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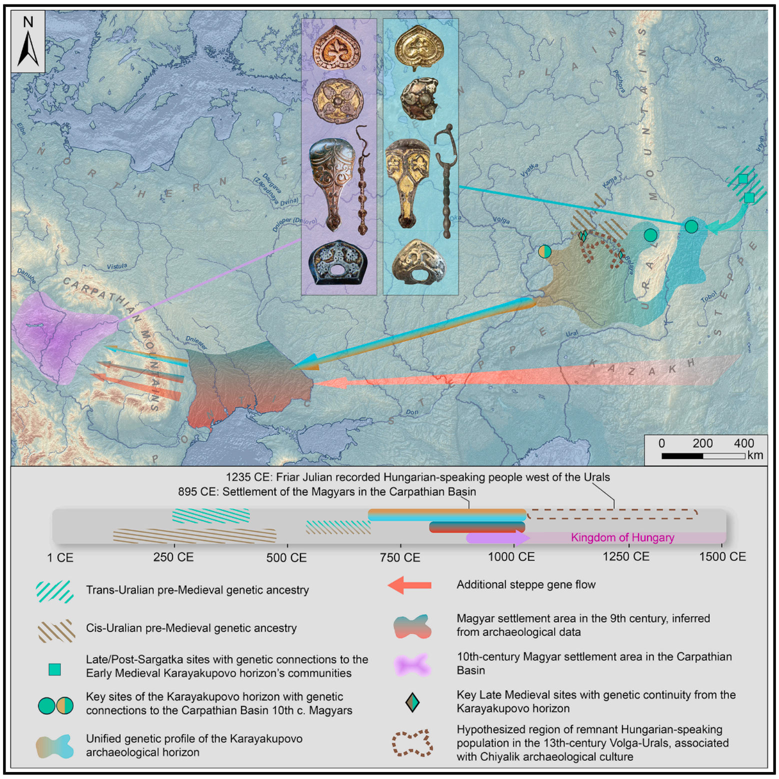
Article

Long shared haplotypes identify the southern Urals as a primary source for the 10th-century Hungarians

Graphical abstract



Highlights

- Genome-wide data of 131 ancient individuals from the Volga-Urals and Carpathian Basin
- 10th-century Carpathian Basin and southern Uralian populations show strong IBD sharing
- Primary southern Uralian origin and rapid migration of Magyars to the Carpathian Basin
- Genetic continuity from the Late Iron Age to the medieval circum-Uralian region

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In brief

Genome-wide ancient DNA data from early medieval populations across the broader Ural region and adjacent areas identify the southern Urals as the primary ancestral source of 10th-century Hungarians.

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Long shared haplotypes identify the southern Urals as a primary source for the 10th-century Hungarians

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SUMMARY

The origins of the early medieval Magyars who appeared in the Carpathian Basin by the end of the 9th century CE remain incompletely understood. Previous archaeogenetic research identified the newcomers as migrants from the Eurasian steppe. However, genome-wide ancient DNA from putative source populations has not been available to test alternative theories of their precise source. We generated genome-wide ancient DNA data for 131 individuals from archaeological sites in the Ural region in northern Eurasia, which are candidates for the source based on historical, linguistic, and archaeological evidence. Our results tightly link the Magyars to people of the early medieval Karayakupovo archaeological horizon on both the European and Asian sides of the southern Urals. The ancestors of the people of the Karayakupovo archaeological horizon were established in the broader Urals by the Late Iron Age, and their descendants persisted in the Volga-Kama region until at least the 14th century.

INTRODUCTION

The Hungarians are the only Uralic-speaking ethnicity in Central Europe, with a history tracing back to the early medieval period, east of the Carpathian Basin (CB). Their history became richly documented beginning with the Hungarian Conquest period (895–1000 CE), which introduced striking innovations in burial rites and artifact assemblages to the CB. These cultural transformations are commonly interpreted as signatures of the arrival of a tribal alliance from the Eurasian steppe, known as the early medieval Magyars (EMMs).[1–6] Chronicles and oral tradition trace the origin of these Magyars to an eastern homeland,[1,2] and a

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significant body of archaeological and linguistic research[1,4,7–11] highlights the cis- or trans-Ural regions as the leading candidate for their homeland. Over the past century, the reconstruction of early Magyar history has seen the emergence of diverse theories, as comprehensively reviewed by Zimonyi,[12] all of which recognize the significance of the broader Volga-south Ural region in the ancestral formation process of the Magyars. The details of the migration speed and routes are more contentious. The Magyars likely encountered Turkic-speaking communities in both the Volga-Ural region and the North-Pontic steppe, based on material culture connections between these regions and the CB. The crossing of the Volga River by the Magyars in a westward direction has been estimated to have occurred between 460 and 830 CE,[1,7,13–17] while their settlement areas in the northwestern Pontic region are inferred to have commenced between 670 and 860 CE.[7,16–22] Although more recent research supports a 9th-century chronology,[3,6] it is challenging to date the beginning of this migration and its intermediate steps. It also remains unclear where and how the language and community structure of the early Magyars were formed, as well as the roles that the circum-Uralian populations played in their ethnogenesis and confederation.

Based on parallels in material culture with the 10th-century CB, archaeologists have attributed some burial sites located around the southern Urals to the Magyars.[8] We hereafter introduce the term “Karayakupovo Horizon” (KH) to cover the diversity of the burial traditions and artefactual assemblages of the southern Urals, including the cis- and trans-Urals, dated to 750–1000 CE and associated with putative EMMs.[8,9] East of the Urals, a reference cemetery of this horizon was excavated at Uyelgi, near Chelyabinsk.[23] On the European side of the Urals, Bolshie Tigany in Tatarstan is a key site, and in the last decades, it was understood as a 9th- to 10th-century cemetery of Magyar groups that remained in the Volga-Urals.[3,5,8,24–27] People attributed to the KH lived in a multilingual and multiethnic context in the circum-Ural region, surrounded by Turkic, Finno-Permic, and Ugric-speaking people.[28] Further evidence supporting the theory that Magyars settled in the Volga region during the Early Middle Ages (EMA) comes from the later reports of a Hungarian-speaking population in the middle Volga and lower Kama regions from European travelers who visited an area known as *Magna Hungaria* in the 1230s.[29] However, the survival of such communities has never been tested using ancient DNA (aDNA) data, the only direct way to verify population continuity and theories of ancestral origin.

aDNA studies have generated large amounts of genetic data on ancient people of Northern Eurasia, which we co-analyze in this study along with our newly reported data.[30–72] However, the Ural region from the Late Iron Age (IA) to medieval times remained unstudied on the genome-wide level. Csáky et al.[73] and Szeifert et al.[74] provided insights into the connections between the 10th- and 11th-century population of the CB and the Volga-Ural populations at the uniparental DNA level, while Maróti et al.[65] and Gnecchi-Ruscone et al.[61] generated genome-wide data for the early medieval CB itself. Maróti et al.[65] reported data from the 5th–10th centuries CB, showing that the Avars and Magyars represent distinct groups with East Eurasian genetic affinities. Based on their analyses, they argued that several source components were plausible for the immigrant 10th-century Magyars (named there as Conqueror Asia Core). This included the modern Ugric-speaking Mansi used as proxy in their ancestry modeling, as well as groups descended from Huns/Xiongnu and early and late Sarmatians. However, these sources do not align with prevailing linguistic and archaeological interpretations. Therefore, it is important to carry out tests with samples from the populations that archaeological evidence suggests are the most plausible proximate sources.

Here, we leverage the first genome-wide aDNA data from the putative sources in the Urals and adjacent populations of EMMs to understand their relationships to the new arrivals in the CB. We then examined the deeper population history of those Volga-Uralian groups (by using Late Bronze Age [BA]/IA and Migration Period reference populations) that showed especially strong connections to 10th-century CB Magyars to document the extent of genetic continuity from the IA to medieval times in the Volga-Urals.

RESULTS

We used in-solution enrichment for more than 1.2 million single-nucleotide polymorphisms (SNPs) (the "1,240k" SNP capture panel[33]) to study the ancestry of 120 newly reported individuals from 40 archaeological sites in the circum-Ural area (see descriptions of relevant geography and sub-regions in Data S1 and a summary of archaeological and genetic context in Table S1A), dated from the Late BA (~1300–1000 BCE) to the late medieval period starting ca. 1400 CE (see Figure 1 and Data S1 for detailed archaeological and genetic descriptions of the newly sampled burials). In addition, we present data for 11 newly reported individuals from the CB dated to the 10th-century CE. For estimating genetic diversity and, in some cases, for modeling genetic origin, we grouped individuals by ecoregions/river basins and chronological periods[75]; see Data S1 section I for details. For brevity, these periods are labeled by prevailing cultural groups in the region, e.g., Russia_Belaya_Chiyalik (Figure 1), but cultural attribution did not play a role in the grouping process with one exception (the KH).

Recent methodological developments have made it possible to detect long shared autosomal haplotypes between pairs of ancient genomes,[76,77] often termed identical-by-descent (IBD) segments.[78] Previously, this method was only applicable to high-quality genomic data for modern populations.[79,80] However, new methods extend its application to ancient individuals as well, even when genome coverage is moderate. This is achieved by statistically imputing genotypes with high confidence, leveraging redundancy in human genetic variation.[76] The IBD-sharing analysis is particularly useful for detecting distant relatives. We coupled this analysis with archaeogenetic methods relying on correlations of allele frequencies: principal-component analysis (PCA),[81] *f*-statistics, and derived methods,[31,81–85] as well as ADMIXTURE.[86]

Our research protocol included several stages. First, we utilized PCA, supervised ADMIXTURE analysis, and network graphs visualizing individuals linked by shared IBD segments (see STAR Methods for further details) to obtain a broad overview of the dataset. In the second stage, we focused on IBD connections between the Volga-Ural region and the population of the 10th- to 11th-century CB. In the third stage, we explored the genetic history of the medieval Volga-Uralian groups using *f*-statistics,[31,81,84] which allow for formal tests of simple non-phylogenetic admixture models. To understand changes in population size and rates of close-kin marriages in this period, we explored runs of homozygosity (ROHs), using hapROH.[87]

Genetic diversity in the Volga-Ural region

The Eurasian PCA in Figure 2B reveals extraordinary genetic heterogeneity in the early medieval Volga-Ural region, with high variability in ancestry among individuals associated with certain regional and chronological groups. In the 1st–3rd principal component (PC) space (Figure 2B), we observe an east-west genetic gradient from Northeast Asian (NEA) to Northwest Eurasian (NWE) genetic affinities. Most ecoregions of interest display high genetic diversity, with individuals from each region spreading over large sections of the gradient. Notably, most of the newly sequenced 10th-century individuals from the CB are positioned along the NWE-NEA and NWE-Eastern Asian (EA) clines, with only two of them demonstrating a Central European genomic profile. We also conducted a supervised ADMIXTURE analysis (Figure 2A; Table S1D), utilizing eight Neolithic and Early BA populations as proxy ancestry sources for the clustering algorithm. In the selection for the ancestral sources, we aimed to reflect the Neolithic/BA variation of north Eurasia (for details, see STAR Methods). Our findings reveal a widespread yet varying presence of Early BA Yamnaya-related ancestry across the region. This persistent Yamnaya-related ancestry,[30] contrasted with the fluctuating levels of other ancestries, such as the Yakutia Late Neolithic and Bronze Age (LNBA), Baikal Neolithic, or Altai Neolithic,[68] reflects a patchwork of local genetic influences in the region.

