



Descent, marriage, and residence practices of a 3,800-year-old pastoral community in Central Eurasia

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Our understanding of prehistoric societal organization at the family level is still limited. Here, we generated genome data from 32 individuals from an approximately 3,800-y-old burial mound attributed to the Bronze Age Srubnaya-Alakul cultural tradition at the site of Nepluyevsky, located in the Southern Ural region of Central Eurasia. We found that life expectancy was generally very low, with adult males living on average 8 y longer than females. A total of 35 first-degree, 40 second-degree, and 48 third-degree biological relationships connected 23 of the studied individuals, allowing us to propose a family tree spanning three generations with six brothers at its center. The oldest of these brothers had eight children with two women and the most children overall, whereas the other relationships were monogamous. Notably, related female children above the age of five were completely absent from the site, and adult females were more genetically diverse than males. These results suggest that biological relationships between male siblings played a structural role in society and that descent group membership was based on patrilineality. Women originated from a larger mating network and moved to join the men, with whom they were buried. Finally, the oldest brother likely held a higher social position, which was expressed in terms of fertility.

biological kinship | prehistoric family | monogamy/polygamy | palaeogenomes

The evolution of family structures in prehistoric Europe has been the subject of great interest and much speculation since the second half of the 19th century (1–3). Although older approaches (Marxist, Weberian, and Eurocentric) emphasized an early divergence in family structures between the Orient and the Occident, more recent ethnohistorical research suggests continuity across Bronze Age Eurasia due to similar production systems and comparable modes of holding and transmitting property (4, 5). Changes in kinship patterns and family organization have also been discussed in the context of major shifts in subsistence and production activities; most notably the emergence of agricultural economies in the Neolithic, and the development of pastoral elites in the Bronze Age (6). Scientific approaches that allow us to assess the validity of these narratives in light of prehistoric data, and with reference to the three dimensions of kinship—descent, marriage, and residence (7)—have only recently emerged. Systems of descent that assume biological relationship, i.e., actual blood ties between members of the group, are common but not universal (8, 9). Recent developments in the field of palaeogenomics provide high-resolution methods to determine biological relationships, and reconstruct ancient pedigrees and possible descent systems in the distant past.

To date, studies combining bioarchaeological, anthropological, and palaeogenetic evidence on kinship have inferred family structure among Upper Palaeolithic foragers (10), Neolithic farmers (11–19), and Bronze Age pastoralists and sedentary farmers (11–15, 20–25), as well as more recent early Medieval populations (26–28). With some exceptions (e.g., ref. 18), most of these studies were based exclusively on genomes from archaeological sites in Western Eurasia. Although earlier Neolithic kinship systems in Anatolia and Europe reflected diverse postmarital residence practices and the occasional absence of biological relationships among coburials (7, 13, 14, 17, 29, 30), later Neolithic and Bronze Age kinship patterns appear to have been to some extent repetitive and were dominated by patrilineal descent and patrilocal residence practices (11–15, 20–25).

Background to the Study

We examined an approximately 3,800-y-old burial group from the Nepluyevsky barrow necropolis in the center of the Eurasian Steppe, more precisely in the Southern Ural region on the border between tectonic Europe and Asia (Fig. 1). The necropolis was

Significance

To date, knowledge about the biological side of familial organization in prehistoric societies has been limited. In particular, little is known about the structure of Bronze Age society in Eurasia at the village or household levels. Here, the skeletal community of a burial mound in the Southern Urals was studied using integrative methods from the fields of archaeology, anthropology, and palaeogenomics. It is suggested that the descent system of the 3,800-y-old livestock herders at Nepluyevsky was patrilineal and primarily determined by consanguinity between brothers. Monogamy was the marriage norm, and postmarital residence was patrilocal, with female membership being transferred to the husband's group.

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Fig. 1. (A) Top view of the kurgan under excavation in the Central Eurasian landscape (photo by S. Sharapova). (B) Location of the Nepluyevsky necropolis in the Southern Urals (in blue) with locations of archaeological sites (red dots) from which individuals were identified sharing two or more IBD segments of at least 12cM with individuals buried at Nepluyevsky.

excavated between 2015 and 2017 and is located on the right bank of the Yandyrka, a small tributary of the Akmulla river, close to the village of Nepluyevka, Kartaly district, in modern-day Russia.

The burial mound under investigation, Kurgan 1 at Nepluyevsky, is one of the largest in a localized cluster of 38 mounds, loosely divided into northern and southern groups, and containing at least 44 individuals in total. Based on ^{14}C dating of the graves and recovered material, Kurgan 1 has been assigned to the so-called “Srubnaya-Alakul” variant (*SI Appendix, section 1*), which is primarily found in the interaction zone between the “Srubnaya” culture, west of the Urals as far as modern-day Ukraine, and the “Alakul” culture further to the East (31).

Societies in the Southern Urals appear to have descended from populations that formed part of the wider Eurasian network first established during the Early Bronze Age, ~3,000 BC (32–38). They are thought to have originated in the Western Eurasian steppe, a region that experienced an influx of Central and Eastern European populations associated with “Corded Ware” and “Fatyanovo” objects and material practices (39, 40). Previous palaeogenomic studies have characterized the temporal genomic patterns on a transregional level (32–38), but little is known about the social and family organization of these Bronze Age societies at the local or community scale.

Traces of settlement occupation associated with a sedentary or semisedentary lifestyle are found at some distance (ca. 1.6 km)

from the necropolis, on the opposite side of the Yandyrka river. Depressions and collected finds indicate that houses were grouped into settlements near the surrounding riverbanks, which were probably used as grazing lands for cattle (41). Traces of metal-working in several houses in the wider locality suggest a well-established local metal industry (31, 42, 43).

Animal husbandry and cattle pastoralism appear to have been the dominant way of life. Traces of milk protein from cattle and sheep were recently found in the dental calculus of two of the individuals (b5-1, b9-1) buried in Kurgan 1 (44). Conversely, there is no evidence for cereal agriculture at Nepluyevsky, and dental pathologies of remains from Nepluyevsky and other contemporary sites of the Southern Ural region are consistent with a diet rich in animal protein and poor in carbohydrates [SI Appendix, section 2, (45–47)]. Although pastoralism tends to lead to social inequality due to the differential accumulation of wealth afforded by large herds, there is currently no evidence for strong hierarchies in Srubnaya-Alakul groups beside the construction of large burial mounds such as Kurgan 1 (48–50). Descent systems have been shown to correlate with subsistence practices and production economies. For instance, human societies that keep large livestock are rarely matrilineal (51). We therefore hypothesized a patrilineal system of descent in Nepluyevsky.

Results

Anthropology, Mortality Profile, and Duration of Occupation.

