HUMAN GENETICS

Late Neolithic collective burial reveals admixture dynamics during the third millennium BCE and the shaping of the European genome

Oğuzhan Parasayan[1]†, Christophe Laurelut[2,3], Christine Bôle[4], Lola Bonnabel[2], Alois Corona[5], Cynthia Domenech-Jaulneau[6], Cécile Paresys[2,7], Isabelle Richard[2,7], Thierry Grange[1]‡*, Eva-Maria Geigl[1]‡*

The third millennium BCE was a pivotal period of profound cultural and genomic transformations in Europe associated with migrations from the Pontic-Caspian steppe, which shaped the ancestry patterns in the present-day European genome. We performed a high-resolution whole-genome analysis including haplotype phasing of seven individuals of a collective burial from ~2500 cal BCE and of a Bell Beaker individual from ~2300 cal BCE in the Paris Basin in France. The collective burial revealed the arrival in real time of steppe ancestry in France. We reconstructed the genome of an unsampled individual through its relatives' genomes, enabling us to shed light on the early-stage admixture patterns, dynamics, and propagation of steppe ancestry in Late Neolithic Europe. We identified two major Neolithic/steppe-related ancestry admixture pulses around 3000/2900 BCE and 2600 BCE. These pulses suggest different population expansion dynamics with striking links to the Corded Ware and Bell Beaker cultural complexes.

INTRODUCTION

Past population migrations followed by admixture between migrating and autochthonous populations have been shown to leave traces in the genomes of the descendants (*1*, *2*). In Holocene Europe, two major population transformations occurred, both involving profound cultural transitions and changes in the genomic composition of descendent populations. The first transformation was associated with the introduction of Neolithic cultures into Europe, leading to a radical lifestyle change from hunting and gathering to farming and animal husbandry. The process started around 6500 BCE in southeast Europe, with the spread of farming across other regions taking around 2000 years to complete [e.g., (*3*)]. The accompanying genomic transformation was the result of admixture between migrating Neolithic farmers descended from populations in western Anatolia and/or the Aegean, and Mesolithic hunter-gatherers (HGs) [e.g., (*4*–*12*)]. The second transformation in Europe was linked to profound social and economic change in Late Neolithic societies in Europe over a relatively short time period of ~600 years [e.g., (*13*, *14*)]. This societal transformation appears associated with Pontic-Caspian Steppe pastoralists migrating westward and admixing with local Late Neolithic populations, as attested by genomic evidence from burials, first in the Corded Ware complex (CWC), later in the Bell Beaker complex (BBC), and ultimately in Bronze Age contexts [e.g., (*5*, *15*–*17*)]. The detailed processes of population transformations, however, are not yet well resolved everywhere in Europe.

In the following paragraphs, we will highlight the main characteristics of the societies involved in the transformation process of the third millennium BCE in Europe with a focus on western Europe, first from the archaeological and second from the paleogenomic perspective.

At the end of the fourth millennium BCE, the Middle Neolithic cultures in Europe diversified and regionalized into a patchwork of cultures with various funerary practices, such as various expressions of the French Late Neolithic ("Néolithique récent") in the west, the Funnel Beaker culture (~4300 to 2800 BCE) in the north, the Baden (~3600 to 2900 BCE) and the Globular Amphora (GAC; ~3200 to 2600 BCE) cultures in the center-east, as well as the Chalcolithic Gumelniţa–Kodžadermen-Karanovo VI (~4500 to 4000 BCE) and the Eneolithic Cucuteni-Trypillia complex (~5500 to 2750 BCE) in the southeast, to name only the most prominent [e.g., (*18*–*26*)]. Starting at the end of the fourth millennium BCE, there is evidence of a remarkable increase in interregional mobility in central and eastern Europe, generating "translocal" communities (*27*, *28*). New cultural elements, such as animal traction using plows, wheels, and wagons, became widespread in eastern and central Europe [reviewed in (*29*)]. In northern and western Europe, however, this period seems to be culturally stable, despite increased competition between groups (*23*). The funerary evidence is dominated by collective tombs with successive deposition of corpses of varying numbers accompanied by grave goods (pottery, axes, ornaments), in monuments that are often megalithic constructions. In the Paris Basin between 3600 and 2900 BCE, gallery tombs and hypogea were constructed [e.g., (*23*)], some of which remained in use into the Late Neolithic (see below).

The situation changed at the turn of the millennium when profound transformations affected most of Europe during the following centuries [e.g., (*14*, *20*, *23*, *29*–*32*)]. The beginning of this transformation is recorded in central and eastern European sites associated with the

---

[1]Université Paris Cité, CNRS, Institut Jacques Monod, F-75013 Paris, France. [2]INRAP Grand Est, Châlons-en-Champagne, France. [3]UMR 8215 Trajectoires (CNRS-University Paris I), Paris, France. [4]Genomics Core Facility, Institut Imagine-Structure Fédérative de Recherche Necker, INSERM U1163 et INSERM US24/CNRS UAR3633, Paris Descartes Sorbonne Université Paris Cité, Paris, France. [5]Service archéologique interdépartemental, 78180 Montigny-le-Bretonneux, France. [6]Service Régional, Direction Régionale des Affaires culturelles d'Île-de-France, UMR 8215 Trajectoires (CNRS-University Paris I), Paris, France. [7]UMR 6472 CEPAM (CNRS-Nice University), Nice, France.
*Corresponding author. Email: eva-maria.geigl@ijm.fr (E.-M.G.); thierry.grange@ijm.fr (T.G.)
†Present address: Institut Pasteur, Université Paris Cité, CNRS UMR2000, Human Evolutionary Genetics Unit, 75015 Paris, France.
‡These authors contributed equally to this work.

GAC (3400 to 2800 BCE) [e.g., (*20*, *23*, *29*)]. There is rich archaeological evidence for three successive Europe-wide cultural expansions in Neolithic Europe during the period between ca. 3100 to ca. 2450 BCE, namely, (i) nomadic cultures from the Pontic-Caspian steppes between the Carpathians and the Ural with an agro-pastoral economy, single, gender-specific pit graves and burial mounds (kurgan/yamna), metallurgy, decorated vessels, and battle axes as common denominators; (ii) the CWC in central and northern Europe that incorporated components of these steppe cultures; and (iii) the BBC [e.g., (*14*, *20*, *22*, *29*–*32*)].

The roots of the transformation process associated with the appearance and spread of the CWC lie in the eastern European steppes. During the second half of the fifth millennium BCE, steppe communities extended their range to the steppe-forest zone and connected at the beginning of the fourth millennium BCE in the west to the Cucuteni-Trypillian communities and in the east to the Maykop communities of the northern Caucasus (3700 to 3000 BCE) (*26*, *30*, *33*, *34*). At the end of the fourth millennium BCE, starting in the Dniester-Dnieper area, this steppe-derived cultural complex spread into eastern and central Europe (Poland, Hungary, Bohemia, and Germany). Single grave burial rituals were introduced in eastern and central Europe through the encounter between steppe communities, such as the Yamnaya, and fourth millennium BCE Eneolithic traditions around the Carpathians, such as the GAC, the Baden, and the Cucuteni-Trypillian cultures (*18*–*21*). Moreover, a new pottery style appeared in Lesser Poland and the adjacent areas up to the Dniestrer river basin: the corded ware vessels, with elements of both the Yamnaya culture and the GAC [e.g., (*20*, *23*, *29*)]. The CWC then spread further north in a patchy fashion, arriving at the Baltic Sea in the 29th c. BCE, lasting until the middle of the 24th c. BCE, and ultimately covering the area from western Russia to the Netherlands and from Switzerland to Norway [e.g., (*13*, *14*, *20*, *21*, *29*) and references therein].

The CWC is marked by strong regional differences in cultural traits, but there are shared elements, such as cord-decorated ceramic beakers, particular stone axes, or mace heads ("battle axes") deposited mostly, but not exclusively, in single graves with gender-specific burial positions [e.g., (*14*, *20*, *22*, *29*–*32*)]. The CWC includes numerous "communities of practice" (*20*) and coexisted with other cultural groups [e.g., (*22*, *35*) and citations therein]. The association of single graves and grave goods considered to be weapons, such as daggers and battle axes, has been interpreted as signs of the rise of social stratification, individual aggrandizement, institutionalized warriorhood and marked gender roles favoring males, and thus an ideology influenced by the steppe people [e.g., (*13*, *14*, *20*–*22*, *29*, *32*) and citations therein]. Around 2600 BCE, All-Over-Ornamented (AOO) and their subgroup the All-Over-Corded (AOC) beakers, a specific type of CW beaker, appear in single graves in the Rhine-Meuse-Delta [e.g., (*35*, *36*)], often in association with Pressignian flint daggers originating from the Paris Basin (*36*–*38*). In northern and west-central France, individual graves with AOC/AOO beakers argue in favor of a fast north-south "leapfrog" dispersal along preexisting Neolithic flint networks (*14*). The AOC burials of Blignicourt dating to 2857 to 2488 cal BCE (*39*) and Ciry-Salsogne « La Bouche à Vesle » dating to 2574 to 2452 cal BCE (*40*) belong to a small series of burials across northern France and the eastern Netherlands containing AOC vessels and Grand Pressigny flint knives that hint at a vast exchange network in western Europe linking the north and the south of western Europe (*22*, *40*, *41*).

The third phenomenon, the BBC, encompassed roughly the second half of the third millennium BCE with a regional-specific chronology, overlapping in time and space with the CWC and in western Europe the AOO/AOC complex [e.g., (*14*, *22*, *42*–*45*)]. In its earlier phase, the BBC was not characterized by a typical form of grave or burial custom. Rather, BBC artefacts were found in preexisting burial contexts, scattered in insular concentrations across a vast area from the Atlantic coast to east-central Europe and the southern Mediterranean. Subsequently, the phenomenon developed into a coherent archaeological culture, in which single burials predominated (*44*). The main cultural expression of this eventually pan-European phenomenon was the characteristic bell-shaped ceramic beaker, the only reliable feature for its identification, sharing similarities throughout time and space [e.g., (*14*, *29*, *32*, *44*) and citations therein]. There is no agreement, however, on the classification of the decorative styles of the beakers, leading to inconsistencies of assignments and their interpretations (*46*).

Graves with Bell Beakers and often daggers and archery equipment were found all over western and central Europe, from Morocco to Scotland, Sicily to northwest Norway, and Denmark to Hungary (*21*). Bell Beaker material was also found in fortified settlements in the Iberian Peninsula and in northern Europe associated with metal production, in megalithic graves and caves in France and Italy, and in single graves with and without gender differentiation in the British Isles and in Central Europe where they overlap with CWC burials [e.g., (*21*, *35*, *47*)]. The origin of the BBC is still debated (see Supplementary Text) but is important to consider if one wants to understand whether its expansion was due to acculturation or demic diffusion, a question that will be addressed in the present study. Radiocarbon dating could not resolve the chronology due to a radiocarbon plateau in the third millennium BCE yielding wide calibration spans (*48*). Nevertheless, there is more archaeological evidence pointing to an Iberian origin than to a Dutch origin and there is agreement that the Maritime Bell Beakers (MBB) mark the beginning of the BBC sequence (see Supplementary Text). These MBBs spread quickly from the Tagus estuary along the Atlantic coast and down the Rhine (*14*, *44*, *49*), as well as along the Mediterranean coast and up the Rhône-Saône valleys, the Upper Rhine being the region with the largest MBB collection known in central Europe (*42*, *44*, *45*, *48*, *50*, *51*). The early Bell Beaker practices seem to have spread along the big European rivers from enclaves and then developed into the Europe-wide Bell Beaker civilization with four geographically distinct Beaker groups in the southwest, south, north, and east of Europe [e.g., (*13*, *14*, *44*, *50*–*55*)].

The Rhine river, a natural environmental boundary and the western edge of the CWC zone, seems to have formed the contact zone where AOO/AOC beaker–associated practices from the Lower Rhine and the MBB-associated practices from the Upper Rhine met, blended, and spread further eastward at a high mobility rate (*51*, *56*) [e.g., (*14*, *42*, *44*, *51*, *56*, *57*) and references therein]. In central Europe, the BBC did not immediately replace the CWC but coexisted with it through a division of territories (*30*, *58*). The BBC eventually replaced the CWC as far as Poland, but assimilated its funerary practices while catalyzing a shift from a herding to an agricultural economy (*59*).