We applied genotype imputation,[76] inferred IBD segments using the approach described in,[77] and constructed a network graph[88] connecting individuals with shared IBD segments on a total of 1,332 individuals (for details see Tables S1B and S1C), comprising published data for 1,231 individuals from Asia and Europe and 101 individuals presented in this study (Figure 3A; see Figure S1 for time-oriented, non-filtered, and PC-projected versions of this network). The graph's edges were weighted based on the length of the most substantial IBD segment shared by two individuals (nodes). To denoise the graph, we restricted the analysis to individuals connected by at least one 9 cM (centimorgan) segment, not separated in time by more than 600 years, and focused on the largest interconnected subgraph. Details of the de-noising, visualization, and clustering approach are described in the STAR Methods. The twelve newly reported IA individuals formed a cluster (with many previously published individuals) in the IBD network that we labeled "Eurasian steppe IA" in Figure 3A (clusters were inferred with the Leiden community detection algorithm,[89] and we refer to them as "IBD-sharing communities" or simply "IBD clusters"). A total of 118 early medieval individuals from both the Volga-Ural region and CB formed another cluster (Figure 3C), labeled as "Urals-Carpathian EMA" in Figure 3A. To discern and quantify the underlying differences among the identified network clusters, we analyzed network topology, similar to that described by Gnecchi-Ruscone et al.,[90] focusing on metrics such as degree centrality (number of links held by a given node) and module strength measured based on summarized IBD sharing between individuals (see STAR Methods). The Urals-Carpathian EMA cluster's average clustering coefficient was close to the mean of the other clusters. At the same time, its relatively high within-module (k_{w}) and low between-module (k_{B}) degree exhibited distributions akin to the most cohesive clusters (Figures S2A and S2B). The Urals-Carpathian EMA cluster was loosely connected to the other IBD-sharing communities. Still, based on the low cluster coefficient, this separation could reflect gaps in sampling in time or space rather than true genetic isolation.

Within the Urals-Carpathian EMA cluster, the published 10th- to 11th-century CB genomes[65] are grouped with our newly sequenced Volga-Ural medieval samples. The KH groups

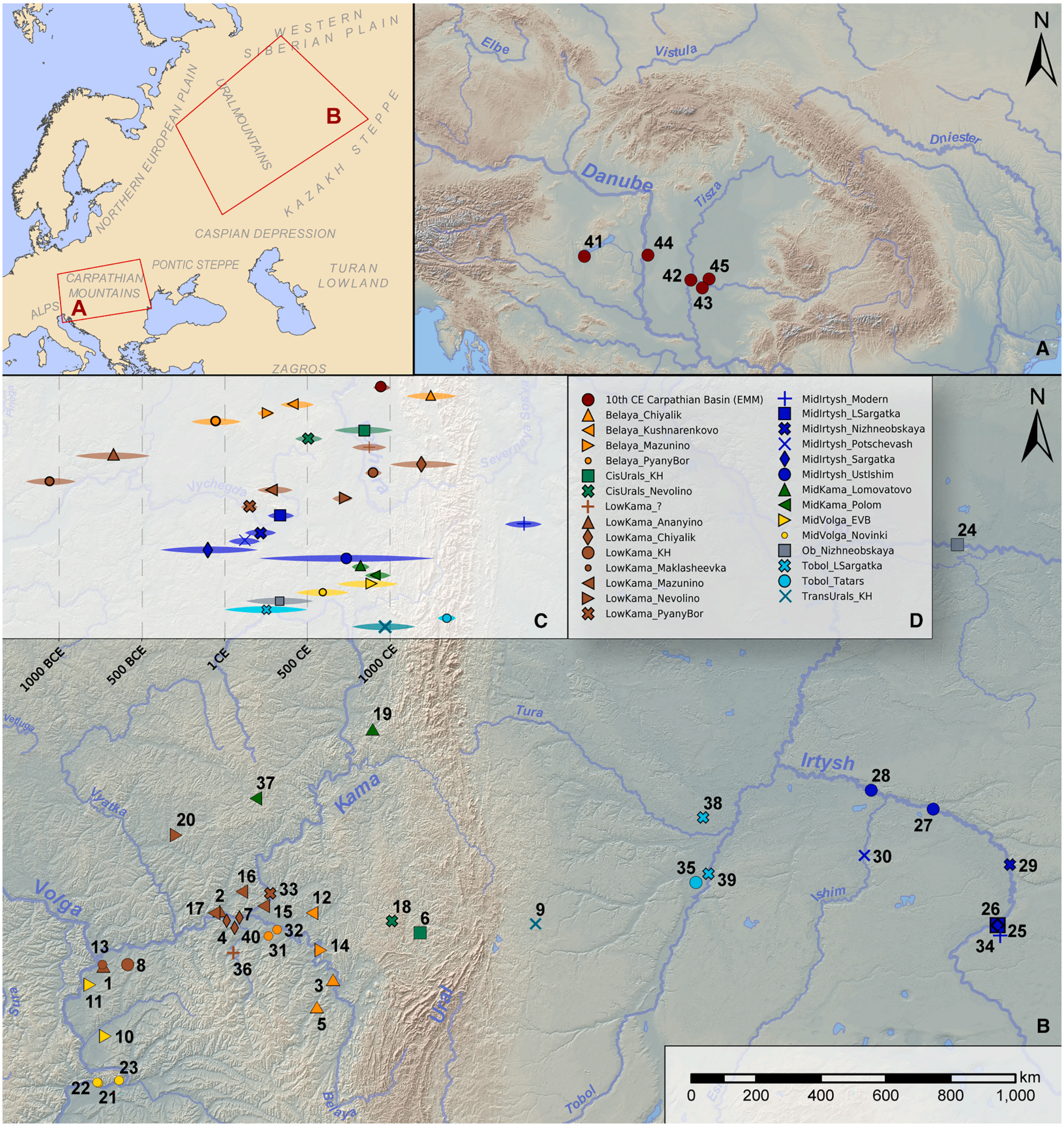

Figure 1. Locations and chronology of the studied burials

Archaeological sites in the CB (A) and in the Volga-Ural region (B) involved in this study are colored according to ecoregions: 1, Izmeri-7; 2, Rysovo-1; 3, Gornovo; 4, Gulyukovo; 5, Novo-Khozyatovo; 6, Karanayevo; 7, Zuyevy-Klyuchi; 8, Bolshie-Tigany; 9, Uyelgi; 10, Mullovka; 11, Tankeyevka; 12, Bustanaevo; 13, Devichiy-Gorodok-4; 14, Birsk-2; 15, Boyarsky-Aray; 16, Dubrovsky; 17, Turaevo-1; 18, Bartym; 19, Bayanovo; 20, Sukhoy-Log; 21, Brusyany; 22, Malaya-Ryazan'; 23, Novinki-1; 24, Barsov-Gorodok; 25, Borovyanka-17; 26, Borovyanka-18; 27, Ivanov-Mys-1; 28, Panovo; 29, Ust-Tarsk; 30, Vikulovo; 31, Kipchakovo; 32, Starokirgizovo; 33, Tarasovo; 34, Bogdanovo-2; 35, Putilovo; 36, Mellyatamak-3; 37, Varni; 38, Ipkul; 39, Starolybaevo-4; 40, Ust-Menzelya; 41, Balatonújlak; 42, Szeged-Öthalom; 43, Kiszombor; 44, Harta-Freifelt; and 45, Makó-Igási járandó. Groups defined in this study are listed in (D), and their chronology is given in (C).

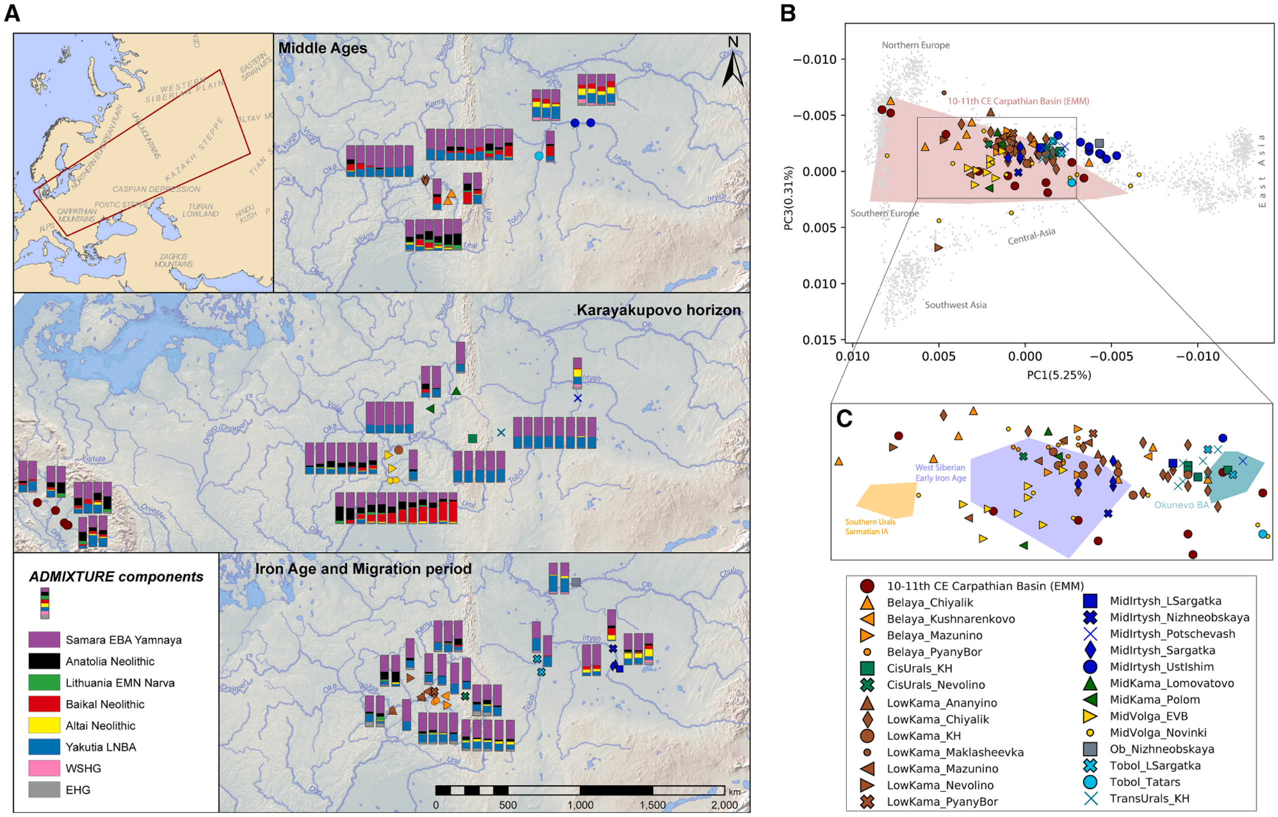

Figure 2. Principal component analysis and supervised ADMIXTURE analysis of the newly sequenced genomes

(A) Supervised ADMIXTURE analysis (K = 8) of the newly presented individuals, plotted on maps, showing their approximate origin and chronology (Iron Age and Migration Period, ca. 250 BCE–650 CE; Karayakupovo horizon, ca. 650–1000 CE; Middle Ages, ca. 1000–1400 CE).

(B and C) (B) Eurasian-scale principal component analysis (PCA), with a projection of the newly sequenced individuals on modern genetic variation after Jeong et al.[50] The PC1 and PC3 dimensions are depicted with the newly presented genomes. Gray dots indicate modern Eurasian genomes on which the ancient samples were projected. Polygons (C) outline ancient reference sample distributions (without displaying individual points): early medieval Magyars (EMMs) from the CB (red),[65] EIA southern Urals (yellow),[49] IA western Siberia (blue),[56] and BA south-central Siberia (green).[38]

See also Figures S3 and S4.

exhibit high degree centrality, suggesting they hold a structurally central position within the cluster (Figure S2C). By contrast, the early medieval CB group displays a more diverse pattern of connectivity. The average IBD per link for both between- and within-module connections (Figure S2D) is moderate for the KH groups compared with other modules. Notably, some 10th-century CB individuals fall into the "East Asia/Carpathian IA-EMA" cluster, reflecting a genetically diverse migration into the region. We have observed that PCA (as well as the other allele-frequency-based methods) and the IBD network highlight distinct yet complementary aspects of population structure: the former is more sensitive to geographically structured genetic gradients, while the latter connects distant or close relatives who may occupy very different positions on these gradients (Figures S1C–S1E).

