65.5%/69.6% Yamnaya Samara/Kalmykia + 34.5%/30.4% Trypillia, respectively (Fig. 4 and table S15). The proportions are similar (69 to 75% Yamnaya + 25 to 31% EF) for Central and Baltic CWC (Fig. 4 and table S15). We also tested these four models with the preceding Volosovo Culture HG

Downloaded from http://advances.sciencemag.org/ on January 21, 2021

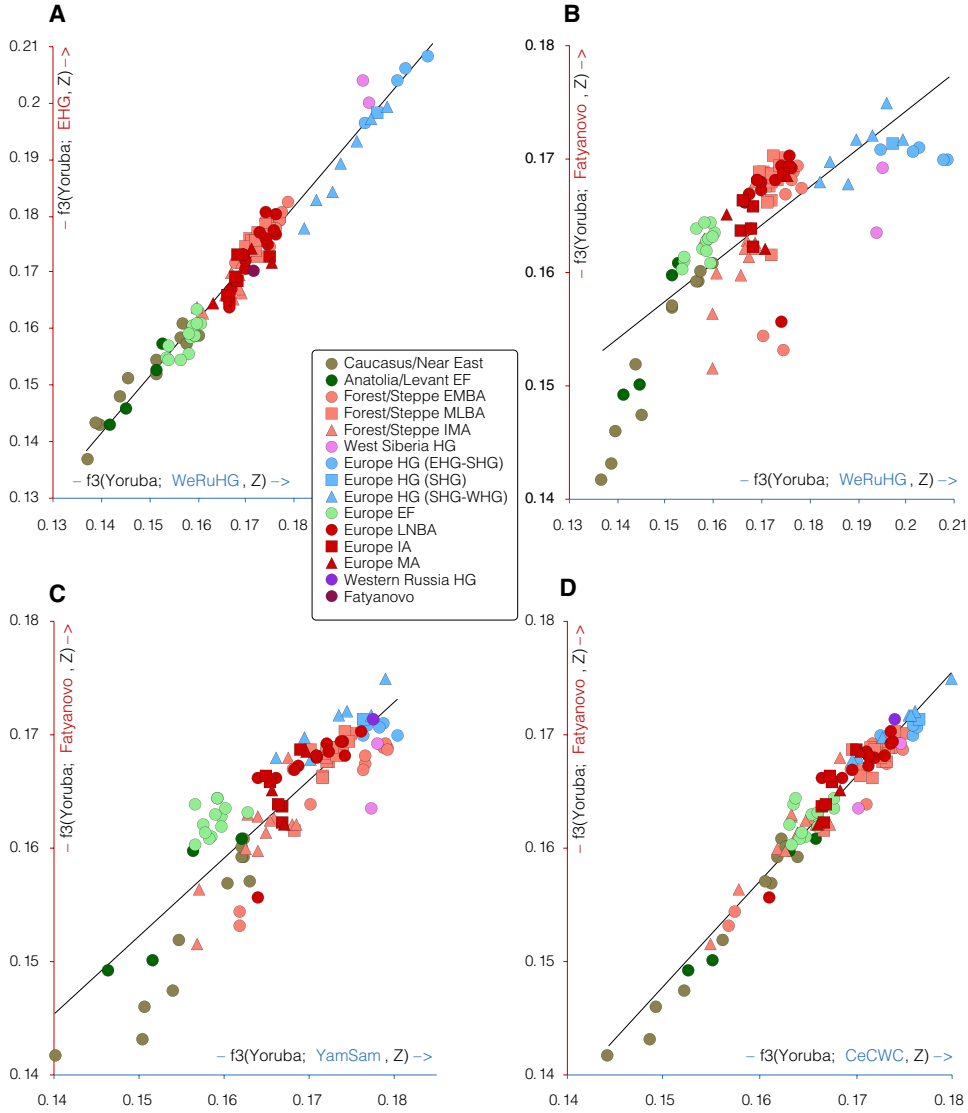

Fig. 3. Outgroup *f*3 statistics' results of comparisons with ancient populations. Outgroup *f*3 statistics' values of form *f*3(Yorubas; study population, ancient) plotted against each other for two study populations (blue and red axes): (**A**) Western Russian HGs (WeRuHG) and Eastern HGs (EHG), (**B**) WeRuHG and Fatyanovo, (**C**) Yamnaya Samara (YamSam) and Fatyanovo, and (**D**) Central Corded Ware Culture (CeCWC) and Fatyanovo. The trend line for all datapoints is shown in black. EMBA, Early/Middle Bronze Age; MLBA, Middle/Late Bronze Age; IMA, Iron/Middle Ages; IA, Iron Age; MA, Middle Ages.

BER001 added to "right" populations to see whether there is shared drift between Volosovo and Fatyanovo that would cause the models with admixing populations without this drift to be rejected. All four models are still not rejected (*P* values of 0.97/0.57 and 0.98/0.59, respectively) (table S15), suggesting that no Volosovo contribution is needed to model Fatyanovo. Ancestry proportions were also calculated using the ChromoPainter/NNLS pipeline with the results 37%/38% Yamnaya Samara + 63%/62% Globular Amphora/Trypillia for Fatyanovo and 51 to 60% Yamnaya + 40 to 49% EF for Central/Baltic CWC (table S16). Although the estimated proportion of EF ancestry is higher for Fatyanovo compared to the other groups in both cases, the difference is significant (*P* value of 0.005 to 0.03) only with Trypillia in the model. Note that qpAdm calculates admixture between populations, while ChromoPainter/NNLS uses single individuals as sources, which might influence the results. Although two-way admixture between Yamnaya and an EF population is enough to explain the genetic variation in Fatyanovo, qpAdm models with an HG population added are also not rejected with EHG, WeRuHG, and Volosovo (*P* values of 0.14 to 0.98) (table S17). Fatyanovo can be modeled as 60 to 63% Yamnaya Samara + 33 to 34% Globular Amphora + 3 to 6% HG. The results are similar for Central and Baltic CWC with 2 to 11% of HG ancestry (except with Volosovo as a source for Central CWC, which gets a negative mixture coefficient).

We estimated the time of admixture for Yamnaya and EF populations to form the Fatyanovo Culture population using DATES (*37*) as 13 ± 2 generations for Yamnaya Samara + Globular Amphora and 19 ± 5 generations for Yamnaya Samara + Trypillia. If a generation time of 25 years and the average calibrated date of the Fatyanovo individuals (~2600 cal BCE) are used, this equates to the admixture happening ~3100 to 2900 BCE.

Next, we investigated the possible difference in affinities between Fatyanovo and other CWC groups (Central and Baltic CWC)

Downloaded from http://advances.sciencemag.org/ on January 21, 2021

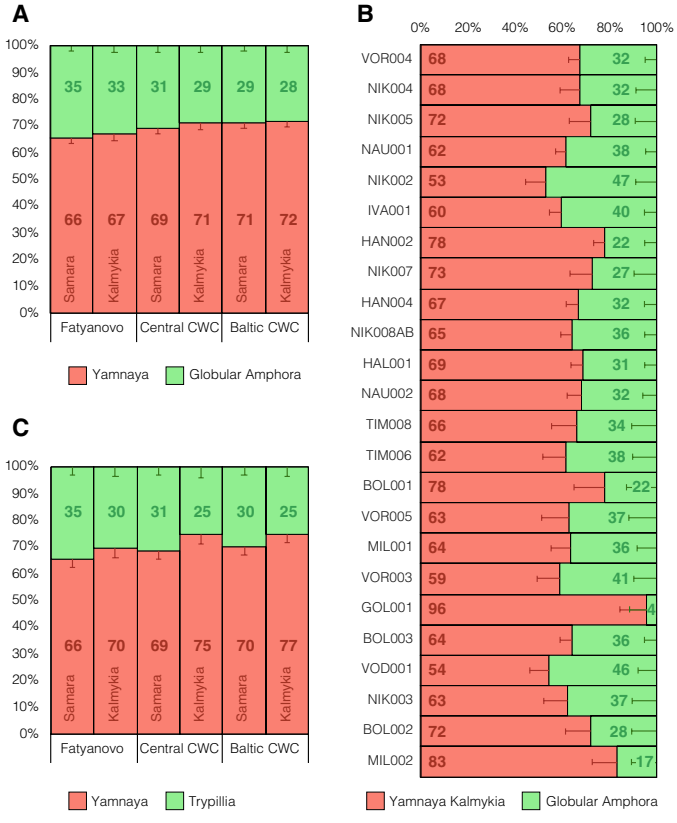

Fig. 4. qpAdm admixture modeling results. (**A**) Models with Yamnaya Samara or Kalmykia and Globular Amphora as sources for Fatyanovo, Central, and Baltic CWC populations. (**B**) Models with Yamnaya Kalmykia and Globular Amphora as sources for Fatyanovo individuals with the oldest radiocarbon date on top and the youngest on the bottom. (**C**) Models with Yamnaya Samara or Kalmykia and Trypillia as sources for Fatyanovo, Central, and Baltic CWC populations.

and found that the populations are similar to each other because a one-way qpAdm model cannot be rejected for Fatyanovo = Central CWC (*P* value of 0.26) or Central CWC = Baltic CWC (*P* value of 0.48) (table S18). On the other hand, there is considerable variation in admixture proportions within populations, visible on PCA (Fig. 2) and ADMIXTURE (fig. S2A) and confirmed by per-individual qpAdm models showing 4 to 47% Globular Amphora ancestry in Fatyanovo (Fig. 4B and table S15) and 7 to 55% in the other two groups (table S15). We tested whether the variation in ancestry correlates with time using the second PC component (PC2) or the qpAdm ancestry proportions and the calibrated radiocarbon dates of the individuals. We found that there is no correlation between time and ancestry proportions in Fatyanovo (*P* value of 0.92/0.23, respectively), but there is a significant change toward more EF ancestry in Baltic CWC using PC2 (*P* value of 0.0003) and in both Central and Baltic CWC using qpAdm proportions (*P* value of 0.02 for both).

Furthermore, we confirmed the presence of sex-biased admixture previously seen in CWC individuals from Estonia, Poland, and Germany (*27*, *38*, *39*) in the Fatyanovo. To that end, we first compared autosomal and chrX outgroup *f*3 results (fig. S5D and tables S11 and S12). Two-sample two-tailed *t* tests assuming unequal variances showed that the mean *f*3 value for EF populations is significantly lower than for HG/Steppe ancestry populations based on autosomal positions (*P* value of 0.000001) but not based on chrX positions (*P* value of 0.14). Next, we calculated admixture proportions on chrX data using qpAdm and the same models as with autosomal data (table S15). Only two of the four models presented for autosomal data (Yamnaya Samara + Globular Amphora/Trypillia) yielded a significant *P* value (0.13/0.36, respectively) due to the low number of chrX SNPs available. The confidence intervals (CIs) were extremely wide with Trypillia, but the chrX data showed 40 to 53% Globular Amphora ancestry in Fatyanovo, in contrast with the 32 to 36% estimated using autosomal data. The sex-biased admixture is also supported by the presence of mtDNA hg N1a in two Fatyanovo individuals—an hg frequent in Linear Pottery Culture (LBK) EFs but not found in Yamnaya individuals so far (*16*, *18*, *40*)—and by all males carrying chrY hg R1a-M417, which appeared in Europe after the Steppe migration (*15*, *18*).

Last, we looked for closely related individuals in the Fatyanovo Culture sample set using READ (*41*). There were no confirmed cases of second-degree or closer relatives (fig. S6), although a second-degree relationship cannot be ruled out for some pairs as the 95% CIs of their point estimates overlap with those of the second-degree relatedness threshold.

Phenotype-informative allele frequency changes in western Russia

We imputed the genotypes of 113 phenotype-informative positions connected to diet (carbohydrate, lipid, and vitamin metabolism), immunity (response to pathogens, autoimmune, and other diseases), and pigmentation (eye, hair, and skin) (tables S20 to S22). We used the individuals of this study and previously published Eastern Baltic individuals for comparison: 3 WeRuHG, 5 Latvian HG, 7 Estonian and Latvian CWC, 24 Fatyanovo, 10 Estonian Bronze Age, 6 Estonian Iron Age, 3 Ingrian Iron Age, and 4 Estonian Medieval individuals (*27*, *28*, *34*). Here, we focus on variants associated with pigmentation (39 SNPs of the HIrisPlex-S system), lactase persistence (rs4988235 and rs182549; *MCM6*), and fatty acid metabolism (rs174546T, *FADS1-2*) (Table 2 and tables S20 to S22). Although the results should be interpreted with due caution because of the small sample size, we inferred that the examined WeRuHG individuals carried alleles connected to brown eyes, dark brown to black hair, and intermediate or dark skin pigmentation, while around a third of the Fatyanovo individuals had blue eyes and/or blond hair. Furthermore, we infer that the frequency of the two alleles associated with lactase persistence (rs4988235 and rs182549; *MCM6*) is 0% in WeRuHG and 17 ± 13% in Fatyanovo Culture based on the individuals of this study (similar to Eastern Baltic populations from the same time periods) but has a significant increase (EstIngIA versus Fatyanovo/EstLatCWC *P* values of 0.03) to ~40% by the Late Bronze Age in the Eastern Baltic (*28*). On the other hand, we find that an allele connected to an increase in cholesterol in serum (rs174546T; *FADS1-2*) significantly decreases from ~90% in Eastern Baltic and Western Russian HG to ~45% in Late Bronze Age individuals from the Eastern Baltic (Fatyanovo versus EstBA, *P* value of 0.01). This has been shown previously by Mathieson and Mathieson (*29*) who observed an increase of the alternative allele C. The change could be a sign of negative selection against high cholesterol or a result of migration of people from a population with a lower frequency of the allele.

DISCUSSION

After the last glacial period, at the end of the 10th and the beginning of the 9th millennium BC, vast areas in the Eastern Baltic, Finland,

Downloaded from http://advances.sciencemag.org/ on January 21, 2021

Table 2. Phenotype prediction results. Phenotype proportions for a selection of pigmentation- and diet-associated phenotypes per period.