These European-wide third millennium BCE cultural transformations were seemingly accompanied by population transformations. Paleogenomic analyses revealed large genomic shifts over short time periods, hinting at migrations to northwest Europe of people from the Samara steppe in present-day Russia, whose genomes can be modeled as a mixture of Steppe Eneolithic, i.e., Zagros-Caucasus and Eastern Hunter Gatherers (*60*), and Caucasus Eneolithic/Maykop ancestry comprising early Neolithic Anatolian farmer ancestry (*61*). Long-lasting cultural interactions between the Balkans and the northern Pontic steppe have been known from the archaeological record (*62*) and involved the exchange of material culture and admixture, since Anatolian Neolithic Farmer (ANF) and steppe ancestry has been identified in fourth millennium Cucuteni-Trypillia farming communities (*33*). Admixture continued between westward moving steppe peoples and local individuals with Neolithic ancestry (i.e., ancestry from Neolithic farmers of northwest Anatolian origin and western Mesolithic HGs, henceforth called "Neo-ancestry") associated with various cultural Late Neolithic practices in eastern Europe, such as the GAC [e.g., (*5*, *11*, *15*–*17*, *61*, *63*–*67*)]. This migration with admixture led to an east-west cline of the proportion of the Pontic-Caspian steppe-related ancestry (hereafter "steppe ancestry") in the CWC-associated population (*68*), with varying proportions of steppe ancestry (*64*). Concomitantly with the dispersal of steppe ancestry throughout central and western Europe, a shift in Y-chromosome haplotypes was detected with rapid expansion of the R1b M269 (R1b1a1b) lineage, similar to the one found in Samara Yamnaya (R1b Z2103, R1b1a1b1b) (*5*, *60*, *64*). The major Y haplogroup spreading in north-eastern Europe during the CWC was the R1a M417 (R1a1a1) and its derivative Z465 (R1a1a1b) (*10*, *69*). Thus, the dispersal of Y-chromosome lineages during the third millennium BCE period suggests both complex steppe ancestry diffusion patterns involving various steppe populations and complex population dynamics in central Europe starting already during the fourth millennium BCE.

This complexity is also observed in Bohemia during the subsequent BBC expansion between 2400 and 2000 BCE, where the R1b-P312 (R1b1a1b1a1a2), another derivative of the L151 lineage, became dominant in tandem with progressive erosion of the percentage of steppe ancestry (*17*). On the basis of the geographic distribution of L151 Y-haplogroups, Papac and colleagues (*17*) suggested that the R1b-P312 lineage originated around the Lower Rhine valley and expanded in association with the BBC, and thus that the BBC expansion into Bohemia was concomitant with an eastward migration from western steppe ancestry groups. These replacement waves of Y-lineages hint to changing male dominance patterns in groups whose movements are associated with cultural shifts.

The expansion of steppe ancestry in western Europe is less precisely documented since the distribution in time and space of genetically analyzed ancient individuals is patchy and uneven. Because of a denser dataset, the timing of the arrival of the steppe ancestry in present-day Switzerland has been estimated to have taken place around 2700 BCE, between 2860 and 2460 BCE, with a rapid increase upon arrival to ~60% followed by a decrease to 25 to 35% over the following 1000 years (*70*). Assuming no sampling bias, the steppe ancestry seems to have arrived slightly earlier in Switzerland than in northern Germany (*5*, *71*), where it is detectable about 100 years later (*70*). Yet, not all individuals in Switzerland carried steppe ancestry, and even 1000 years after its arrival, there were still individuals without the corresponding signature. This pattern suggests limited admixture between carriers of steppe ancestry and local farmers with Neo-ancestry.

In the Iberian Peninsula, steppe ancestry arrived later and was detected in northern Spain around 2400 BCE (*72*) and in southern Spain around 2200 BCE (*73*). Here, BBC-associated individuals with and without steppe ancestry lived together for a few hundred years but ultimately steppe ancestry permeated into all genomes (*15*, *72*, *73*). Steppe ancestry arrived in the British Isles at a similar period, around 2450 BCE, and this arrival is associated with the spread of the BBC (*15*) and the introduction of Y-haplogroup R1b L21 (R1b1a1b1a1a2c1), derived from the P312 haplogroup (*74*).

Since its initial observation, a male bias in the steppe ancestry propagation in Europe has been contentious (*75*, *76*). The sensitivity and specificity of the sex bias detected depend both on the methods used and the quality and richness of the X-chromosome data, with particular variations linked to the single-nucleotide polymorphism (SNP) density of the capture array and to the coverage of the shotgun genomes. Papac *et al.* (*17*) report a female-biased assimilation process of pre-CW people into early CW societies in Bohemia, while in CWC individuals from Germany, a male sex bias was detected in two individuals dated around 2600 BCE but was not detectable in later Bronze Age individuals (*77*). A sex bias has also been observed in Switzerland where the increase of Neo-ancestry between 2700 and 2000 BCE was driven by women (*70*). In Estonia, during the CWC between 2800 and 2000 BCE, steppe ancestry propagation was male-biased, although it involved a population distinct from the Yamnaya that carried Y-haplogroup R1a Z645 (*69*).

To better understand the spread of steppe ancestry in western Europe in conjunction with the cultural transformations, a clear view of the phenomenon in France is required. France represents a keystone geographic position not only between eastern and central Europe and the far west (British Isles) but also between the northwest and southwest of Europe (Iberian Peninsula) and thus between the CWC zone and the area in which the BBC expansion unfolded. The third millennium BCE transformation of the genomic landscape in France has, however, been sketched only in broad strokes. The genomes of roughly a dozen individuals in Bell Beaker and Bronze Age contexts in both northern and southern France are characterized by a substantial steppe ancestry–related genomic portion, around 50% (38 to 68%), and by males who were carriers of the steppe-related Y-chromosome haplotype group R1b-M269, with most individuals typed at higher resolution belonging to the P312 group (*11*, *15*, *65*). The aforementioned AOC burial CBV95 (Ciry-Salsogne « La Bouche à Vesle » in northern France), a single burial dated to 2574 to 2452 cal BCE, was a carrier of both a substantial genomic portion of steppe ancestry and the Y-chromosome R1bM269 lineage (*11*), while PEI2, an individual from a BBC collective grave dated to 2562 to 2308 BCE (Dolmen des Peirières, Villedubert, Aude, southern France), had no substantial steppe ancestry (*11*) akin to individual I1392 from Hegenheim, Alsace, dated to 2832 to 2476 cal BCE (*15*). This heterogeneous situation is also seen in the Iberian Peninsula where only some BBC-associated burials carry steppe ancestry, and individuals without any steppe-related ancestry were present until at least 1950 BCE (*15*, *73*).

From these various lines of evidence arises a picture of third millennium BCE European societies with diverse genetic origins facing each other, with regionally different outcomes. The CWC seems to have emerged after the encounter between Neolithic populations in Central Europe, mainly GAC-associated, and various migrating steppe people from eastern Europe (*17*, *66*, *67*). In contrast, it is not clear whether the BBC resulted from the encounter between local people with Neo-ancestry and migrants with steppe ancestry, or if it developed before the arrival of steppe ancestry. Most of the early Iberian MBB-associated individuals were found to be unadmixed descendants of the previous Neolithic populations (*15*). The propagation of the MBBs from the southwest/west to Europe's north and east, such as southern Poland, apparently involved carriers of both Neo-ancestry and steppe ancestry of the R1b M269 and its derivative P312 (*17*, *64*). Little is known, however, about the speed and fine-scale processes that led to these profound genomic transformations accompanying the cultural transformations at the individual level. Genetic data from archaeologically contextualized individuals involved in these processes are necessary to compensate for this limitation and fill in the information gap, in particular in areas with a dearth of genomic data, such as in northern France.

It is with this aim that we present here the paleogenomic study of seven individuals of a Late Neolithic collective burial dated to ~2500 BCE from the Paris Basin in northern France, Bréviandes les Pointes. We produced whole genome sequences for these individuals, including mitogenome and Y-chromosome sequences, as well as radiocarbon dates and $^{87}Sr/^{86}Sr$ data. We report a "real-time" observation of steppe ancestry introduction into the Neolithic gene pool in northern France. Moreover, we model the origins of the different ancestral components, shedding light on the admixture dynamics and the origins, directions, timing, and mechanisms of the expansion of steppe ancestry at the end of the fourth to the first half of the third millennium BCE in western Europe, i.e., at the beginning of a cultural transition period between the Stone Age and the Metal Ages that coincides with the BBC. We correlate movements of populations and individuals with archaeological evidence to address questions about the evolution of the CWC and the BBC. Finally, we analyze an individual BBC burial from Saint-Martin-la-Garenne dated to ~2300 BCE, representing the first genomic analysis of a proper BBC burial in the Île-de-France, in the middle of the Paris Basin where BBC burials are rare. The results of these analyses uncover important features of the admixture processes associated with the CWC and the BBC.

RESULTS

Archaeological context of a Late Neolithic collective burial

The archaeological site of "Bréviandes les Pointes" et les Grèvottes (hereafter "Bréviandes"), near Troyes in the southern Paris Basin, was repeatedly used as a burial ground from the Early Neolithic (~5200 cal BCE) to the beginning of the Final Bronze Age (~1200 cal BCE). Several noncontemporaneous graves with few or no associated artifacts, hampering cultural assignment, were radiocarbon-dated to the later Neolithic. A collective burial of seven individuals in a subcircular pit named BRE445 (Fig. 1A) produced no other finds apart from a circular bone bead and a dog paw (fig. S3). This burial mode lacking diagnostic artefacts was typical for the period in the Île-de-France and in Champagne [e.g., (*78*, *79*)]. The bones of the individuals (BRE445 A-E, FK, HI, hereafter abbreviated as A, B, C, D, E, FK, HI) are well preserved and unfragmented. The burial comprises three adult women, an adult man, two young children. and a neonate. Anthropological analysis estimated age at death of the three women A, B, and E to be respectively 20 to 39, 20 to 30, and about 60, while the adult man was estimated to be 20 to 30 years old at death. The two children HI and C were estimated to be respectively 4 to 8 and 6 to 10 years old at death. Direct radiocarbon dates were obtained from bones of individuals B, FK, and E and range between 2580 and 2275 cal BCE (98.9%), 2580 and 2284 cal BCE (99.6%), and 2706 and 2287 cal BCE (96.9%), respectively (see table S1 and fig. S8), assigning the burials to the last part of the Late Neolithic period. There is one additional burial excavated that is contemporaneous to the burial BRE445, but the skeleton lacked the skull and DNA was poorly preserved, preventing its full analysis. The neighboring graves date to earlier periods. No osteological indications of pathology were found apart from signs of general stress and ageing (see Supplementary Text). Variations in bone morphology discriminate individual FK from the others and suggest biological relatedness between individuals E and HI (see Supplementary Text). Signs of violence were not identified. A temporal succession of the inhumations could partially be determined from stratigraphic data (see Supplementary Text). The spatial layout of the skeletons shows that some bones of the earlier burials had been disturbed by the later arrival of a new corpse, although there was no evidence of intentional spatial displacement. The archaeological and anthropological analysis suggested that this was most likely a family burial (see Supplementary Text).

Genetic and isotopic characterization of the individuals of the collective burial at Bréviandes

To better understand the BRE445 burial, we produced whole genomes from the petrous bones of each individual with coverage from 0.75× to 4.6× (median coverage 1×) through untargeted shotgun sequencing (table S1). Mitochondrial and Y-chromosome haplogroups yielded a first glimpse of the biological relationships in the burial (Fig. 1B and table S1). Shared mitochondrial haplotypes suggest individuals FK, HI, and D to be related to the women E, A, and B, respectively. FK and HI shared the same Y-chromosome haplotype R1b-L151, suggesting, given their ages at death, that they could be biological father and son. Only individual C does not share her mitochondrial haplotype with any other individual of the burial. These conclusions were further confirmed following whole genome analysis with NgsRelate (*80*) and READ (*81*), allowing us to reconstruct the genealogies (Fig. 1C and table S2). The burial consists of one biological family comprising three generations, a second mother and her biological child, and a single child who were not related genetically to the individuals of the nuclear family. Analysis of genomic runs of homozygosity using hapROH (*82*) showed that none of the individuals were inbred (fig. S9). The combination of genetic, anthropological, and archaeological results also enabled reconstruction of the most likely temporal sequence of the burials (Supplementary Materials). Since the adult man FK and his son HI were the first to be buried, the mother of FK and grandmother of HI in the middle of the burial at an intermediate time point, and the mother of HI at the end, we can surmise that the genetically unrelated individuals embedded within the burial structure must have been part of the social community buried here.