EMMs fall within the genetic diversity of the Volga-Ural region

We examined closely the genetic links between the Volga-Uralian groups and the 10th-century CB population forming the Urals-Carpathian EMA IBD cluster. The analysis showed that 10th-century Magyars in the CB exhibit significant genetic variation along PC1 (Figure 2B), indicative of admixture during their migration westward or within the CB. As observed earlier, ancestries tracing back to the Baikal Neolithic and the Yakutian Late Neolithic/BA varied across the EMM individuals. We mapped the proportions of these proxy ancestry sources onto our PCA (Figure S3A). Consistent with the previously identified NWE-NEA and NWE-EA gradients, the EMMs demonstrate ancestry from two different East Eurasian sources. Specifically, those aligned with the NWE-NEA gradient exhibited a pronounced Yakutian Late Neolithic/BA ancestry, whereas those on the NWE-EA cline displayed higher levels of Baikal Neolithic ancestry (Figures S3A and S3B). These ancestry components should not be interpreted as reflecting direct gene flows from Yakutia or the Baikal region; rather, the proxy sources are reference groups for broad geographical regions and chronological periods. All of these results suggest that substantially different genetic sources on the Siberian genetic landscape could have contributed to the Urals-Carpathian EMA cluster of distant relatives in the 10th-century CB.

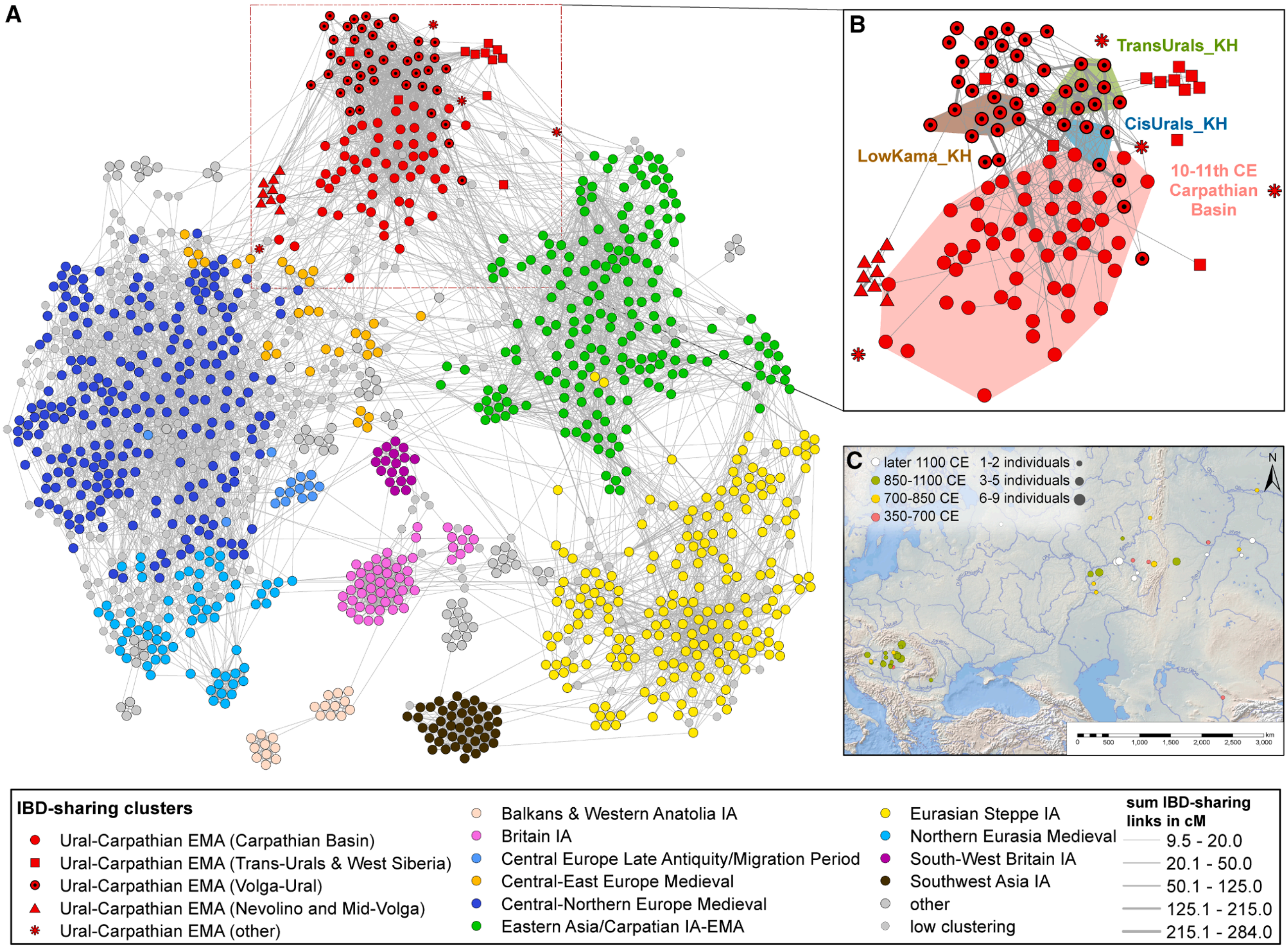

Figure 3. IBD network and visualization of the major IBD connections on a map

(A) A network graph of IBD sharing visualizing clusters of distant relatives for 1,332 ancient Eurasian individuals from the IA to the medieval period (MultiGravity ForceAtlas 2, a force-directed layout algorithm,[88] was used, with the additional Leiden algorithm[89] for clustering).

(B) Close up of the Urals-Carpathian EMA cluster within the network, highlighting the KH and 10th- to 11th-century CB individuals in the cluster.

(C) Geographical distribution of the individuals from the Urals-Carpathian EMA IBD-sharing community.

See also Figures S1–S5.

Next, we focused on specific cases of strong IBD links between EMMs and the population of the Volga-Ural region, providing examples of long-distance migration within a few generations. We identified 28 pairs of individuals sharing more than two genome segments of 12 cM or longer (Table S2), and of these, 11 pairs with the longest IBD segments are presented in Table 1. For their ancestry proportions estimated with ADMIXTURE, see Figure S3B. It is most likely that the degree of kinship for these pairs of individuals indicates distant biological relatedness (even up to the 6th degree)[77] (Figure S3C).

Dating based on archaeological context and radiocarbon analysis (Table S1G) shows that most IBD segments link individuals within a couple of hundred years of each other. Owing to the broad chronological ranges provided by radiocarbon and archaeological dating, the observed connections between pairs of sixth-degree (or more distant) relatives may reflect either collateral relatedness through a shared common ancestor or direct ancestor-descendant relationships. The majority of the strong connections (>2 segments above 12 cM) of the EMM individuals are detected with the KH individuals from various ecoregions. To better understand the connection between the two regions, we conducted a qpWave analysis-based cladality test[85] (see STAR Methods for details). This test assesses whether two populations of interest (referred to as left populations) form a clade or show genetic continuity, given a set of reference (right) populations (see STAR Methods). As proxy ancestry sources for Urals-Carpathian EMA cluster individuals, we used medieval Volga-Ural region groups that each included at least five individuals (Mid-Irtysh_Usthim, TransUral_KH, CisUral_KH, LowKama_KH, and MidVolga_Early Volga Bulghar [EVB]), representing a diverse genetic composition spanning from the trans-Uralian/western Siberian to the mid-Volga region. We paired each group with Urals-Carpathian EMA cluster individuals from the CB and found that individuals from the CB

Table 1. IBD connections between medieval Volga-Uralian and Carpathian Basin individuals

10th- to 11th-century EMMs in the Carpathian Basin				Volga-Uralian individuals					
Ind1	Date	Sex	Y/mtDNA	Group	Ind	Sex	Y/mtDNA	Date	Total length of shared IBD segments > 2 × 12 cM
SEO-4	900–1000 CE	male	G2a/T2g1a	mid-Volga EVB	I25526	male	Q/B5b4	850–1050 CE	144
SZAK-1	900–1000 CE	male	N1a/T2d1b1	trans-Urals KH	I19117	male	N1a/N1a	**771–937 calCE**	92
K2-61	900–950 CE	male	R1/U4d2	cis-Urals KH	I25538	male	N1a/U5a1g1	664–1016 CE[a]	67
SZAK-7	900–1000 CE	female	–/D5a1	trans-Urals KH	I19118	male	G2a/A+152	772–1152 CE[a]	42
SZAK-7	900–1000 CE	female	–/D5a1	cis-Urals KH	I25538	male	N1a/U5a1g1	664–1016 CE[a]	63
SZAK-4	900–1000 CE	female	–/HV4a2a	cis-Urals KH	I25537	male	N1a/H6a1b	664–1016 CE[a]	43
SZA-154	900–1000 CE	female	–/B5b4	trans-Urals KH	I19120	male	N1a/A12a	772–1152 CE[a]	42
SZAK-6	900–1000 CE	female	–/A16	low-Kama KH	I19105	female	–/A12a	850–950 CE	45
SZAK-1	900–1000 CE	male	N1a/T2d1b1	trans-Urals KH	I19121	male	N1a/U5a1a1	**879–1150 calCE**	46
K3-6	900–1000 CE	female	–/B4d1	cis-Urals KH	I25536	male	N1a/C4a2	**664–827 calCE**	46

Radiocarbon dates (calibrated [cal], 95% confidence interval) are highlighted in bold. In other cases, the dating is based on the archaeological chronology of the material culture.

[a] Summed probability densities, based on samples radiocarbon dated from the same site.

with the highest levels of genomic segment (IBD) sharing with KH groups (Table 1) primarily showed feasible models with the cis and trans-Uralian KH groups (Table S3)—an outcome also mirrored in their ADMIXTURE profiles (Table S1D). When paired with the low-Kama group, only four individuals fit the model, while none fit with the mid-Volga EVB or mid-Irtysh group. Our cladality test thus provides a second, independent line of evidence—alongside the IBD links—supporting a genetic connection between the 10th-century CB EMMs and the circum-Uralian KH groups.

We conducted a genetic mobility estimation analysis (mobest; see STAR Methods for details and Table S1H for reference samples) to identify the most likely spatial origin of the EMMs. This analysis (Figure S4) indicated that most EMMs from the Urals-Carpathian EMA cluster were associated with three potential source regions: one primarily from Europe (Figure S4A), one from the Ural region (Figure S4B), and another from somewhere in Central Asia (Figure S4C). Among the EMMs, those with the strongest IBD sharing with the KH individuals and a high level of Yakutian LNBA ancestry mostly displayed the highest similarity probabilities to the Ural region (e.g., the Szakony [SZAK] individuals). The Baikal Neolithic ancestry-bearing individuals indicated the highest similarities for yet preliminarily defined Eastern Eurasian sources. In some cases, dual or tri-regional affinities were observed; however, this pattern was not evident in the KH individuals (Figure S4D; for reference samples, see Figure S4E).