	Proportion in period						
	Western Russian HGs	Latvian HGs	Estonian and Latvian Corded Ware complex farmers	Fatyanovo	Estonian Late Bronze Age	Estonian/ Ingrian Iron Age	Estonian Middle Age
Phenotype	*N* = 3	*N* = 5	*N* = 7	*N* = 24	*N* = 10	*N* = 9	*N* = 4
Blue eyes	0.00	0.60	0.29	0.21	0.70	1.00	1.00
Brown eyes	1.00	0.40	0.71	0.79	0.30	0.00	0.00
Blond + dark blond hair	0.00	0.20	0.00	0.04	0.10	0.78	0.75
Red hair	0.00	0.00	0.00	0.00	0.00	0.00	0.25
Brown/dark brown hair	0.00	0.00	0.14	0.21	0.30	0.11	0.00
Dark brown + black hair	1.00	0.80	0.86	0.75	0.60	0.11	0.00
Very pale + pale skin	0.00	0.00	0.00	0.00	0.10	0.00	0.00
Mixed/unpredictable very pale-pale-intermediate skin	0.00	0.00	0.00	0.00	0.10	0.22	0.50
Intermediate skin	0.33	0.60	0.57	0.58	0.80	0.67	0.50
Mixed/unpredictable intermediate-dark + dark + black skin	0.67	0.40	0.43	0.42	0.00	0.11	0.00
Lactase persistence (rs4988235)	0.00	0.00	0.07	0.17	0.40	0.50	0.75
High cholesterol (rs174546)	1.00	0.90	0.57	0.83	0.45	0.56	0.13

and northern parts of Russia were populated relatively quickly by HG groups (*42*–*44*). Flint originating from several places in the Eastern Baltic and the European part of Russia and the similarities in lithic and bone technologies and artifacts suggest the existence of extensive social networks in the forest belt of Eastern and Northern Europe after it was populated (*43*, *45*, *46*). This has led to the hypothesis that the descendants of Final Paleolithic HG from eastern Poland to the central areas of European Russia took part in the process (*8*, *47*) and remained connected to their origin, creating a somewhat stretched social network (*4*). However, these connections ceased after a few centuries, as can be witnessed from the production of stone tools from mostly local materials, and new geographically smaller social units appeared in the middle of the 9th millennium BCE (*4*). aDNA studies of this area have included Mesolithic individuals that are from the 8th millennium BC or younger and reveal two genetic groups: WHG in the Eastern Baltic and EHG in northwestern Russia (*14*–*17*, *27*, *34*). However, no human genomes from the settlement period have been published so far, leaving the genetic ancestry/ancestries of the settlers up for discussion. The individual PES001 from around 10,700 cal BCE presented here with 5× coverage provides evidence for EHG ancestry in northwestern Russia close to the time it was populated. This, in turn, raises the question—hopefully answered by future studies—of the ancestry of the first people of the Eastern Baltic: Did they have EHG ancestry, as suggested by the shared social network of the two areas at the time of settlement, and an influx of WHG ancestry people later, not accompanied by a change in archaeological material, or did WHG ancestry people live in the Eastern Baltic from the beginning, representing a case of groups with different ancestry sharing a similar culture?

The formation of Fatyanovo Culture is one of the main factors that affected the population, culture, and lifestyle of the previously hunter/fisher-gatherer culture of the Eastern European forest belt. The Fatyanovo Culture people were the first farmers in the area, and the arrival of the culture has been associated with migration (*21*, *24*). This is supported by our results as the Stone Age HG and the Bronze Age Fatyanovo individuals are genetically clearly distinguishable. The sample size of our HG is low, but the three individuals form a genetically homogenous group with previously reported EHG individuals (*14*, *16*), and the newly reported PES001 is the highest-coverage whole-genome sequenced EHG individual so far, providing a valuable resource for future studies. What is more, the Fatyanovo Culture individuals (similarly to other CWC people) have not only mostly Steppe ancestry but also some EF ancestry that was not present in the area before and thus excludes the northward migration of Yamnaya Culture people with only Steppe ancestry as the source of Fatyanovo Culture population. The strongest connections for Fatyanovo Culture in archaeological material can be seen with the Middle Dnieper Culture (*23*, *48*) spread in present-day Belarus and Ukraine (*49*, *50*). The territory of what is now Ukraine is where the most eastern individuals with European EF ancestry and the most western Yamnaya Culture individuals are from based on published genomic data (*13*, *51*) (Fig. 1 and data S1). Furthermore, archaeological finds show that LBK reached western Ukraine around 5300 BCE (*52*), and the Yamnaya complex (burial mounds) arrived in southeastern Europe around 3000 BCE and spread further as far as Romania, Bulgaria, Serbia, and Hungary (*53*). This is in accordance with our genetic results as the two populations that proved to be plausible mixture sources for Fatyanovo, with the

Downloaded from http://advances.sciencemag.org/ on January 21, 2021

other source being either of the two Russian Yamnaya groups (Kalmykia or Samara), were Globular Amphora that includes individuals from Ukraine and Poland, and Trypillia that is composed of individuals from Ukraine. These findings suggest present-day Ukraine as the possible origin of the migration leading to the formation of the Fatyanovo Culture and of the Corded Ware cultures in general.

The exact timing of and processes involved in the emergence of the Fatyanovo Culture in European Russia and the local processes following it have also remained unclear. Until recently, the Fatyanovo Culture was thought to have developed later than other CWC groups and over a longer period of time (*21*, *23*). However, radiocarbon dates published last year (*24*), in combination with the 25 new dates presented here and the estimate for Yamnaya and EF admixture ~300 to 500 years before the Fatyanovo individuals of this study lived, point toward a fast process, similar in time to CWC people reaching the Eastern Baltic and southern Fennoscandia (*54*–*56*). The archaeological cultures are clearly differentiated between the areas. What is more, it has been suggested that the Fatyanovo Culture people admixed with the local Volosovo Culture HG after their arrival in European Russia (*21*, *57*, *58*). Our results do not support this as they do not reveal more HG ancestry in the Fatyanovo people compared to two other CWC groups; the three groups are shown to be similar by nonrejected one-way qpAdm models, and correlating radiocarbon dates with PC values or qpAdm ancestry proportions reveals no change in ancestry proportions of the Fatyanovo people during the period covered by our samples (2900 to 2050 BCE).

Last, allele frequency changes in western Russia and the Eastern Baltic revealed similar patterns in both areas: The frequencies of alleles in the *MCM6* and *FADS1-2* genes, which have been hypothesized to have changed due to dietary shifts from the Neolithic onward (*16*, *29*, *59*), change significantly during the Bronze Age, although the first signals of change can be seen already from the Neolithic. In accordance with a recent publication on lactase persistence (*60*), we find a low frequency of the rs4988235A allele in the initial Steppe ancestry samples [90% CI, 0 to 2.7% in (*60*), 0 to 33.8% in this study]. This suggests that the factors affecting these allele frequency shifts over time were complex and may have involved several environmental factors and genetic forces, as has already been suggested previously (*14*, *16*, *18*, *28*, *29*, *60*, *61*).

MATERIALS AND METHODS

Experimental design

The teeth used for DNA extraction were obtained with relevant institutional permissions from the Institute of Ethnology and Anthropology of Russian Academy of Sciences (Russia), Cherepovets Museum Association (Russia), and Archaeological Research Collection of Tallinn University (Estonia). DNA was extracted from the teeth of 48 individuals: 3 from Stone Age HGs from western Russia (WeRuHG; 10,800 to 4250 cal BCE), 44 from Bronze Age Fatyanovo Culture individuals from western Russia (Fatyanovo; 2900 to 2050 cal BCE), and 1 from a Corded Ware Culture individual from Estonia (EstCWC; 2850 to 2500 cal BCE) (Fig. 1, data S1, table S1, and text S1). Petrous bones of 13 of the Fatyanovo Culture individuals have been sampled for another project. More detailed information about the archaeological periods and the specific sites and burials of this study is given below.

All of the laboratory work was performed in dedicated aDNA laboratories of the Institute of Genomics, University of Tartu. The library quantification and sequencing were performed at the Institute of Genomics Core Facility, University of Tartu. The main steps of the laboratory work are detailed below.

Laboratory methods

DNA extraction

The teeth of 48 individuals were used to extract DNA. One individual was sampled twice from different teeth. Apical tooth roots were cut off with a drill and used for extraction because root cementum has been shown to contain more endogenous DNA than crown dentine (*62*). The root pieces were used whole to avoid heat damage during powdering with a drill and to reduce the risk of cross-contamination between samples. Contaminants were removed from the surface of tooth roots by soaking in 6% bleach for 5 min, then rinsing three times with Milli-Q water (Millipore), and lastly soaking in 70% ethanol for 2 min, shaking the tubes during each round to dislodge particles. Last, the samples were left to dry under an ultraviolet light for 2 hours.

Next, the samples were weighed, [20 * sample mass (mg)] μl of EDTA and [sample mass (mg) / 2] μl of proteinase K were added, and the samples were left to digest for 72 hours on a rotating mixer at 20°C to compensate for the smaller surface area of the whole root compared to powder. Undigested material was stored for a second DNA extraction if need be.

The DNA solution was concentrated to 250 μl (Vivaspin Turbo 15, 30,000 MWCO PES, Sartorius) and purified in large-volume columns (High Pure Viral Nucleic Acid Large Volume Kit, Roche) using 2.5 ml of PB buffer, 1 ml of PE buffer, and 100 μl of EB buffer (MinElute PCR Purification Kit, QIAGEN).

Library preparation

Sequencing libraries were built using NEBNext DNA Library Prep Master Mix Set for 454 (E6070, New England Biolabs) and Illumina-specific adaptors (*63*) following established protocols (*63*–*65*). The end repair module was implemented using 30 μl of DNA extract, 12.5 μl of water, 5 μl of buffer, and 2.5 μl of enzyme mix, incubating at 20°C for 30 min. The samples were purified using 500 μl of PB and 650 μl of PE buffer and eluted in 30 μl of EB buffer (MinElute PCR Purification Kit, QIAGEN). The adaptor ligation module was implemented using 10 μl of buffer, 5 μl of T4 ligase, and 5 μl of adaptor mix (*63*), incubating at 20°C for 15 min. The samples were purified as in the previous step and eluted in 30 μl of EB buffer (MinElute PCR Purification Kit, QIAGEN). The adaptor fill-in module was implemented using 13 μl of water, 5 μl of buffer, and 2 μl of Bst DNA polymerase, incubating at 37°C for 30 min and at 80°C for 20 min. The libraries were amplified, and both the indexed and universal primers (NEBNext Multiplex Oligos for Illumina, New England Biolabs) were added by polymerase chain reaction (PCR) using HGS Diamond Taq DNA polymerase (Eurogentec). The samples were purified and eluted in 35 μl of EB buffer (MinElute PCR Purification Kit, QIAGEN). Three verification steps were implemented to make sure library preparation was successful and to measure the concentration of double-stranded DNA/sequencing libraries—fluorometric quantitation (Qubit, Thermo Fisher Scientific), parallel capillary electrophoresis (Fragment Analyzer, Agilent Technologies), and quantitative PCR. One sample (TIM004) had a DNA concentration lower than our threshold for sequencing and was

Downloaded from http://advances.sciencemag.org/ on January 21, 2021

hence excluded, leaving 48 samples from 47 individuals to be sequenced.

DNA sequencing

DNA was sequenced using the Illumina NextSeq 500 platform with the 75–base pair (bp) single-end method. First, 15 samples were sequenced together on one flow cell. Later, additional data were generated for some samples to increase coverage.

Statistical analysis

Mapping

Before mapping, the sequences of adaptors and indexes and poly-G tails occurring due to the specifics of the NextSeq 500 technology were cut from the ends of DNA sequences using cutadapt 1.11 (*66*). Sequences shorter than 30 bp were also removed with the same program to avoid random mapping of sequences from other species. The sequences were mapped to reference sequence GRCh37 (hs37d5) using Burrows-Wheeler Aligner (BWA 0.7.12) (*67*) and command mem with reseeding disabled.

After mapping, the sequences were converted to BAM format, and only sequences that mapped to the human genome were kept with samtools 1.3 (*68*). Next, data from different flow cell lanes were merged and duplicates were removed with picard 2.12 (http://broadinstitute.github.io/picard/index.html). Indels were realigned with GATK 3.5 (*69*), and lastly, reads with mapping quality under 10 were filtered out with samtools 1.3 (*68*).

The average endogenous DNA content (proportion of reads mapping to the human genome) for the 48 samples is 29% (table S1). The endogenous DNA content is variable as is common in aDNA studies, ranging from under 1 to around 78% (table S1).

aDNA authentication

As a result of degrading over time, aDNA can be distinguished from modern DNA by certain characteristics: short fragments and a high frequency of C→T substitutions at the 5′ ends of sequences due to cytosine deamination. The program mapDamage2.0 (*70*) was used to estimate the frequency of 5′ C→T transitions.

mtDNA contamination was estimated using the method from (*71*).This included calling an mtDNA consensus sequence based on reads with mapping quality of at least 30 and positions with at least 5× coverage, aligning the consensus with 311 other human mtDNA sequences from (*71*), mapping the original mtDNA reads to the consensus sequence, and running contamMix 1.0-10 with the reads mapping to the consensus and the 312 aligned mtDNA sequences while trimming seven bases from the ends of reads with the option trimBases. For the male individuals, contamination was also estimated on the basis of chrX using the two contamination estimation methods first described in (*72*) and incorporated in the ANGSD software (*73*) in the script contamination.R.

The samples show 10% C→T substitutions at the 5′ ends on average, ranging from 6 to 17% (table S1). The mtDNA contamination point estimate for samples with >5× mtDNA coverage ranges from 0.03 to 2.02% with an average of 0.4% (table S1). The average of the two chrX contamination methods of male individuals with average chrX coverage of >0.1× is between 0.4 and 0.87% with an average of 0.7% (table S1).