Anthropological examination of the remains revealed no significant signs of trauma indicative of sustained conflict or intergroup violence—only signs of minor healed fractures in five women and two men (49). The distribution of heritable dental traits provides some evidence of close biological relatedness among those buried beneath the kurgan [SI Appendix, section 2; (52)]. We observed an unequal distribution of the sexes among the anthropological age groups. A life table with all identifiable individuals ($N = 44$) showed that the proportion of females ($N = 15$) was not significantly different from males ($N = 12$) in the 0 to 5 y age group ($P = 0.70$). However, males ($N = 9$) were more frequent than females ($N = 1$) among children and adolescents (age group 5 to 20 y; $P = 0.02$). Among adults, a sex ratio of one could not be rejected (males: $N = 6$, females: $N = 9$; $P = 0.60$). An estimated 39% of all identifiable individuals died/disappeared before the age of 5, and 57% before reaching reproductive age (>15 y). Life expectancy was estimated to be 14 y (e_0) at birth, and 31.6 y (e_{20}) for those reaching adulthood. When analyzed separately, females had shorter life expectancies compared to males, both as newborns (females: 12 y vs. males: 13.4 y) and adults (females: 27.8 y vs. males: 36.2 y; see SI Dataset).

Radiocarbon data were used to model the duration of use of Kurgan 1. Dates obtained for 26 individuals ranged from 1914 to 1751 cal BC (MAMS 54915), to 1744 to 1626 cal BC (MAMS 54926; see Table 1 and SI Appendix, Fig. S3.6). Using OxCal (53), we estimated an upper limit of 52 y (99.7% probability, SI Appendix, Figs. S3.4 and S3.5) for the duration of use. However, the agreement indices for individuals b2a-1 and j15-2 indicate that they were probably buried at a slightly different time. We then devised an approach to directly test whether the interred individuals died at around the same time or within small windows of time (2, 3, and 10 y; see Materials and Methods for details on the approach). Although the model that all individuals died within a 2-y window (SI Appendix, Fig. S3.7) could be rejected, models with 3- and 10-y windows could not (SI Appendix, Fig. S3.7). Taken together, the results leave open the possibility of a relatively short deposition period for the entire burial population. However,

it should be recognized that the power to reject models of near-contemporaneous death is low due to the wide posterior distribution of calibrated dates stemming from the wiggled shape of the ^{14}C calibration curve in that period.

Palaeogenomes. Full genomes originating from 30 human petrous bones were sequenced to an average autosomal read depth of 1.46X (0.8 to 2.3X). In addition, DNA extracts from 25 teeth were enriched for 1240k single-nucleotide polymorphisms (SNPs), of which 24 yielded sufficient human DNA (SI Dataset). In total, genomic data from 32 individuals were available for further analysis (10 shotgun only; 3 capture only; 19 shotgun and capture). DNA damage patterns consistent with ancient DNA (aDNA) were present in all libraries. Contamination levels in mitochondrial (MT) sequences (55) were estimated to be below 1% in all genomes, consistent with estimates based on autosomal reads (56), except for one library from individual b7-1, which showed an autosomal contamination estimate of over 15% and was therefore excluded from further analysis (SI Dataset). We found that two petrous bone samples originated from the same individual (b6). Molecular sexing following the approach described in ref. 57 revealed 18 males (XY) and 14 females (XX) and was consistent with the morphological/anthropological assessments as far as they could be made on the available skeletal elements, except for b4-1 who was initially classified as female (SI Appendix, Table S2).

Diversity in Uniparental Markers. MT haplogroup diversity was high among the individuals from Nepluyevsky Kurgan 1 (h_{mt} : 0.7204 ± 0.0166). The assigned mtDNA lineages belonged to haplogroups H, N, K, T, and U, which are typically associated with Western Eurasian populations (58). In contrast, the Y-haplogroup diversity was low (h_{y} : 0.2157 ± 0.0679), with all male individuals belonging to haplogroup Q1b, except individuals b8-2 and b24-1 who were assigned to haplogroup R1a. Haplogroups of the R1a branch have previously been reported for Srubnaya-Alakul individuals from the Southern Urals (36) and were frequent among Bronze Age individuals from the Eurasian Steppe and Eastern Europe (32, 37, 38). In contrast, the prevailing Q1b(2) family of Y-chromosomal lineages is more commonly found among contemporary southern Siberian and Mongolian populations (35, 37, 38, 59, 60).

Kinship and Pedigree Reconstruction. No excess of long runs of homozygosity (ROHs)—indicative of recent inbreeding—was detected (61). We observed a general decrease in the length and number of ROHs over time in the region (SI Appendix, section 6.4), similar to the results described in ref. 36. Applying KIN (62) to the dataset led to the detection of 35 first-degree, 40 second-degree, and 48 third-degree relationships. All pairwise relationships were further confirmed, using the approach described in ref. 17. Pairwise relatedness coefficients (r) were higher between males, compared to females, especially when assessed only for adult individuals (r_{m} : 0.1133 ± 0.1435 ; r_{f} : 0.0260 ± 0.1447 ; $t = -6.096$, $P < 2.820\text{e-}09$, SI Appendix, Fig. S6.6). This finding is in agreement with sex-specific outgroup f_3 statistics in the form of $f_3(\text{Khomani}; \text{Test}_X, \text{Test}_Y)$, with Test_X and Test_Y being all possible combinations of adult Nepluyevsky individuals (SI Appendix, Fig. S6.3), yielding a significantly higher mean pairwise f_3 value for males compared to females (male mean: 0.1345 ± 0.0176 vs. female mean: 0.1169 ± 0.0011 , $P < 4.2441\text{e-}07$, $t = 5.4140$). This result indicates a higher average degree of relatedness among men than among women, which is consistent with the observation of low overall Y-lineage diversity compared to MT diversity.

We reconstructed the pedigree of a multigenerational family based on the degrees of biological relatedness (see Fig. 2; see

Table 1. Information pertaining to the 32 individuals sequenced as part of this study