Iron Age genetic continuity in the medieval Volga-Ural region

To provide deeper insights into the genetic landscape of the Volga-Ural region, we applied f_4-statistics (for details see Table S1E), aiming to test if there was a significant genetic shift in this region since the BA. For this purpose, we compared allele sharing between the newly sequenced individuals and selected BA reference individuals from the southern Urals (attributed to the Sintashta culture) and south-central Siberia (attributed to the Okunevo culture, from the Minusinsk Basin), as shown in Figure 4A. Our analysis revealed that during the late phase of the Early IA (EIA), the level of allele sharing was similar with both distant reference populations for the circum-Uralian individuals dated to this period (culturally associated with the Pyany-Bor and Sargatka contexts). Over time, particularly by the medieval period, an increasing number of individuals displayed a stronger genetic affinity to one of these reference groups. Notably, the two individuals attributed to the transitional period from the late Sargatka to the Migration Period cultural groups and buried in the Tobol region (see Data S1 section I.C), stood out from the homogeneous IA genetic continuum, showing a pronounced affinity with the south-central Siberian BA reference group. One of these two individuals, ID I33844, comes from a burial dated to 250–320 CE at Ipkul in the Tobol River area—the latest site preserving the late Sargatka tradition, which persisted in the remote periphery of its cultural area in admixture with a taiga-derived cultural environment (see Data S1 sections I.C and IV.B.2). Notably, this individual clusters with the Urals-Carpathian EMA. Similarly, the trans- and cis-Uralian KH individuals exhibited a strong affinity with this BA reference group. These results highlight the diverse population interactions during the Migration and, later, medieval periods compared with those of the IA.

To test the IA/Migration Period (for a detailed description of the archaeological chronology in the region, see Data S1 sections I.A, I.B, and I.C) individuals for evidence of continuity with early medieval KH individuals, we used two complementary f_4-statistics (for details, see Table S1E). Initially, we tested allele sharing between our focal (KH) group and both the EIA southern Uralian (associated with the Sarmatian culture context) and western Siberian groups (Sargatka horizon), which revealed reduced allele sharing of the KH groups with the Sarmatian cultural context when comparing to the western Siberian groups (Figure 4B). In the second stage, we analyzed Late IA/Migration Period

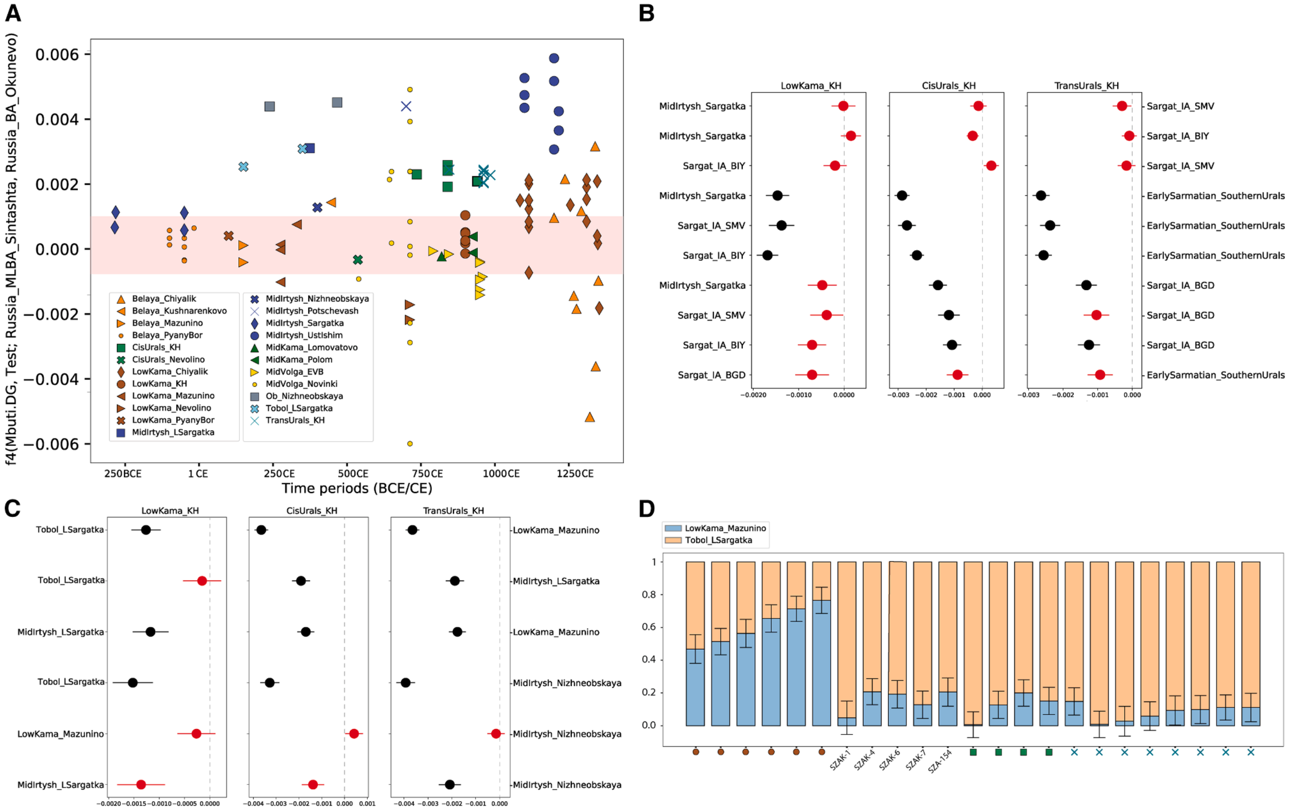

Figure 4. f_4-statistics and admixture models illustrating allele sharing and genetic affinities among newly sequenced individuals and BA/IA reference groups

(A) f_4-statistics for the newly sequenced individuals from the Volga-Ural regions, excluding those from the Maklasheevka and Ananyino cultural contexts. The y axis represents the allele sharing values with two BA reference groups (red band indicates $|Z \text{ score}| < 3$). The x axis shows the timeline.

(B) f_4-statistics in the form of $f4$(Mbuti, KH_group; EIA_test_1, EIA_test_2) assess allele sharing among KH groups and various EIA references. These analyses include individuals from the Sargatka horizon at the Shmakovo (SMV), Bogdanovka (BGD), and Mountain Bitiya (BIY) sites as described by Gnecchi-Ruscone et al.[61] Additionally, it features groups from the southern Uralian and Sarmatian cultures as reported by Järve et al.,[49] alongside our newly introduced early IA groups. Red markers denote $|Z \text{ score}| < 3$; error bars showing the respective standard errors estimated by block jackknife.

(C) f_4-statistics comparing allele sharing between KH groups and Migration Period Volga-Uralian reference groups in the form of f_4 (Mbuti.DG, KH_test_group; MigrationPeriod_reference_group1, MigrationPeriod_reference_group2). The locations of the dots indicate affinities with left and right reference groups. Red markers denote $|Z \text{ score}| < 3$; error bars showing the respective standard errors estimated by block jackknife.

(D) A two-way admixture model (qpAdm, $p > 0.05$; ancestry proportions with respective standard errors, estimated by block jackknife) for the KH and EMM individuals from the 10th- to 11th-century CB (from Table 1) that exhibited strong IBD sharing (>42 cM in IBD segments longer than 12 cM; see Table S2 for additional details). For additional EMMs modeled with this two-way qpAdm setup, see Table S1F.

See also Figure S4.

reference populations from the wider Volga-Ural region and tested allele sharing between them and the KH groups (Figure 4C). This included the low-Kama Mazunino group and groups from the Tobol and mid-Irtysh regions from the Sargatka sites, including the latest ones in the Tobol region, and the Nizhneobskaya cultural contexts. The latter is distinct both archaeologically and genetically from the local continuum. Compared with the other reference populations, we observed significant allele sharing between the KH groups and the Tobol reference groups associated with the residual Sargatka sites. These findings indicate genetic continuity in the KH groups from the end of the EIA, suggesting their ancestry is rooted in the Irtysh and Tobol River regions.

To model possible admixture scenarios and quantify the proportion of the Migration Period ancestral sources (for KHs and EMMs with direct connections to KH individuals [Table 1]), we employed qpAdm analysis (Figure 4D) (for the detailed settings, see STAR Methods). We purposely avoided rotating modeling approaches, exploring large sets of alternative proxy sources.[91] Instead, we utilized a two-way modeling strategy with proxy sources on both sides of the Urals in the Late IA/Migration Period: the residual Sargatka group in the Tobol basins and Mazunino in the low-Kama basin. Their separation in the spaces of f_4-statistics (Figure 4A) and differences in ADMIXTURE proportions (Figure 2A) justified the use of these sources for qpAdm analysis. Archaeological context also supports the significance of these groups, as they potentially influenced the Kushnarenkovo and later Karayakupovo archaeological cultures.[8] In the case of the Mazunino group, we used the low-Kama subgroup, which has sufficient coverage in our dataset. Out of the 20 analyzed KH individuals, the two-way model provided a good fit (p value > 0.05) in 18 cases (for the list of outgroups, see STAR Methods). The Tobol late Sargatka ancestry was notably prevalent among the trans-Ural KH, cis-Ural KH, and EMM individuals, representing at least ~70% of their ancestry (for detailed results, see Table S1F). While all EMM and KH groups likely share the same trans-Uralian ancestry, some (low-Kama KH, see Figure 4D) mixed extensively with local groups to the west of the Urals.

A time-ordered IBD graph in Figure S1A illustrates biological continuity, especially between the early medieval KH groups and those from the late medieval Chiyalik cultural contexts in the Belaya and especially low-Kama regions. The similarity in ADMIXTURE profiles (Figure 2A) further supports the continuity of the KH-type ancestry into the later medieval period. By contrast, the Belaya region in the late medieval period is more diverse genetically, with several individuals having European and East Asian genetic profiles (supported also by IBD connections outside the Urals-Carpathian EMA cluster).

To explore the demographic history of the Volga-Ural groups from a different perspective, we utilized the hapROH method to identify long ROHs, as shown in Figures S5A and S5B.[87] This analysis revealed that KH individuals probably had a small effective population size (N_e), evidenced by the ROH segments in their genomes. Our N_e analysis further indicated that both the early medieval low-Kama KH and late medieval low-Kama Chiyalik groups had consistently smaller population sizes than neighboring groups across different periods (Table S4).

DISCUSSION

In this study, we report genome-wide data for 131 ancient human genomes from 1300 BCE to 1400 CE in the circum-Ural region and the CB. The genetic gradients displayed on the PCA by the Volga-Ural region groups (Figure 2B) align with the modern genetic variation found in Eurasia's forest and forest-steppe zones (the northern one) and the steppe zone (the southern one), respectively.[68] The Asian end of the northern gradient is linked to the Yakutian LNBA population, which is described as a genetic "tracer dye" for the spread of Uralic speakers in north Eurasia.[68] The IBD analysis of autosomal chromosome segments reveals distant relatedness between early medieval circum-Uralian individuals from the KH sites and the EMM 10th- to 11th-century population from the CB. We term the IBD cluster of distant relatives as "Urals-Carpathian EMA" (Figure 3C), which shows a genetic gradient stretching from Europe to Northeast Asia on PCA, and is distinct from the Eurasian steppe IA and East-Asia/Carpathian IA-EMA IBD clusters (Figures 3A and S1C–S1E).