Kinship analysis

A total of 4,375,438 biallelic single-nucleotide variant sites, with minor allele frequency (MAF) > 0.1 in a set of more than 2000 high-coverage genomes of Estonian Genome Center (EGC) (*74*), were identified and called with ANGSD (*73*) command --doHaploCall from the 25 BAM files of 24 Fatyanovo individuals with coverage of >0.03×. The ANGSD output files were converted to .tped format as an input for the analyses with READ script to infer pairs with first- and second-degree relatedness (*41*).

The results are reported for the 100 most similar pairs of individuals of the 300 tested, and the analysis confirmed that the two samples from one individual (NIK008A and NIK008B) were indeed genetically identical (fig. S6). The data from the two samples from one individual were merged (NIK008AB) with samtools 1.3 option merge (*68*).

Calculating general statistics and determining genetic sex

Samtools 1.3 (*68*) option stats was used to determine the number of final reads, average read length, average coverage, etc. Genetic sex was calculated using the script sexing.py from (*75*), estimating the fraction of reads mapping to chrY out of all reads mapping to either X or Y chromosome.

The average coverage of the whole genome for the samples is between 0.00004× and 5.03× (table S1). Of these, 2 samples have an average coverage of >0.01×, 18 samples have >0.1×, 9 samples have >1×, 1 sample have around 5×, and the rest are lower than 0.01× (table S1). Genetic sexing confirms morphological sex estimates or provides additional information about the sex of the individuals involved in the study. Genetic sex was estimated for samples with an average genomic coverage of >0.005×. The study involves 16 females and 20 males (Table 1 and table S1).

Determining mtDNA hgs

The program bcftools (*76*) was used to produce VCF files for mitochondrial positions; genotype likelihoods were calculated using the option mpileup, and genotype calls were made using the option call. mtDNA hgs were determined by submitting the mtDNA VCF files to HaploGrep2 (*77*, *78*). Subsequently, the results were checked by looking at all the identified polymorphisms and confirming the hg assignments in PhyloTree (*78*). Hgs for 41 of the 47 individuals were successfully determined (Table 1, fig. S1, and table S1).

No female samples have reads on the chrY consistent with a hg, indicating that levels of male contamination are negligible. Hgs for 17 (with coverage of >0.005×) of the 20 males were successfully determined (Table 1 and tables S1 and S2).

chrY variant calling and hg determination

In total, 113,217 haplogroup informative chrY variants from regions that uniquely map to chrY (*36*, *79*–*82*) were called as haploid from the BAM files of the samples using the --doHaploCall function in ANGSD (*73*). Derived and ancestral allele and hg annotations for each of the called variants were added using BEDTools 2.19.0 intersect option (*83*). Hg assignments of each individual sample were made manually by determining the hg with the highest proportion of informative positions called in the derived state in the given sample. chrY haplogrouping was blindly performed on all samples regardless of their sex assignment.

Genome-wide variant calling

Genome-wide variants were called with the ANGSD software (*73*) command --doHaploCall, sampling a random base for the positions that are present in the 1240K dataset (https://reich.hms.harvard.edu/downloadable-genotypes-present-day-and-ancient-dna-data-compiled-published-papers).

Preparing the datasets for autosomal analyses

The HO array dataset (https://reich.hms.harvard.edu/downloadable-genotypes-present-day-and-ancient-dna-data-compiled-published-papers) was used as the modern DNA background. Individuals

Downloaded from http://advances.sciencemag.org/ on January 21, 2021

from the 1240K dataset (https://reich.hms.harvard.edu/downloadable-genotypes-present-day-and-ancient-dna-data-compiled-published-papers) were used as the aDNA background.

The data of the comparison datasets and of the individuals of this study were converted to BED format using PLINK 1.90 (http://pngu.mgh.harvard.edu/purcell/plink/) (*84*), and the datasets were merged. Two datasets were prepared for analyses: one with HO and 1240K individuals and the individuals of this study, where 584,901 autosomal SNPs of the HO dataset were kept; the other with 1240K individuals and the individuals of this study, where 1,136,395 autosomal and 48,284 chrX SNPs of the 1240K dataset were kept.

Individuals with <10,000 SNPs overlapping with the HO autosomal dataset were removed from further autosomal analyses, leaving 30 individuals of this study to be used in autosomal analyses. These included 3 from WeRuHG, 26 from Fatyanovo, and 1 from EstCWC (table S1).

Principal components analysis

To prepare for PCA, a reduced comparison sample set composed of 813 modern individuals from 53 populations of Europe, Caucasus, and Near East and 737 ancient individuals from 107 populations was assembled (tables S3 and S4). The data were converted to EIGENSTRAT format using the program convertf from the EIGENSOFT 7.2.0 package (*85*). PCA was performed with the program smartpca from the same package, projecting ancient individuals onto the components constructed based on the modern genotypes using the option lsqproject and trying to account for the shrinkage problem introduced by projecting by using the option autoshrink.

Admixture analysis

For Admixture analysis (*86*), the same ancient sample set was used as for PCA, and the modern sample set was increased to 1861 individuals from 144 populations from all over the world (tables S3 and S4). The analysis was carried out using ADMIXTURE 1.3 (*86*) with the P option, projecting ancient individuals into the genetic structure calculated on the modern dataset due to missing data in the ancient samples. The HO dataset of modern individuals was pruned to decrease linkage disequilibrium using the option indep-pairwise with parameters 1000 250 0.4 in PLINK 1.90 (http://pngu.mgh.harvard.edu/purcell/plink/) (*84*). This resulted in a set of 269,966 SNPs. Admixture was run on this set using $K = 3$ to $K = 18$ in 100 replicates. This enabled us to assess convergence of the different models. $K = 10$ and $K = 9$ were the models with the largest number of inferred genetic clusters for which >10% of the runs that reached the highest log likelihood values yielded very similar results. This was used as a proxy to assume that the global likelihood maximum for this particular model was indeed reached. Then, the inferred genetic cluster proportions and allele frequencies of the best run at $K = 9$ were used to run Admixture to project the aDNA individuals, for which the intersection with the LD pruned modern dataset yielded data for more than 10,000 SNPs, on the inferred clusters. The same projecting approach was taken for all models for which there is good indication that the global likelihood maximum was reached (K3 to 18). We present all ancient individuals in fig. S2 but only population averages in Fig. 2B. The resulting membership proportions to K genetic clusters are sometimes called "ancestry components," which can lead to overinterpretation of the results. The clustering itself is, however, an objective description of genetic structure and hence a valuable tool in population comparisons.

Outgroup f3 statistics

For calculating autosomal outgroup *f*3 statistics, the same ancient sample set as for previous analyses was used, and the modern sample set included 1177 individuals from 80 populations from Europe, Caucasus, Near East, Siberia and Central Asia, and Yoruba as outgroup (tables S3 and S4). The data were converted to EIGENSTRAT format using the program convertf from the EIGENSOFT 5.0.2 package (*85*). Outgroup *f*3 statistics of the form *f*3(Yoruba; West_Siberia_N/EHG/CentralRussiaHG/Fatyanovo/ Yamnaya_Samara/Poland_CWC/Baltic_CWC/Central_CWC, modern/ancient) were computed using the ADMIXTOOLS 6.0 program qp3Pop (*87*).

To allow chrX versus autosome comparison for ancient populations, outgroup *f*3 statistics using chrX SNPs were computed. To allow the use of the bigger number of positions in the 1240K over the HO dataset, Mbuti from the Simons Genome Diversity Project (*88*) was used as the outgroup. The outgroup *f*3 analyses of the form *f*3(Mbuti; West_Siberia_N/EHG/CentralRussiaHG/Fatyanovo/Yamnaya_Samara/Poland_CWC/Baltic_CWC/Central_CWC, ancient) were run both using not only 1,136,395 autosomal SNPs but also 48,284 chrX positions available in the 1240K dataset. Because all children inherit half of their autosomal material from their father but only female children inherit their chrX from their father, then in this comparison chrX data give more information about the female and autosomal data about the male ancestors of a population.

The autosomal outgroup *f*3 results of the two different SNP sets were compared to each other and to the results based on the chrX positions of the 1240K dataset to see whether the SNPs used affect the trends seen. Outgroup *f*3 analyses were also run with the form *f*3(Mbuti; PES001/I0061/Sidelkino, Paleolithic/Mesolithic HG) and admixture *f*3 analyses with the form *f*3(Fatyanovo; Yamnaya, EF) using the autosomal positions of the 1240K dataset.

D statistics

D statistics of the form *D*(Yoruba, West_Siberia_N/EHG/CentralRussiaHG/Fatyanovo/ Yamnaya_Samara/Poland_CWC/Baltic_CWC/Central_CWC; Russian, modern/ancient) were calculated on the same dataset as outgroup *f*3 statistics (tables S3 and S4) using the autosomal positions of the HO dataset. The ADMIXTOOLS 6.0 package program qpDstat was used (*87*).

In addition, *D* statistics of the form *D*(Mbuti, ancient; Yamnaya_Samara, Fatyanovo/Baltic_CWC/ Central_CWC) and *D*(Mbuti, ancient; Poland_CWC/Baltic_CWC/ Central_CWC, Fatyanovo) were calculated using the autosomal positions of the 1240K dataset. However, comparing very similar populations directly using *D* statistics seems to be affected by batch biases—Central_CWC comes out as significantly closer to almost all populations than Fatyanovo, while this is not the case when comparing less similar Fatyanovo and Yamnaya_Samara. Because of this, the results of *D*(Mbuti, ancient; Poland_CWC/Baltic_CWC/Central_CWC, Fatyanovo) are not discussed in the main text, but the data are included in table S19.

F_{ST}

Weir and Cockerham pairwise average F_{ST} (*89*) was calculated for the dataset used for outgroup *f*3 and *D* statistics using the autosomal positions of the HO dataset using a custom script.

qpAdm

The ADMIXTOOLS 6.0 (*87*) package programs qpWave and qpAdm were used to estimate which populations and in which proportions are suitable proxies of admixture to form the populations or individuals of this study. The autosomal positions of the 1240K dataset were used. Only samples with more than 100,000 SNPs were used in the analyses. Mota, Ust-Ishim, Kostenki14, GoyetQ116, Vestonice16, MA1, AfontovaGora3, ElMiron, Villabruna, WHG,

Downloaded from http://advances.sciencemag.org/ on January 21, 2021

EHG, CHG, Iran_N, Natufian, Levant_N, and Anatolia_N (and Volosovo in some cases indicated in table S15) were used as right populations. Yamnaya_Samara or Yamnaya_Kalmykia was used as the left population representing Steppe ancestry. Levant_N, Anatolia_N, LBK_EN, Central_MN, Globular_Amphora, Trypillia, Ukraine_Eneolithic, or Ukraine_Neolithic was used as the left population representing EF ancestry. In some cases, WHG, EHG, WesternRussiaHG, or Volosovo was used as the left population representing HG ancestry. Alternatively, one-way models between Fatyanovo, Baltic_CWC, and Central_CWC were tested. Also, PES001 was modeled as a mixture of WHG and AfontovaGora3, MA1, or CHG.

To look at sex bias, four models that were not rejected using autosomal data were also tested using the 48,284 chrX positions of the 1240K dataset. The same samples were used as in the autosomal modeling.

ChromoPainter/NNLS

To infer the admixture proportions of ancient individuals, the ChromoPainter/NNLS pipeline was applied (*28*). Because of the low coverage of the ancient data, it is not possible to infer haplotypes, and the analysis was performed in unlinked mode (option -u). The autosomal positions of the HO dataset were used. Only samples with more than 20,000 SNPs were used in the analyses. Because ChromoPainter (*90*) does not tolerate missing data, every ancient target individual was iteratively painted together with one representative individual from potential source populations as recipients. All the remaining modern individuals from the sample set used for Admixture analysis were used as donors (tables S3 and S4). Subsequently, we reconstructed the profile of each target individual as a combination of two or more ancient individuals, using the non-negative least square approach. Let **Xg** and **Yp** be vectors summarizing the proportion of DNA that source and target individuals copy from each of the modern donor groups as inferred by ChromoPainter. $\mathbf{Yp} = \beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_z X_z$ was reconstructed using a slight modification of the nnls function in R (*91*) and implemented in GlobeTrotter (*92*) under the conditions $\beta_g \geq 0$ and $\cdot\beta_g = 1$. To evaluate the fitness of the NNLS estimation, we inferred the sum of the squared residual for every tested model (*93*). Models identified as plausible with qpAdm with Yamnaya_Samara and Globular_Amphora/Trypillia as sources were used. The resulting painting profiles, which summarize the fraction of the individual's DNA inherited by each donor individual, were summed over individuals from the same population.

DATES

The time of admixture between Yamnaya and EF populations forming the Fatyanovo Culture population was estimated using the program DATES (*37*). The autosomal positions of the 1240K dataset were used.

Phenotyping

To predict eye, hair, and skin color in the ancient individuals (tables S20 to S22), the HIrisPlex-S variants from 19 genes in nine autosomes were selected (*94*–*96*), and the region to be analyzed was selected adding 2 Mb around each SNP, collapsing in the same region the variants separated by less than 5 Mb. A total of 10 regions (2 for chromosome 15 and 1 for each of the remaining autosomes) were obtained, ranging from about 6 to about 1.5 Mb. Similarly, to analyze the other phenotype-informative markers (diet, immunity, and diseases), 2 Mb around each variant was selected, and the overlapping regions were merged, for a total of 47 regions (45 regions in 17 autosomes and 2 regions on chrX). For the local imputation, we used a two-step pipeline (*97*) as follows: (i) variant calling, (ii) first imputation step using a reference panel as much similar as possible to the target samples, (iii) variant filtering, (iv) second imputation step using a larger worldwide reference panel, and (v) final variant filtering. This pipeline has been validated by randomly downsampling a high-coverage Neolithic sample (NE1) (*98*) to 0.05× and comparing the imputed variants in the low-coverage version with the called variants from the original genome. For a local imputation approach on 2 Mb, we obtained a concordance rate higher than 90% for all the variants, a figure that increased to 99% for frequent variants (MAF ≥ 0.3). The variants were called using ATLAS v0.9.0 (*99*) (task = call and method = MLE commands) (step 1) at biallelic SNPs with a MAF ≥ 0.1% in a reference panel composed of more than 2000 high-coverage Estonian genomes (EGC) (*74*). The variants were called separately for each sample and merged in one VCF file per chromosomal region. The merged VCFs were used as input for the first step of our two-step imputation pipeline [genotype likelihood update; -gl command on Beagle 4.1 (*100*)], using the EGC panel as reference (step 2). Then, the variants with a genotype probability (GP) less than 0.99 were discarded (step 3), and the missing genotype was imputed with the -gt command of Beagle 5.0 (*101*) using the large HRC as reference panel (*102*), with the exception of variants rs333 and rs2430561 [not present in the HRC (Haplotype Reference Consortium)], imputed using the 1000 Genomes as reference panel (step 4) (*103*). Last, a second GP filter was applied to keep variants with GP ≥ 0.85 (step 5). Then, the 113 phenotype-informative SNPs were extracted, recoded, and organized in tables, using VCFtools (*104*), PLINK 1.9 (http://pngu.mgh.harvard.edu/purcell/plink/) (*84*), and R (*91*) (tables S21 and S22). The HIrisPlex-S variants were uploaded on the HIrisPlex webtool (https://hirisplex.erasmusmc.nl/) to perform the pigmentation prediction, after tabulating them according to the manual of the tool. Out of 41 variants of the HIrisPlex-s system, two markers were not analyzed, namely, the rs312262906 indel and the rare (MAF = 0 in the HRC) rs201326893 SNP, because of the difficulties in the imputation of such variants.