To further characterize the individuals of this group and to reveal potential individual mobility, we performed stable strontium isotope analysis ($^{87}Sr/^{86}Sr$ ratio) on both teeth and bones of the adult individuals and on faunal remains (Supplementary Text and table S9). The rationale behind this analysis is that the $^{87}Sr/^{86}Sr$ ratio in teeth show the incorporation into the forming teeth of water- and food-borne Sr isotopes during early childhood, while Sr isotopes in bones correspond to Sr incorporation during the last 10 and 20 years before death (*52*, *56*, *83*). The Sr values obtained from these individuals were compared with those of contemporaneous faunal remains representing the local signature (table S9 and Supplementary Text). Only individuals E and B had $^{87}Sr/^{86}Sr$ ratio values that differed in teeth and bones, suggesting lifetime mobility of these two individuals but not

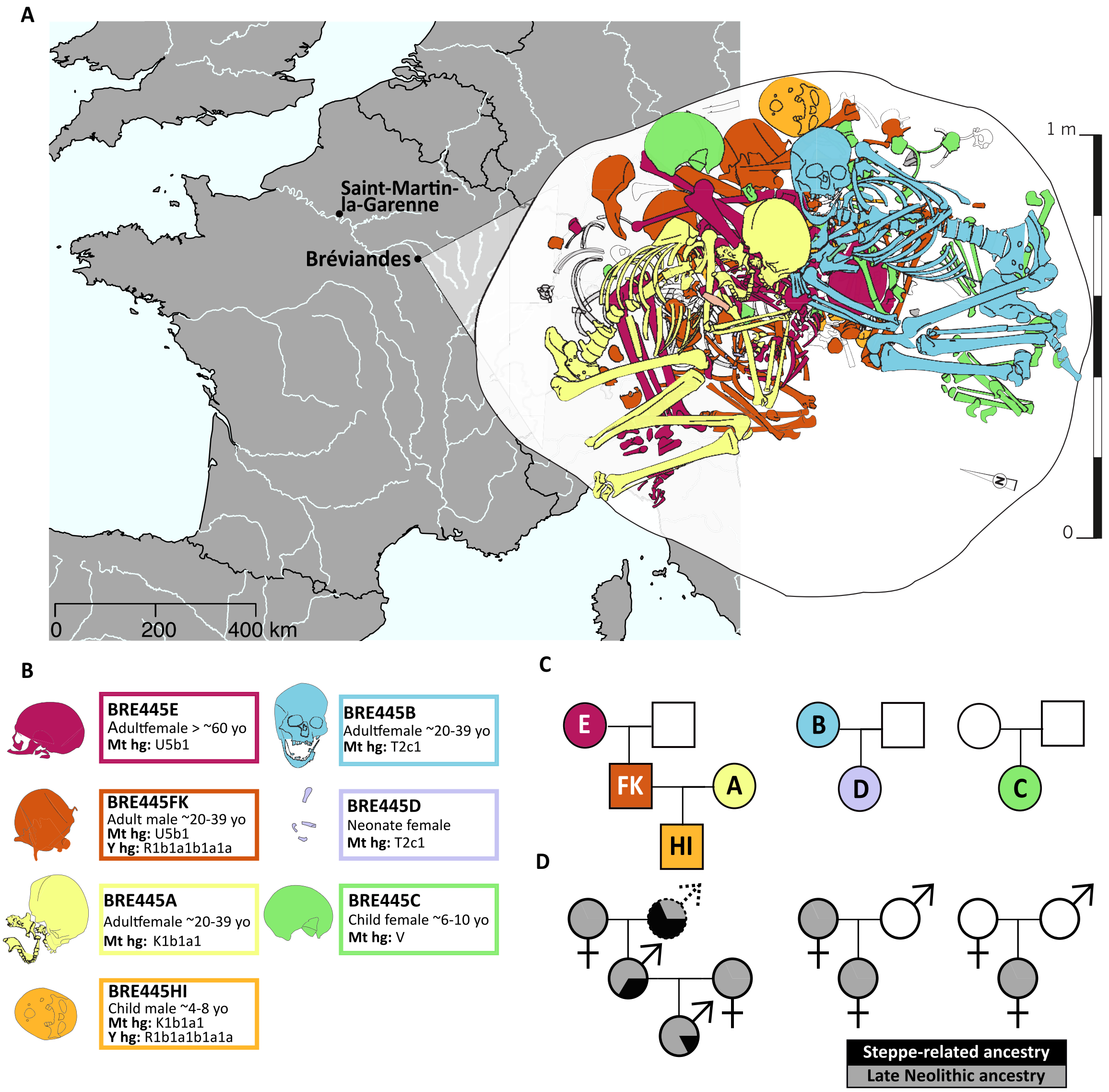

Fig. 1. A collective burial in the Paris Basin. (**A**) Map showing geographical locations of samples analyzed in this study. Schematic representation of the collective burial at Bréviandes. (**B**) Estimated age of death and uniparental haplogroup information of the Bréviandes individuals. (**C**) Pedigree plots showing kin relationships between the Bréviandes individuals. (**D**) Pedigree plots showing the genomic component of steppe-related and Late Neolithic ancestries between the Bréviandes individuals. The steppe ancestry proportions were plotted based on three-way qpAdm admixture modeling using northwest Anatolian Neolithic farmers (ANFs), Western hunter-gatherers (WHGs), and individuals with steppe ancestry represented by individuals associated with the Yamnaya culture of the Pontic steppe (see table S7). The sum of ANF and WHG ancestry proportions shown as the Late Neolithic ancestry. Empty boxes and circles indicate unsampled individuals. Dotted lines indicate the individual whose genome is reconstructed. The white bones in the iconographic reconstruction of the burial, done by E. Vauquelin, are unassigned bones.

of the other ones. The comparison of the individual $^{87}Sr/^{86}Sr$ ratio values with the strontium isoscape map of present-day France (fig. S7) (*84*) suggests that individuals E and B moved to Bréviandes following childhood in another location, either in the Paris Basin or beyond from areas of similar geology, including the northeast or southeast of France.

Genomic composition of the individuals of the BRE445 burial and haplotype reconstruction of the missing grandfather

To obtain deeper insight into the potential genetic origins of the Bréviandes individuals, we performed ChromoPainter analysis (*85*) on a dataset of 116 imputed ancient genomes. To this, we added one representative from each "biological family" of the collective grave of Bréviandes 445, identified as described above, excluding all other related individuals to avoid biases and artificial subclustering caused by excessive haplotype sharing among related individuals. Throughout the following analyses, related individuals will thus be analyzed independently of each other alongside all other unrelated individuals. The corresponding results will be presented either in the Supplementary Materials or, whenever possible without misrepresenting the results, combined within a single representation. With this dataset, we generated a haplotypic coancestry matrix, on which principal components analysis (PCA) and fineSTRUCTURE (*85*) were performed (rather than ignoring haplotype phasing information and projecting the ancient genomes on a PCA defined by present-day genomes as often done). Both the dimensionality reduction through PCA and the dendrogram analysis with fineSTRUCTURE allowed us to identify and visualize different genetic clusters and structures within the dataset. The first two PCs strongly differentiate three ancestral populations, i.e., northwest ANFs, Western hunter-gatherers (WHG), and individuals with steppe ancestry represented by individuals associated with the Yamnaya culture of the Pontic steppe (Fig. 2A and figs. S10 and S11). PC1 separates ANF from HG/steppe ancestries, whereas PC2 separates WHG from the steppe ancestries. The European individuals from Neolithic to Bronze Age contexts, including those from Bréviandes, are positioned between the three ancestry poles in a manner that reflects their ancestry proportions (Fig. 2A and figs. S10 and S11). Neo-ancestry individuals without any steppe ancestry are distributed on a line that can be drawn between the ANF and the WHG clusters. The proportion of steppe ancestry in the genomes of Late Neolithic and Yamnaya-associated individuals, estimated using SOURCEFIND [(*86*); Fig. 2B], positions on the PCA the carriers of steppe ancestry along a line of increasing steppe ancestry [compare the individuals grouped in four clusters (a to d) in Fig. 2, A and B]. The five female individuals from Bréviandes cluster with Neolithic and Chalcolithic genomes from France and Spain, respectively, in cluster "a" and are devoid of steppe ancestry (Fig. 2, A and B, and figs. S10 and S11). In contrast, the two related male individuals HI and FK are positioned within clusters "b" and "c," respectively, because of varying steppe ancestry proportions, the steppe ancestry of the son HI being half of that of his father, FK, in agreement with the absence of steppe ancestry found in his mother A (Fig. 2, A and B, and figs. S10 and S11). This finding reveals that individuals FK and HI represent the early arrival of steppe ancestry in a Neolithic context in northern France.

Since the proportion of steppe ancestry found in FK was about 35%, we predicted that this proportion should be twice as high again in his father, as the mother of FK, individual E, is devoid of this steppe ancestry (Fig. 2, A and B, and table S5). This high steppe ancestry proportion in FK indicates that his father would have a dominant proportion of steppe ancestry, around 70% (represented in the pedigree analyses of Fig. 1D). This would make it the earliest arrival of steppe ancestry in France hitherto detected (fig. S8), which prompted us to reconstruct the phased genotype of the unsampled father of FK, herein referred to as YY, using the phased genotypes of FK and E. Since only one haploid genome of YY could be inferred, that of the gamete (the spermatozoid) that led to FK, we modeled YY as a pseudo-diploid homozygous at all positions, using only the positions where the phased genotypes of FK and E allowed for unambiguous deduction of the allele contributed to FK by YY (fig. S12). The date associated with the arrival of this individual was inferred from the radiocarbon date of his son FK who was between 20 to 30 years old when he died, as inferred from anthropological analyses (see Supplementary Text and table S1). The pseudo-diploid genome of reconstructed individual YY is found on the PCA in cluster "d" (fig. S11B) along with other individuals of similar dates and showing similarly high steppe ancestry proportions, in particular an AOC individual from Ciry-Salsogne « La Bouche à Vesle » from northeastern France, CBV95 [(*11*) and table S4], and one of the earliest BBC-associated individuals from the Netherlands, I5748 [(*15*) and table S4], who are roughly contemporaneous to the Bréviandes individuals. This reconstructed genome of YY increases our ability to analyze the dynamics of the arrival of this ancestry in western Europe.

A new genome from a Bell Beaker–associated individual in northern France is carrier of steppe ancestry

The identification of steppe ancestry in the individual FK and the scarcity of contemporaneous shotgun genomes from northern France prompted us to improve the resolution of our analysis by adding another genome from an individual of nearby area and time period who was associated with the BBC, a cultural context linked to steppe ancestry. We produced the genome of an individual from Saint-Martin-la-Garenne (SMGB54), west of Paris in the Île-de-France (Yvelines), radiocarbon-dated to 2410 to 2129 cal BCE (97.8%) and representing a 30- to 49-year-old man buried with BBC funerary rituals, including a BBC-type shale wrist guard (figs. S4 and S5 and table S1). This individual is also a carrier of 35 to 36% steppe ancestry (Fig. 2, A blue diamond, and B), similar to that of individual FK (table S5), and was therefore included in further analyses. SMGB54 is found in cluster c with FK and other BBC and Bronze Age individuals from France as well as Bronze Age Hungarian and Croatian individuals.

Spatiotemporal high-resolution analysis of Late Neolithic genomes

Our fineSTRUCTURE analysis reveals similar relationships between individuals as seen with the PC1-PC2 plot, yet it further defines clusters with respect to geographical origins (Fig. 2C and fig. S13). The fineSTRUCTURE dendrogram first separates individuals with a high proportion of steppe or HG ancestry from those with high ANF ancestry (branches 1 and 2, respectively, in Fig. 2C). Within the dendrogram's first group, the next bifurcation separates steppe and HG ancestry (branches 11 and 12, respectively), and then, among the steppe ancestry group, the group comprising BBC, CWC, and Early Bronze Age–associated Europeans with high steppe ancestry from Yamnaya individuals (branches 111 and 112, respectively). The reconstituted YY genome belongs to a subgroup of the Europeans with high steppe ancestry comprising mostly western individuals. Among the group with high ANF ancestry (branch 2), the first bifurcation separates individuals with and without steppe ancestry (branches 21 and 22, respectively). Among those with no steppe ancestry, the next bifurcation separates individuals according to their extent of WHG ancestry: a first group (branch 221) comprises all initial ANF and early European Neolithic individuals with low divergence from this initial population, whereas a second group (branch 222) comprises most European Neolithic individuals with WHG ancestry, themselves subdivided at fine scale roughly according to their geographic origin. The Bréviandes individuals devoid of steppe ancestry (namely, the females A, B, C, D, and E) are found in a subgroup consisting mostly of individuals with southern France/Iberian origin. Branch 21 comprises individuals with both substantial WHG and steppe ancestries, dating to periods corresponding to the Late Neolithic and the Middle Bronze Age. This branch gives rise to two clusters discriminated by their extent of steppe ancestry: a first group (branch 211) with higher steppe ancestry later subdivided into two subgroups of different geographical origins, Central Europe and France, the latter one including individual FK. The second group (branch 212) carries lower steppe ancestry and is subdivided into two subgroups, one including mostly Iberian individuals as well as individual HI.