Our findings demonstrate that cis- and trans-Uralian KH sites are linked to 10th- to 11th-century CB individuals in the IBD-sharing network. These connections are supported by similarity in ADMIXTURE profiles, qpWave-based cladality tests, and mobest mobility estimation. Notably, individuals from the western Hungarian Szakony-Kavicsbánya site display the highest similarities to the Volga-Ural population in ADMIXTURE clustering and IBD sharing. Archaeological artifacts from this site and burial customs show direct parallels with Uralian cultural contexts.[92] These combined findings provide the first compelling genetic evidence supporting a dominant Uralian origin for a significant portion of the ancestry of 10th-century Magyars in the CB. EMMs from the CB mostly demonstrate Yakutian LNBA-type ancestry associated with the northern (forest and forest-steppe) Eurasian gradient. Still, some also demonstrate Baikal Neolithic-related ancestry associated with the southern (steppe) Eurasian gradient (Figure S3A). The genetic mobility estimation analysis of the EMMs also indicates that a significant portion of the EMMs originated from the Ural region. Some of them may have migrated rapidly, possibly within the span of a single generation (e.g., individuals from the Szakony-Kavicsbánya site). Additionally, we identified other potential regions, likely in Central Asia, as sources of gene flow into the EMMs. However, it is important to note that this gene flow was not observed in the early medieval KH individuals (Figure S4D), suggesting that this admixture likely occurred outside the Volga-Ural region, during the EMMs' westward migration. These results imply that they (or their ancestors) have at least two genetic sources outside the CB, and we confirmed the circum-Uralian one. Considering the archaeological, historical, and genetic results, our findings are consistent with a scenario in which the starting point of the EMM migration to the CB was located in the circum-Ural region. In the KH groups, no traces of admixture are detectable with Central/East Eurasian ancestry-bearing groups (such as those usually attributed to Turkic speakers).[38,50] The results presented in our paper align with the Uralic (Ugric) basis of the Hungarian language, which has its first written documents only as late as 11th-century Hungary.[93] Among the possible early medieval influxes to the CB, the Hungarian language was most probably brought from the southern Ural region (by descendants of the members of the Karayakupovo archaeological horizon), among others by those Magyars who shared the Urals-Carpathian EMA cluster. However, it is important to emphasize that the Magyar-associated archaeological assemblages demonstrate diverse cultural backgrounds and likely reflect multiethnic/multilingual communities.[16,94,95] The most recent reconstructions of the Magyar migration based on material culture evidence favor the subsequent population movement from the Volga to the Pontic Steppe as late as the early 9th-century CE, and from there to the CB by the end (or second half) of that century.[3,6] The tight connectedness of the Urals-Carpathian EMA cluster and the genetic characteristics of a part of the EMMs indicate a rapid migration from the Volga-Ural to the CB and a rather short stop in the North-Pontic area. This later area could have been the site for the integration and alliance with the Turkic-speaking steppe population.[3]

We propose referring to this specific type of ancestry, best observed among Uralian early medieval individuals and later identified in the EMMs, as the "Karayakupovo-type." We detect the first emergence of it to the west of the Urals by 550 CE. This ancestry did not extend as far west as the Volga-Kama confluence or the Volga's west bank by the Samara Bend, as it is absent in the group with Novinki-type burial practices (for the description of the Novinki group, see Data S1 section II.F). Furthermore, our findings indicate that individuals from the EVB Mullovka and Tankeyevka cemeteries also differ from the KH sites (for the description of the EVB group, see Data S1 section II.G). Our analyses also indicate a low level of IBD connection between the KH and medieval Ob (possibly proto-Ob-Ugric) groups in western Siberia, despite their close geographical proximity for 1,500–2,000 years after their estimated linguistic split.[74]

As the KH groups demonstrated notably strong IBD connectivity despite considerable geographical distances (low-Kama, cis-Urals, and trans-Urals), we investigated the extent of their shared population history. Multiple f_4-statistics demonstrate that the KH groups share the most alleles with groups from the Irtysh and Tobol regions throughout the IA and Migration Period. This evidence supports the hypothesis of a trans-Uralian origin for the later Karayakupovo-type ancestry. Our proximal qpAdm analysis shows that the low-Kama KH group can be modeled as a combination of Pyany-Bor/Mazunino and Tobol residual Sargatka-related ancestries, resulting in a distinct local KH variant. By contrast, the other KH groups have much lower Pyany-Bor/Mazunino ancestry. We demonstrate that the proxy ancestry sources we use in our qpAdm analyses (Pyany-Bor/Mazunino to the west of the Urals and Tobol late Sargatka to the east of the Urals) are much closer to the actual sources than those used in the Maróti et al. qpAdm approach,[65] which used modern Mansis, early/late Sarmatians, and Xiongnu as proxies for modeling the ancestors of the EMMs. Based on the connections with the KH individuals, we show that an important stratum of the EMMs (named by Maróti et al. as "Conqueror Asia Core") can be traced to the early medieval circum-Uralian region. Also, with qpAdm modeling, we detect local biological continuity from the IA to the early medieval times in these regions. However, unlike Maróti et al.,[65] we avoided extensive qpAdm screenings across multiple ancestry sources, closely timed to target groups, due to the high risk of false discoveries, as demonstrated by Flegontova et al.[91] Additionally, archaeologists have determined that the area east of the Ural Mountains, extending to the Ob River in the present-day Omsk region, had an extremely low population density in the EMA. The total number of excavated graves from the 6th to the 10th centuries CE does not exceed 300.[96] We have detected extended genetic signals indicating small population sizes both east of the Urals and in the cis-Urals KH group. These findings provide significant evidence of sparse and small population in these regions during this period.

The late medieval Chiyalik group that occupied the lower Kama region shows strong continuity within the Urals-Carpathian EMA IBD cluster. This is indicated by a high level of connectivity within the IBD-sharing community and limited IBD sharing beyond it. Moreover, they are similar to the KH groups on an allele frequency level. By contrast, individuals attributed to the Chiyalik culture in the Belaya River basin are more diverse genetically and the majority of them fall outside the Urals-Carpathian EMA IBD-sharing cluster. These findings suggest the potential influx of newcomers during the Golden Horde domination, when heightened transcontinental communications likely introduced various East Eurasian genetic ancestries that were rare in the Urals before (Data S1 section III.H). Considering the late 14th-century radiocarbon dates for the Chiyalik individuals, it is reasonable to assume the presence of remaining Magyars, archaeologically represented by a local variety of the Chiyalik culture, mainly in the lower Kama River Valley.[97,98] We also did not detect widespread Central European ancestry among the Chiyalik period individuals, suggesting no back migration from the late medieval CB. By analyzing the effective population size, we estimate that the low-Kama Chiyalik group comprised at least a few thousand individuals during late medieval times. These results suggest that descendants of the Urals-Carpathian EMA IBD-sharing community survived in late medieval times in considerable numbers in the Kama region. We assume that the low-Kama region near the Belaya-Kama confluence was the area that was called *Magna Hungaria* by Friar Julian in the 13th century.[29] In addition to this historically documented data, the regional toponymy suggests the presence of Hungarian-speaking groups there until the 16th century, when, after the collapse of the Golden Horde imperial space, they were absorbed into the late medieval populations of modern-day Bashkortostan, Tatarstan, and Udmurtia.[6,99,100]

Limitations of the study

The results of this study link the 10th-century CB with the medieval circum-Uralian region through the westward migration of the EMMs. Nevertheless, the scarce availability of medieval genomes spanning the vast space from Eastern Europe to western Siberia restricts our ability to assess contributions from many regions. While it was possible to identify one source of EMM ancestry in this study (in the Volga-Ural region), detecting the origin of other genetic components (e.g., the Baikal Neolithic-type ancestry) is challenging with the current data. Future research on samples from the whole migration route of the EMMs and their adjacent territories will be essential to reveal the full set of genetic sources of the 10th-century CB population.

RESOURCE AVAILABILITY

Lead contact

Requests for further information and resources should be directed to and will be fulfilled by the lead contact, Anna Szécsényi-Nagy (szecsenyi-nagy.anna@abtk.hu).

Materials availability

This study did not generate new, unique reagents.

Data and code availability

- Newly reported ancient sequencing data have been deposited at the European Nucleotide Archive (ENA) with the following accession number: ENA: PRJEB83577.
- This paper does not report original code.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

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AUTHOR CONTRIBUTIONS

Designed the study: B.G., L.V., A.T., P.F., D.R., and A.S.-N.; collected/provided archaeological material: L.V., A.T., P.L., D.A.S., A.S., N.P.M., A.S.Z., S.G.B., I.V.G., B.G.M., I.C., R.P., O.C., O.E.P., R.R.R., E.V.V., M.P.R., A.G. K., A.A.C., A.A. Khokhlov, I.R.G., S.Z., and F.S.; laboratory analysis: B.S. and N.R.; performed bioinformatics processing of the data: H.R., A.A., and S.M.; performed analysis: B.G., L.V., and A.S.-N.; wrote the paper: B.G., L. V., B.S., V.C., and A.S.-N.; wrote archaeological supplement: L.V., D.A.S., A. S.Z., S.G.B., I.V.G., O.K., D.G.B., A.A. Krasnoperov, and O.E.P.; supervised the manuscript: P.F., A.T., D.R., and A.S.-N.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Biological samples		
131 newly reported ancient individuals	This paper	N/A
Chemicals, peptides, and recombinant proteins		
23 HI-RPM hybridization buffer	Agilent Technologies	5190-0403
Herculase II Fusion DNA Polymerase	Agilent Technologies	600679
Pfu Turbo Cx Hotstart DNA Polymerase	Agilent Technologies	600412
50% PEG 8000	Anatrace	OPTIMIZE-82 100 ML
0.5 M EDTA pH 8.0	BioExpress	E177
Sera-Mag SpeedBead CarboxylateModified [E3] Magnetic Particles	Cytiva Life Sciences	65152105050250
silica magnetic beads	G-Biosciences	786–916
10 x T4 RNA Ligase Buffer	New England Biolabs	B0216L
Bst DNA Polymerase2.0, large frag.	New England Biolabs	M0537
UGI	New England Biolabs	M0281
USER enzyme	New England Biolabs	M5505
Buffer PB	QIAGEN	19066
Buffer PE concentrate	QIAGEN	19065
1 M Tris-HCl pH 8.0	Sigma Aldrich	AM9856
1 M NaOH	Sigma Aldrich	71463
20% SDS	Sigma Aldrich	5030
3 M Sodium Acetate (pH 5.2)	Sigma Aldrich	S7899
5 M NaCl	Sigma Aldrich	S5150
Ethanol	Sigma Aldrich	E7023
Guanidine hydrochloride	Sigma Aldrich	G3272
Isopropanol	Sigma Aldrich	650447
PEG-8000	Sigma Aldrich	89510
Proteinase K	Sigma Aldrich	P6556
Tween-20	Sigma Aldrich	P9416
Water	Sigma Aldrich	W4502
10x Buffer Tango	Thermo Fisher Scientific	BY5
50x Denhardt's solution	Thermo Fisher Scientific	750018
AccuPrime Pfx Polymerase (2.5 U/ul)	Thermo Fisher Scientific	12344032
ATP	Thermo Fisher Scientific	R0441
dNTP Mix	Thermo Fisher Scientific	R1121
Dyna MyOne Streptavidin C1 beads	Thermo Fisher Scientific	65002
FastAP (1 U/mL)	Thermo Fisher Scientific	EF0651
GeneAmp 103 PCR Gold Buffer	Thermo Fisher Scientific	4379874
Human Cot-I DNA	Thermo Fisher Scientific	15279011
Klenow Fragment (10 U/mL)	Thermo Fisher Scientific	EP0052
Maxima Probe qPCR 2xMM	Thermo Fisher Scientific	K0233
Maxima SYBR Green kit	Thermo Fisher Scientific	K0251
Maxima SYBR Green kit	Thermo Fisher Scientific	K0253
Salmon sperm DNA	Thermo Fisher Scientific	15632-011

(*Continued on next page*)

Continued

REAGENT or RESOURCE	SOURCE	IDENTIFIER
SSC Buffer (203)	Thermo Fisher Scientific	AM9770
T4 DNA Ligase	Thermo Fisher Scientific	EL0012
T4 DNA Ligase, HC (30U/mL)	Thermo Fisher Scientific	EL0013
T4 DNA Polymerase	Thermo Fisher Scientific	EP0062
T4 Polynucleotide Kinase	Thermo Fisher Scientific	EK0032
23 HI-RPM hybridization buffer	Agilent Technologies	5190-0403
Critical commercial assays		
Twist Alliance Ancient Human DNA Panel	Twist BioSciences	part number 106658
High Pure Viral Nucleic Acid Large Volume Kit	Roche	part number 05114403001
HiSeq X Ten Reagent Kit v2.5	Illumina	FC-501-2521
NextSeq 500/550 High Output Kit v2.5	Illumina	Cat.# 20024906
Deposited data		
Sequencing data from 131 newly reported ancient individual	This paper	ENA: PRJEB83577
Isotopic data of newly reported ancient individual	This paper	Table S1G
Software and algorithms		
BWA	Li and Durbin[101]	https://maq.sourceforge.net
ADNA-Tools	https://github.com/dReichLab/ADNA-Tools	https://github.com/dReichLab/ADNA-Tools
adna-workflow	https://github.com/dReichLab/adna-workflow	https://github.com/dReichLab/adna-workflow
EIGENSOFT	Patterson et al.[102]	https://github.com/DReichLab/EIG
ADMIXTURE	Alexander et al.[86]	https://dalexander.github.io/admixture
PLINK	Chang et al.[103]	https://www.cog-genomics.org/plink/2.0
GLIMPSE	Rubinacci et al.[76]	https://odelaneau.github.io/GLIMPSE
ancIBD	Ringbauer et al.[77]	https://github.com/hringbauer/ancIBD
Gephi	Bastian et al.[104]	https://gephi.org
ForceAtlas2	Jacomy et al.[88]	N/A
NetworkX	Hagberg et al.[105]	https://networkx.org
ADMIXTOOLS 2	Maier et al.[85]	https://uqrmaie1.github.io/admixtools
hapROH	Ringbauer et al.[87]	https://github.com/hringbauer/hapROH
Mobest	Schmid and Schiffels[106]	https://github.com/nevrome/mobest
KIN	Popli et al.[107]	https://github.com/DivyaratanPopli/Kinship_Inference
OxCal v4.4.2	Ramsey[108]	https://c14.arch.ox.ac.uk/oxcal.html

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Ancient individuals

Extensive description of the archeological context for the ancient individuals analyzed in this study is available in Data S1.