The 28 samples analyzed here were compared with 34 ancient samples from surrounding geographical regions from literature, gathering them in seven groups according to their region and/or culture: (i) 3 Western Russian Stone Age HGs (present study); (ii) 5 Latvian Mesolithic HGs (*34*); (iii) 7 Estonian and Latvian Corded Ware Culture farmers [present study and (*27*, *34*)]; (iv) 24 Fatyanovo Culture individuals (present study); (v) 10 Estonian Bronze Age individuals (*28*); (vi) 9 Estonian and Ingrian Iron Age individuals (*28*); (vii) 4 Estonian Middle Age individuals (*28*). For each variant, an analysis of variance (ANOVA) test was performed between the seven groups, applying Bonferroni's correction by the number of tested variants to set the significance threshold (table S20). For the significant variant, a Tukey test was performed to identify the significant pairs of groups.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/7/4/eabd6535/DC1

View/request a protocol for this paper from *Bio-protocol*.

REFERENCES AND NOTES

1. J. Krause, A. W. Briggs, M. Kircher, T. Maricic, N. Zwyns, A. Derevianko, S. Pääbo, A complete mtDNA genome of an early modern human from Kostenki, Russia. *Curr. Biol.* **20**, 231–236 (2010).

Downloaded from http://advances.sciencemag.org/ on January 21, 2021

2. A. Seguin-Orlando, T. S. Korneliussen, M. Sikora, A.-S. Malaspinas, A. Manica, I. Moltke, A. Albrechtsen, A. Ko, A. Margaryan, V. Moiseyev, T. Goebel, M. Westaway, D. Lambert, V. Khartanovich, J. D. Wall, P. R. Nigst, R. A. Foley, M. M. Lahr, R. Nielsen, L. Orlando, E. Willerslev, Genomic structure in Europeans dating back at least 36,200 years. *Science* **346**, 1113–1118 (2014).
3. M. Sikora, A. Seguin-Orlando, V. C. Sousa, A. Albrechtsen, T. Korneliussen, A. Ko, S. Rasmussen, I. Dupanloup, P. R. Nigst, M. D. Bosch, G. Renaud, M. E. Allentoft, A. Margaryan, S. V. Vasilyev, E. V. Veselovskaya, S. B. Borutskaya, T. Deviese, D. Comeskey, T. Higham, A. Manica, R. Foley, D. J. Meltzer, R. Nielsen, L. Excoffier, M. M. Lahr, L. Orlando, E. Willerslev, Ancient genomes show social and reproductive behavior of early Upper Paleolithic foragers. *Science* **358**, 659–662 (2017).
4. A. Kriiska, T. Rostedt, T. Jussila, The development of the Early Mesolithic social networks during the settlement of Virgin Lands in the Eastern Baltic Sea Zone—Interpreted through comparison of two sites in Finland, in *Comparative Perspectives on Past Colonisation, Maritime Interaction and Cultural Integration*, L. Melheim, H. Glørstad, Z. Glørstad, Eds. (Equinox Publishing, 2016), pp. 19–40.
5. M. G. Zhilin, L. V. Koltsov, *Финальный палеолит лесной зоны Европы (культурное своеобразие и адаптация)* (Институт археологии Российской академии наук, 2008).
6. R. Indreko, *Die mittlere Steinzeit in Estland. Mit einer Übersicht "Über die Geologie des Kunda-Sees". Kungl. Vitterhets Historie och Antikvitets Akademiens Handlingar, 66* (1948).
7. V. Luho, *Die Suomusjärvi-Kultur. Die mittel- und spätmesolithische Zeit in Finnland. Suomen Muinaismuistoyhdistyksen aikakauskirja, 66* (1967).
8. L. V. Koltsov, M. G. Zhilin, *Мезолит Волго-Окского междуречья. Памятники бутовской культуры* (Hayka, 1999).
9. A. Vybornov, S. Kondratiev, I. Tolpygina, Chronology of Pit-Comb Ware in the Middle Volga region (Russia): 14C dates of organic substances within pottery matrix. *Est. J. Archaeol.* **22**, 83–95 (2018).
10. N. N. Gurina, D. A. Krainov, Льяловская культура, in Неолит Северной Евразии, S. V. Oshibkina, Ed. (Hayka, 1996), pp. 173–182.
11. D. A. Krainov, Волосовская культура, in Эпоха бронзы лесной полосы СССР. Археология СССР (Наука, 1987), pp. 10–28.
12. I. Olalde, S. Mallick, N. Patterson, N. Rohland, V. Villalba-Mouco, M. Silva, K. Dulias, C. J. Edwards, F. Gandini, M. Pala, P. Soares, M. Ferrando-Bernal, N. Adamski, N. Broomandkhoshbacht, O. Cheronet, B. J. Culleton, D. Fernandes, A. M. Lawson, M. Mah, J. Oppenheimer, K. Stewardson, Z. Zhang, J. M. J. Arenas, I. J. T. Moyano, D. C. Salazar-García, P. Castanyer, M. Santos, J. Tremoleda, M. Lozano, P. G. Borja, J. Fernández-Eraso, J. A. Mujika-Alustiza, C. Barroso, F. J. Bermúdez, E. V. Mínguez, J. Burch, N. Coromina, D. Vivó, A. Cebrià, J. M. Fullola, O. García-Puchol, J. I. Morales, F. X. Oms, T. Majó, J. M. Vergès, A. Díaz-Carvajal, I. Ollich-Castanyer, F. J. López-Cachero, A. M. Silva, C. Alonso-Fernández, G. D. de Castro, J. J. Echevarría, A. Moreno-Márquez, G. P. Berlanga, P. Ramos-García, J. Ramos-Muñoz, E. V. Vila, G. A. Arzo, Á. E. Arroyo, K. T. Lillios, J. Mack, J. Velasco-Vázquez, A. Waterman, L. B. de Lugo Enrich, M. B. Sánchez, B. Agustí, F. Codina, G. de Prado, A. Estalrrich, Á. F. Flores, C. Finlayson, G. Finlayson, S. Finlayson, F. Giles-Guzmán, A. Rosas, V. B. González, G. G. Atiénzar, M. S. Hernández Pérez, A. Llanos, Y. C. Marco, I. C. Beneyto, D. López-Serrano, M. S. Tormo, A. C. Valera, C. Blasco, C. Liesau, P. Ríos, J. Daura, M. J. de Pedro Michó, A. A. Diez-Castillo, R. F. Fernández, J. F. Farré, R. Garrido-Pena, V. S. Gonçalves, E. Guerra-Doce, A. M. Herrero-Corral, J. Juan-Cabanilles, D. López-Reyes, S. B. McClure, M. M. Pérez, A. O. Foix, M. S. Borràs, A. C. Sousa, J. M. V. Encinas, D. J. Kennett, M. B. Richards, K. W. Alt, W. Haak, R. Pinhasi, C. Lalueza-Fox, D. Reich, The genomic history of the Iberian Peninsula over the past 8000 years. *Science* **363**, 1230–1234 (2019).
13. I. Mathieson, S. Alpaslan-Roodenberg, C. Posth, A. Szécsényi-Nagy, N. Rohland, S. Mallick, I. Olalde, N. Broomandkhoshbacht, F. Candilio, O. Cheronet, D. Fernandes, M. Ferry, B. Gamarra, G. G. Fortes, W. Haak, E. Harney, E. Jones, D. Keating, B. Krause-Kyora, I. Kucukkalipci, M. Michel, A. Mittnik, K. Nägele, M. Novak, J. Oppenheimer, N. Patterson, S. Pfrengle, K. Sirak, K. Stewardson, S. Vai, S. Alexandrov, K. W. Alt, R. Andreescu, D. Antonović, A. Ash, N. Atanassova, K. Bacvarov, M. B. Gusztáv, H. Bocherens, M. Bolus, A. Boroneanţ, Y. Boyadzhiev, A. Budnik, J. Burmaz, S. Chohadzhiev, N. J. Conard, R. Cottiaux, M. Čuka, C. Cupillard, D. G. Drucker, N. Elenski, M. Francken, B. Galabova, G. Ganetsovski, B. Gély, T. Hajdu, V. Handzhyiska, K. Harvati, T. Higham, S. Iliev, I. Janković, I. Karavanić, D. J. Kennett, D. Komšo, A. Kozak, D. Labuda, M. Lari, C. Lazar, M. Leppek, K. Leshtakov, D. L. Vetro, D. Los, I. Lozanov, M. Malina, F. Martini, K. M. Sweeney, H. Meller, M. Menđušić, P. Mirea, V. Moiseyev, V. Petrova, T. D. Price, A. Simalcsik, L. Sineo, M. Šlaus, V. Slavchev, P. Stanev, A. Starović, T. Szeniczey, S. Talamo, M. Teschler-Nicola, C. Thevenet, I. Valchev, F. Valentin, S. Vasilyev, F. Veljanovska, S. Venelinova, E. Veselovskaya, B. Viola, C. Virag, J. Zaninović, S. Zäuner, P. W. Stockhammer, G. Catalano, R. Krauß, D. Caramelli, G. Zariņa, B. Gaydarska, M. Lillie, A. G. Nikitin, I. Potekhina, A. Papathanasiou, D. Borić, C. Bonsall, J. Krause, R. Pinhasi, D. Reich, The genomic history of southeastern Europe. *Nature* **555**, 197–203 (2018).
14. A. Mittnik, C.-C. Wang, S. Pfrengle, M. Daubaras, G. Zariņa, F. Hallgren, R. Allmäe, V. Khartanovich, V. Moiseyev, M. Tõrv, A. Furtwängler, A. A. Valtueña, M. Feldman, C. Economou, M. Oinonen, A. Vasks, E. Balanovska, D. Reich, R. Jankauskas, W. Haak, S. Schiffels, J. Krause, The genetic prehistory of the Baltic Sea region. *Nat. Commun.* **9**, 442 (2018).
15. W. Haak, I. Lazaridis, N. Patterson, N. Rohland, S. Mallick, B. Llamas, G. Brandt, S. Nordenfelt, E. Harney, K. Stewardson, Q. Fu, A. Mittnik, E. Bánffy, C. Economou, M. Francken, S. Friederich, R. G. Pena, F. Hallgren, V. Khartanovich, A. Khokhlov, M. Kunst, P. Kuznetsov, H. Meller, O. Mochalov, V. Moiseyev, N. Nicklisch, S. L. Pichler, R. Risch, M. A. Rojo Guerra, C. Roth, A. Szécsényi-Nagy, J. Wahl, M. Meyer, J. Krause, D. Brown, D. Anthony, A. Cooper, K. W. Alt, D. Reich, Massive migration from the steppe was a source for Indo-European languages in Europe. *Nature* **522**, 207–211 (2015).
16. I. Mathieson, I. Lazaridis, N. Rohland, S. Mallick, N. Patterson, S. A. Roodenberg, E. Harney, K. Stewardson, D. Fernandes, M. Novak, K. Sirak, C. Gamba, E. R. Jones, B. Llamas, S. Dryomov, J. Pickrell, J. L. Arsuaga, J. M. B. de Castro, E. Carbonell, F. Gerritsen, A. Khokhlov, P. Kuznetsov, M. Lozano, H. Meller, O. Mochalov, V. Moiseyev, M. A. Rojo Guerra, J. Roodenberg, J. M. Vergès, J. Krause, A. Cooper, K. W. Alt, D. Brown, D. Anthony, C. Lalueza-Fox, W. Haak, R. Pinhasi, D. Reich, Genome-wide patterns of selection in 230 ancient Eurasians. *Nature* **528**, 499–503 (2015).
17. P. de Barros Damgaard, R. Martiniano, J. Kamm, J. V. Moreno-Mayar, G. Kroonen, M. Peyrot, G. Barjamovic, S. Rasmussen, C. Zacho, N. Baimukhanov, V. Zaibert, V. Merz, A. Biddanda, I. Merz, V. Loman, V. Evdokimov, E. Usmanova, B. Hemphill, A. Seguin-Orlando, F. E. Yediay, I. Ullah, K.-G. Sjögren, K. H. Iversen, J. Choin, C. de la Fuente, M. Ilardo, H. Schroeder, V. Moiseyev, A. Gromov, A. Polyakov, S. Omura, S. Y. Senyurt, H. Ahmad, C. M. Kenzie, A. Margaryan, A. Hameed, A. Samad, N. Gul, M. H. Khokhar, O. I. Goriunova, V. I. Bazaliiskii, J. Novembre, A. W. Weber, L. Orlando, M. E. Allentoft, R. Nielsen, K. Kristiansen, M. Sikora, A. K. Outram, R. Durbin, E. Willerslev, The first horse herders and the impact of early Bronze Age steppe expansions into Asia. *Science* **360**, eaar7711 (2018).
18. M. E. Allentoft, M. Sikora, K.-G. Sjögren, S. Rasmussen, M. Rasmussen, J. Stenderup, P. B. Damgaard, H. Schroeder, T. Ahlström, L. Vinner, A.-S. Malaspinas, A. Margaryan, T. Higham, D. Chivall, N. Lynnerup, L. Harvig, J. Baron, P. D. Casa, P. Dąbrowski, P. R. Duffy, A. V. Ebel, A. Epimakhov, K. Frei, M. Furmanek, T. Gralak, A. Gromov, S. Gronkiewicz, G. Grupe, T. Hajdu, R. Jarysz, V. Khartanovich, A. Khokhlov, V. Kiss, J. Kolář, A. Kriiska, I. Lasak, C. Longhi, G. M. Glynn, A. Merkevicius, I. Merkyte, M. Metspalu, R. Mkrtchyan, V. Moiseyev, L. Paja, G. Pálfi, D. Pokutta, Ł. Pospieszny, T. D. Price, L. Saag, M. Sablin, N. Shishlina, V. Smrčka, V. I. Soenov, V. Szeverényi, G. Tóth, S. V. Trifanova, L. Varul, M. Vicze, L. Yepiskoposyan, V. Zhitenev, L. Orlando, T. Sicheritz-Pontén, S. Brunak, R. Nielsen, K. Kristiansen, E. Willerslev, Population genomics of Bronze Age Eurasia. *Nature* **522**, 167–172 (2015).
19. P. Włodarczak, Radiocarbon and dendrochronological dates of the Corded Ware culture. *Radiocarbon* **51**, 737–749 (2009).
20. F. Racimo, J. Woodbridge, R. M. Fyfe, M. Sikora, K.-G. Sjögren, K. Kristiansen, M. V. Linden, The spatiotemporal spread of human migrations during the European Holocene. *Proc. Natl. Acad. Sci.* **117**, 8989–9000 (2020).
21. D. A. Krainov, Древнейшая история Волго-Окского междуречья. Фатьяновская культура. (Prehistory of the Volga-Oka interfluve. The Fatyanovo culture) (1972).
22. J. Kruk, S. Milisauskas, *Rozkwit i upadek społeczeństw rolniczych Neolitu* (Instytut Archeologii i Etnologii Polskiej Akademii Nauk, 1999).
23. D. A. Krainov, Фатьяновская культура, in *Эпоха бронзы лесной полосы СССР. Археология СССР* (Наука, 1987), pp. 58–76.
24. N. A. Krenke, Радиоуглеродная хронология фатьяновской культуры. *Российская Археология.* **3**, 110–116 (2019).
25. O. N. Bader, A. H. Khalikov, Балановская культура, in Эпоха бронзы лесной полосы СССР. Археология СССР (Наука, 1987), pp. 76–84.
26. I. Lazaridis, D. Nadel, G. Rollefson, D. C. Merrett, N. Rohland, S. Mallick, D. Fernandes, M. Novak, B. Gamarra, K. Sirak, S. Connell, K. Stewardson, E. Harney, Q. Fu, G. Gonzalez-Fortes, E. R. Jones, S. A. Roodenberg, G. Lengyel, F. Bocquentin, B. Gasparian, J. M. Monge, M. Gregg, V. Eshed, A.-S. Mizrahi, C. Meiklejohn, F. Gerritsen, L. Bejenaru, M. Blüher, A. Campbell, G. Cavalleri, D. Comas, P. Froguel, E. Gilbert, S. M. Kerr, P. Kovacs, J. Krause, D. M. Gettigan, M. Merrigan, D. A. Merriwether, S. O'Reilly, M. B. Richards, O. Semino, M. Shamoon-Pour, G. Stefanescu, M. Stumvoll, A. Tönjes, A. Torroni, J. F. Wilson, L. Yengo, N. A. Hovhannisyan, N. Patterson, R. Pinhasi, D. Reich, Genomic insights into the origin of farming in the ancient Near East. *Nature* **536**, 419–424 (2016).
27. L. Saag, L. Varul, C. L. Scheib, J. Stenderup, M. E. Allentoft, L. Saag, L. Pagani, M. Reidla, K. Tambets, E. Metspalu, A. Kriiska, E. Willerslev, T. Kivisild, M. Metspalu, Extensive farming in Estonia started through a sex-biased migration from the Steppe. *Curr. Biol.* **27**, 2185–2193.e6 (2017).
28. L. Saag, M. Laneman, L. Varul, M. Malve, H. Valk, M. A. Razzak, I. G. Shirobokov, V. I. Khartanovich, E. R. Mikhaylova, A. Kushniarevich, C. L. Scheib, A. Solnik, T. Reisberg, J. Parik, L. Saag, E. Metspalu, S. Rootsi, F. Montinaro, M. Remm, R. Mägi, E. D'Atanasio, E. R. Crema, D. Díez-del-Molino, M. G. Thomas, A. Kriiska, T. Kivisild, R. Villems, V. Lang, M. Metspalu, K. Tambets, The arrival of siberian ancestry connecting the Eastern Baltic to Uralic Speakers further East. *Curr. Biol.* **29**, 1701–1711.e16 (2019).
29. S. Mathieson, I. Mathieson, *FADS1* and the timing of human adaptation to agriculture. *Mol. Biol. Evol.* **35**, 2957–2970 (2018).