Burial and individual ID	Genetic sex	Age (years)	Calibrated date BC 2 σ range (95.4%)	Data	MT	Y
b1-1	XY	13 to 17	1882 to 1747	S,C	H15a1	Q1b2b
b1-2	XY	7 to 11	1881 to 1699	S,C	H15a1	Q1b2b
b2a-1	XY	18 to 20	1878 to 1689	S,C	U2e2a1a2	Q1b
b2a-2	XX	20 to 25	1914 to 1751	S,C	U4b1a1a	
b2b-1	XY	20 to 30	1895 to 1706	S,C	U2e2a1a2	Q1b2b
b3-1	XX	3 to 4		C	U2e2a1	
b4-1	XY	18 to 20		C	H15a1	Q1b2
b6-1	XY	4 to 6	1880 to 1694/1862 to 1622	S,C	H6a1b	Q1b2b
b7-1	XY	9.5 to 12.5	1871 to 1627	S,C	T2b34	Q1b2b
b8-1	XX	18 to 22	1874 to 1640/1878 to 1693	S,C	U5a1b1f	
b8-2	XY	17 to 19	1877 to 1642	S,C	U5b1b	R1a1a1b2a
b10-2	XY	4 to 8	1875 to 1688	S,C	K2b1a1	Q1b
b13-1	XY	6 to 8	1878 to 1692	S,C	U5a1b1	Q1b2b
b17-1	XX	4 to 8 M		S	H2b	
b22-1	XY	6 to 12 M	1880 to 1694	S	U1b2	Q1b2b
b24-1	XY	13.5 to 16		C	T2b4e	R1a1a1b2
b25-1	XX	25 to 35	1873 to 1635	S,C	T2b34	
b26-1	XX	14 to 16	1875 to 1660	S,C	N1a1a1a1	
b27-1	XX	<6 M	1878 to 1691	S	H15a1	
b28-1	XY	35 to 45	1866 to 1628	S,C	H15a1	Q1b
b28-2 (from b29)	XX	26 to 42	1881 to 1699	S	K2b1a1	
b30-1	XY	18 to 22	1879 to 1689	S,C	T1a1	Q1b2b
b31-1	XY	3 to 5	1881 to 1694/1878 to 1693	S,C	T1a1	Q1b2b
b32-1	XY	>50	1874 to 1637	S,C	U2e2a1a2	Q1b2b
b32-2	XX	25 to 35	1879 to 1693	S,C	H15a1	
b33-1	XX	3 to 5	1873 to 1641	S,C	U1b2	
j3-1	XY	Newborn	1876 to 1642	S	U5a1g1	Q1b2b1a
j6-1	XY	4 to 8 M		S	U2e2a1d	Q1b2b
j9-1 (bones in pot)	XX	<1.5	1879 to 1694	S	U5b2c	
j11-1	XX	<2		S	H2b	
j15-1	XX	8 to 16 M	1875 to 1688	S	H3g	
j15-2	XX	<6 M	1744 to 1626	S	H15a1	

The combination of the first letter (b = burial and j = jama) and the number indicates the burial; the trailing number refers to the respective individual. Anthropological age at death estimates are reported in years, except in cases where M [month] is present in the column. The column "Data" indicates the sequencing strategy used [S: shotgun, C: 1240K capture]; MT and Y report mitochondrial and Y-chromosomal (ISOGG) haplogroups, respectively. All dates were calibrated in OxCal v4.4.4 (53) using atmospheric data from ref. 54. Multiple entries correspond to separate dates for the same individual. See *SI Appendix, Figs. S3.1 and S3.2* for details.

SI Appendix, section 2 for a comparison with morphological traits), accounting for all constraints imposed by genetic sex, age at death, ^{14}C dates, and MT- and Y-lineages. The reconstructed pedigree spanned three generations and connected 33 individuals, of whom 21 were sequenced in this study. The existence of the remaining 12 people was indirectly inferred from the gaps in the family tree. At the center of the tree were six brothers with their wives (or partners), children, and grandchildren. The founding parents of the six brothers could not be identified among the individuals buried in Kurgan 1. Three brothers and their wives were directly detected among our sequenced individuals, whereas the remaining three were indirectly inferred through their children.

B32-1, a male more than 50 y of age, was the only man who was found to have had children with more than one woman. He was buried with a woman (b32-2) between 25 and 35 y of age, with whom he had at least seven children: two daughters (b27-1 and j15-2) and five sons. Four sons could be found in the kurgan

(b1-1, b1-2, and adult sons b28-1 and b4-1), one son was inferred through the presence of a grandson (b6-1). In addition, that same male (b32-1) was found to have another son (b10-2) with female b28-2, who was buried close to one of his adult sons (b28-1). Individuals b2b-1 (adult male) and b25-1 (adult female) were connected through a son, b7-1. An additional adult brother, b2a-1, was buried with an adult woman, b2a-2, but without a common child. Furthermore, the r estimates revealed that j11-1 and b17-1, both of whom were sampled from a left pars petrosa, were monozygous twins who could be placed in the tree as nieces to the existing three brothers in the second generation. Similarly, b30-1 and b22-1 were also found to be nephews of the three brothers in our dataset. For b22-1, additional relatives were identified, including a nephew (j3-1) through a brother and a niece (b33-1) through a sister.

Eleven individuals could not be placed in the pedigree based on the available information. However, four of them—namely,