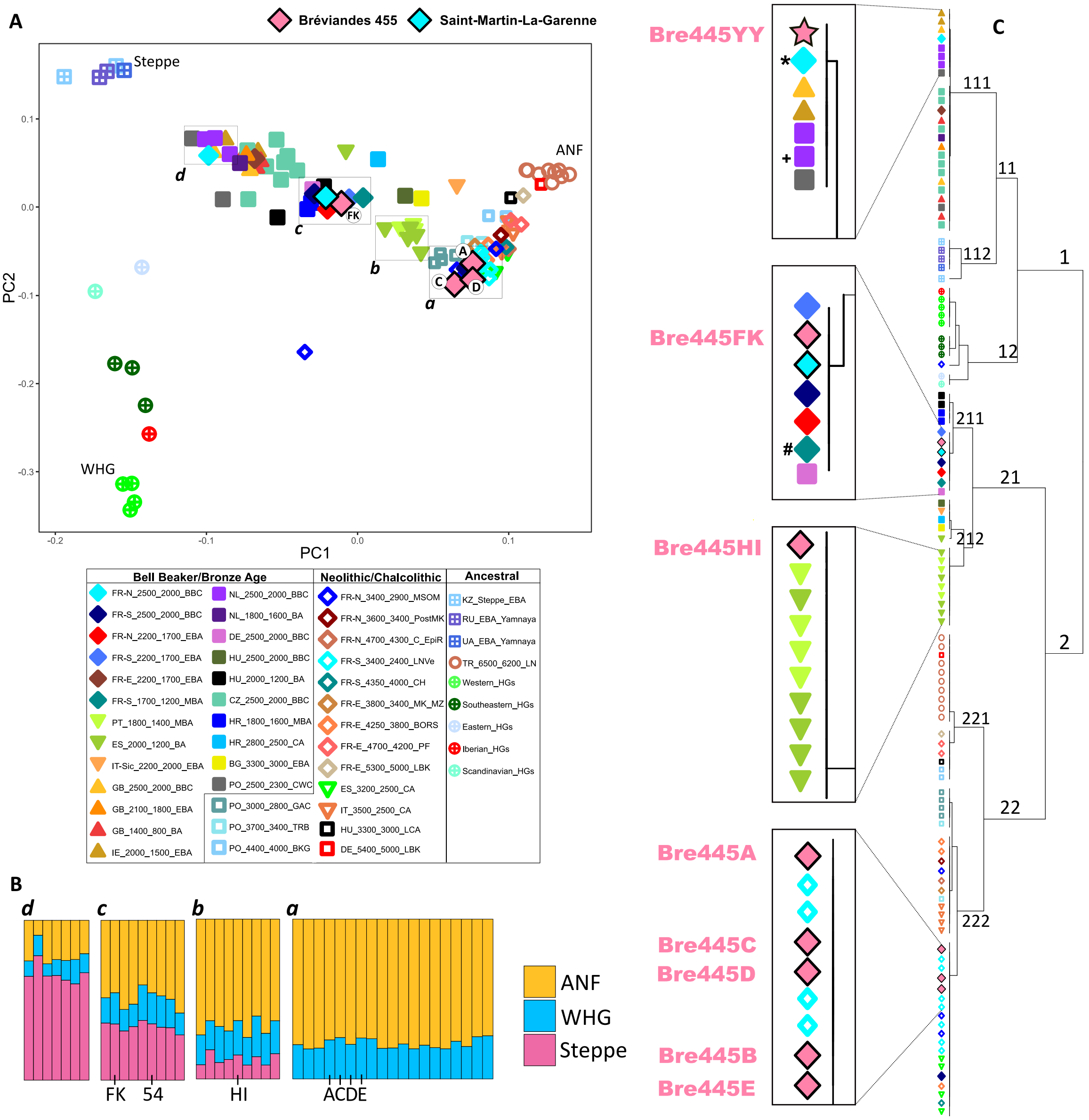

Fig. 2. Haplotype-based clustering of Neolithic and Bronze Age individuals. (**A**) Principal components analysis (PCA) based on ChromoPainter haplotypic coancestry matrix of unrelated subsets of individuals. The fractions of variance explained by PC1 and PC2 are, respectively, 45.8% and 30.5%. Individuals E and HI were added to the ancestry plot independently of the PCA. To avoid biases and artificial subclustering caused by excessive haplotype sharing among related individuals, the PCA was performed using unrelated individuals (see fig. S11 for the PCA plots performed independently using other family members from the Bréviandes grave). (**B**) SOURCEFIND ancestry component estimates of selected individuals in the PCA plot (see tables S4 and S5). The clusters a to d are ordered according to increasing steppe ancestry content and correspond to those shown on the PCA plot in (A). Individuals E and HI, who were not represented on this PCA plot, were attributed to clusters a and b, respectively, based on the PCA plots of Fig. S11. (**C**) fineSTRUCTURE clustering dendrogram based on the same coancestry matrix. Zoomed clusters correspond to different fineSTRUCTURE dendrograms based on coancestry matrices including other related Bréviandes individuals as shown on fig. S13. From top to bottom, zoomed dendrograms originate from dendrograms in fig. S13 [(A) to (C)] and integrate data from figs. S13 [(B) and (D)]. Some individuals referred to in the text are highlighted with symbols: CBV95 (*), I5748 (+), GBVPK (#). Two-letter country codes according to the International Organization for Standardization (ISO) are used in the group labels [FR: France (-N: North, -E: East, -S: South), DE: Germany, NL: Netherlands, ES: Spain, PT: Portugal, IT: Italy, GB: Great Britain, IE: Ireland, HR: Croatia, HU: Hungary, BG: Bulgaria, TR: Turkey, CZ: Czechia, PO: Poland, KZ: Kazakhstan, RU: Russia, UA: Ukraine].

Since the hierarchical clustering approach of the fineSTRUCTURE analysis produced clusters first reflecting admixture from the three source populations, but also reflecting, at a finer scale, the geographic origin, we explored whether this geographic signal could also be detected in the PCA. Although the proportion of the three source ancestries account for most of the signal detected in PC1 and PC2, PC3-PC4 reveals a correlation between haplotypes and geography, predominantly for later samples dating from the Late Neolithic to the Middle Bronze Age (see Fig. 3A showing individuals colored according to geographic origin and where the presence of steppe ancestry is indicated by a square; see figs. S14, S16, and S17 showing the lack of influence on PC3-PC4 of cultural association and steppe ancestry levels; and see fig. S15 for the Procrustes analysis showing that the best correlation with geography is obtained with PC3-PC4). West to east and south to north clines are clearly visible in Fig. 3A, irrespective of the extent of steppe ancestry of the individuals, indicating that a fine-scale genetic structure was already established at the continental level during this time, possibly due to the accumulation of genetic drift and/or admixture during the Neolithic expansion with genetically distinct HG populations in different parts of Europe. Furthermore, Late Neolithic individuals from southern France and Iberia group together and are clearly distinct from most samples from northern France, with the notable exception of the five female Bréviandes individuals with no steppe ancestry: A, B, C, D, and E (see fig. S16). The BBC individual SMGB54 is also associated with the southern France cluster. This association suggests that these individuals all have a stronger genetic link with southern than with local populations. In contrast, the reconstituted YY individual has a clear northern signature and is localized in PC3 to PC4 at the outer boundary of the cluster of individuals from northern France/Netherlands/British Isles/Czechia, referred to hereafter as the northern European cluster (fig. S16B). YY's son FK occupies an intermediate position between the southern and northern European clusters due to the southern component brought about by his mother E, which puts him in the middle of the northern European cluster (Fig. 3A). Finally, YY's grandson HI is again located halfway between his father, FK, of northern European affinity and his mother, A, of southern affinity (fig. S16D). To substantiate the inference that the Late Neolithic ancestry of the BRE445 individuals was from southern origin, we performed a normalized haplotype donor test focused on Neo ancestry (Materials and Methods) using two reference donor populations from the same period, Late Neolithic, and geographic area, France: one is representative of northern France from the hypogea of Mont-Aimé (Marne), and one is representative of southern France, from the Rouquet cave (Hérault) (*65*). In the haplotype donation analysis represented in Fig. 3B, we used as recipients, in addition to the Bréviandes 445 individuals devoid of steppe ancestry, two control individuals from the same sites of the reference populations but that were not included in the donor pools used, 1H04 from northern France and ROUQH from southern France, two Late Neolithic individuals from southwestern Europe from distinct sites, GBVPL from a southern France site near the Rouquet cave (*65*), and I5835, a Chalcolithic individual from the Atapuerca cave in northern Spain [Burgos, (*9*)]. The results show that the Bréviandes individuals share more alleles with the individuals from southern France than from northern France comparable to all other individuals from southwestern Europe tested (Fig. 3B). Thus, members of the Bre445 grave carry ancestry typical of southwestern Europe despite the northern France location of the grave.

Steppe ancestry admixture dynamics in Europe reflected in the Bréviandes burial

To explore whether we could extend our findings to a larger number of individuals than those for whom complete genome data allowed haplotype inference, we used SNP-based approaches to incorporate individuals who had been genotyped using sequence capture with the 1240k SNP array. We used qpAdm analysis (*87*) to group samples based on their locations and associated cultural or contextual dates (Fig. 4A and tables S6 and S7). As previously reported (*15*), we observe a dilution of steppe-related ancestry through a northeast to southwest cline. It is striking that the Bréviandes burial recapitulates the general continental admixture dynamics, particularly the dilution of steppe ancestry with ANF-WHG ancestry. To better pinpoint the date when this ancestry dilution took place, we plotted individuals' percentages of steppe ancestry as a function of their calibrated radiocarbon ages and color-coded them according to geographical location (Fig. 4B), and to visualize better the global trends, we represented the local polynomial regression fitting of relative steppe ancestry proportions using the LOESS method (Fig. 4C). In steppe ancestry carriers, we observe a progressive decrease in the proportion of genomic steppe ancestry in western Europe over a 1000-year period between ~3000 and ~2000 BCE starting from levels above ~75% found in early CWC-associated individuals from Czechia in the 3000 to 2500 BCE period, slowly decreasing to ~50% for the late CWC- and BBC-associated individuals from Central Europe, as previously reported (*17*). In the following 1000 years (2000 to 1000 BCE), the percentage of steppe ancestry appears to reach regional equilibria. In the Netherlands and the British Isles, steppe ancestry mounted to ~50% and remained at this level for over 500 years, arguing for the almost complete absence of admixture with local peoples of Neo-ancestry [Fig. 4, B and C, and (*15*)]. In France, we observe a decrease in steppe ancestry within a few hundred years between 2500 and 2250 BCE to around 35 to 40%, a value that appears to remain stable to at least 1700 BCE. Further incorporation of Neo-ancestry into the steppe ancestry background occurred during the southward migration of steppe ancestry carriers toward the Iberian Peninsula, leading to the dilution of steppe ancestry from ~25% during the Chalcolithic to ~13% during the Bronze Age [(*15*) and Fig. 4, B and C]. This north-south gradient of steppe ancestry persisted in Europe up to the present (*5*).

Strikingly, the Bréviandes collective grave gives a real-time snapshot of the dilution process of steppe ancestry during the southward migration, capturing it in action at the precise moment it occurred. The reconstituted YY corresponds to the earliest documented arrival of steppe ancestry in France, between 2600 and 2500 BCE, followed by the nearly contemporaneous individual CBV95 from nearby Ciry-Salsogne. This ancestry is found later in BBC individuals, whereas earlier individuals from these same regions do not carry this ancestry, whether associated with the BBC or not (table S7).

Two major pulses of steppe ancestry admixture

To infer the admixture dates between European Neo-ancestry– and steppe ancestry–related groups, we used fastGLOBETROTTER relying on phased haplotypes (*88*) and applied it to admixed individuals, FK and SMGB54, as well as 21 other admixed individuals post-2500 cal BCE. We estimated the timing of the admixture events in generations using a jackknife procedure to generate 95% confidence intervals (see Materials and Methods and raw results in table S8). We plotted the calibrated mean sample age and inferred admixture dates assuming 28 years per generation (Fig. 5A and table S8). Since the distribution was suggestive of distinct pulses of steppe ancestry admixture, we evaluated whether every 21 measurements generated per individual through the jackknife procedure could reveal a multimodal distribution using a Gaussian mixture modeling (GMM) probabilistic clustering approach to represent the presence of subpopulations. These 440 measurements led to a trimodal Pareto density estimation represented in Fig. 5B that was used to estimate the probability density function, and after using the expectation maximization algorithm for finding the local maximum likelihood, the data could be clustered in three Gaussian distributions (Fig. 5B), the best