Downloaded from http://advances.sciencemag.org/ on January 21, 2021

30. A. Goldberg, T. Günther, N. A. Rosenberg, M. Jakobsson, Ancient X chromosomes reveal contrasting sex bias in Neolithic and Bronze Age Eurasian migrations. *Proc. Natl. Acad. Sci. U.S.A.* **114**, 2657–2662 (2017).
31. I. Lazaridis, D. Reich, Failure to replicate a genetic signal for sex bias in the steppe migration into central Europe. *Proc. Natl. Acad. Sci. U.S.A.* **114**, E3873–E3874 (2017).
32. A. Goldberg, T. Günther, N. A. Rosenberg, M. Jakobsson, Reply to Lazaridis and Reich: Robust model-based inference of male-biased admixture during Bronze Age migration from the Pontic-Caspian Steppe. *Proc. Natl. Acad. Sci. U.S.A.* **114**, E3875–E3877 (2017).
33. J. Meadows, V. Bērziņš, U. Brinker, H. Lübke, U. Schmölcke, A. Staude, I. Zagorska, G. Zariņa, Dietary freshwater reservoir effects and the radiocarbon ages of prehistoric human bones from Zvejnieki, Latvia. *J. Archaeol. Sci. Rep.* **6**, 678–689 (2016).
34. E. R. Jones, G. Zarina, V. Moiseyev, E. Lightfoot, P. R. Nigst, A. Manica, R. Pinhasi, D. G. Bradley, The Neolithic transition in the Baltic was not driven by admixture with early European farmers. *Curr. Biol.* **27**, 576–582 (2017).
35. D. M. Behar, M. van Oven, S. Rosset, M. Metspalu, E.-L. Loogväli, N. M. Silva, T. Kivisild, A. Torroni, R. Villems, A "Copernican" reassessment of the human mitochondrial DNA tree from its Root. *Am. J. Hum. Genet.* **90**, 675–684 (2012).
36. M. Karmin, L. Saag, M. Vicente, M. A. Wilson Sayres, M. Järve, U. G. Talas, S. Rootsi, A.-M. Ilumäe, R. Mägi, M. Mitt, L. Pagani, T. Puurand, Z. Faltyskova, F. Clemente, A. Cardona, E. Metspalu, H. Sahakyan, B. Yunusbayev, G. Hudjashov, M. De Giorgio, E.-L. Loogväli, C. Eichstaedt, M. Eelmets, G. Chaubey, K. Tambets, S. Litvinov, M. Mormina, Y. Xue, Q. Ayub, G. Zoraqi, T. S. Korneliussen, F. Akhatova, J. Lachance, S. Tishkoff, K. Momynaliev, F.-X. Ricaut, P. Kusuma, H. Razafindrazaka, D. Pierron, M. P. Cox, G. N. N. Sultana, R. Willerslev, C. Muller, M. Westaway, D. Lambert, V. Skaro, L. Kovačevic, S. Turdikulova, D. Dalimova, R. Khusainova, N. Trofimova, V. Akhmetova, I. Khidiyatova, D. V. Lichman, J. Isakova, E. Pocheshkhova, Z. Sabitov, N. A. Barashkov, P. Nymadawa, E. Mihailov, J. W. T. Seng, I. Evseeva, A. B. Migliano, S. Abdullah, G. Andriadze, D. Primorac, L. Atramentova, O. Utevska, L. Yepiskoposyan, D. Marjanovic, A. Kushniarevich, D. M. Behar, C. Gilissen, L. Vissers, J. A. Veltman, E. Balanovska, M. Derenko, B. Malyarchuk, A. Metspalu, S. Fedorova, A. Eriksson, A. Manica, F. L. Mendez, T. M. Karafet, K. R. Veeramah, N. Bradman, M. F. Hammer, L. P. Osipova, O. Balanovsky, E. K. Khusnutdinova, K. Johnsen, M. Remm, M. G. Thomas, C. Tyler-Smith, P. A. Underhill, E. Willerslev, R. Nielsen, M. Metspalu, R. Villems, T. Kivisild, A recent bottleneck of Y chromosome diversity coincides with a global change in culture. *Genome Res.* **25**, 459–466 (2015).
37. V. M. Narasimhan, N. Patterson, P. Moorjani, N. Rohland, R. Bernardos, S. Mallick, I. Lazaridis, N. Nakatsuka, I. Olalde, M. Lipson, A. M. Kim, L. M. Olivieri, A. Coppa, M. Vidale, J. Mallory, V. Moiseyev, E. Kitov, J. Monge, N. Adamski, N. Alex, N. Broomandkhoshbacht, F. Candilio, K. Callan, O. Cheronet, B. J. Culleton, M. Ferry, D. Fernandes, S. Freilich, B. Gamarra, D. Gaudio, M. Hajdinjak, É. Harney, T. K. Harper, D. Keating, A. M. Lawson, M. Mah, K. Mandl, M. Michel, M. Novak, J. Oppenheimer, N. Rai, K. Sirak, V. Slon, K. Stewardson, F. Zalzala, Z. Zhang, G. Akhatov, A. N. Bagashev, A. Bagnera, B. Baitanayev, J. Bendezu-Sarmiento, A. A. Bissembaev, G. L. Bonora, T. T. Chargynov, T. Chikisheva, P. K. Dashkovskiy, A. Derevianko, M. Dobeš, K. Douka, N. Dubova, M. N. Duisengali, D. Enshin, A. Epimakhov, A. V. Fribus, D. Fuller, A. Goryachev, A. Gromov, S. P. Grushin, B. Hanks, M. Judd, E. Kazizov, A. Khokhlov, A. P. Krygin, E. Kupriyanova, P. Kuznetsov, D. Luiselli, F. Maksudov, A. M. Mamedov, T. B. Mamirov, C. Meiklejohn, D. C. Merrett, R. Micheli, O. Mochalov, S. Mustafokulov, A. Nayak, D. Pettener, R. Potts, D. Razhev, M. Rykun, S. Sarno, T. M. Savenkova, K. Sikhymbaeva, S. M. Slepchenko, O. A. Soltobaev, N. Stepanova, S. Svyatko, K. Tabaldiev, M. Teschler-Nicola, A. A. Tishkin, V. V. Tkachev, S. Vasilyev, P. Velemínský, D. Voyakin, A. Yermolayeva, M. Zahir, V. S. Zubkov, A. Zubova, V. S. Shinde, C. Lalueza-Fox, M. Meyer, D. Anthony, N. Boivin, K. Thangaraj, D. J. Kennett, M. Frachetti, R. Pinhasi, D. Reich, The formation of human populations in South and Central Asia. *Science* **365**, eaat7487 (2019).
38. A. Mittnik, K. Massy, C. Knipper, F. Wittenborn, R. Friedrich, S. Pfrengle, M. Burri, N. Carlichi-Witjes, H. Deeg, A. Furtwängler, M. Harbeck, K. von Heyking, C. Kociumaka, I. Kucukkalipci, S. Lindauer, S. Metz, A. Staskiewicz, A. Thiel, J. Wahl, W. Haak, E. Pernicka, S. Schiffels, P. W. Stockhammer, J. Krause, Kinship-based social inequality in Bronze Age Europe. *Science* **366**, 731–734 (2019).
39. A. Linderholm, G. M. Kılınç, A. Szczepanek, P. Włodarczak, P. Jarosz, Z. Belka, J. Dopieralska, K. Werens, J. Górski, M. Mazurek, M. Hozer, M. Rybicka, M. Ostrowski, J. Bagińska, W. Koman, R. Rodríguez-Varela, J. Storå, A. Götherström, M. Krzewińska, Corded Ware cultural complexity uncovered using genomic and isotopic analysis from south-eastern Poland. *Sci. Rep.* **10**, 6885 (2020).
40. W. Haak, P. Forster, B. Bramanti, S. Matsumura, G. Brandt, M. Tänzer, R. Villems, C. Renfrew, D. Gronenborn, K. W. Alt, J. Burger, Ancient DNA from the first European farmers in 7500-year-old Neolithic sites. *Science* **310**, 1016–1018 (2005).
41. J. M. Monroy Kuhn, M. Jakobsson, T. Günther, Estimating genetic kin relationships in prehistoric populations. *PLOS ONE* **13**, e0195491 (2018).
42. A. V. Volokitin, Мезолитические стоянки Парч 1 и Парч 2 на Вычегде (Коми научный центр Уральского отделения Российской академии наук, 2006).
43. T. Jussila, A. Kriiska, T. Rostedt, Saarenoja 2—An Early Mesolithic Site in South-Eastern Finland: Preliminary Results and Interpretations of Studies Conducted in 2000 and 2008–10, in *Fennoscandia archaeologica, 2012. XXIX.* (2012), pp. 3–27.
44. P. Pesonen, E. Hertell, L. Simponen, K. Mannermaa, M. A. Manninen, T. Rostedt, N. Taipale, M. Tallavaara, Postglacial pioneer settlement in the Lake Sarvinki area, eastern Finland, in *Lateglacial and Postglacial Pioneers in Northern Europe. British Archaeological Reports, International Series*, F. Riede, M. Tallavaara, Eds. (Archaeopress, 2014), vol. 2599, pp. 174–190.
45. M. G. Zhilin, Early Mesolithic communications networks in the East European forest zone, in *Mesolithic on the Move: Papers Presented at the Sixth International Conference on the Mesolithic in Europe, Stockholm*, L. Larsson, H. Kindgren, K. Knutsson, D. Loeffler, A. Akerlund, Eds. (Oxbow Books, 2003), pp. 688–693.
46. S. V. Oshibkina, Мезолитическая культура веретье. *Хронология и периодизация. Российская Археология*. **1**, 100–110 (2004).
47. L. L. Zaliznyak, Tanged point cultures in the Western Part of Eastern Europe, in *Tanged Points Cultures in Europe: Read at the International Archaeological Symposium, Lublin, September, 13–16, 1993. Lubelskie Materiały Archeologiczne XIII*, S. K. Kozłowski, J. Gurba, L.L. Zaliznyak, Eds. (Marie Curie-Skłodowska University Press, 1999), pp. 202–218.
48. V. V. Sidorov, A. V. Engovatova, Ханевский могильник и древнейшие памятники фатьяновской культуры, in *Археологические памятники Волго-Клязьминского междуречья, 7* (1992), pp. 28–37.
49. I. I. Artemenko, Культуры раннего бронзового века южной полосы лесов европейской части СССР, in *Эпоха бронзы лесной полосы СССР. Археология СССР* (Наука, 1987), pp. 35–51.
50. M. Kryvaltsevich, N. Kovalyukh, Radiocarbon dating of the Middle Dnieper culture from Belarus, in *The Foundations of Radiocarbon Chronology of Cultures between the Vistula and Dnieper. Baltic-Pontic Studies*, A. Kośko, Ed. (1999), vol. 7, pp. 151–162.
51. M. Järve, L. Saag, C. L. Scheib, A. K. Pathak, F. Montinaro, L. Pagani, R. Flores, M. Guellil, L. Saag, K. Tambets, A. Kushniarevich, A. Solnik, L. Varul, S. Zadnikov, O. Petrauskas, M. Avramenko, B. Magomedov, S. Didenko, G. Toshev, I. Bruyako, D. Grechko, V. Okatenko, K. Gorbenko, O. Smyrnov, A. Heiko, R. Reida, S. Sapiehin, S. Sirotin, A. Tairov, A. Beisenov, M. Starodubtsev, V. Vasilev, A. Nechvaloda, B. Atabiev, S. Litvinov, N. Ekomasova, M. Dzhaubermezov, S. Voroniatov, O. Utevska, I. Shramko, E. Khusnutdinova, M. Metspalu, N. Savelev, A. Kriiska, T. Kivisild, R. Villems, Shifts in the genetic landscape of the western eurasian steppe associated with the beginning and end of the scythian dominance. *Curr. Biol.* **29**, 2430–2441.e10 (2019).
52. G. Motuzaitė Matuzevičiūtė, S. Telizhenko, The first farmers of ukraine: An Archaeobotanical investigation and AMS dating of wheat grains from the ratniv-2 site. *Archaeol. Litu.* **17**, 100–111 (2017).
53. B. Preda-Bălănică, A. Frînculeas, V. Heyd, Review of the current state of the art in assessing Yamnaya migrations, The Yamnaya Impact North of the Lower Danube, A Tale of Newcomers and Locals. *Bull. Soc. Préhist. Fr.* **117**, 85–101 (2020).
54. A. Kriiska, K. Nordqvist, D. V. Gerasimov, S. Sandel, Preliminary results of the research at Corded Ware sites in the Narva–Luga interfluve, Estonian–Russian border area in 2008–2014. *Archeol. Fieldwork Est.* **2014**, 39–50 (2015).
55. P. Pesonen, Å. M. Larsson, E. Holmqvist-Sipilä, The chronology of Corded Ware culture in Finland – reviewing new data. *Fennosc. Archaeol.* **36**, 130–141 (2020).
56. Å. M. Larsson, *Making and Breaking Bodies and Pots, Material and Ritual Practices in Sweden in the Third Millennium BC* (Department of Archaeology and Ancient History, Uppsala University, 2009).
57. P. N. Tretyakov, Финно-угры, балты и славяне на Днепре и Волге (Наука, 1966).
58. P. M. Dolukhanov, *The Early Slavs: Eastern Europe from the Initial Settlement to the Kievan Rus* (Longman, 1996).
59. Y. Itan, A. Powell, M. A. Beaumont, J. Burger, M. G. Thomas, The origins of lactase persistence in Europe. *PLOS Comput. Biol.* **5**, e1000491 (2009).
60. J. Burger, V. Link, J. Blöcher, A. Schulz, C. Sell, Z. Pochon, Y. Diekmann, A. Žegarac, Z. Hofmanová, L. Winkelbach, C. S. Reyna-Blanco, V. Bieker, J. Orschiedt, U. Brinker, A. Scheu, C. Leuenberger, T. S. Bertino, R. Bollongino, G. Lidke, S. Stefanović, D. Jantzen, E. Kaiser, T. Terberger, M. G. Thomas, K. R. Veeramah, D. Wegmann, Low prevalence of lactase persistence in bronze age europe indicates ongoing strong selection over the last 3,000 years. *Curr. Biol.* **30**, 4307–4315.e13 (2020).
61. C. Jeong, S. Wilkin, T. Amgalantugs, A. S. Bouwman, W. T. T. Taylor, R. W. Hagan, S. Bromage, S. Tsolmon, C. Trachsel, J. Grossmann, J. Littleton, C. A. Makarewicz, J. Krigbaum, M. Burri, A. Scott, G. Davaasambuu, J. Wright, F. Irmer, E. Myagmar, N. Boivin, M. Robbeets, F. J. Rühli, J. Krause, B. Frohlich, J. Hendy, C. Warinner, Bronze Age population dynamics and the rise of dairy pastoralism on the eastern Eurasian steppe. *Proc. Natl. Acad. Sci. U.S.A.* **115**, E11248–E11255 (2018).
62. P. B. Damgaard, A. Margaryan, H. Schroeder, L. Orlando, E. Willerslev, M. E. Allentoft, Improving access to endogenous DNA in ancient bones and teeth. *Sci. Rep.* **5**, 11184 (2015).
63. M. Meyer, M. Kircher, Illumina sequencing library preparation for highly multiplexed target capture and sequencing. *Cold Spring Harb. Protoc.* **2010**, pdb.prot5448 (2010).