Sampling and sample selection

Based on years of collaborations with local archaeological experts governed by bilateral collaboration agreements, we selected the most relevant and available samples, which were in certain cases verified by radiocarbon dating. We did not perform a priori sample size calculations. Our aim was to achieve equal/representative sampling across the sites based on archaeological relevance and sample availability. Allocation to experimental groups was determined by geographical and chronological frameworks (see results and Data S1 for details). We aimed to collect graves for this research with archaeological materials characteristic of local cultures (see Data S1 section I for details). In the **trans-Urals**, our sampling involves individuals buried in the Sargatka cultural context from the middle Irtysh (300 BCE - 200 CE) and the Tobol (100-350 CE) River basins. The later trans-Uralian population groups are represented by burials attributed to the Medieval Nizhneobskaya, Potchevash, and Ust'-Ishim cultures, and the Uyelgi cemetery attributed to the Karayakupovo Horizon. In cases of inconsistency between radiocarbon dates and archaeological context dating at trans-Uralic sites, we preferred the dates based on the archaeological context due to the high probability of a freshwater reservoir effect in human bones from this area. In the c**is-Urals**, we undertook a dense sampling from sites attributed to the Maklasheevka Late Bronze Age (1100-900 BCE), Post-Maklasheevka Ananyino Early Iron Age (900-250 BCE), Pyany Bor Early Iron Age (250 BCE-150 CE), Mazunino (150-450 CE), and Nevolino (400-850 CE) archaeological entities. The Migration Period population archaeologically related to the cis-Uralian groups is represented by one individual from the Kushnarenkovo cultural context (550-700 CE). The sampling of the Medieval individuals of the Volga-Ural region involves the peripheral regions of the Volga Bulgaria, to the east of the main cities and densely populated areas. Our Medieval samples originate from burials carried out according to Muslim rites with some pagan elements, a pattern typically attributed to the Chiyalik culture. The sites of the **Karayakupovo Horizon** to the west of the Urals are represented by Bolshiye Tigany from the lower Kama region (800-900 CE). We also included some sites contemporaneous with the Karayakupovo Horizon, but archaeologically attributed to other groups: the Novinki-type sites (700-850 CE) and the Tankeevka cemetery (850-1000 CE), a local group of the Khazar-Khaganate nomads and the Early Volga Bulghars respectively (see further details in the supplemental information). Two individuals from the Polom cultural context and one from Lomovatovo represent the mid-Kama population groups that are contemporaneous with the people of the Karayakupovo Horizon sites.

Ethics declaration

The individuals studied here were all analyzed with the goal of minimizing damage, with permission from local authorities for each site of origin. Every sample is represented by archaeologists who hold the scientific copyright of the samples, have research agreements with either Hungarian, Austrian, Czech, or American scientific institutions affiliated with the authors, and are leading archaeological experts with specific knowledge of the samples and their archaeological context. They are authors of this paper or named in the Acknowledgments. Open science principles require making all data used to support the conclusions of a study maximally available, and we support these principles here by making fully publicly available not only the digital copies of molecules (the uploaded sequences) but also the molecular copies (the ancient DNA libraries themselves, which constitute molecular data storage). Those researchers who wish to carry out deeper sequencing of libraries published in this study should make a request to corresponding author D.R. We commit to granting reasonable requests as long as the libraries remain preserved in our laboratories, with no requirement that we be included as collaborators or co-authors on any resulting publications.

METHOD DETAILS

Ancient DNA data generation

A total of 77 samples were processed in the Budapest Laboratory of Archaeogenetics (Institute of Archaeology RCH) and shipped to Harvard Medical School. Sample surfaces were cleaned using mechanical methods and also UV irradiation. After that the bone powder was generated from petrous bones or teeth.[74] Three samples were prepared in Vienna, and seven samples were prepared in Ostrava and shipped to the Harvard laboratory (for further details see Table S1A). In dedicated clean rooms, we extracted DNA manually with spin columns[109,110] or automated using silica magnetic beads and Qiagen PB buffer on the Agilent Bravo NGS workstation[111] and converted it into barcoded double-stranded partial Uracil-treated libraries[112] or USER-treated single-stranded libraries[113] which we enriched in solution for sequences overlapping 1.24 million SNPs [1240k: Mathieson et al.,[33] Twist: Rohland et al.[114]] as well as the mitochondrial genome. For each library, we sequenced approximately 30 million read pairs (median of 29.747M reads) of each enriched library using Illumina instruments [NextSeq500, HiSeq X]; we also sequenced several hundred thousand sequences of the unenriched libraries (Table S1A). Each sample was processed individually, while the laboratory procedures were conducted alongside extraction blanks. Although there was no biological replication during the laboratory processing, we performed next-generation sequencing (NGS), which generated millions of sequencing reads.

Bioinformatic data processing

Samples were sequenced to generate raw paired-end reads; these were prepared for analysis by performing the following steps: preprocessing/alignment, and post-alignment filtering to enable variant calling. Raw reads were demultiplexed by using identifying barcodes and indices to assign each read to a particular sample, prior to stripping these identifying tags. Paired-end reads were merged into a single molecule using the base overlaps as a guide, Single-ended reads were aligned to the hg19 human reference genome (https://www.internationalgenome.org/category/grch37/) and the basal Reconstructed Sapiens Reference Sequence (RSRS)[115] mitochondrial genome using the same aligner of BWA (v0.7.15-r1140).[101] Duplicate molecules were marked based on barcoding bin, start/stop positions and orientation. For calling variants, a pseudo-haploid approach was used at targeted SNPs, where a single base was randomly selected from a pool of possible bases at that position filtering by a minimum mapping quality of 10 and base quality 20, after trimming reads by 2 base pairs at both 5' and 3' ends to remove damage artifacts. Sex determination, contamination estimation, mtDNA and Y-chromosomal haplogroup determination were conducted along with the mentioned other steps using tools implemented in the computational pipelines of the Harvard laboratory. Scripts with specific parameters are publicly available on GitHub at: https://github.com/dReichLab/ADNA-Tools and https://github.com/dReichLab/adna-workflow. Ancient DNA authenticity was verified using contamMix (v1.0.10511)[116] to detect heterogeneity in mitochondrial DNA sequences and ANGSD (0.921-3-g40ac3d6)[117] to detect heterogeneity in X chromosome sequences. Authenticity of the ancient samples was also evaluated by using pmdtools(v0.60.5).[118] A consensus for mitochondrial DNA was determined by using bcftools[119] and SAMTools.[120] Mitochondrial haplogroups were determined using HaploGrep2,[121] based on the phylotree database (mtDNA tree build 17).[122] For Y-chromosome haplogroup determination, we used YFull YTree v.8.09 (https://www.yfull.com/).

QUANTIFICATION AND STATISTICAL ANALYSIS

Principal component analysis (PCA)

PCA analysis was carried out with EIGENSOFT software[102] (version 5.0) with lsqproject: YES and shrink mode: YES settings. For the calculation of the PCs, we used modern-day Eurasians from the Affymetrix Human Origin array,[50] and projected the ancient samples onto the top PCs.

ADMIXTURE analysis

Before running ADMIXTURE[86] we pruned our dataset with PLINK (version 3).[103] We used the -geno 0.95 option to ensure that we included sites where most individuals were covered at least once. After that we used –indep-pairwise 200 25 0.4 parameters for linkage disequilibrium (LD) pruning. We performed supervised ADMIXTURE clustering with K=8. We used Neolithic/Early Bronze Age populations as sources to reflect the overall distribution of different ancestries through Eurasia. We aimed to include well-represented groups (more than 4 individuals) with high-coverage data and no close relatedness (up to third degree). We intentionally aimed to reconstruct a similar ADMIXTURE reference set presented in Zeng et al.[68] (Table S1D): Russia_Samara_EBA_Yamnaya, Turkey_N, Lithuania_EMN_Narva, Russia_Baikal_N, Russia_Altai_N, Russia_Yakutia_LNBA, Russia_WSHG and Russia_EHG. We have found this set useful in understanding the pre-historical genetic composition of our newly analysed individuals.

Genotype imputation

For imputation, we applied the software GLIMPSE (v.1.1.1)[76] with the 1000 Genome Project data as the haplotype reference panel to estimate genotype posterior probabilities and phased genotypes at bi-allelic SNP sites in the 1000G data, as described previously in Ringbauer et al.[77] For IBD analysis, we then restricted to variants in the 1240k SNP panel, which are informative for ancient DNA studies. These VCF files were generated by downsampling the imputed 1000G SNP set to 1240k SNPs. A full description of the imputation pipeline is provided in Supplementary Note 3 (see also Figure 1b of Ringbauer et al.[77]).

IBD-sharing analysis

To infer identical by descent (IBD) segments, we applied the program *ancIBD (v0.7)*[77] to the imputed genotype data. As recommended by Ringbauer et al.[77] for accurate IBD detection, we only included individuals that have a maximum genotype probability >0.99 for at least 70% of all imputed 1240k SNPs on Chromosome 3[77] and call IBD segments >8 centimorgan long. In the downstream IBD segment analysis, we included all individuals that matched our research criteria, based on geographical location (coordinates in North Eurasia) and on timeframe (from ~1000 BCE to modern times).