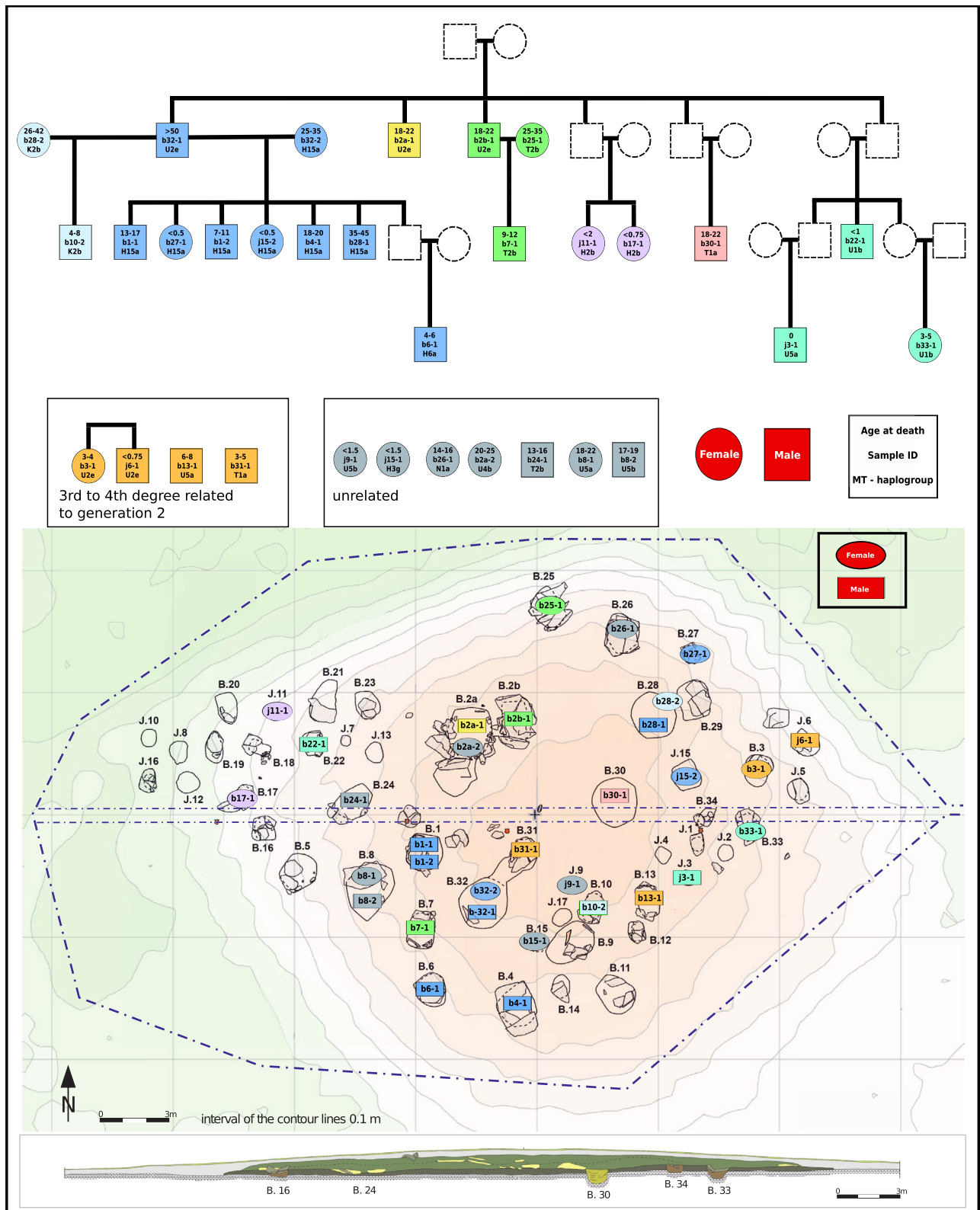


Fig. 2. A representation of the pedigree, inferred from relationship coefficients r , genetic sex, age at death in years, and MT- and Y-haplogroups. The reconstructed pedigree spans three generations and connects 33 individuals, 21 of which were sequenced in this study; the existence of the remaining 12 was inferred (uncolored). First-generation individuals, their spouses, and their descendants are grouped by color. The same color code is used to indicate individual associations with graves and “jamas” (pits) in the kurgan. A larger version of both can be found in *SI Appendix, Figs. S6.7 and S6.8*.

male infants b13-1, b31-1, as well as male infant j6-1 and his older sister b3-1—were related to individuals of the pedigree to the third or fourth degree. The remaining seven individuals—two adult females (b8-1 and b2a-2), one juvenile female (b26-1), two female

infants (j9-1 and j15-1), and two male juveniles (b8-2 and b24-1)—were not related to any of the other individuals closer than the fifth degree. However, there were shared identity-by-descent (IBD) segments of more than 12 cM between each of them and

one or more family members. Although they cannot be considered close biological relatives, these individuals were at least members of the same population. The two males in this group of distant relations were the only ones with a Y haplogroup other than Q1b(2), namely R1a1a1b2.

By extending the ancIBD approach to a larger set of over 1,000 contemporary genomes from the broader steppe region, we identified several additional individuals sharing two or more IBD segments ≥ 12 cM with one or more Nepluyevsky individuals. They originated from 21 archaeological sites, many of which were nearby, such as Kamennyi Ambar or Bolshekaraganski. However, several sites were from regions hundreds or even thousands of kilometers away (Fig. 1 and *SI Appendix, section 6* and *SI Dataset*).

Summary Patterns of Genomic Variation. Projection PCA on autosomal markers showed that the majority of the Nepluyevsky individuals clustered in close proximity to published Srubnaya-Alakul-associated individuals (36). This “main cluster” was located near Middle Bronze Age Sintashta individuals, as well as individuals from the Fatyanovo culture from modern-day Russia (63). Only two individuals were found outside this main cluster: b28-2, a female who is located further to the lower right in Fig. 3 in close proximity to Iron Age Sarmatians, and b10-2, a young male who fell in between b28-2 and the main cluster. The location of the main cluster is consistent with the hypothesis that Srubnaya-Alakul individuals derived the majority of their ancestry from Eastern European sources, similar to the individuals from the preceding Sintashta culture, whereas the location of the two “outliers,” who were buried in the same kurgan, indicates contact with Eurasian populations from the East.

To test whether Srubnaya-Alakul individuals received additional ancestry from populations east of the Urals, we computed *D*-statistics in the form of *D*(Khomani, Eneolithic Russian Shamanka; Sintashta, Test), with “Test” being the Nepluyevsky individuals. This analysis resulted in significant positive *D*-values for five of the Nepluyevsky individuals (b10-2, b13-1, b17-1, b27-1, and b28-2), indicating at least some gene flow from an eastern source deriving ancestry from a population similar to Eneolithic Shamanka into the ancestors of the sampled individuals (*SI Dataset*).

Similarly, we modeled the ancestry of the Nepluyevsky individuals as a three-way mixture between Russian Middle Bronze Age individuals belonging to the Sintashta culture, Eneolithic Shamanka hunter-gatherers from Lake Baikal, and people from the Russian Eneolithic Steppe. For half of the individuals ($N = 16$), the component found in Sintashta individuals was sufficient to describe their ancestry. For 15 of the remaining individuals, adding at least one further component to the model increased *P* values substantially. Although the ancestry of nine individuals could be described by a two-way model consisting of Sintashta-like ancestry and an additional ~20 to 60% Russian Eneolithic Steppe ancestry, four individuals were best modeled as Sintashta-like individuals with up to 10% additional ancestry from a source similar to Eneolithic Shamanka. For the two individuals outside of the main PCA cluster (b28-2 and b10-2), ancestry was best described by a three-component model that consisted of ~25 to 35% ancestry as found in Sintashta individuals, 50 to 60% Eneolithic Steppe ancestry, and a small (less than 10%) addition of Shamanka ancestry (Fig. 3). None of the models led to a sufficient fit for b13-1 ($P > 0.01$). These results are consistent with people associated with the Srubnaya-Alakul culture originating from the substrate of preceding Sintashta-like people, with additional admixture from populations local to the Russian Steppe as well as further to the east.

Discussion

Regional Continuity in Ancestry and Occasional Long Distance Mate Procurement in the Eurasian Steppe. The burial mound of Nepluyevsky belongs to a broader cultural horizon in the Southern Urals, described by archaeologists as Srubnaya-Alakul (49, 65) and dating to the period c. 1,800 to 1,200 BC (31). The Srubnaya-Alakul cultural horizon is traditionally assumed to have developed in connection with the preceding Sintashta culture, c. 2100 to 1800 BC, based on similarities in burial and material practices (31). Our analysis of ancient genomes from the Nepluyevsky cemetery corroborates this hypothesis, as we found similar ancestry profiles and an accumulation of shared IBD segments among Sintashta and Srubnaya-Alakul-related individuals (32, 36–38).

Indeed, most of the genomes sequenced from Nepluyevsky could be modeled as a simple mixture of Sintashta-like ancestors, projecting close to earlier (Fatyanovo–Sintashta cultural horizons) and contemporary steppe populations with a Srubnaya cultural background on a PCA. Several Nepluyevsky individuals showed signs of a small amount of additional gene flow from Eneolithic Steppe populations ($N = 9$), Eneolithic hunter-gatherers from Lake Baikal ($N = 4$), or both ($N = 2$). Genomic data from the kurgan provide important insight into how gene flow from the east could have occurred at the family level; specifically, “Central Asian”-like adult female b28-2 had a son (b10-2) with one of the six brothers (b32-1). All three individuals were buried under the kurgan without evidence of significant differences in terms of burial practices or grave goods.