Downloaded from http://advances.sciencemag.org/ on January 21, 2021

64. L. Orlando, A. Ginolhac, G. Zhang, D. Froese, A. Albrechtsen, M. Stiller, M. Schubert, E. Cappellini, B. Petersen, I. Moltke, P. L. F. Johnson, M. Fumagalli, J. T. Vilstrup, M. Raghavan, T. Korneliussen, A.-S. Malaspinas, J. Vogt, D. Szklarczyk, C. D. Kelstrup, J. Vinther, A. Dolocan, J. Stenderup, A. M. V. Velazquez, J. Cahill, M. Rasmussen, X. Wang, J. Min, G. D. Zazula, A. Seguin-Orlando, C. Mortensen, K. Magnussen, J. F. Thompson, J. Weinstock, K. Gregersen, K. H. Røed, V. Eisenmann, C. J. Rubin, D. C. Miller, D. F. Antczak, M. F. Bertelsen, S. Brunak, K. A. S. Al-Rasheid, O. Ryder, L. Andersson, J. Mundy, A. Krogh, M. T. P. Gilbert, K. Kjær, T. Sicheritz-Ponten, L. J. Jensen, J. V. Olsen, M. Hofreiter, R. Nielsen, B. Shapiro, J. Wang, E. Willerslev, Recalibrating *Equus* evolution using the genome sequence of an early Middle Pleistocene horse. *Nature* **499**, 74–78 (2013).
65. A.-S. Malaspinas, O. Lao, H. Schroeder, M. Rasmussen, M. Raghavan, I. Moltke, P. F. Campos, F. S. Sagredo, S. Rasmussen, V. F. Gonçalves, A. Albrechtsen, M. E. Allentoft, P. L. F. Johnson, M. Li, S. Reis, D. V. Bernardo, M. De Giorgio, A. T. Duggan, M. Bastos, Y. Wang, J. Stenderup, J. V. Moreno-Mayar, S. Brunak, T. Sicheritz-Ponten, E. Hodges, G. J. Hannon, L. Orlando, T. D. Price, J. D. Jensen, R. Nielsen, J. Heinemeier, J. Olsen, C. Rodrigues-Carvalho, M. M. Lahr, W. A. Neves, M. Kayser, T. Higham, M. Stoneking, S. D. J. Pena, E. Willerslev, Two ancient human genomes reveal Polynesian ancestry among the indigenous Botocudos of Brazil. *Curr. Biol.* **24**, R1035–R1037 (2014).
66. M. Martin, Cutadapt removes adapter sequences from high-throughput sequencing reads. *EMBnet.journal.* **17**, 10–12 (2011).
67. H. Li, R. Durbin, Fast and accurate short read alignment with Burrows-Wheeler transform. *Bioinforma. Oxf. Engl.* **25**, 1754–1760 (2009).
68. H. Li, B. Handsaker, A. Wysoker, T. Fennell, J. Ruan, N. Homer, G. Marth, G. Abecasis, R. Durbin, 1000 Genome Project Data Processing Subgroup, The Sequence Alignment/Map format and SAMtools. *Bioinforma. Oxf. Engl.* **25**, 2078–2079 (2009).
69. A. McKenna, M. Hanna, E. Banks, A. Sivachenko, K. Cibulskis, A. Kernytsky, K. Garimella, D. Altshuler, S. Gabriel, M. Daly, M. A. DePristo, The Genome Analysis Toolkit: A MapReduce framework for analyzing next-generation DNA sequencing data. *Genome Res.* **20**, 1297–1303 (2010).
70. H. Jónsson, A. Ginolhac, M. Schubert, P. L. F. Johnson, L. Orlando, mapDamage2.0: Fast approximate Bayesian estimates of ancient DNA damage parameters. *Bioinforma. Oxf. Engl.* **29**, 1682–1684 (2013).
71. Q. Fu, A. Mittnik, P. L. F. Johnson, K. Bos, M. Lari, R. Bollongino, C. Sun, L. Giemsch, R. Schmitz, J. Burger, A. M. Ronchitelli, F. Martini, R. G. Cremonesi, J. Svoboda, P. Bauer, D. Caramelli, S. Castellano, D. Reich, S. Pääbo, J. Krause, A revised timescale for human evolution based on ancient mitochondrial genomes. *Curr. Biol.* **23**, 553–559 (2013).
72. M. Rasmussen, X. Guo, Y. Wang, K. E. Lohmueller, S. Rasmussen, A. Albrechtsen, L. Skotte, S. Lindgreen, M. Metspalu, T. Jombart, T. Kivisild, W. Zhai, A. Eriksson, A. Manica, L. Orlando, F. M. De La Vega, S. Tridico, E. Metspalu, K. Nielsen, M. C. Ávila-Arcos, J. V. Moreno-Mayar, C. Muller, J. Dortch, M. T. P. Gilbert, O. Lund, A. Wesolowska, M. Karmin, L. A. Weinert, B. Wang, J. Li, S. Tai, F. Xiao, T. Hanihara, G. van Driem, A. R. Jha, F.-X. Ricaut, P. de Knijff, A. B. Migliano, I. G. Romero, K. Kristiansen, D. M. Lambert, S. Brunak, P. Forster, B. Brinkmann, O. Nehlich, M. Bunce, M. Richards, R. Gupta, C. D. Bustamante, A. Krogh, R. A. Foley, M. M. Lahr, F. Balloux, T. Sicheritz-Pontén, R. Villems, R. Nielsen, J. Wang, E. Willerslev, An Aboriginal Australian genome reveals separate human dispersals into Asia. *Science* **334**, 94–98 (2011).
73. T. S. Korneliussen, A. Albrechtsen, R. Nielsen, ANGSD: Analysis of next generation sequencing data. *BMC Bioinformatics* **15**, 356 (2014).
74. V. Pankratov, F. Montinaro, A. Kushniarevich, G. Hudjashov, F. Jay, L. Saag, R. Flores, D. Marnetto, M. Seppel, M. Kals, U. Võsa, C. Taccioli, M. Möls, L. Milani, A. Aasa, D. J. Lawson, T. Esko, R. Mägi, L. Pagani, A. Metspalu, M. Metspalu, Differences in local population history at the finest level: The case of the Estonian population. *Eur. J. Hum. Genet.* **58**, 1580–1591 (2020).
75. P. Skoglund, J. Storå, A. Götherström, M. Jakobsson, Accurate sex identification of ancient human remains using DNA shotgun sequencing. *J. Archaeol. Sci.* **40**, 4477–4482 (2013).
76. H. Li, A statistical framework for SNP calling, mutation discovery, association mapping and population genetical parameter estimation from sequencing data. *Bioinformatics* **27**, 2987–2993 (2011).
77. H. Weissensteiner, D. Pacher, A. Kloss-Brandstätter, L. Forer, G. Specht, H.-J. Bandelt, F. Kronenberg, A. Salas, S. Schönherr, HaploGrep 2: Mitochondrial haplogroup classification in the era of high-throughput sequencing. *Nucleic Acids Res.* **44**, W58–W63 (2016).
78. M. van Oven, M. Kayser, Updated comprehensive phylogenetic tree of global human mitochondrial DNA variation. *Hum. Mutat.* **30**, E386–E394 (2009).
79. G. D. Poznik, Y. Xue, F. L. Mendez, T. F. Willems, A. Massaia, M. A. W. Sayres, Q. Ayub, S. A. McCarthy, A. Narechania, S. Kashin, Y. Chen, R. Banerjee, J. L. Rodriguez-Flores, M. Cerezo, H. Shao, M. Gymrek, A. Malhotra, S. Louzada, R. Desalle, G. R. S. Ritchie, E. Cerveira, T. W. Fitzgerald, E. Garrison, A. Marcketta, D. Mittelman, M. Romanovitch, C. Zhang, X. Zheng-Bradley, G. R. Abecasis, S. A. M. Carroll, P. Flicek, P. A. Underhill, L. Coin, D. R. Zerbino, F. Yang, C. Lee, L. Clarke, A. Auton, Y. Erlich, R. E. Handsaker; The Genomes Project Consortium, C. D. Bustamante, C. Tyler-Smith, Punctuated bursts in human male demography inferred from 1,244 worldwide Y-chromosome sequences. *Nat. Genet.* **48**, 593–599 (2016).
80. ISOGG 2019 Y-DNA Haplogroup Tree; https://isogg.org/tree/.
81. YFull | Analysis and comparing your NextGen Y-Chr sequencing data; www.yfull.com/.
82. M. Mitt, M. Kals, K. Pärn, S. B. Gabriel, E. S. Lander, A. Palotie, S. Ripatti, A. P. Morris, A. Metspalu, T. Esko, R. Mägi, P. Palta, Improved imputation accuracy of rare and low-frequency variants using population-specific high-coverage WGS-based imputation reference panel. *Eur. J. Hum. Genet.* **25**, 869–876 (2017).
83. A. R. Quinlan, BEDTools: The Swiss-army tool for genome feature analysis. *Curr. Protoc. Bioinformatics* **47**, 11.12.1–11.12.34 (2014).
84. S. Purcell, B. Neale, K. Todd-Brown, L. Thomas, M. A. R. Ferreira, D. Bender, J. Maller, P. Sklar, P. I. W. de Bakker, M. J. Daly, P. C. Sham, PLINK: A tool set for whole-genome association and population-based linkage analyses. *Am. J. Hum. Genet.* **81**, 559–575 (2007).
85. N. Patterson, A. L. Price, D. Reich, Population structure and eigenanalysis. *PLOS Genet.* **2**, e190 (2006).
86. D. H. Alexander, J. Novembre, K. Lange, Fast model-based estimation of ancestry in unrelated individuals. *Genome Res.* **19**, 1655–1664 (2009).
87. N. Patterson, P. Moorjani, Y. Luo, S. Mallick, N. Rohland, Y. Zhan, T. Genschoreck, T. Webster, D. Reich, Ancient admixture in human history. *Genetics* **192**, 1065–1093 (2012).
88. S. Mallick, H. Li, M. Lipson, I. Mathieson, M. Gymrek, F. Racimo, M. Zhao, N. Chennagiri, S. Nordenfelt, A. Tandon, P. Skoglund, I. Lazaridis, S. Sankararaman, Q. Fu, N. Rohland, G. Renaud, Y. Erlich, T. Willems, C. Gallo, J. P. Spence, Y. S. Song, G. Poletti, F. Balloux, G. van Driem, P. de Knijff, I. G. Romero, A. R. Jha, D. M. Behar, C. M. Bravi, C. Capelli, T. Hervig, A. Moreno-Estrada, O. L. Posukh, E. Balanovska, O. Balanovsky, S. Karachanak-Yankova, H. Sahakyan, D. Toncheva, L. Yepiskoposyan, C. Tyler-Smith, Y. Xue, M. S. Abdullah, A. Ruiz-Linares, C. M. Beall, A. D. Rienzo, C. Jeong, E. B. Starikovskaya, E. Metspalu, J. Parik, R. Villems, B. M. Henn, U. Hodoglugil, R. Mahley, A. Sajantila, G. Stamatoyannopoulos, J. T. S. Wee, R. Khusainova, E. Khusnutdinova, S. Litvinov, G. Ayodo, D. Comas, M. F. Hammer, T. Kivisild, W. Klitz, C. A. Winkler, D. Labuda, M. Bamshad, L. B. Jorde, S. A. Tishkoff, W. S. Watkins, M. Metspalu, S. Dryomov, R. Sukernik, L. Singh, K. Thangaraj, S. Pääbo, J. Kelso, N. Patterson, D. Reich, The Simons Genome Diversity Project: 300 genomes from 142 diverse populations. *Nature* **538**, 201–206 (2016).
89. B. S. Weir, C. C. Cockerham, Estimating F-statistics for the analysis of population structure. *Evolution* **38**, 1358–1370 (1984).
90. D. J. Lawson, G. Hellenthal, S. Myers, D. Falush, Inference of population structure using dense haplotype data. *PLOS Genet.* **8**, e1002453 (2012).
91. R Core Team, *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, 2017); www.R-project.org/.
92. G. Hellenthal, G. B. J. Busby, G. Band, J. F. Wilson, C. Capelli, D. Falush, S. Myers, A genetic atlas of human admixture history. *Science* **343**, 747–751 (2014).
93. A. Raveane, S. Aneli, F. Montinaro, G. Athanasiadis, S. Barlera, G. Birolo, G. Boncoraglio, A. M. Di Blasio, C. Di Gaetano, L. Pagani, S. Parolo, P. Paschou, A. Piazza, G. Stamatoyannopoulos, A. Angius, N. Brucato, F. Cucca, G. Hellenthal, A. Mulas, M. Peyret-Guzzon, M. Zoledziewska, A. Baali, C. Bycroft, M. Cherkaoui, C. Dina, J. M. Dugoujon, P. Galan, J. Giemza, T. Kivisild, M. Melhaoui, M. Metspalu, S. Myers, L. M. Pereira, F. X. Ricaut, F. Brisighelli, I. Cardinali, V. Grugni, H. Lancioni, V. L. Pascali, A. Torroni, O. Semino, G. Matullo, A. Achilli, A. Olivieri, C. Capelli, Population structure of modern-day Italians reveals patterns of ancient and archaic ancestries in Southern Europe. *Sci. Adv.* **5**, eaaw3492 (2019).
94. S. Walsh, L. Chaitanya, L. Clarisse, L. Wirken, J. Draus-Barini, L. Kovatsi, H. Maeda, T. Ishikawa, T. Sijen, P. de Knijff, W. Branicki, F. Liu, M. Kayser, Developmental validation of the HIrisPlex system: DNA-based eye and hair colour prediction for forensic and anthropological usage. *Forensic Sci. Int. Genet.* **9**, 150–161 (2014).
95. S. Walsh, L. Chaitanya, K. Breslin, C. Muralidharan, A. Bronikowska, E. Pospiech, J. Koller, L. Kovatsi, A. Wollstein, W. Branicki, F. Liu, M. Kayser, Global skin colour prediction from DNA. *Hum. Genet.* **136**, 847–863 (2017).
96. L. Chaitanya, K. Breslin, S. Zuñiga, L. Wirken, E. Pośpiech, M. Kukla-Bartoszek, T. Sijen, P. de Knijff, F. Liu, W. Branicki, M. Kayser, S. Walsh, The HIrisPlex-S system for eye, hair and skin colour prediction from DNA: Introduction and forensic developmental validation. *Forensic Sci. Int. Genet.* **35**, 123–135 (2018).
97. R. Hui, E. D'Atanasio, L. M. Cassidy, C. L. Scheib, T. Kivisild, Evaluating genotype imputation pipeline for ultra-low coverage ancient genomes. *Sci. Rep.* **10**, 18542 (2020).
98. C. Gamba, E. R. Jones, M. D. Teasdale, R. L. McLaughlin, G. Gonzalez-Fortes, V. Mattiangeli, L. Domboróczki, I. Kővári, I. Pap, A. Anders, A. Whittle, J. Dani, P. Raczky, T. F. G. Higham, M. Hofreiter, D. G. Bradley, R. Pinhasi, Genome flux and stasis in a five millennium transect of European prehistory. *Nat. Commun.* **5**, 5257 (2014).
99. V. Link, A. Kousathanas, K. Veeramah, C. Sell, A. Scheu, D. Wegmann, ATLAS: Analysis Tools for Low-depth and Ancient Samples. bioRxiv 105346 [**Preprint**]. 2 February 2017. https://doi.org/10.1101/105346.