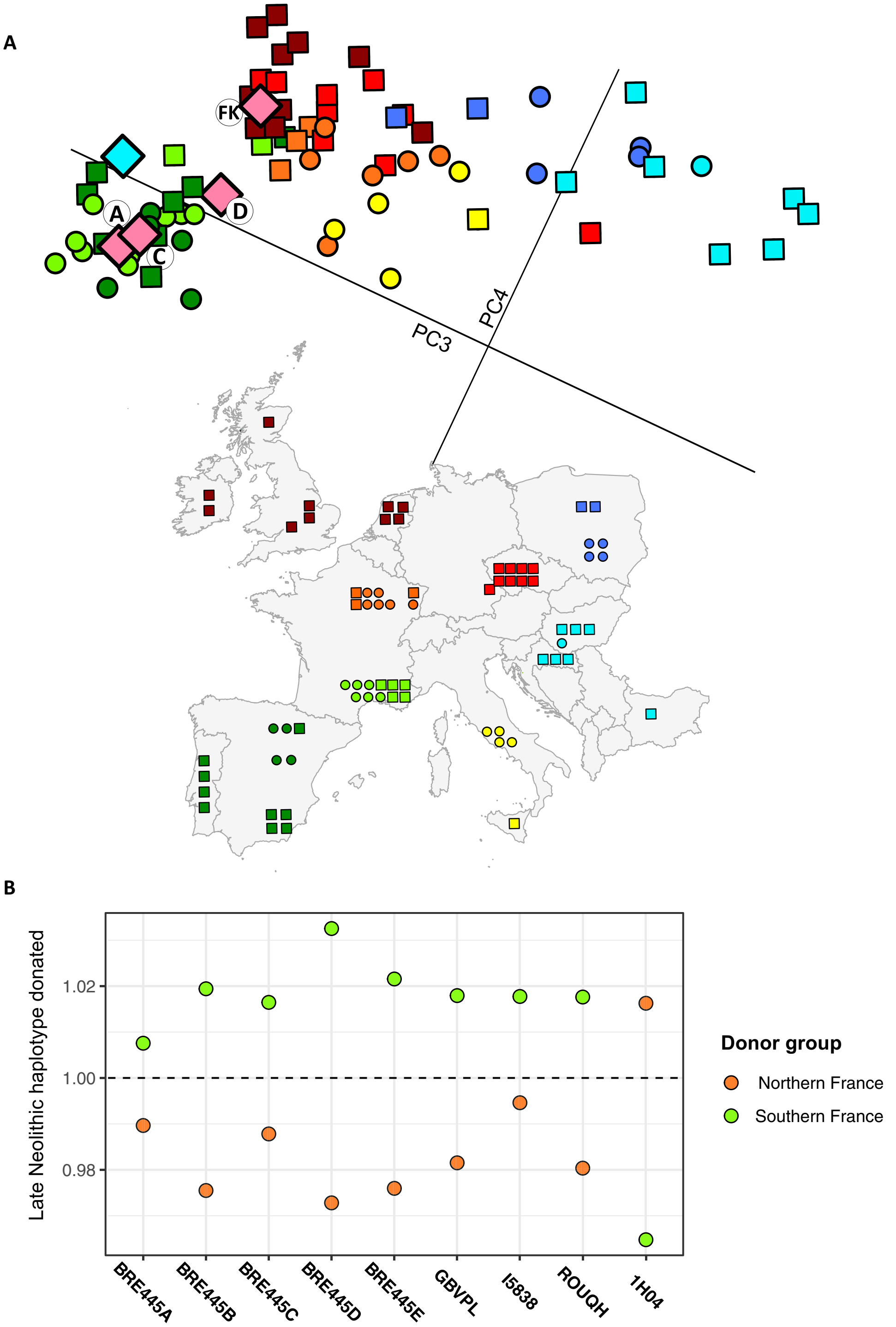

Fig. 3. Fine-scale genetic structure of Late Neolithic ancestries. (**A**) The PC3-PC4 plot of the same PCA (top) showing only European Late Neolithic and Bronze Age samples colored based on their geographical locations and the locations of these samples on the geographical map (bottom). Individuals with and without steppe ancestry are shown with squares and circles, respectively. The plot has been rotated clockwise to have a similar orientation as the geographical map. The fractions of variance explained by PC3 and PC4 are, respectively, 2.9% and 2.5%. (**B**) Normalized haplotypic length donations from two Late Neolithic groups, Northern France (Mont-Aimé) and Southern France (Rouquet), to the five female individuals from Bréviandes and other tested Late Neolithic individuals.

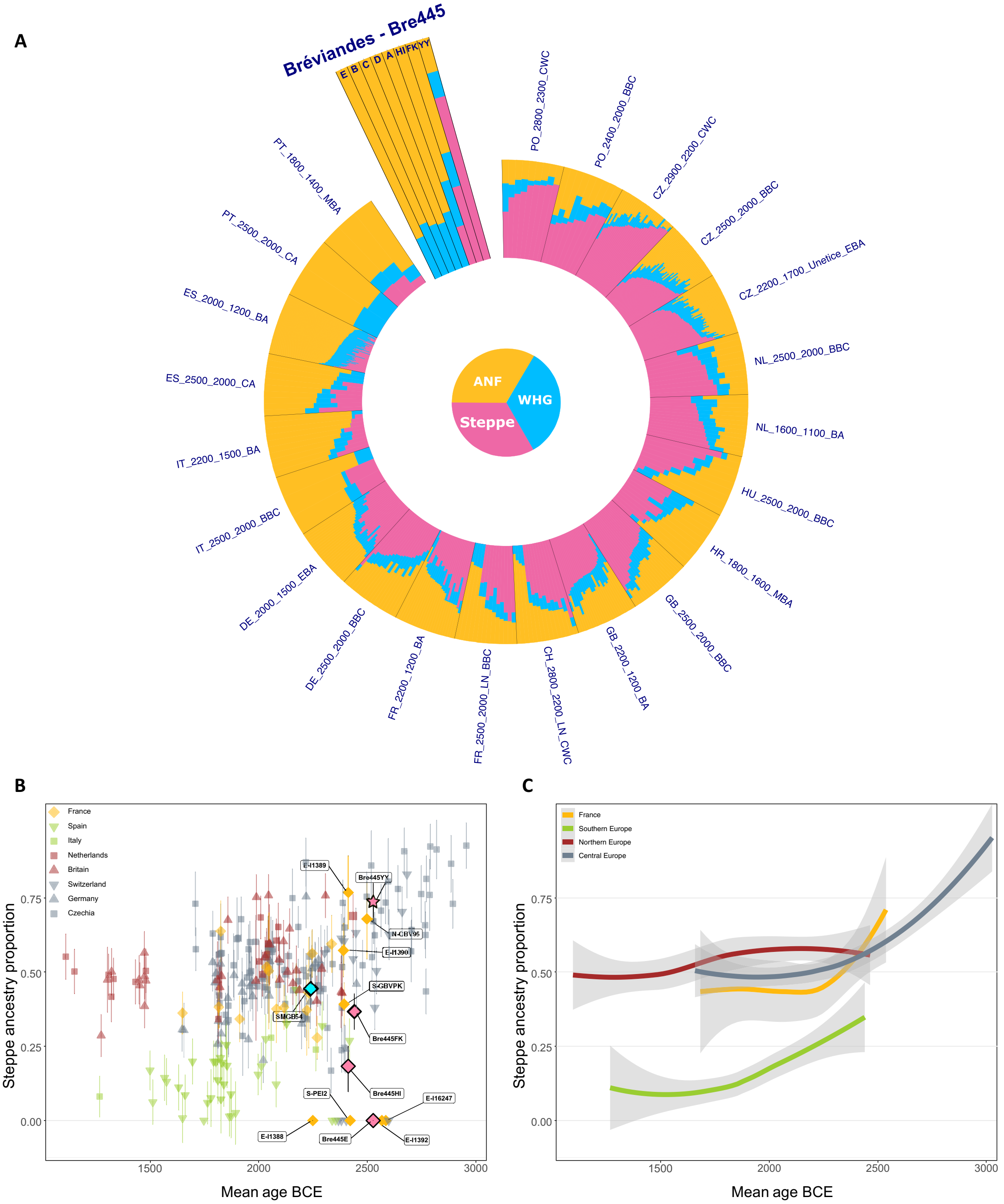

Fig. 4. Spatiotemporal analysis of steppe ancestry. (**A**) Circular graph display of the three-way qpAdm models for Late Neolithic and Bronze Age individuals grouped by location, archaeological context, and dates. (**B**) Relative steppe ancestry proportions plotted against mean radiocarbon dating values. The names of individuals from France are shown with boxes and indication of geographical regions in France (E: East, W: West, S: South, N: North). For Bre445YY, the radiocarbon date of Bre445E is used. For Bre445HI, the radiocarbon date of Bre445FK minus one generation (28 years) is used. (**C**) Local polynomial regression fitting of relative steppe ancestry proportions plotted against mean radiocarbon dating values, excluding Bréviandes individuals and those without steppe ancestry. Gray areas represent a level of confidence intervals of 0.95.

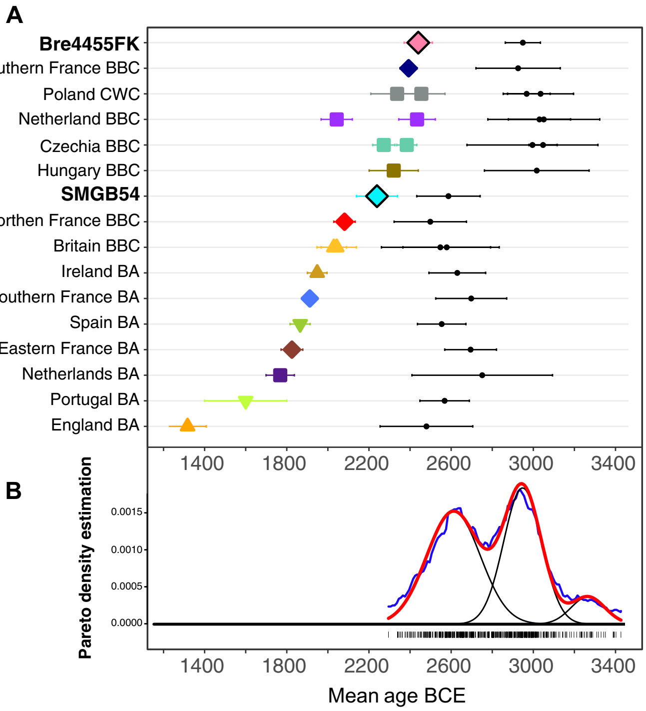

Fig. 5. Inference of admixture dates. (**A**) Admixture dates and their 95% confidence interval of generation times (in black) inferred by the fastGLOBETROTTER software and mean radiocarbon dating values of individuals. (**B**) Density curve of admixture dates calculated from the number of inferred generations per autosome subset of individuals that were estimated by the jackknife resampling step of fastGLOBETROTTER, corresponding to 22 estimations from each chromosome subsets per individual from a total of 20 individuals or grouped individuals. The 440 date estimations are represented at the bottom of the graph as bars. The blue curve represents the Pareto density estimation computed from these 440 measurements that was used for Gaussian mixture modeling (GMM) probabilistic clustering. The three Gaussian issued from the best supported model (see Materials and Methods) are represented by black lines, whereas the red line represents the best GMM model corresponding to the Pareto density estimation of the data.

model supported by both the Bayesian information criterion (BIC) and a Pearson's chi-square goodness of fit test (see Materials and Methods). The mean, SD, and proportion of these three Gaussian were estimated to be 2611 ± 130 BCE (49.9%), 2947 ± 92 BCE (42.5%), and 3266 ± 82 BCE (7.6%), and thus, the two most recent pulses account for more than 90% of the data. Strikingly, the admixture dates of the two individuals FK and SMGB54, 2949 ± 92 BCE and 2587 ± 154 BCE, respectively, correspond almost exactly to the center of these two major pulses, showing that they are indeed representative of the global trends. Note that dating estimates of fastGLOBETROTTER rely on the size distribution of ancestral haplotype blocks, which are progressively reduced by meiosis-dependent recombination following admixture. Since FK is an F1 hybrid between his steppe ancestry father YY and his Neolithic ancestry mother E devoid of steppe ancestry, no recombination event has yet taken place, and thus, the admixture date estimated between the two ancestries is that concerning his father YY. Nevertheless, FK is the product of an admixture event that took place around 2500 BCE, and is thus a direct witness of this most recent admixture pulse, although it cannot be detected from the size distribution of his haplotype blocks. Individuals associated with the BBC from southern France, the Netherlands, and Czechia showed initial admixture dates corresponding to the ancient major pulse, dating back to ~2950 BCE (YY showed a similar date, table S8). In contrast, admixture dates corresponding to around 2600 BCE, i.e., the most recent major admixture pulse, were inferred for other individuals from France including SMGB54, but also from the British Isles and Iberia.

We explored the results that could be inferred using an alternative admixture approach, DATES, which is based on unphased data (*89*), and thus does not leverage the extra resolution provided by haplotype blocks. Instead, DATES relies on the ancestry covariance pattern between the test genome and those of two source populations. Previously, simulations revealed that DATES provides varying values in cases of complex admixture involving unequal contributions of three ancestral groups (*89*). Accordingly, when using DATES to evaluate admixture between steppe ancestry and Neo-ancestry farmers that are themselves admixed between ANFs and HGs, very different admixture dates were obtained for some test individuals, depending on which individuals were used to represent the Late Neolithic source population. These results show that the method is highly sensitive to uncertainties in the true structure of the source population: This is the case here as the east-west migration of steppe ancestry occurs on a population substrate shaped by the east-west migration of Early Neolithic farmers of Anatolian origin increasingly admixing with HGs (table S10). In contrast, admixture dates estimated with fastGLOBETROTTER appear to be much more resistant to such uncertainties in the source population (table S10) as previously discussed (*88*).

The presence of admixture pulses between individuals with steppe ancestry and Neo-ancestry suggests that most steppe ancestry individuals preferentially interbred with individuals of similar ancestries and only rarely mated with Neo-ancestry carriers except during the pulse periods, thus preserving high levels of steppe ancestry for many generations. In contrast, when an individual with steppe ancestry integrated into a Neo-ancestry farmers' group, his/her steppe ancestry would have been diluted in a few generations. Such an event can be detected clearly only in the first generations, as observed here in the collective burial of Bréviandes.