IBD-sharing network

All IBD networks were built using the Gephi (v.0.10.1) software.[104] The graph's edges were weighted based on the length of the most substantial shared IBD segment between two individuals, referred to as nodes. To filter spurious connections, we removed IBD segments below a threshold of 9 cM and connections that spanned over 600 years (for non-filtered network see Figure S1B). Additionally, we maintained nodes connected by at least two edges and focused on the largest interconnected segment of the graph. Visualization was achieved using the MultiGravity ForceAtlas 2, a force-directed layout algorithm.[88] In the processed graph, clusters were discerned using the Leiden algorithm,[89] maintaining algorithmic independence. We explored several key metrics using the Python package NetworkX[105]: degree centrality as well as within-module degree (k_W), representing connections within each predefined cluster; and between-module degree (k_B), capturing connections between different clusters. To assess the average IBD per link within and between modules, we used sum IBD segments > 12 cM as weighted edges, considering our predefined groups as modules.

f-statistics-based methods

We computed f_4-statistics (for samples with >200k SNPs covered on the 1240k panel) with the ADMIXTOOLS 2 software package[85] with the qpDstat (f4Mode: YES; printsd: YES) packages. For f_4-statistics we used the form (Mbuti, Target; Test1, Test2) to check the genetic affinities between two possible ancestral populations. For the pairwise cladality test, we used the 'qpWave pairs' test from the R software package ADMIXTOOLS 2 with default settings.[81,85] We designated 10th to 11th-century Carpathian Basin individuals as targets (each individual was analyzed separately) and the five Medieval Volga-Ural region groups as left populations (MidIrtysh_Usthim, TransUral_KH, CisUral_KH, LowKama_KH, and MidVolga_EVB). The right populations included Mbuti, Italy_North_Villabruna_HG, Russia_MA1_HG, Russia_Caucasus_Eneolithic, Russia_Ekven_IA, Russia_DevilsCave_N, Russia_UstIda_LN.SG, Russia_KolymaRiver_LN, Russia_EHG, Turkey_N, and Iran_GanjDareh_N. For the qpAdm analysis (for samples with >200k SNPs covered on the 1240k panel), we used the ADMIXTOOLS 2 R package,[85] with the following elected outgroups: Mbuti, Ami, Italy_North_Villabruna_HG, Turkey_N.SG, Russia_Ekven_IA.SG, Russia_DevilsCave_N.SG, Russia_Sidelkino_HG.SG, Russia_Caucasus_Eneolithic, Tarim_EMBA1. We avoided using the rotating approach as in complex demographic histories the direction of the gene flows cannot be defined accurately.[91]

Mobility estimation (mobest)

To investigate potential origins of the Early Medieval Magyars, as well as the Karayakupovo Horizon individuals, we conducted a mobility estimation analysis (mobest).[106] For comparison, we included Late Iron Age/Migration Period samples, as detailed in Table S1H and Figure S4E. The analysis was based on the first two principal components of the PCA described above, using the standard settings (https://nevrome.de/mobest).

Consanguinity test (ROHs)

Detecting runs of homozygous blocks with *hapROH*[87] software can provide signals of consanguinity, whereas small homozygous runs are indicative of a small recent effective population size. The program was used with default parameters for pseudo-haploid genotypes with at least 400k SNP covered. The N_e module of this program was also used to estimate effective population sizes with confidence interval, considering 4-20 cM ROHs.

Biological relatedness

We used KIN[107] to assess potential relatedness among the newly sampled individuals. KIN can detect relationships up to the third degree and distinguish between parent–child and sibling pairs. We applied a log-likelihood ratio threshold of >2 (Table S1I).

Radiocarbon dating

Radiocarbon dating of 14 DNA samples was performed in the Penn State's Radiocarbon Laboratory (PSUAMS codes). The BP values were calibrated in the OxCal program 4.4 with a calibration curve IntCal 20.[108,123]

Supplemental figures

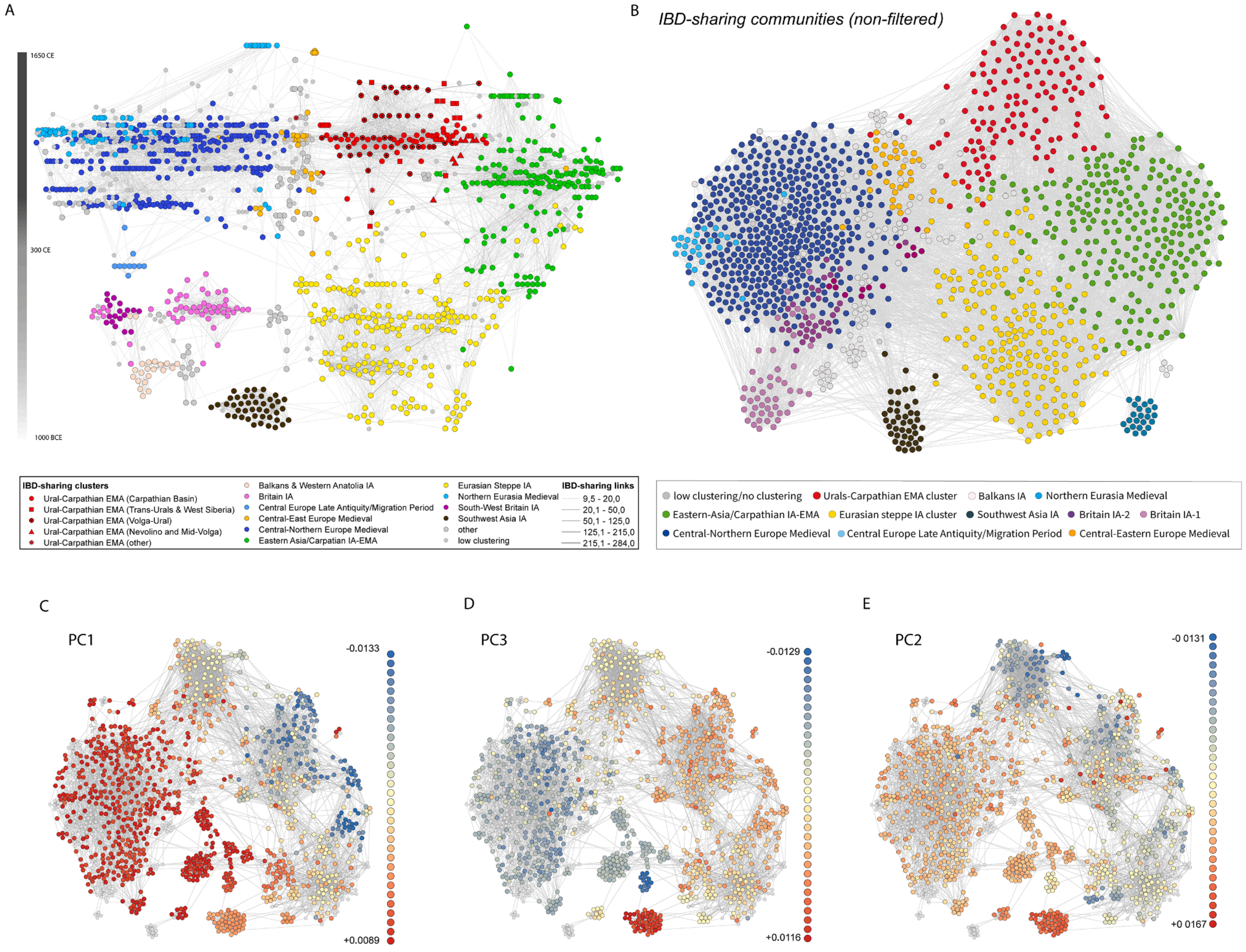


Figure S1. Detailed analyses of the IBD network: Time-ordered network and PC projections, related to Figure 3

(A) Time-ordered IBD-sharing network version of Figure 3.

(B–E) (B) The non-filtered version of the IBD-sharing network, corresponding to Figure 3. The cluster symbols are simplified here for the Urals-Carpathian EMA cluster individuals for easier interpretation. Individuals of the IBD-sharing network (Figure 3) are also colored using PC1 (C), PC3 (D) and PC2 (E) values, calculated based on modern Eurasian individuals.[50]