Our study thus demonstrates the integration by marriage or partnership of far-distant, Central Asian, individuals into the relatively stable Srubnaya-Alakul gene pool. Such occasional episodes of gene flow must have already occurred in the preceding Sintashta period. Positive *D*-statistics in the form of *D*(Khomani, Eneolithic Shamanka, Sintashta, Nepluyevsky) indicated gene flow from a population east of the Urals into at least some of the ancestors of the people buried at Nepluyevsky. In addition, the fact that all but two Nepluyevsky males carried a Q1b(2) Y-haplogroup is consistent with a contribution of Central Asian ancestry along the male line to the ancestors of the Srubnaya-Alakul population. The Q1b(2) Y-haplogroup is common among contemporary populations east of the Urals (35, 37, 38, 59, 60). Furthermore, we found derived G alleles in the EDAR gene (SNP rs3827760), of two individuals (b32-2 and j6-1) a variant commonly found in East Asian and Native American populations (66).

Central or East Asian ancestry surged in the region during later historical periods, i.e., among Iron Age populations such as the Sarmatians, or, broadly speaking, groups associated with the Scythian cultural complex (36, 67). Our study indicates that low levels of gene flow from Central Asia had already occurred by the start of the Late Bronze Age, c. 1,800 BC. Considering the extent and boundless nature of the Eurasian Steppe zone, which harbored a wide range of populations with correspondingly different genomic profiles (35, 37, 38), the fact that gene flow from East Eurasian populations occurred only episodically is surprising, and contradictory in the geographic context. Our findings indicate that cultural and/or ethnic boundaries constrained random mating from the East into the Nepluyevsky community. By contrast, the observed patterns of IBD-sharing suggest that populations related to the Nepluyevsky group were distributed over an area of hundreds to thousands of kilometers to both, the west and the east of Nepluyevsky during the Middle to Late Bronze Age (Fig. 1).

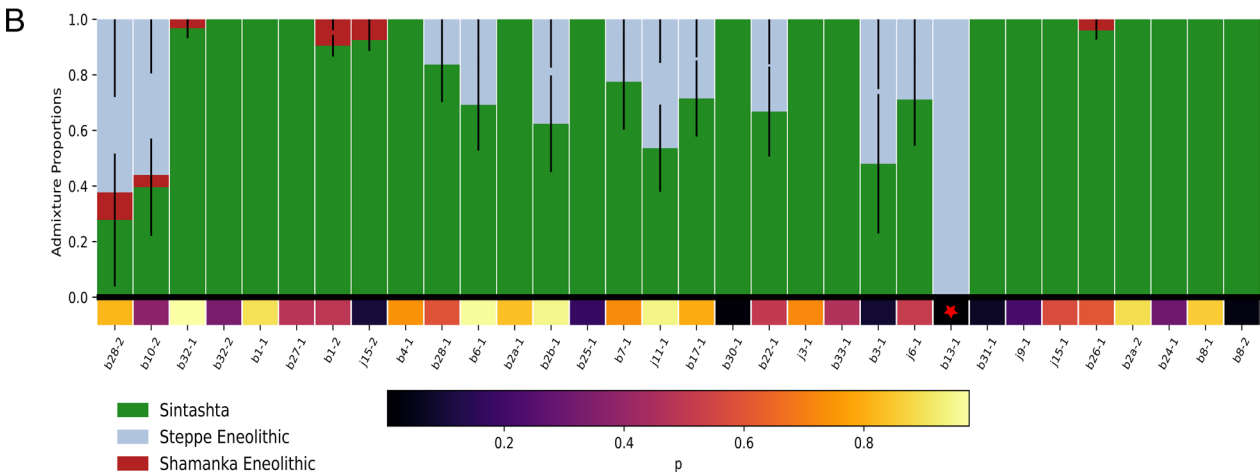
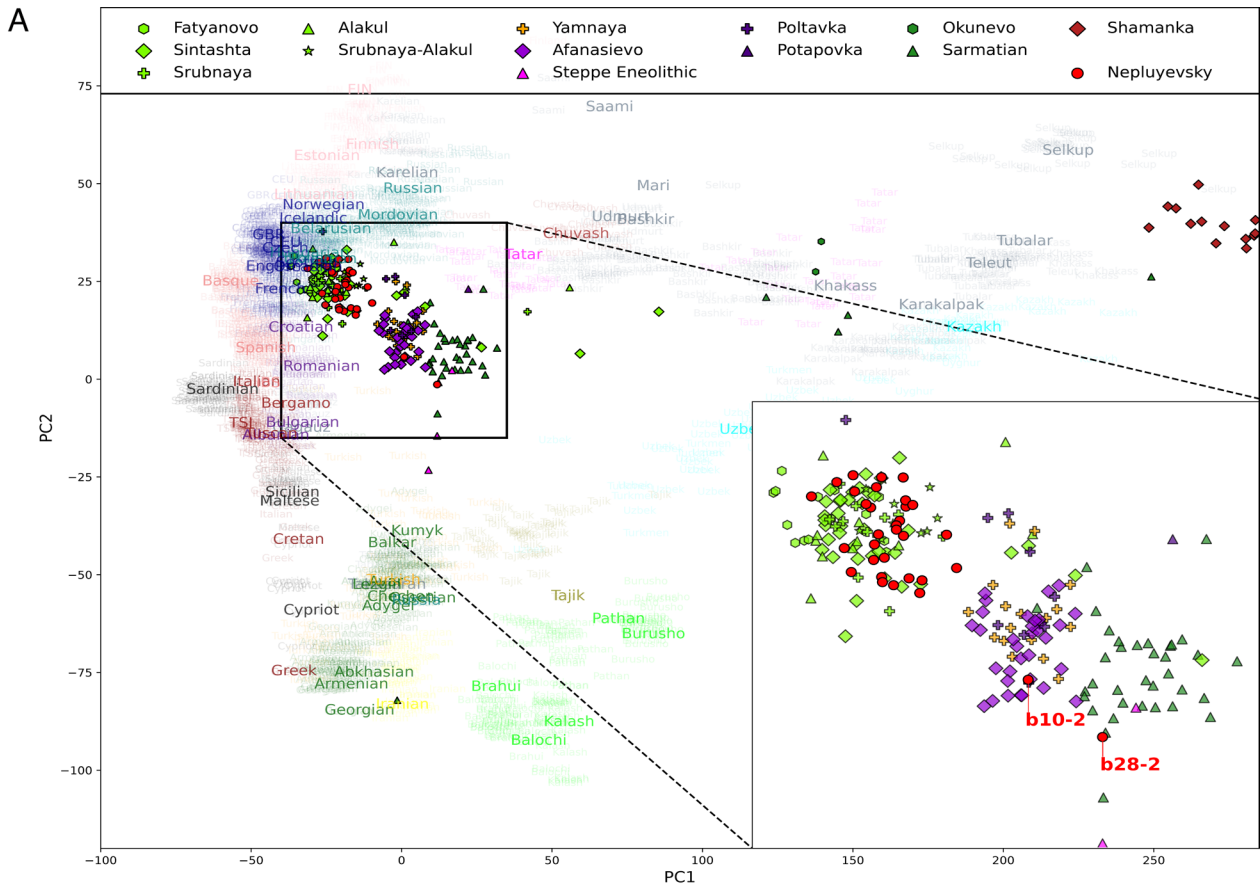