Sex-biased spread of steppe ancestry

To detect any potential sex bias in the spread of steppe ancestry, we performed a ChromoPainter analysis on the imputed X-chromosome dataset of the best covered whole genomes, followed by a SOURCEFIND analysis to compare, in steppe ancestry carriers, the ancestry proportions on the X chromosome with those found on the autosomes (Fig. 6 and table S11). To quantify potential sex biases, we calculated the ratio of steppe ancestry on the X chromosome to that of the autosomes and used a $\log_2$ transformation. An excess of steppe ancestry on the X chromosome gives rise to a positive value, whereas a depletion, resembling an excess of Neo-ancestry, yields a negative value (e.g., +1 reveals a twofold steppe excess and −1 reveals a twofold steppe depletion and thus corresponding to Late Neo excess, i.e., ANF + WHG). As seen in Fig. 6, there is variability among individuals in the extent of ancestry transmitted preferentially on the maternal side, with some individuals showing a slight excess of steppe ancestry on the X and others showing an excess of Neo ancestry. Among the 38 steppe ancestry carriers from CWC, BBC, and Bronze Age Europe for whom whole genomes are available, 18 showed at least 20% excess of steppe ancestry on the X [$\log_2(\text{ratio}) > 0.26$], while

12 showed a similar depletion of steppe ancestry, and thus at least 20% excess Neo-ancestry on the X [$\log_2(\text{ratio}) < -0.26$], and the remaining 8 were balanced [$-0.26 < \log_2(\text{ratio}) < 0.26$] (Fig. 6 and table S11). Among the 12 individuals with depleted steppe ancestry on the X chromosome, 5 had an even lower level (ratio of steppe ancestry X:A < 0.4 corresponding to a 2.5-fold or more higher Neo-ancestry on the X): the 3 individuals from southern France, 1 BBC man from the British Isles (I2445), and individual Bre445FK who had no steppe ancestry on the X. Although there were more individuals with an excess of steppe ancestry on the maternal lineage, this excess was generally of smaller amplitude: Among these 18 steppe ancestry individuals, only 1 showed steppe ancestry that approached the level of excess observed for the individuals with high Neo ancestry: the male BBC individual SMGB54. He had a 2.4-fold excess of steppe ancestry on the X, reaching 86% on this chromosome, well above the 36% found on the autosomes, indicating that his maternal lineage had a higher proportion of steppe ancestry than his paternal lineage, although his Y chromosome showed characteristic steppe ancestry (R1b1a1b1a1a, also known as P310/PF6546/S129). SMGB54, as well as two BBC or early Bronze Age individuals from the British Isles, two BBC individuals from the Netherlands, two BBC individuals from Czechia, and one CWC individual from Poland, have very high proportions of steppe ancestry (>80%) on the X chromosome. This pattern of maternal lineages with strong steppe dominance indicates that steppe ancestry women mated less frequently with Neo-ancestry men than steppe ancestry–carrying men mated with Neo-ancestry women. These asymmetric admixture events, when captured a few generations after the mating event, at the F1 level as in the case of BRE445 males, or a few generations later, as in the case of the southern France individuals or the British Isle BBC individual, led to a marked imbalance of Neo-ancestry on the X chromosome. Thus, the sex bias appears bimodal when analyzed on the present dataset, with Neo-ancestry women admixing more frequently with steppe ancestry men than Neo-ancestry men admixing with steppe ancestry women. This low frequency of admixture involving Neo-ancestry men is also visible on the Y chromosome since out of 21 men of steppe ancestry in this well-covered genome dataset, only 2 carried a Y chromosome distinct from the typical steppe ancestry R1b1a1b1 (Fig. 6 and table S11), as previously observed in several studies (*11*, *15*).

DISCUSSION

Our high-resolution genomic analysis of the Late Neolithic collective burial BRE445 illuminated the mechanisms and direction of admixture processes in western Europe between Neolithic farmers and descendants of Pontic-Caspian steppe nomads. The genome coverage was sufficiently high to impute and phase the haplotypes and enabled us to use tools that maximize the precision inherent to haplotype analyses, and thus detect signatures distinguishing Neo-ancestry individuals by geographic origin.

Biological and social relatedness between the individuals of a Late Neolithic collective burial in the Paris Basin

In the collective grave of Bréviandes 445, the genomes of the three Neo-ancestry women show closer affinity to Neo-ancestry individuals from southern France and the Iberian Peninsula than to contemporary individuals from northern Europe, suggesting that either the women or their ancestors came from southwestern Europe (Fig. 3). Among these women, only two show ^{87}Sr/^{86}Sr isotopic signatures that might reveal lifetime mobility, whereas all other individuals show signatures of lifetime residency in the area. The isotopic signatures obtained for the BRE445 individuals do not provide unambiguous identification of the origins of these two women, but in tandem with their genetic signatures, they are compatible with earlier-life mobility from southern France. This result would be in line with previous results of combined genetic and isotopic analyses of BBC burials revealing large-scale mobility and at least partial female exogamy during the Middle Neolithic, BBC, and Bronze Age periods (*90*, *91*). Although it cannot be firmly established that the point of origin of the lifetime mobility of these two women is in southern France, we note that for a southern genetic signal to be preserved in northern France, one would need to consider preferential mating over generations among Neolithic people of southern ancestry. The southern genetic signature detected in all BRE445 women of pure Late Neolithic ancestry buried in the same grave suggests that this common southern origin may be one of the factors that have contributed to their shared identity, i.e., their cognate kinship relations maintained beyond death, which is in support of a preferential mating pattern. The more generations separate the southern source population from the migrant individuals living in northern France, however, the stronger the mating preference must have been to maintain for several generations a genomic signature from the south. Therefore, it seems more parsimonious to us to consider that the Bréviandes individuals or their ancestors migrated recently from the south to the north, women E and B possibly during their lifetimes as this is compatible with their strontium isotope signatures.

Through use of ancestry profiles, genealogies, and ^{87}Sr/^{86}Sr isotopic signatures, we propose the following narrative, although others are possible: E moved to Bréviandes before or after having met YY, likely a member of an ethnic group descending from steppe nomads. YY might have been a member of the "warrior youth bands," hypothesized by Kristiansen and colleagues (*31*), who "abducted" Neo-ancestry women, but this remains speculation. Neo-ancestry E, however, continued her life in a Neolithic community where she gave birth to FK who grew up in this Neolithic context. FK had a son, HI, with the Neo-ancestry woman A. Father FK and son HI died at the same time, or HI shortly after his father. FK, A, and B, all died as middle-aged adults. The only older individual belonging to the first generation was E. Individual B, who might also have come from another location, maybe as a child, settled at Bréviandes and had a child with a Neo-ancestry man not present in the burial. Individual C might have been a foster child. The combined genetic, anthropological, and archaeological results identify this collective grave as a kin group with both purely social and biological ties important enough to be conserved in the burial. Kingroups are indeed recognized as social constructions and kinship practices known to vary largely (*92*). The physical appearance of the individuals, as determined through genotyping analysis on the forensic HIrisPlex-S assay (*93*), did not distinguish them from other Neolithic individuals [e.g., (*63*, *64*, *71*, *94*)]. They all had genetic signatures suggesting brown eyes, intermediate to darker skin, and dark hair, except for FK and E whose hair could have been chestnut-colored. Thus, their physical appearance does not deviate much from other Neolithic individuals published.

European-wide sex-biased admixture process involving steppe ancestry revealed in genomes of the Bréviandes burial

While most details of these individuals' life histories cannot be reconstructed, this peculiar burial reveals some aspects of the arrival

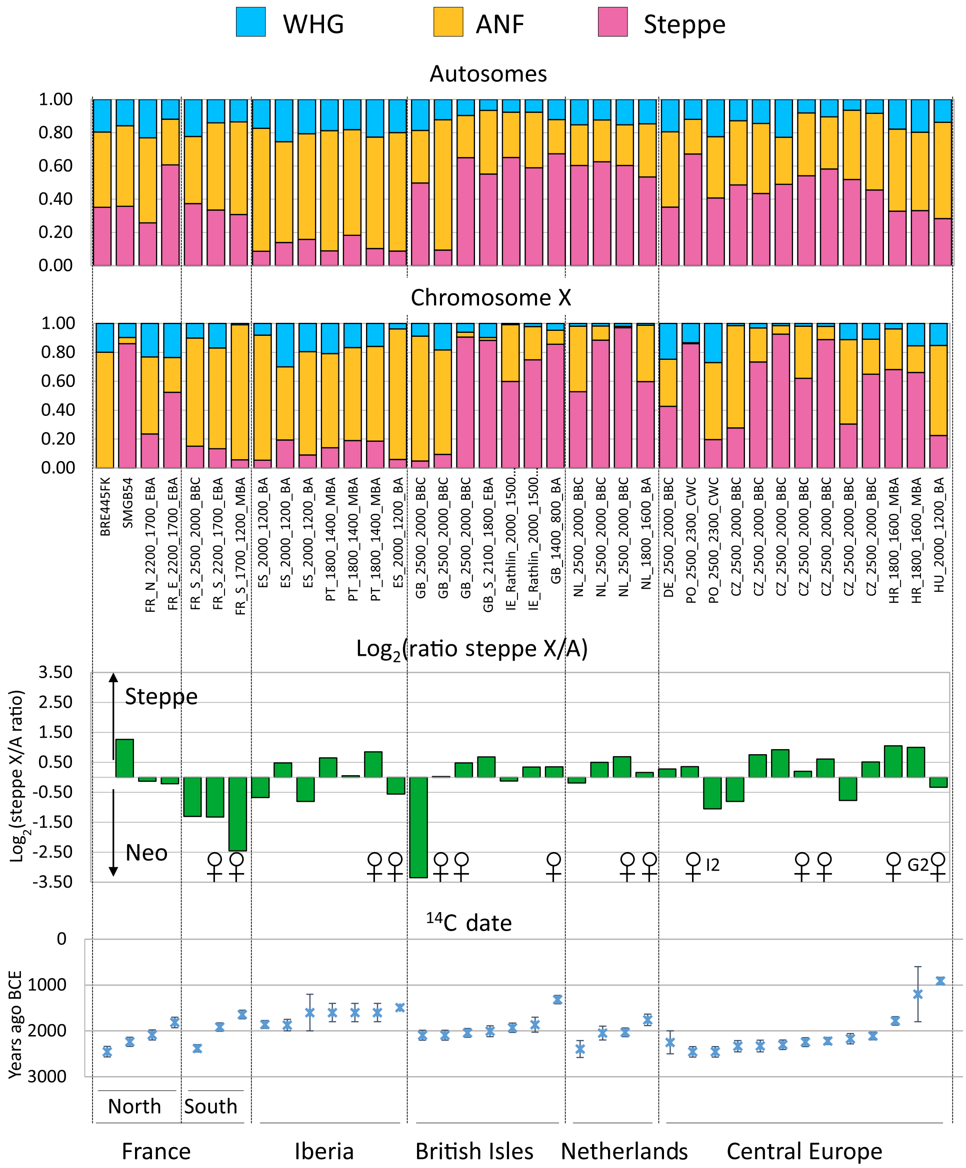

Fig. 6. Comparative analyses of the extent of steppe ancestry on chromosome X and autosomes. The two upper panels represent the proportion of steppe, WHG, and ANF ancestry as estimated using SOURCEFIND on either the autosomes or the X chromosome (top and bottom panels, respectively). The third panel represents the $\log_2$ of the ratio of steppe ancestry of the X chromosome to that of the autosomes. The fourth and lower panel represents the radiocarbon dating of the samples (average and 95% confidence interval). The women whose steppe ancestry proportion on the X is contributed by two chromosomes are indicated by the Venus symbol. The Y-chromosome haplogroup of the two men that do not carry the typical steppe ancestry (Y haplogroup R1b1a1b1) are indicated: One CWC man from Poland (haplogroup I2a1b1a2b1) is indicated as I2, and one man from Bronze Age Croatia (haplogroup G2a2a1a2a2a1) is indicated as G2 (see table S11 for the various ancestry proportions and ratios and the precise Y haplotypes).

of steppe ancestry in France. Grandfather YY was the carrier of the steppe ancestry that we found in the genomes of his son FK and grandson HI (Figs. 2B and 4A). While the proportion of steppe ancestry in the reconstructed pseudodiploid genome of YY (~66%) resembles that seen in contemporary CWC individuals in Poland (*16*, *64*) and Bohemia (*17*), it is reduced twofold in his son FK to a proportion otherwise found in Late Neolithic and Bronze Age individuals from Germany, Switzerland, and southern France (*15*, *65*, *70*, *77*). In YY's grandson, this steppe ancestry is further reduced twofold to levels found in Bronze Age Spain and Italy (*15*, *95*, *96*). Thus, within only two generations, incorporation of Neo-ancestry into the admixed steppe-Neo gene pool reduced steppe ancestry to a level otherwise observed in individuals post-2500 cal BCE. The speed of this ancestry reduction, and the low frequency of admixture during the initial steppe ancestry expansion in western Europe, might explain why steppe-Neo admixture has escaped observation so far: It must be captured in real time to be visible, as was possible in BRE445. This burial is a lucky case, a snapshot of a mating event involving a steppe ancestry individual who could be considered as an early steppe ancestry pioneer. He probably came to France from the Lower Rhine, given his northern European genetic signature.

This result unveils the fundamental elements of the early-phase admixture process between local Neo-ancestry and migrating steppe ancestry groups, as well as the groups' most likely mating behavior. The stark dilution of steppe ancestry within two generations following admixture as observed in the Bréviandes family snapshot highlights the difference in mating behavior in this case versus situations when steppe ancestry dilution was much slower or almost inexistent. For individuals to retain substantial steppe ancestry across generations, exceeding the at least 70% found in most Late Neolithic and Bronze Age individuals from eastern and Central Europe (*5*, *15–17*, *70*, *77*, *95*), they must have mated mostly with people of similar ancestry, and only sporadically with Neo-ancestry farmers. This mating pattern matches previous demographic inferences based on modeling of captured genomic data (*97*).