Downloaded from http://advances.sciencemag.org/ on January 21, 2021

100. B. L. Browning, S. R. Browning, Genotype imputation with millions of reference samples. *Am. J. Hum. Genet.* **98**, 116–126 (2016).
101. B. L. Browning, Y. Zhou, S. R. Browning, A one-penny imputed genome from next-generation reference panels. *Am. J. Hum. Genet.* **103**, 338–348 (2018).
102. Haplotype Reference Consortium, A reference panel of 64,976 haplotypes for genotype imputation. *Nat. Genet.* **48**, 1279–1283 (2016).
103. The 1000 Genomes Project Consortium, A global reference for human genetic variation. *Nature* **526**, 68–74 (2015).
104. P. Danecek, A. Auton, G. Abecasis, C. A. Albers, E. Banks, M. A. DePristo, R. E. Handsaker, G. Lunter, G. T. Marth, S. T. Sherry, G. McVean, R. Durbin, 1000 Genomes Project Analysis Group, The variant call format and VCFtools. *Bioinforma. Oxf. Engl.* **27**, 2156–2158 (2011).
105. C. Bronk Ramsey, Bayesian analysis of radiocarbon dates. *Radiocarbon* **51**, 337–360 (2009).
106. P. J. Reimer, E. Bard, A. Bayliss, J. W. Beck, P. G. Blackwell, C. B. Ramsey, C. E. Buck, H. Cheng, R. L. Edwards, M. Friedrich, P. M. Grootes, T. P. Guilderson, H. Haflidason, I. Hajdas, C. Hatté, T. J. Heaton, D. L. Hoffmann, A. G. Hogg, K. A. Hughen, K. F. Kaiser, B. Kromer, S. W. Manning, M. Niu, R. W. Reimer, D. A. Richards, E. M. Scott, J. R. Southon; R. A. Staff, C. S. M. Turney, J. van der Plicht, IntCal13 and Marine13 radiocarbon age calibration curves 0-50,000 years cal BP. *Radiocarbon* **55**, 1869–1887 (2013).
107. A. Juras, M. Krzewińska, A. G. Nikitin, E. Ehler, M. Chyleński, S. Łukasik, M. Krenz-Niedbała, V. Sinika, J. Piontek, S. Ivanova, M. Dabert, A. Götherström, Diverse origin of mitochondrial lineages in Iron Age Black Sea Scythians. *Sci. Rep.* **7**, 43950 (2017).
108. C. Knipper, A. Mittnik, K. Massy, C. Kociumaka, I. Kucukkalipci, M. Maus, F. Wittenborn, S. E. Metz, A. Staskiewicz, J. Krause, P. W. Stockhammer, Female exogamy and gene pool diversification at the transition from the Final Neolithic to the Early Bronze Age in central Europe. *Proc. Natl. Acad. Sci. U.S.A.* **114**, 10083–10088 (2017).
109. D. M. Fernandes, D. Strapagiel, P. Borówka, B. Marciniak, E. Żądzińska, K. Sirak, V. Siska, R. Grygiel, J. Carlsson, A. Manica, W. Lorkiewicz, R. Pinhasi, A genomic Neolithic time transect of hunter-farmer admixture in central Poland. *Sci. Rep.* **8**, 14879 (2018).
110. M. Krzewińska, G. M. Kılınç, A. Juras, D. Koptekin, M. Chyleński, A. G. Nikitin, N. Shcherbakov, I. Shuteleva, T. Leonova, L. Kraeva, F. A. Sungatov, A. N. Sultanova, I. Potekhina, S. Łukasik, M. Krenz-Niedbała, L. Dalén, V. Sinika, M. Jakobsson, J. Storå, A. Götherström, Ancient genomes suggest the eastern Pontic-Caspian steppe as the source of western Iron Age nomads. *Sci. Adv.* **4**, eaat4457 (2018).
111. C. Valdiosera, T. Günther, J. C. Vera-Rodríguez, I. Ureña, E. Iriarte, R. Rodríguez-Varela, L. G. Simões, R. M. Martínez-Sánchez, E. M. Svensson, H. Malmström, L. Rodríguez, J.-M. B. de Castro, E. Carbonell, A. Alday, J. A. H. Vera, A. Götherström, J.-M. Carretero, J. L. Arsuaga, C. I. Smith, M. Jakobsson, Four millennia of Iberian biomolecular prehistory illustrate the impact of prehistoric migrations at the far end of Eurasia. *Proc. Natl. Acad. Sci. U.S.A.* **115**, 3428–3433 (2018).
112. H. Malmström, T. Günther, E. M. Svensson, A. Juras, M. Fraser, A. R. Munters, Ł. Pospieszny, M. Tõrv, J. Lindström, A. Götherström, J. Storå, M. Jakobsson, The genomic ancestry of the Scandinavian Battle Axe Culture people and their relation to the broader Corded Ware horizon. *Proc. R. Soc. B Biol. Sci.* **286**, 20191528 (2019).
113. A. Modi, D. Nesheva, S. Sarno, S. Vai, S. Karachanak-Yankova, D. Luiselli, E. Pilli, M. Lari, C. Vergata, Y. Yordanov, D. Dimitrova, P. Kalcev, R. Staneva, O. Antonova, S. Hadjidekova, A. Galabov, D. Toncheva, D. Caramelli, Ancient human mitochondrial genomes from Bronze Age Bulgaria: New insights into the genetic history of Thracians. *Sci. Rep.* **9**, 5412 (2019).
114. S. Översti, K. Majander, E. Salmela, K. Salo, L. Arppe, S. Belskiy, H. Etu-Sihvola, V. Laakso, E. Mikkola, S. Pfrengle, M. Putkonen, J.-P. Taavitsainen, K. Vuoristo, A. Wessman, A. Sajantila, M. Oinonen, W. Haak, V. J. Schuenemann, J. Krause, J. U. Palo, P. Onkamo, Human mitochondrial DNA lineages in Iron-Age Fennoscandia suggest incipient admixture and eastern introduction of farming-related maternal ancestry. *Sci. Rep.* **9**, 16883 (2019).
115. A. Furtwängler, A. B. Rohrlach, T. C. Lamnidis, L. Papac, G. U. Neumann, I. Siebke, E. Reiter, N. Steuri, J. Hald, A. Denaire, B. Schnitzler, J. Wahl, M. Ramstein, V. J. Schuenemann, P. W. Stockhammer, A. Hafner, S. Lösch, W. Haak, S. Schiffels, J. Krause, Ancient genomes reveal social and genetic structure of Late Neolithic Switzerland. *Nat. Commun.* **11**, 1915 (2020).
116. S. V. Oshibkina, Мезолит бассейна Сухоны и Восточного Прионежья (Hayka, 1983).
117. S. V. Oshibkina, Мезолит Восточного Прионежья. Культура Веретье (Институт археологии Российской академии наук, 2006).
118. S. V. Oshibkina, Веретье 1. Поселение эпохи мезолита на Севере Восточной Европы (Hayka, 1997).
119. M. E. Foss, Стоянка Веретье *(Отчёт Северной экспедиции ГИМ о раскопках 1929–1934 гг. торфяника в бассейне р. Лача)*. (1941), *Труды Государственного Исторического музея, XII*.
120. N. V. Kosorukova, M. A. Kulkova, H. Piezonka, Хронология раннего неолита бассейна озера Воже. *Уральский Исторический Вестник.* **3**, 78–86 (2018).
121. S. V. Oshibkina, Мезолитический могильник «Попово» на р. Кинеме. *Советская Археология*, 122–138 (1982).
122. S. V. Oshibkina, Funeral rituals of the population of the Eastern Lake Onega region (based on materials from Popovo and Peschanitsa cemeteries), in *Mesolithic burials—Rites, Symbols and Social Organisation of Early Postglacial Communities, International Conference Halle (Saale), Germany, 18th-21st September 2013,* J. M. Grünberg, B. Gramsch, L. Larsson, Y. Orschiedt, H. Meller, Eds. (Verlag Beier-Beran, 2017), pp. 793–808.
123. A. Y. Bryusov, Караваевская стоянка, in Сборник по археологии Вологодской области, A. Y. Bryusov, Ed. (Вологодское книжное издательство, 1961), pp. 72–162.
124. A. V. Utkin, E. L. Kostyleva, Погребения на стоянке Караваиха. Российская Археология, 55–66 (2001).
125. N. V. Kosorukova, H. Piezonka, Новые материалы по эпохе неолита в бассейне озера Воже, in Археология Озерных Поселений: Хронология Культур И Природно-Климатические Ритмы (Периферия, 2014), pp. 69–174.
126. A. Y. Bryusov, Свайное поселение на реке Модлоне и другие стоянки в Чарозерском районе Вологодской области, in Поселения Эпохи Неолита и Раннего Металла на Севере Европейской Части СССР, M. E. Foss, Ed. (Издательство Академии Наук СССР, 1951), pp. 7–76.
127. N. E. Zaretskaya, E. L. Kostyleva, Новые данные по абсолютной хронологии льяловской культуры, in Тверской Археологический Сборник, 8 (1), I. N. Chernyh, ed. (ООО «Издательство «Триада», 2011), pp. 175–183.
128. E. L. Kostyleva, A. V. Utkin, Нео-энеолитические могильники Верхнего Поволжья и Волго-Окского междуречья, in Планиграфические И Хронологические Структуры (ТАУС, 2010).
129. M. G. Zhilin, E. L. Kostyleva, A. V. Utkin, A. V. Engovatova, *Мезолитические и неолитические культуры Верхнего Поволжья. По материалам стоянки Ивановское VII* (Hayka, 2002).
130. A. L. Nikitin, Существовала ли «волосовская культура». *Советская Археология*, 27–33 (1974).
131. A. L. Nikitin, Эволюция жилищ эпох камня и раннего металла в Марийском Поволжье, in *Тверской археологический сборник, 5,* I. N. Chernyh, Ed. (Тверская областная типография, 2002), pp. 363–369.
132. A. Macāne, K. Nordqvist, E. Kostyleva, Marmot incisors and bear tooth pendants in Volosovo hunter-gatherer burials. New radiocarbon and stable isotope data from the Sakhtysh complex, Upper-Volga region. *J. Archaeol. Sci. Rep.* **26**, 101908 (2019).
133. A. L. Nikitin, Поздний неолит в лесной полосе бассейна Волги (к проблеме истоков волосовской культуры и её локальных вариантов), in *Тверской археологический сборник, 8 (1)*, I. N. Chernyh, Ed. (ООО «Издательство «Триада», 2011), pp. 213–219.
134. A. H. Khalikov, *Древняя история Среднего Поволжья* (Hayka, 1969).