Fig. 3. (A) Principal component analysis based on modern Eurasian populations taken from the Human Origins dataset [colored population names, (64), for a detailed list, see *S1 Dataset*]. The box in the middle indicates the area of the lower right *Insert*. The Nepluyevsky samples (red dots) fall on top of other Bronze Age genomes from the broader steppe area associated with the Fatyanovo, Srubnaya and Alakul cultures (green diamonds, crosses and triangles) and the Sintashta culture (green rectangles), except for individuals b10-2 and b28-2. (B) qpAdm results, modeling the Nepluyevsky individuals as a mixture of Russian Sintashta and Eneolithic Steppe individuals with Eneolithic Shamanka individuals from Lake Baikal. *P* Values for each model are color-coded below the stacked bars. The model for individual b13-1 was rejected ($P < 0.01$, red star).

Descent Was Patrilineal, and Blood Relations among Brothers Played a Structural Role in Society. The reconstructed pedigree (Fig. 2) connected 33 individuals (21 sequenced and 12 inferred) over three generations, starting with six brothers and their unrelated wives, their children, and grandchildren. The founding couple and parents of the six brothers are unknown. Another four individuals, including young siblings (brother–sister), were identified as being related to the third or fourth degree to several other individuals in Kurgan 1 but could not be precisely attached

to the pedigree. Only seven of the 32 sequenced individuals were determined to be unrelated in the narrower family sense—(defined here as all relations beyond fourth degree), which suggests that at Nepluyevsky descent was primarily and almost exclusively determined by biological relationships.

Several hypotheses may explain the presence of individuals in Kurgan 1 who were not closely related by blood. These people may represent nonbiological kins, i.e., individuals accepted into the descent group for social reasons, such as becoming allies (68).

Alternatively, these individuals could have been linked to others by affinal ties (i.e., marriage), but the absence of common children excludes them from the pedigree. They may have had more distant blood relations that could not be detected at such sequencing depth using current methods for estimating biological relatedness, or they could be nonkin, with burial proximity resulting from, for example, the intrusion or reuse of the burial mound by different descent groups. At present, our data cannot distinguish among these hypotheses. Grave goods did not greatly differ between the inhumations at the site, which limits the ability to draw conclusions about status differences or inheritance (*SI Appendix, Fig. S6.9 and Table S1*); only two young females (b26-1 and b8-2), who were not part of the pedigree, showed elevation in grave goods, including bronze objects.

Unlike early Neolithic sites, where unrelated coburials are common (7, 13), most of the deceased individuals in Kurgan 1 belonged to three generations of a single patrilineal descent group. Biological kinship relations between sibling brothers appear to have played a structural role beyond childhood. The observed and partly inferred presence of six brothers and their children and grandchildren, as well as the absence of adult sisters at the site, suggests that affiliation with the descent group was based on patriliney. However, one exception is worth noting: female b33-1, who was buried at the site despite being linked to other individuals through her mother rather than her father, as might be expected in a strict patrilineal descent system. Most kinship systems are flexible and tolerate exceptions. For example, in patrilineal descent systems, it would be common to bring an unrelated man into the family line through marriage if there were no surviving male children (69).

Monogamy Was Apparently the Norm, but Polygamous Partnership Cannot Be Excluded. While the position of the graves within the kurgan, the distribution of grave goods, and the nutritional status of the deceased (45) do not indicate any obvious intrafamilial stratification, one adult male (b32-1) stands out. At least eight children from two mothers, including the woman with a presumed Central Asian ancestry background, can be attributed to this individual. By contrast, the other five brothers had no more than three children, all with one wife each. Although sampling bias is possible, it is highly unlikely that the ratio of children to parents would be altered drastically enough to change this fundamental interpretation. Hence, b32-1 is the only brother to show evidence of polygamy or sequential monogamy. Whether the man was living in a relationship with the two women and their children at the same time cannot be determined. Given b32-1's age at death (>50 y) and his position within the pedigree, he is likely to have been the oldest of the six brothers, or even the firstborn (son), suggesting preferential treatment and/or differential fertility based on birth order privileges. Although monogamous relationships appear to have been the norm at Nepluyevsky, polygamous partnerships cannot be excluded in general; second or third partnerships may have been treated differently in the grave or simply did not result in common children.

Assuming that the numbers of spouses and children in historical societies correlate with wealth and status (70, 71), the potential marriage trio represented by adult male b32-1 and his two wives could be ascribed to a commanding role within the family. Also, a link between polygyny (serial or simultaneous) and large numbers of children can be established in this case. Polygyny is common among either shifting horticultural or pastoralist communities worldwide but is almost absent among plow agriculturalists (72, 73). This ethnographically documented trend is in line with the archaeologically reconstructed evidence of the lifestyle of the Nepluyevsky

population, who lived largely on livestock with little evidence of cereal cultivation (*SI Appendix, section 1*).

An Absence of Young Women Suggested by the Unusual Demographic Profile of the Nepluyevsky Population. The complete absence of females in the kurgan between the ages of 5 and 14 is distinctly unusual. Given that male individuals of all ages were present at the site, this finding is notable because it indicates a differential treatment of females in this age category. Outmarriage at a young age is an unlikely explanation for this, because it would, in turn, require the presence of unrelated young females, who were not observed. The observed demographic patterns are more likely to reflect differential burial customs for female children, as is known for children from other sites (74). Burial sites containing only subadult remains (Nepluyevsky Kurgan 5 and 9, Yulaly-8 kurgan 2 in the Trans-Urals) or subadult plus adult female remains (Nikolayevsky kurgan 1 in the Pre-Ural region) have been found over a wider area (75–77). Because sexing subadult individuals is difficult osteologically, a systematic genetic survey at the sites could provide insight by clarifying the molecular sex of the children.