One minor and two major steppe-Neo admixture pulses

Using an admixture dating tool adapted to haplotypes, fastGLOBETROTTER (*88*), we estimated that admixture between individuals with steppe- and Neo-ancestry was not linear but rather followed a trimodal distribution pattern (Fig. 5 and table S8). A first but small admixture pulse observed around 3300 BCE may have resulted from the encounter of steppe nomads and Late Neolithic individuals in the steppe-forest zone between the Dniester and Dnieper. These pastoralists were genetically distinct from the Eneolithic steppe groups as they bore also small amounts of ANF-related ancestry in their genomes that can be explained by occasional admixture between Early Bronze Age individuals from the western Black Sea region and steppe pastoralists whose graves have been found as far west as the Carpathian Basin (*61*).

This first admixture event seems to have been of limited extent. It was followed some 300 years later by a larger admixture pulse around 2950 BCE (Fig. 5), identified in individuals from central and northern Europe [e.g., (*5*, *16*, *17*, *66*, *98*)]. The second admixture pulse involved many more individuals than the first, and we therefore refer to it henceforth as the "first major admixture pulse." This major admixture process corresponds to the admixture observed in previous studies (*5*, *66*, *67*, *99*, *100*). The corresponding communities must have been steppe-related on one hand and GAC-related on the other. The genetic legacy of the GAC-associated individuals has been identified as major contributors to later CWC-associated individuals (*66*). These first minor and major admixture pulses between migrating individuals with steppe ancestry and local individuals with Neo-ancestry appear sex-biased, as early CWC-associated individuals were detected with higher steppe ancestry on the autosomes than on the X chromosome (*77*). These first admixture pulses were followed by a period of relative stasis, when CWC-associated individuals mated preferentially with individuals of similar, predominantly steppe ancestry, leading to many generations of individuals with stable 70 to 80% steppe ancestry. This slightly admixed population pursued its migration to the north and west of Europe and only occasionally mated with local Neo-ancestry farmers, as described, for example, in southern Poland (*64*).

In western Europe, around 2600 BCE, we detect a new pulse of admixture between Neo-ancestry and steppe ancestry in the genome of SMGB54 from Saint-Martin-la-Garenne "Les Bretelles" associated with the BBC (2339 to 2139 cal BCE) and harboring ~40% steppe ancestry (Fig. 5 and table S8). The high proportion of steppe ancestry and the long steppe ancestry haplotype chunks in the SMGB54 genome point to a recent admixture event, about 12 generations before his birth. This event could have occurred in northern France, where individuals with northern steppe ancestry admixed with carriers of southwestern Neolithic genomes without steppe ancestry as seen in the BRE445 grave. Thus, both SMGB54 and the male individual FK from the Bréviandes grave are evidence of the major second pulse of admixture between steppe- and Neo-ancestry individuals. FK being an F1 hybrid, his haplotype block length was not yet reduced by recombination, and therefore did not affect the admixture date inferred from the size distribution of the haplotype blocks, but this new admixture could be inferred from its F1 hybrid status. The high amount of steppe ancestry introduced by this second admixture pulse is detected also in later Bronze Age individuals from western Europe who, like SMGB54, do not show further erosion of steppe ancestry. This observation let us infer that following the major second pulse, most individuals resumed their traditional mating preference for steppe ancestry carriers (*44*, *77*).

Sex bias of the admixture process

Using a haplotype-based approach, we also detect differences in the extent of steppe ancestry on the X chromosome and autosomes in European individuals around 2000 BCE (Fig. 6 and table S11). The pattern reveals a bimodal sex bias of the admixture process between steppe- and Neo-ancestry individuals. Some individuals show a marked excess of Neo ancestry on the X chromosome. The two male individuals of BRE445 have an infinite excess of Neo-ancestry on the X chromosome since their mothers were devoid of steppe ancestry. A male BBC individual from England [I12445, (*15*)] also showed a high excess of Neo-ancestry on the X chromosome. His maternal X chromosome, however, bore traces of steppe ancestry, and his steppe ancestry amounts to half of his genome, indicating that the maternal autosomes must have substantially contributed, although he was not an F1 hybrid between parents of pure Neo-ancestry and steppe ancestry. The excess of Neo-ancestry on the X chromosome of this BBC individual from England reveals a history of several generations of admixture with women of Neo-ancestry. Such an excess of Neo-ancestry on the X chromosome is also visible in the three individuals from southern France whose genomes were amenable to this analysis. This high frequency of Neo-ancestry excess on the X chromosome in southern France may indicate regional biases in the pattern of admixture. The finer evaluation of such regional and temporal differences in the admixture pattern, however, will require more extensive and high-quality whole-genome sequencing to be reliably detected.

In contrast, many individuals did not show an excess of Neo-ancestry on the X chromosome. On the contrary, a larger proportion of individuals showed an excess of steppe ancestry on the X chromosome, although this excess was not as high as that found in individuals with very recent maternal Neo-ancestry. The highest excess of steppe ancestry on the X chromosome was found in the male BBC individual from the Parisian Basin, SMGB54, whose maternal X chromosome has more than 80% of steppe ancestry. Twenty percent of the individuals analyzed (8 of 40) showed an excess of 80% steppe ancestry on the X chromosome. The maintenance of such a high proportion of steppe ancestry on the X chromosome indicates that for many generations women have not received an X chromosome with full Neo-ancestry from their father, since such a situation would have introduced large chunks of Neo-ancestry on the X chromosome. Thus, the bimodal pattern of ancestry on the X-chromosome appears to result from a mating bias: Men of steppe ancestry occasionally mated with women of Neo-ancestry, whereas women of steppe ancestry mated less frequently with men of

Neo-ancestry. Such a pattern of admixture is also supported by the vast excess of steppe ancestry Y haplotypes detected during the Late Neolithic to Bronze Age transition in western Europe (*11*, *15*) as well as in the dataset analyzed herein where 22 of 24 male individuals carry a R1b1a1 Y haplotype. Although admixture of steppe ancestry men with Neo-ancestry women occurred at various points in time, the bimodal pattern detected in the admixture timing indicates that these admixture events were more frequent during the two phases of westward expansion of individuals with steppe ancestry. Individual FK could be considered the earliest representative of this major second sex-biased admixture pulse, detected as it occurred.

This brief but rather general pattern of admixture with Neo-ancestry women in western Europe around 2600 BCE suggests a modification of the modalities or rhythm of the westward expansion of steppe ancestry carriers when reaching the Rhine. Between the first and the second pulse, wandering pioneers would have maintained contacts with their original CWC groups, a behavior that would have presented sufficient opportunities for mating with partners with similar steppe ancestry. An exchange pattern of females of steppe ancestry was detected in the Lech Valley in Germany during the BBC and Bronze Age (*77*). This pattern may thus have been a general trend associated with steppe ancestry groups, which could explain the relative population stasis after the first pulse of admixture. The three admixture pulses suggest rapid expansion of male-dominated pioneer groups moving in a single generation over distances too long to maintain “mating links” with their community of origin. This process would have led to more active recruitment of local women of Neo-ancestry and more rapid dilution of steppe ancestry, as seen in Bréviandes where we observed the phenomenon in real time. Grandfather YY likely represents such a pioneer and is the first witness of the arrival of steppe ancestry in France. The traces left in the later steppe ancestry descendants reveal that similar events happened elsewhere. This dilution of the steppe ancestry in the Neo gene pool is in agreement with archaeological data and provides no evidence for a replacement of the local Neolithic cultures by the early phase BBC (*44*). Strikingly, the second major admixture pulse occurred at the time when the BBC spread throughout Europe, in association with steppe ancestry. It is tempting to speculate that these two events were linked, particularly in light of the proposal that the MBBs originated from a Neolithic/Chalcolithic community of Neo-ancestry in the Iberian Peninsula (*54*).

Blending of populations and associated cultures

Encounters between steppe people and Neolithic communities and the emergence of the CWC

The first minor admixture pulse must have occurred around 3270 BCE in the steppe-forest contact zone in eastern Europe between emerging Yamnaya pastoralists from the steppes, whose graves have been found as far west as the Carpathian Basin, and the Neolithic world further west. This admixture must have taken place when steppe people moved to the west and the Baden culture expanded to the east and the GAC from eastern Poland to the Danube delta and the Dnieper area [e.g., (*20*, *48*)]. The contact between these communities did not lead to large-scale cultural transformations identifiable in the archaeological record and might have been driven by small pioneer groups.

The first major admixture pulse that peaked around 3000 to 2900 BCE was a large-scale event, and it likely drove the spread of the regionally diversified material cultures unified under the term CWC/single grave culture manifested in eastern Europe at the turn of the third millennium BCE (*20*). The earliest radiocarbon-dated single graves associated with the CWC have been found in northern Germany and Denmark around 2900 BCE [e.g., (*48*)]. This first major admixture pulse came to a halt rather quickly, less than 10 generations later, and can be explained only with a stark diminution of the interactions between CWC-associated and other Neolithic groups. There is archaeological evidence in support of this hypothesis. For instance, in the Netherlands, a lack of interaction is recorded between CWC-associated and coexisting Late Neolithic Vlaardingen/Stein–associated groups (~3400 to 2450 BCE), and exotic objects originated exclusively from areas occupied by other CWC communities (*22*). It also has been recognized that throughout the third millennium BCE, the CWC communities were strongly interconnected and individual mobility was high (*21*, *27*).

North-south and south-north movements of pots and people in western Europe

In the middle of the third millennium BCE, French Pressignian daggers appeared in AOO/AOC graves and exotic objects were traded over long distances throughout Europe (*22*). These elements coincide with the second major admixture pulse inferred around 2600 BCE and recorded in the archaeological record of France. The cultural attributes of the 2574 to 2452 cal BCE individual CBV95 from Ciry-Salsogne [notably an AOC beaker and a Grand-Pressigny flint dagger (*40*)] associate him with the single grave AOC/AOO complex. His cultural origin is reflected in both his high steppe ancestry proportion (~68% steppe ancestry) and his Neolithic genomic proportion that relates him to the northern/central European cluster associated with the Late Neolithic and Early Bronze Age single burial complex established in central Europe (*5*, *29*). This individual could be the descendant of an admixture event dated to the first major admixture pulse, but the genome coverage was not high enough for a high-resolution analysis. The genome of the male individual from Saint-Martin-la-Garenne (SMGB54) is characterized by ~36% steppe ancestry. SMGB54 was buried according to BBC funeral rituals (body in a crouched position on the left side, head oriented to the north-east), and his shale wrist guard might be the attribute of an archer, either a hunter and/or a warrior, but could also be symbolic (*58*, *101*). Stone wrist guards are prestigious grave goods only found in some BBC graves and rarely in domestic contexts. While their functional role is debated, they might indicate a higher-ranked social status (*22*, *32*, *58*, *101*). This cultural attribute, along with his steppe ancestry and genomic clustering with people from southwestern Europe, could make SMGB54 a witness of admixture in one of his ancestors between northern AOC pioneers moving southward and Neolithic/Chalcolithic MBB users from southern France or the Iberian Peninsula moving northward. Thus, SMGB54 might reflect both northward movement of his ancestors during the early stage of the BBC along the Atlantic coast followed by inland incursion along the river Loire and across the Gâtinais to the Seine valley, and southward movement from AOO/AOC pioneers (see also Supplementary Text).

Although thus far in northern France, the individuals found buried with AOO/AOC beakers and MBBs have all been carriers of steppe ancestry, this is not the case in southern France and the Rhine valley. The collective grave goods in southern France showing Iberian influence assigned to the early BBC period can be associated with individuals who are not steppe ancestry carriers, as follows: (i) two individuals from the Grotte Basse de la Vigne Perdue, one of whom (GBVPL; 2574 to 2473 cal BCE) was contemporaneous to the classical Veraza culture when the first BBC intrusions could have taken place, whereas the other (GBVPK; 2461 to 2299 cal BCE) belonged to the Late Pyrenean BBC, carrying steppe ancestry (*65*); (ii) an individual from the BBC period buried with others in the Dolmen des Peirières [PEI2; 2563 to 2308 cal BCE (*11*)]; (iii) a BBC burial at Hegenheim in Alsace accompanied by a vessel decorated in mixed maritime style from the early BBC tradition [I1392; 2832 to 2476 cal BCE (*15*)]. These individuals may be evidence of the Rhône-Saône valley BBC expansion through traveling craftspeople such as potters or archers (*51*). The Upper Rhône Valley records discontinuities between the Neolithic and the Bronze Age funerary pottery styles change between 2600/500 and 2200 BCE (*51*). The modifications of funerary monuments and stele engravings, as well as the individualization and modification of grave goods indicate a profound cultural change in these interconnected "communities of practice" (*51*). This change is also reflected in the shift from distant raw material sources (such as the Grand-Pressigny flint mines) to local ones, thus hinting at a transformation of exchange networks (*51*).

The establishment of the BBC in France

The genomic heterogeneity in the BBC horizon in France can be considered as a representative snapshot of the continuous assimilation of the BBC sociocultural model without abrupt population replacement by people with steppe ancestry, contrasting the situation in the British Isles where the population with Neo-ancestry seems to have been replaced by steppe ancestry carriers (*15*). The transformation process in southern France may thus have integrated regionally diverse trends with varying rejection and acculturation, as observed in the archaeological record [(*102*) and citations therein]. The spread of this new BBC ideology in France seems to have been accompanied by heterogeneous local and intra-regional admixture, involving only certain individuals. Their admixed descendants were absorbed in the Late Neolithic communities, as at Bréviandes, and buried in collective graves following various Middle and Late Neolithic deposition customs that differ from those of the CWC and later BBC traditions (see text S1), or alternatively, the admixed descendants were not buried, thus escaping archaeological and paleogenomic studies. Other admixed individuals of groups that had developed or adopted the new ideology, however, were buried in single graves (*29*, *59*). Those individuals that have been excavated and analyzed genomically revealed that further admixture with the local population was not common, leading to both the gradual disappearance of the former Neolithic culture and the transformation of the Neolithic genome.