135. V. V. Sidorov, A. V. Engovatova, Протоволосовский этап или культура? in *Тверской археологический сборник, 2*, I. N. Chernyh, Ed. (Тверская областная типография, 1996), pp. 164–181.
136. O. N. Bader, К вопросу о балановской культуре, in *Советская Этнография, 1* (1950), pp. 64–85.
137. N. A. Krenke, Москворецкие памятники фатьяновской культуры, in *Российская Археология* (2014), pp. 5–18.
138. N. A. Krenke, Древности бассейна Москвы-реки от неолита до Средневековья: этапы культурного развития, формирование производящей экономики и антропогенного ландшафта (2019).
139. E. V. Volkova, Новинковские Могильники Фатьяновской Культуры (Институт археологии Российской академии наук, 2010).
140. O. N. Bader, К истории первобытного хозяйства на Оке и в верхнем Поволжье в эпоху металла, in *Вестник Древней Истории, 3* (1939), pp. 110–123.
141. E. G. Ershova, Природное окружение фатьяновских поселений и могильников в долине Москвы-реки по данным спорово-пыльцевого анализа, in *Российская Археология* (2014), pp. 19–23.
142. R. Y. Denisova, Новые данные об антропологическом типе населения фатьяновской культуры, in *Советская этнография, 4* (1966), pp. 24–37.
143. L. Varul, R. M. Galeev, A. A. Malytina, M. Tõrv, S. V. Vasilyev, L. Lõugas, A. Kriiska, Complex mortuary treatment of a Corded Ware Culture individual from the Eastern Baltic: A case study of a secondary deposit in Sope, Estonia. *J. Archaeol. Sci. Rep.* **24**, 463–472 (2019).
144. D. A. Krainov, Болшневский могильник фатьяновской культуры, in *Памятники древнейшей истории Евразии*, P. M. Kožin, L. V. Koltsov, M. P. Zimina, Eds. (1975), pp. 173–180.
145. D. A. Krainov, O. S. Gadzyatskaya, Фатьяновская культура. Ярославское Поволжье, in Свод археологических источников. Археология СССР (Hayka, 1987), vol. 1, pp. 1–22.
146. D. A. Krainov, Памятники фатьяновской культуры. Московская группа, in Свод археологических источников. Археология СССР (Изд-во Академии наук СССР, 1963), vol. 1, pp. 1–19.
147. A. L. Nikitin, Фатьяновский могильник у с. Халдеево, in Советская Археология (Ростовский район Ярославской области, 1964), pp. 277–282.
148. O. S. Gadzyatskaya, Милославский фатьяновский могильник, in Памятники Каменного и бронзового веков Евразии, O. N. Bader, Ed. (Hayka, 1964).
149. O. N. Bader, Мытищинский могильник фатьяновского типа, in *Краткие сообщения о докладах и полевых исследованиях Института истории материальной культуры, 75* (Издательство Академии наук СССР, 1959), pp. 143–153.

Downloaded from http://advances.sciencemag.org/ on January 21, 2021

150. N. A. Kirianova, Наумовский фатьяновский могильник. (Ярославская область), in *Бронзовый век на территории СССР*. (1973), *Краткие сообщения Института археологии, 134*, pp. 73–77.
151. V. M. Raushenbah, Фатьяновское погребение на неолитической стоянке Николо-Перевоз, in *Археологический сборник. Труды Государственного исторического музея, 37*, V. P. Levasheva, Ed. (1960), pp. 28–37.
152. O. S. Gadzyatskaya, Памятники фатьяновской культуры. Ивановско-Горьковская группа, *Археология СССР. Свод археологических источников*, (Hayka, 1976), pp. 1–21.
153. D. A. Krainov, *Памятники фатьяновской культуры. Ярославско-Калининская группа*. (Изд-во Академии наук СССР, 1964), vol. 1 of *Свод археологических источников. Археология СССР, 1–20*.
154. K. Nordqvist, From separation to interaction: Corded Ware in the Eastern Gulf of Finland. *Acta Archaeol.* **87**, 49–84 (2016).
155. A. Kriiska, K. Nordqvist, D. V. Gerasimov, Эстонский вариант шнуровой керамики, in *V (XXI) всероссийский археологический съезд. Сборник научных трудов*, A. P. Derevyanko, A. A. Tushkin, Eds. (Алтайский государственный университет, 2017), pp. 557–558.
156. L. Jaanits, Über die estnischen Bootäxte vom Karlova-Typus. *Fin. Mus.* **78**, 46–76 (1973).
157. K. Nordqvist, P. Häkälä, Distribution of Corded Ware in the Areas North of the Gulf of Finland: An update. *Est. J. Archaeol.* **18**, 3–29 (2014).
158. A. M. Tallgren, in *Acta et Commentationes Universitatis Tartuensis (Dorpatensis), III:6* (1922).
159. R. Indreko, Ein Hockergrab in Ardu, Ksp. Kose, in *Õpetatud Eesti Seltsi Toimetised 30* (1937), pp. 185–200.
160. L. Jaanits, Venekirveste kultuuri asulatest Eestis, in *Pronksiajast varase feodalismini. Uurimusi Baltimaade ja naaberalade arheoloogiast*, J. Selirand, H. Moora, Eds. (1966), pp. 60–66.
161. A. Kriiska, Corded Ware Culture Sites in North-Eastern Estonia, in *De temporibus antiquissimus ad honorem Lembit Jaanits*, *Muinasaja teadus, 8*. V. Lang, A. Kriiska, Eds. (Ajaloo Instituut, 2000), pp. 59–79.
162. R. Indreko, Sépultures néolithiques en Estonie, in *Õpetatud Eesti Seltsi Aastaraamat 1933* (1935), pp. 202–223.
163. L. Lõugas, A. Kriiska, L. Maldre, New dates for the Late Neolithic Corded Ware Culture burials and early husbandry in the East Baltic region. *Archaeofauna* **16**, 21–31 (2007).

Acknowledgments: We thank M. Keller for help with coordinates. Analyses were carried out using the facilities of the High Performance Computing Center of the University of Tartu. **Funding:** This work was funded by research projects of the Estonian Research Council IUT20-7 (to A.K.) and PRG243 (to M.M., Lauri Saag, C.L.S., Lehti Saag, and A.S.); the EU European Regional Development Fund 2014-2020.4.01.16-0030, 2014-2020.4.01.16-0125, and 2014-2020.4.01.15-0012; and Arheograator Ltd. (to L.V. and A.K.). We would like to thank the University of Tartu Development Fund for support to the Collegium for Transdisciplinary Studies in Archaeology, Genetics and Linguistics. **Author contributions:** Lehti Saag, A.K., and M.M. conceived the study. S.V.V., L.V., N.V.K., D.V.G., S.V.O., and A.K. assembled skeletal samples and performed osteological analyses. Lehti Saag, S.J.G., K.T., C.L.S., and A.S. performed aDNA extraction and sequencing. Lehti Saag, Lauri Saag, E.D., E.M., M.R., S.R., and T.K. analyzed data. Lehti Saag, L.V., N.V.K., D.V.G., T.K., K.T., A.K., and M.M. wrote the manuscript with input from the remaining authors. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. The DNA sequences are available through the data depository of the EBC (http://evolbio.ut.ee) and through the European Nucleotide Archive (accession code PRJEB40698). Additional data related to this paper may be requested from the authors.

Submitted 3 July 2020
Accepted 1 December 2020
Published 20 January 2021
10.1126/sciadv.abd6535

Citation: L. Saag, S. V. Vasilyev, L. Varul, N. V. Kosorukova, D. V. Gerasimov, S. V. Oshibkina, S. J. Griffith, A. Solnik, L. Saag, E. D'Atanasio, E. Metspalu, M. Reidla, S. Rootsi, T. Kivisild, C. L. Scheib, K. Tambets, A. Kriiska, M. Metspalu, Genetic ancestry changes in Stone to Bronze Age transition in the East European plain. *Sci. Adv.* **7**, eabd6535 (2021).

Downloaded from http://advances.sciencemag.org/ on January 21, 2021

Science Advances

Genetic ancestry changes in Stone to Bronze Age transition in the East European plain

Lehti Saag, Sergey V. Vasilyev, Liivi Varul, Natalia V. Kosorukova, Dmitri V. Gerasimov, Svetlana V. Oshibkina, Samuel J. Griffith, Anu Solnik, Lauri Saag, Eugenia D'Atanasio, Ene Metspalu, Maere Reidla, Siiri Rootsi, Toomas Kivisild, Christiana Lyn Scheib, Kristiina Tambets, Aivar Kriiska and Mait Metspalu

Sci Adv **7** (4), eabd6535.
DOI: 10.1126/sciadv.abd6535

ARTICLE TOOLS http://advances.sciencemag.org/content/7/4/eabd6535

SUPPLEMENTARY MATERIALS http://advances.sciencemag.org/content/suppl/2021/01/14/7.4.eabd6535.DC1

REFERENCES This article cites 93 articles, 23 of which you can access for free
http://advances.sciencemag.org/content/7/4/eabd6535#BIBL

PERMISSIONS http://www.sciencemag.org/help/reprints-and-permissions

Use of this article is subject to the Terms of Service

Science Advances (ISSN 2375-2548) is published by the American Association for the Advancement of Science, 1200 New York Avenue NW, Washington, DC 20005. The title *Science Advances* is a registered trademark of AAAS.

Copyright © 2021 The Authors, some rights reserved; exclusive licensee American Association for the Advancement of Science. No claim to original U.S. Government Works. Distributed under a Creative Commons Attribution NonCommercial License 4.0 (CC BY-NC).

Downloaded from http://advances.sciencemag.org/ on January 21, 2021