Life expectancy at birth was found to be low for both females and males, although the estimate for females may be biased by cultural factors, such as burial custom. A low life expectancy at birth is thought to reflect high fertility rates among young females, as well as a high newborn mortality (78). Although elevated levels of child mortality were common in preindustrial societies (79), the child mortality estimates for the Nepluyevsky population are high compared to other Bronze Age societies outside of the Urals. Nevertheless, the pattern observed in this study is in line with that observed in other steppe populations of the Ural region. High proportions of nonadults have been found at the Middle Bronze Age Sintashta sites of Kamennyi Ambar 5 and Bolshekaraganski Kurgan 25 (80–82), as well as at other Sintashta, Petrovka, and Alakul cemeteries in the Southern Urals (74). The life expectancy of adults in Nepluyevsky was short compared with other prehistoric populations. This was especially true for females, for whom life expectancy was estimated to be more than 8 y shorter than for males (females: 27.8 y vs. males: 36.2 y, *SI Appendix, section 2*). If longevity is considered to be an indicator for societal health (83), the life expectancy values reported here, as well as those for other contemporary sites in the area, suggest the possibility of health constraints such as recurring human or livestock diseases.

Postmarital Residence Was Patrilocal, and a Woman's Membership Was Transferred to Her Husband's Group. No inbreeding was detected in Kurgan 1, despite a high degree of relatedness among interred males. The absence of long ROHs, and the fact that the wives and mothers of the first Nepluyevsky generation were not biologically related to each other, indicates the existence of a wider mating network. Patrilocal exogamy can be regarded as an efficient way to avoid inbreeding in small societies. At Nepluyevsky, a woman's membership was transferred to her husband's group; we can exclude a scenario in which women were returned to their group's cemetery. Female exogamy is a frequent, but nonuniversal practice in human societies. Recent strontium isotope and aDNA studies have shown that Neolithic societies had diverse postmarital residence practices (7), sometimes including, but not restricted to, patrilocality—hence the range of distinct signatures observed among close kin (13, 14, 17, 29, 30). Evidence of a patrilocal residence system has been frequently revealed among the Eneolithic and Bronze Age societies of Central (11, 12, 84, 85) and Eastern Europe (14) and appears to have persisted until more recent times (26–28).

However, there are notable exceptions to the patrilineal pattern that we identified. For example, Žegarac et al. (22) found no

evidence for patrilineality at the Mokrin cemetery associated with the Bronze Age Maros culture in modern-day Serbia. They found evidence for the inheritance of wealth through the local female lineage. Another example from medieval Bavaria points to a mixed form, including local men and women and the additional immigration of ethnically and culturally diverse women from distant areas (26).

The Period of Use of Kurgan 1 Was Too Short to Reflect a Natural Die-Off Pattern, Suggesting an Abrupt End to This Descent Line.

Modeling the occupation time based on ^{14}C dates in OxCal indicated a duration of use of the kurgan of less than 52 y, whereas our developed simulation approach suggested a minimum of 3 y as the lowest possible limit. Alternatively, age-at-death estimates in the context of the reconstructed pedigree can also be considered. The age-at-death distributions—especially in the second and third generations, which are characterized by an overall small number of adults—suggest an abrupt end of use for Kurgan 1 rather than a natural die-off pattern. The possible duration of use can be narrowed down further by focusing on the family surrounding b32-2, who died at an estimated age of 25 to 35 y, and her son b28-1, who was between 35 and 45 y old at the time of his death. Assuming a maternal age of 15 y for b32-2 at the time of giving birth, a lower boundary for the duration of use of 15 y may be estimated based on the highest and lowest estimated ages at death of mother and son, respectively. The young ages of the individuals in the third generation and the small number of adults in the second generation could indicate that the overall duration of use was not considerably longer than that.

Conclusions

Burial practices and the treatment of the deceased provide only limited information about the lives of prehistoric communities. Although no approach truly provides a “direct window into the past,” our study demonstrates that high-resolution genetic “kinship” analysis, combined with traditional archaeological and anthropological proxies such as burial location, age determination, and ^{14}C dates, can significantly enhance our possible understanding of past family structure and social organization. Biological relatedness patterns allow for the reconstruction of pedigrees that bear a remarkable resemblance to the kinship diagrams created by social anthropologists (86). The inferred family tree at Nepluyevsky spans three generations and is centered around six brothers and their wives, children, and grandchildren. All these people were buried under Kurgan 1, implying that biological relatedness was a central component of the kinship system in this part of Bronze Age Eurasia. The IBD network shown in Fig. 1 suggests that populations related to Nepluyevsky have settled throughout much of the Eurasian Steppe belt; thus, the insights derived from this study may have implications for the larger geographic area.

The Nepluyevsky people, who relied on livestock herding, derived most of their ancestry from “Sintashta-like” ancestors. The genetic picture is remarkably stable despite the wide-open nature of the steppe. Our findings indicate that the community was a participant in a broader mating network, with only few individual contributions of Central Asian ancestry to the local gene pool. Female exogamy was common, and women were not returned to their original group after death but instead were buried alongside their husband and children at Nepluyevsky. High overall levels of child mortality, combined with short life expectancies at this site and other sites in the region, suggest that the local living conditions were demanding.

Our results suggest that certain kinship patterns previously observed at older and contemporary sites in Central and Eastern Europe (patrilineality, female exogamy) were practiced thousands of kilometers to the east in the Southern Urals, providing support for the notion of Eurasian Bronze Age continuity (4). Further studies will reveal whether the observed characteristics and attributes of the Nepluyevsky society, such as the existence of brotherhood and the higher fertility of the putative firstborn son, as well as the absence of local lineage daughters, are particular to the local area or represent more general cross-space Bronze Age patterns.

Materials and Methods

The Burials. Nepluyevsky Kurgan 1 consisted of at least 44 individuals in 34 burial features, as well as 10 pits with depositions of ceramic vessels and four empty grave-like structures or cenotaphs. Based on the stratigraphy and cross-section of the mound (Fig. 3B), it is possible that all of the graves were dug within a short period of time, as none of them intersected. Several graves were capped by stone boulders and cist-like constructions that extended over multiple burial features. In general, the burials contained few grave goods, although some adolescent and young adult females were buried with bracelets, rings, and other bronze objects (SI Appendix, Table S1 and Fig. S6.9). For instance, grave 26 contained the well-preserved skeletal remains of a 14- to 16-y-old girl buried with several bronze items along with Srubnaya pottery. By contrast, intact male burials did not include any bronze artifacts, although some long bones showed traces of bronze oxides associated with residues from ornamented clothing items [SI Appendix, section 1, (49)]. In addition, some burials showed signs of looting or later retrieval, perhaps to recover heirlooms (burials 2a and 28).

Life Tables. Life expectancy, reflecting the overall mortality level of the population, was assessed via life tables calculated according to ref. 87. We used a 5-y span to define age groups and life expectancy was estimated for all identifiable individuals ($N = 44$, see SI Dataset), as well as for females and males separately. Individuals without a genomic or anthropological sex estimation were counted once in the male and once in the female age groups, as appropriate to their age (SI Appendix, section 2.2 and SI Dataset). To address potential limitations inherent to life tables (88), additional palaeodemographic indexes (89–92) were estimated (SI Appendix, section 2.2).