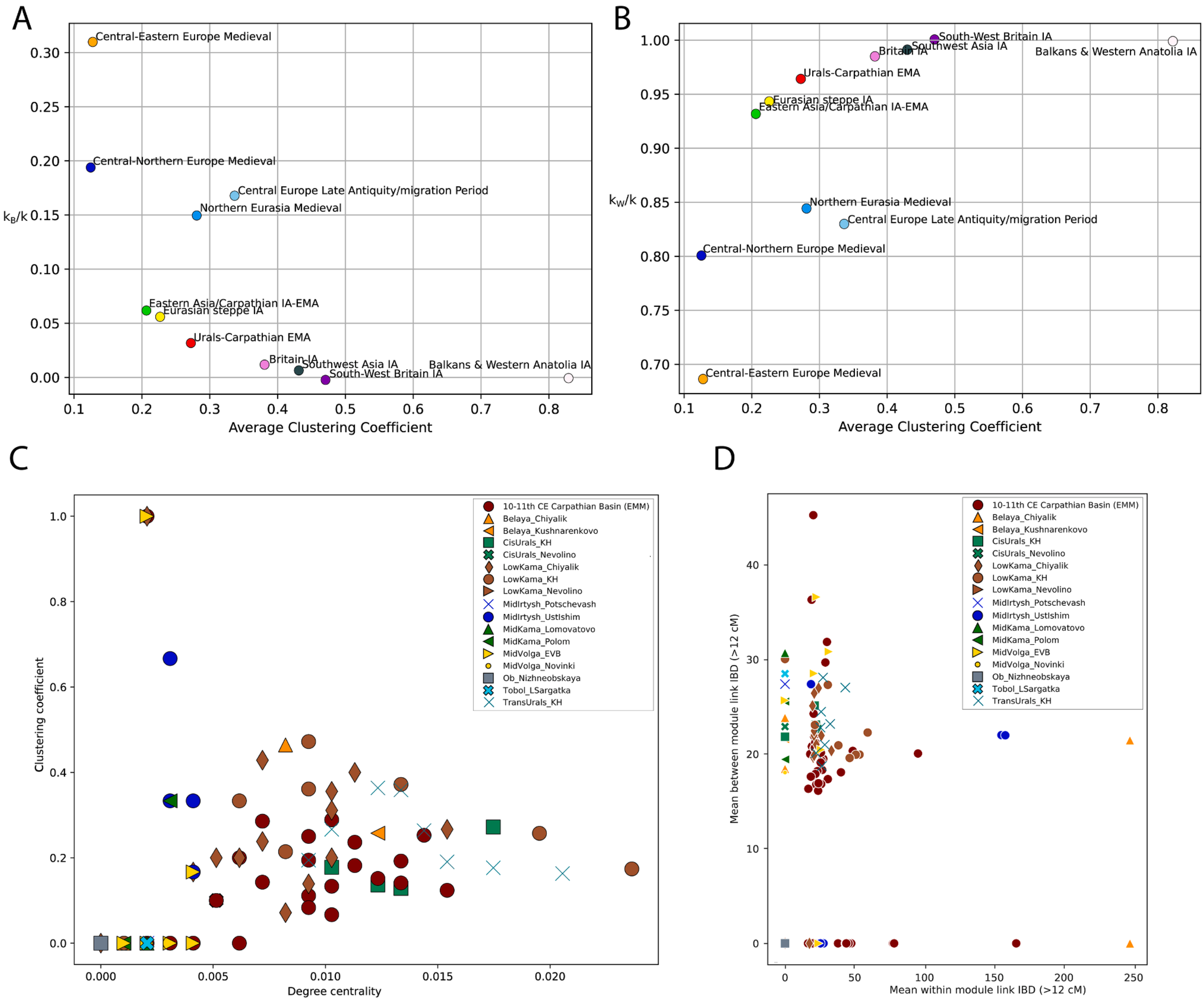


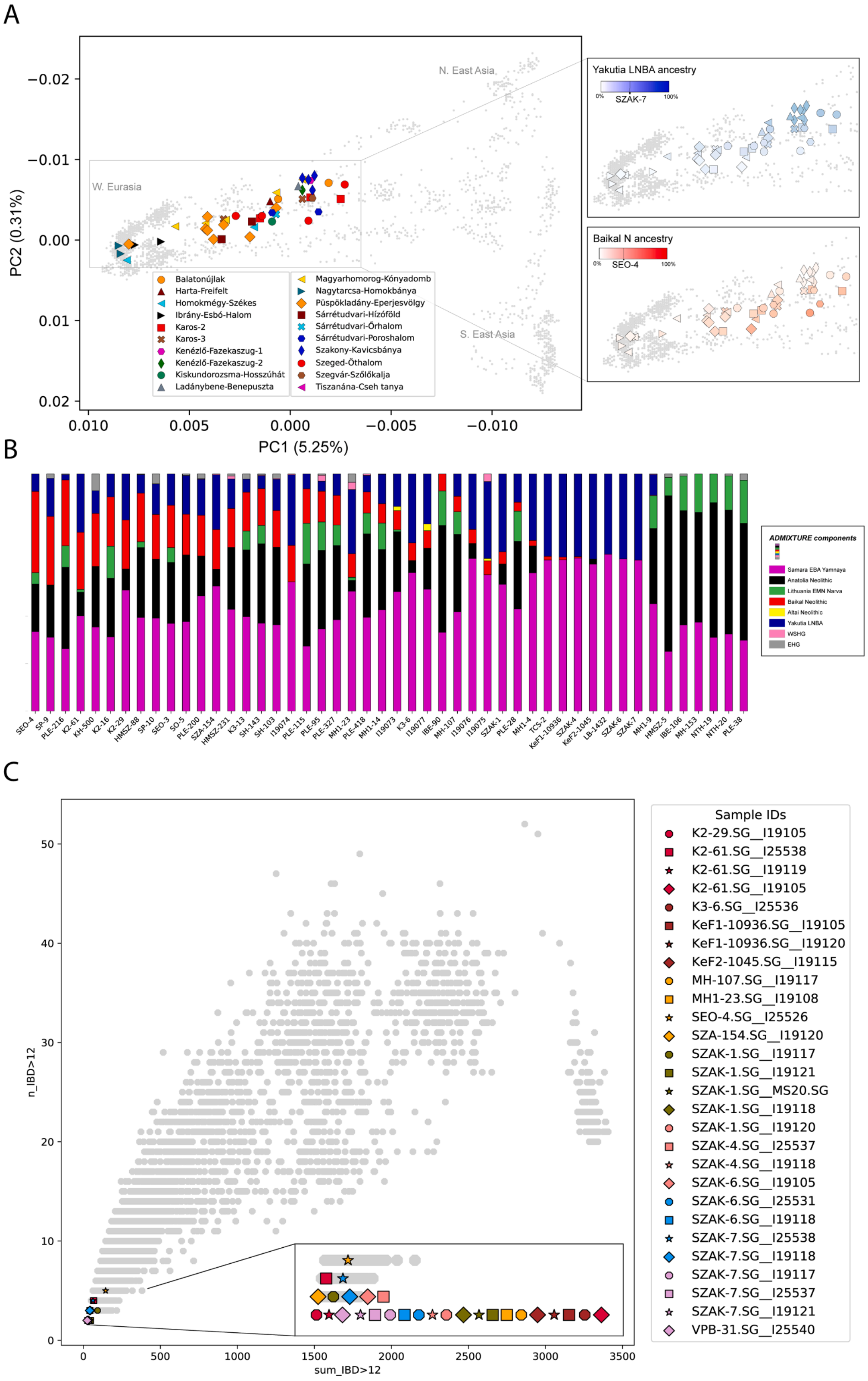
Figure S2. Analysis of clustering coefficients and module connections in IBD-sharing networks, related to Figure 3

(A) A scatterplot displaying the average clustering coefficient of each cluster versus the ratio of between-module connections (kB) to the total degree (k) of the cluster. Each cluster is identified using the Leiden algorithm, which determines community structure in the network. The 'modules' in this context refer to the clusters defined by this algorithm.

(B) A scatterplot displaying the average clustering coefficient of each cluster versus the ratio of within-module connections (kw) to the total degree (k) of the cluster. Each cluster is identified using the Leiden algorithm, which determines community structure in the network. The "modules" in this context refer to the clusters defined by this algorithm.

(C) Scatterplot of degree centrality versus clustering coefficient for individuals in the Urals-Carpathian EMA cluster.

(D) Scatterplot of between-module strength versus within-module strength in the Urals-Carpathian EMA cluster (modules defined by groups).



(legend on next page)

Figure S3. Comprehensive analysis of EMMs in the Urals-Carpathian EMA cluster: PCA projections, IBD segment distribution, and supervised ADMIXTURE analysis, related to Figures 2 and 3 and Table 1

(A) PCA projection with estimates of the Yakutian LNBA and Baikal Neolithic ancestry components from the supervised ADMIXTURE analysis presented in Figure 2B is shown on the right. In the case of the Yakutian LNBA ancestry, a deeper blue color means a higher proportion of this ancestry, while a deeper red color means a higher proportion of the Baikal Neolithic ancestry. Gradients as legends represent the scale of the respective ancestry, with two given EMM samples exhibiting the highest level of each component in the analyzed dataset.

(B) A supervised ADMIXTURE (K = 8) analysis of 10th-century CB individuals from the Urals-Carpathian EMA IBD-sharing community.

(C) IBD segment sharing patterns between individuals from the Volga-Ural region and early medieval CB (Table S2). Only pairs of individuals sharing at least two segments longer than 12 cM were considered. Grey dots indicate reference relations, presented as in Ringbauer et al.[77]

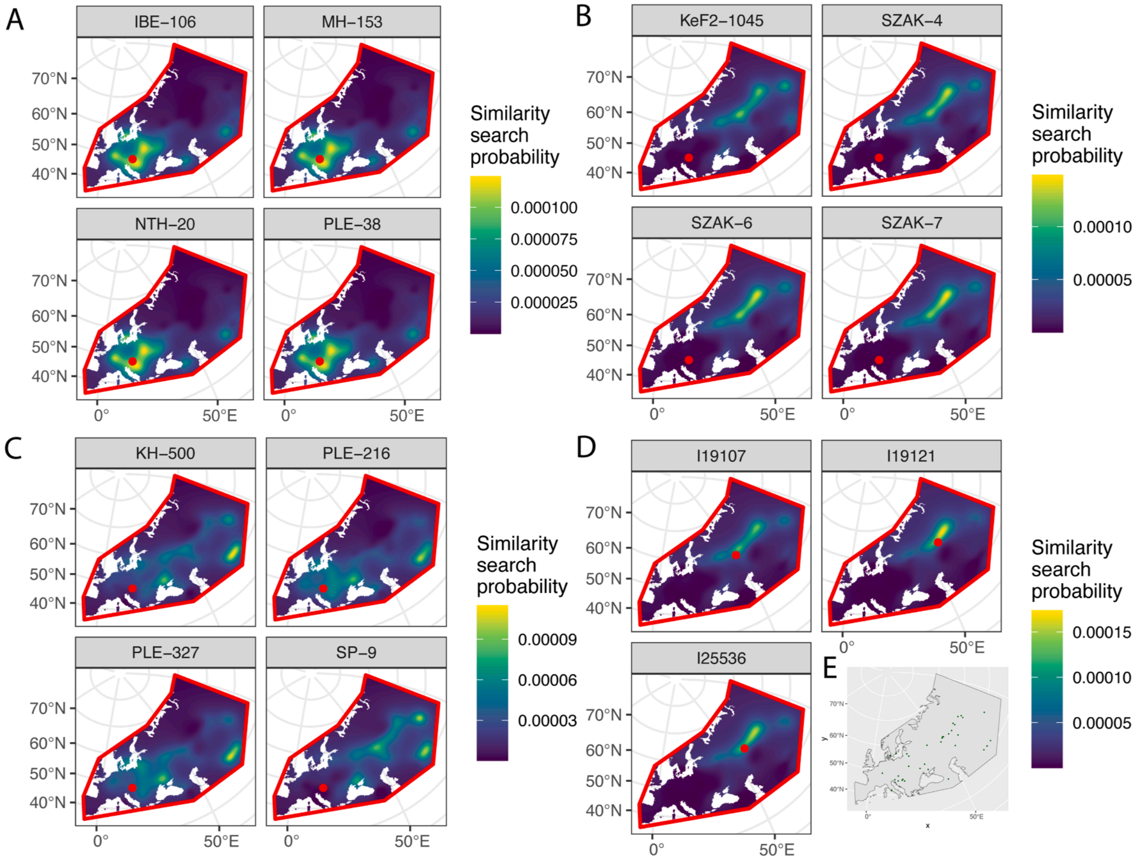


Figure S4. Mobest estimation for individuals in the Urals-Carpathian EMA cluster, related to Figures 2, 3, and 4

(A) Four individuals are presented with high levels of European ancestry from the Urals-Carpathian EMA cluster.

(B) Four individuals are presented with high levels of Yakutian LNBA ancestry from the Urals-Carpathian EMA cluster.

(C) Four individuals are presented with high levels of Baikal Neolithic ancestry from the Urals-Carpathian EMA cluster. (A–C) Red dots indicate the geographical coordinates of the respective sites of the samples.

(D) Three individuals are shown, each representing one sample from the low-Kama, trans-Urals, and cis-Urals KH groups, with red dots marking their geographical coordinates.

(E) Distribution of reference samples used in the mobility estimation is shown; precise dating and geographical origins are detailed in Table S1H.

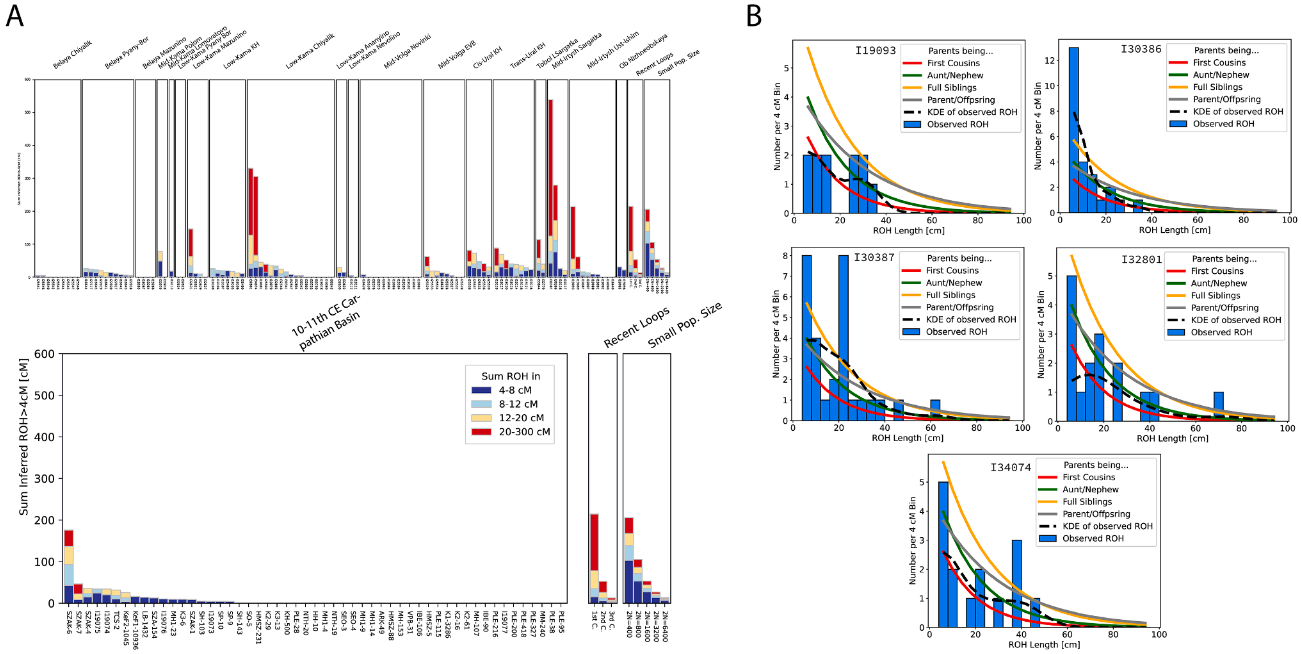


Figure S5. hapROH analysis and individual ROH histograms: Volga-Uralian and 10th–11th CE CB individuals, related to Figure 3

(A) hapROH results for the Volga-Uralian and 10th–11th CE CB individuals (both newly presented and previously published data[65]).

(B) Individual ROH histograms of individuals that show a high (>50 cM sum IBD from >20 cM segment) signal of parental relatedness. They show marriages of at least first-cousin-level relatives.