Dating. Uncalibrated dates were calibrated in R using the rcarbon library (93) and calibration curve IntCal20 (54). Uncalibrated dates of individuals who were dated twice (Table 1 and SI Dataset) were merged with OxCal's R_combine command (94) prior to recalibration [T statistic ≤ 3.8 (5% significance threshold) in all cases]. We used OxCal v4.4.4 (53) to assess the maximum duration of use by jointly analyzing all ^{14}C dates. (SI Appendix, section 3). We further implemented a procedure to test whether the death of a set of n individuals within a particular time window can be rejected. First, we determined the time window of the desired size that maximized the product of normalized calibrated probabilities in all individuals (for numerical stability, we actually considered the sum of log probabilities). Then, n calendar dates were sampled from that window, and converted to uncalibrated mean dates using the function uncalibrateCalendarDates() from the ADMUR library (95). Corresponding SEs were sampled from the kernel density estimate of the SEs actually observed in the n individuals, and the resulting uncalibrated dates are calibrated. The product of probabilities in the same time window was computed for the n simulated curves and recorded. The whole sampling procedure was repeated 10,000 times to construct a null distribution of joint probabilities expected if the n individuals had actually died in the stipulated time window. Finally, an empirical one-tailed P value was computed by dividing the number of simulated probabilities below the observed one by 10,000. Implementation of this approach can be found at https://github.com/ydiemann/Bloecher_PNAS_2023.

Sample Preparation, DNA Library Construction, and Sequencing. Sample preparation and library construction followed the protocol described in ref. 22. After surface removal and UV irradiation, the petrous bone (pars petrosa ossis temporalis) samples were milled into fine bone powder. DNA extraction was performed following the protocol in ref. 96, with modifications after refs. 22, 97,

and 98. After a 10-min prelysis step at room temperature with EDTA, the bone powder was incubated twice, in a solution of EDTA, Tris-HCl, N-Laurylsarcosine, and Proteinase K at 37 °C for 24 h under constant shaking. The lysate was then washed with Tris-EDTA using an Amicon Filter (Amicon Ultra-4 30 kDa, Merck Millipore) and subsequently purified using the QIAgen MinElute kit. Prior to library construction, 5 µL of USER enzyme (1U/µL) was added to 16.25 µL of DNA extract and incubated at 37 °C for 3 h (99). Double-indexed libraries were built as described in ref. 22 following the protocol by (100) with minor modifications and sequenced on an Illumina NovaSeq 6000 system (S2 flow cell, 100 bp, single end) (SI Appendix, section 4).

In addition, teeth from 25 individuals were processed independently in the ancient DNA facility of the Department of Archaeogenetics at the Max Planck Institute for the Science of Human History, Jena, which is now part of the Max Planck Institute for Evolutionary Anthropology, Leipzig. The sampling of teeth (101), DNA extraction, and double-stranded, UDG-half-treated DNA library preparation (102) were carried out using well-described standard procedures, available at protocols.io [https://www.protocols.io/workspaces/mpieva-archaeogenetics/publications, (103)]. In brief, DNA libraries were screened in-house via shotgun sequencing of 5 million reads on an Illumina HiSeq 4000 platform (75 bp, single end). After an initial quality criteria assessment (human DNA content and DNA damage profiles) using EAGER v. 1.92.56 (104), libraries containing >0.1% endogenous human DNA were enriched for ~1.2 million SNPs using a targeted in-solution capture ["1240K SNP capture"; (105)] following the protocol described in ref. 106. Following capture, an average of 20 million single-end reads were generated from each target-enriched DNA library.

Read Processing and Variant Calls. Residual adapter sequences were removed from individual fastq files with trimmomatic 0.36 (107), discarding reads shorter than 30 bp. Trimmed reads were aligned against GRCh37/hg19 using bwa aln, with disabled seeding (-l 1024 -n 0.02) (108, 109) and converted to the binary sequence alignment format (BAM), discarding reads with a mapping quality ≤30. PCR duplicates were removed with sambamba markdup (110), and the remaining reads were realigned around known SNPs and InDels with GATK 3.6 (111). The ATLAS software (112) was used to create pseudohaploid genotype calls overlapping the 1240K capture regions (105), as well as for the MT-chromosomes. In addition, diploid genotype calls for a genome-wide panel overlapping biallelic SNPs in the 1,000 Genomes dataset (113) were prepared using the MLE call function. Phasing and imputation were done using GLIMPSE (114), with the 1,000 Genomes dataset as a reference panel. Potential contamination rates were estimated based on MT-reads using contamMix-1.0.9 (55) and with ContamLD (56) in combination with ANGSD (115) for reads aligned to the autosomes and the X chromosome in males, respectively. The genetic sex of each individual was estimated following ref. 57. MT- and Y-chromosomal haplotypes were assessed with HaploGrep2 (116), and Clean_tree2 (117) based on the ISOGG 2018 tree (International Society of Genetic Genealogy), respectively. Haplogroup diversity was estimated as described in ref. 22.

Summary Statistics and Clustering Methods. Principal component analysis was performed with LASER 2.04 (118). Ancestry components were modeled using the qpAdm (119) framework with Mbuti.DG, Russia_Ust_Ishim.DG, USA_Anzick_realigned.SG, Russia_Kostenki14.SG, Switzerland_Bichon.SG, Israel_Natufian, and Russia_MA1_HG.SG used as right populations and varying source populations used as left. Outgroup f_3 - and D-statistics were performed

using ADMIXTOOLS, qp3pop, and qpDstat respectively (119). Potential ROHs were inferred using hapROH (61).

Kinship Estimation and Pedigree Reconstruction. KIN (62) was used with default parameters and contamination corrections disabled (-cnc 0) to estimate relatedness directly from the BAMs, focusing on the biallelic 1240K capture SNPs (105). Additionally, we estimated the kinship coefficient r for all pairs of individuals following (17) based on the pairwise mismatch rate x as: $r = 1 - (2^x - (b/2))/b$. The following procedure was used for pedigree reconstruction: In a first round, all individuals with first-degree relationships from both methods were linked (r : 0.375 to 0.75, KIN: parent-offspring/siblings), taking into account potential violations due to age at death, genetic sex, and MT- and Y-haplogroup information. In a second round, all second-degree relationships (r : 0.1875 to 0.375) were assessed to validate previously drawn connections and place additional individuals into the pedigree (SI Appendix, section 6.5). Relatedness beyond the third degree was assessed using anclBD (120) in combination with a large dataset of previously published contemporary genomes (for details, see SI Appendix, section 6 and SI Dataset).

Data, Materials, and Software Availability. Sequencing data are available in FASTQ and BAM format at the European Nucleotide Archive [https://www.ebi.ac.uk/ena/] under the accession number PRJEB63318 (121). Code for the ^{14}C related simulations can be found at https://github.com/ydielmann/Bloecher_PNAS_2023 (122). Previously published data were used for this work (https://reich.hms.harvard.edu/allen-ancient-dna-resource-aadr-downloadable-genotypes-present-day-and-ancient-dna-data) (123).

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