The integrated analysis of genomic data from this study with previously published genomes from other areas unveil that northward traveling MBB and collective grave users from southwestern Europe and southward-traveling AOO/AOC beaker–using steppe ancestry carriers met in northern France. We propose that this meeting led to the second major admixture pulse detected in this study. Therefore, we hypothesize that the BBC arose as a synthesis of cultural elements from the encounter in France of southwestern Chalcolithic MBB and collective grave users and northwestern AOO/AOC beaker users with single grave burial rituals, leading to an admixed group, in agreement with the proposal that both the CWC and the BBC arose through interaction and mixing of individuals with a migrant background and people with stronger local roots (*13*, *29*). While the BBC integrated into the preexisting cultural fabrics, most settlements associated with the previous Neolithic traditions ceased to exist a few generations after the emergence of the single grave burial rituals in these regions [e.g., (*29*, *45*, *101*)]. This observation suggests that the populations with local roots increasingly adopted elements related to the settlement and economic customs of the immigrants by adopting their lifestyle [e.g., (*29*, *44*, *45*, *51*, *102*)].

After 2500 cal BCE, the descendants of this admixed group moved southward, as postulated by the "Rückstrom hypothesis" (*103*), probably via ancient western Alpine jadeite trade routes, mating in southern France and the Iberian Peninsula with individuals associated with preexisting Neolithic traditions and forming Mediterranean enclaves, thus recruiting additional southwestern Neo-ancestry into the admixed steppe-Neo ancestry. Interactions between MBB users and local Neolithic groups have been reported from graves in southwest and southern Mediterranean areas containing beakers of both styles, AOO/AOC and MBB, with the local traditions being more associated with the indigenous production of the latest Neolithic [(*102*) and citations therein]. This process would explain the establishment of a north-south steppe ancestry gradient, as it is still present today. The persistence of this ancestry gradient, and the maintenance of steppe ancestry in the European genome to the present day, argues for a higher reproductive rate of individuals with steppe ancestry in the later phase of the BBC, ultimately outcompeting the farmers carrying solely Neo-ancestry. The merging of genomes and cultural practices would have led to the emergence of a "hybrid" culture that continued to evolve and rapidly spread all over Europe. In support of this hypothesis are various bell beaker decorative styles in northwestern France that have been interpreted as hybrids, reflecting mutual influences between the Iberian and the Rhine decorative traditions (*46*). Thus, the hypothesis of merging genomes and blending of cultural elements matches and supports previous propositions solely based on archaeological evidence.

To conclude, our study of a Late Neolithic burial enables direct, quasi–real-time observation of the trimodal admixture processes in Europe between 3300 and 2600 cal BCE as steppe ancestry people dispersed and mixed with local Neo-ancestry groups or individuals. The generalization of the results obtained from our data suggests that this genomic transformation took place during a period of profound cultural change. The proposed admixture processes via two major pulses would also explain a shift to the profoundly different societal system observed in the Bronze Age (*77*) that eventually led to the replacement of the Neolithic genomes. Thus, this transformation concerned both the cultures and the biology of the populations involved, and led to the establishment of the genomic structure of the European population that still exists today.

MATERIALS AND METHODS

Radiocarbon dating and strontium isotope analysis

The samples were AMS ^{14}C-dated at Tandem Laboratory, Uppsala University, Uppsala, Sweden. The ^{87}Sr/^{86}Sr isotope analyses were performed by P. Fullagar under the direction of T. D. Price (Archaeological Chemistry, University of Chapel Hill, NC 27599, USA).

DNA extraction and library construction

Ancient DNA work was carried out in a high containment laboratory as described (*104*–*106*). The dense pyramidal parts of the petrous bones of the individual BRE445 and the individual SMBG54 were isolated using a flame-sterilized diamond disc of a Dremel. Bone pieces were then ground to fine powder in a 6775 Freezer/Mill-Spex SamplePrep in liquid nitrogen as described previously (*11*). The further protocol deviated from the previous one. Briefly, about 100 mg of bone powder was washed three times for 15 min each with 1 ml of 0.5 M sodium phosphate buffer at pH 8.0. Each sample was rinsed with 1 ml of TT buffer made of 10 mM tris-HCl (pH 8.0) and 0.1% Tween 20. One milliliter of extraction buffer [0.5 M EDTA (pH 8.0), 0.05% Tween 20, proteinase K (250 μg/ml), and 0.14 M β-mercaptoethanol] was added to each sample and incubated on a rotating wheel for ~30 hours at 37°C. After this first incubation, the samples were centrifuged at 6000*g* for 1 min. The supernatant was removed and kept for purification. Another 1 ml of extraction buffer was added to the pellet and, after resuspension, incubated for another 30 hours on a rotating wheel at 37°C. After this second incubation step, all samples were centrifuged at 6000*g* for 1 min. The supernatants from both incubation periods were pooled together in 2-ml tubes, mixed well, and then centrifuged at maximum speed for 2 min. One milliliter of the supernatant was used for the following purification step using 5M40 binding buffer [5 M guanidine HCl, 40% isopropanol, 120 mM sodium acetate (NaAc) (pH 5.2), 0.05% Tween 20; (*107*)]. One milliliter of each sample extract was purified with ~10 ml of 5M40 binding buffer through Qiagen columns under vacuum, rinsed twice with 1 ml of Buffer PE (Qiagen), and eluted with twice 30 μl of TET buffer [10 mM tris-HCl (pH 8.0), 1 mM EDTA, 0.05% Tween 20] following (*108*).

Libraries were constructed using 6 μl of extract and the NEBNext Ultra II DNA Library Prep Kit for Illumina (NEB, Ipswich, MA, USA) after a pretreatment with USER enzyme mix (NEB, Ipswich, MA, USA) as described by the manufacturer. An unindexed Y-shaped adapter was ligated, the ligated libraries were first amplified for eight cycles with the Illumina Rd1 and Rd2 sequencing primers, and then 20% of the library was further amplified for 12 cycles with Illumina unique dual indexed adapter primers. The libraries were purified using 1.3 volume of SPRI beads (Macherey-Nagel NucleoMag NGS Clean-up and Size Select) for two successive rounds of purification.

Processing of sequencing data

All data processing steps were performed using shell instructions and in-house written scripts. The raw output of Illumina sequencers was in the BCL format. Because of the high number of in-house barcodes used, we performed the initial demultiplexing and fastq conversion using bcl2fastq (Illumina) on the laboratory server. Sequence quality was assessed using FastQC (Babraham Bioinformatics, http://www.bioinformatics.babraham.ac.uk/projects/fastqc). Paired-end reads were merged and trimmed for adapters using leeHom (*109*). Reads larger than 28 base pairs were selected using awk and mapped onto the Human Reference Genome hs37d5 using BWA (Burrows-Wheeler Aligner) version 0.7.17 (*110*) with a seed length of 18. Aligned sequences in BAM format were processed with Samtools v.1.9 (*111*) to create index files and flagstat reports and to select and sort mapped reads. Picard tools (http://broadinstitute.github.io/picard/) was used to remove duplicates. Multiple libraries were merged by Samtools v.1.9 before filtering by mapping quality (-q 20). Damage patterns were analyzed using mapDamage v.2.2.1 followed by end-clipping using BamUtil (https://genome.sph.umich.edu/wiki/BamUtil:_trimBam). According to the damage pattern, three to four bases at the ends of each read were clipped for the User-treated libraries and 10 bases for non–User-treated libraries. Five Mbuti genome sequences (SRR1157019, SRR1157021, SRR1157023, SRR1157024, and SRR1157055) were mapped onto the hs37d5 human genome using bwa mem deduplicated and filtered for a mapping quality higher than 30.

Uniparental haplogroups, sex identification, and contamination estimation

To determine the sex of each individual, chromosome counts were performed using index statistics (idxstats) of Samtools on bam files by using exclusively the reads with mapping quality higher than 20 to prevent confounding effects from repetitive regions. Then, the ratio of the proportion of read counts normalized to chromosome length for both the X and Y, normalized for each to the average of the autosomal proportion, was used. Mitochondrial and Y-chromosome variants were called using bcftools mpileup (options -B -q30 -Q30) and call (option –ploidy GRCh37) for all female and male individuals, respectively. The output mtDNA and Y chr vcf files were used as input to run HaploGrouper (*112*) to classify mitochondrial and Y haplogroups, respectively, following the example provided online (https://gitlab.com/bio_anth_decode/haploGrouper) (table S1). The clipped bam files were used as input to run Haplocheck (*113*, *114*) for the estimation of contamination level. No contamination was detected in the mtDNA data. We used the ANGSD software to estimate contamination based on the X chromosome for male individuals (*115*).

Genotype calling and dataset preparation

We followed two different genotyping approaches, genotype imputation and pseudo-haploid calling, to prevent possible false calls from direct diploid genotyping due to low coverage of most ancient samples. To generate an imputed and phased dataset, first GLIMPSE (v.1.1.1) (*116*) was used to impute the ancient genomes, namely, 8 individuals from the current study and 111 publicly available ancient individuals. We followed the procedure described in the online Glimpse tutorial (https://odelaneau.github.io/GLIMPSE/glimpse1/tutorial_hg19.html), using Genotype Likelihoods (GL) computed with Bcftools (mpileup -I -E, call -Aim parameters) using the 1000 Genomes Project phase 3 reference panel excluding the indels. Following imputation, we filtered out positions with minor allele frequency lower than 5% in the 1000G reference panel. Under these conditions, based on the imputation accuracy (r^2) estimated using the same procedure and reference dataset for ancient European genomes (*117*), we estimate that the imputation accuracy would range from about 0.95 for the least covered genome (BRE445A) to about 0.99 for the best covered one (BRE445FK). Then, we applied a further filtration to remove positions with any posterior genotype probability lower than 0.99 and any missing genotype. For the bam files from shotgun sequencing or in-solution target capture, we used the autosomal sites in the 1240k SNP capture (*71*) using Samtools mpileup and the pileupCaller pipeline (https://github.com/stschiff/sequenceTools), the bam files resulting from either shotgun sequencing or in-solution target capture.

Estimation of genealogy, pigmentation profile, and runs of homozygosity

We inferred the relatedness between individuals coming from the complex burial described in the current study using a combination of two complementary approaches, NgsRelate and READ (*80*, *81*). We used a mixed group of 56 ancient western European individuals covering the periods of the Middle Neolithic and Late Neolithic, as well as Bronze Age to provide a distribution of background allele frequencies with ancestry proportions similar to those found in the complex burial. The first NgsRelate (v.2) analysis was performed using the allele frequency of these 56 individuals calculated from the genotype likelihoods of the bam files for all autosomes processed through ANGSD. To infer the pedigree, we performed a second NgsRelate analysis using ANGSD and the X chromosome data in the same manner. A third NgsRelate analysis was performed using the imputed genotypes of these 56 individuals in vcf format. The estimated genetic relationship (theta) and Cotterman (k0, k1, k2) coefficients from these three analyses were compared to the ideal values obtained using simulations by Yaka *et al.* (*118*) (table S2). READ was used to analyze pseudo-haploidized genotypes of individuals from the complex burial to further corroborate the NgsRelate-inferred relationships. We also calculated the normalized 1-P0 (mismatch rate) values from the output of Read as described (*118*) (table S2). To establish the pedigree shown in Fig. 1, we used the genetic relationships determined by these analyses, the uniparental haplogroups (mitogenomes and Y chromosomes), the genetic sex, and the anthropological estimation of the ages at death.

To predict the pigmentation profile of the newly reported individuals, we used HIrisplex-S (*93*) on the imputed genotypes. We checked the HIrisplex-S output for consistency by manual verification of the genotypes and allele depths obtained without imputation. Inbreeding was analyzed through HapROH (*82*) to identify ROH (runs of homozygosity) blocks longer than 4 cM on the Neolithic individuals from France.

Population genetic analyses

We ran ChromoPainter/fineSTRUCTURE (*85*) on the imputed and phased data using different sets of individuals so that no relatives were analyzed simultaneously. We used four datasets including all unrelated individuals with the related individuals grouped as follows: (i) FK-A-D, (ii) E-A-B, (iii) HI-B, and (iv) YY-A-D. After estimation of switch and mutation rates using 10 expectation-maximization (EM) iterations, each haplotype was painted using the others (-a 0 0). We applied fineSTRUCTURE's Markov chain Monte Carlo (MCMC) model on the resulting coancestry matrices with 3,000,000 burn-in and 2,000,000 sampling iterations. After the extraction of the maximum observed posterior probability state and 100,000 hill-climbing iterations, the trees were inferred by using the maximum concordance state as it is used in the PoBI study (*119*). The PCA and the dendrogram constructions were performed using the R functions from FinestructureLibrary.R (https://people.maths.bris.ac.uk/~madjl/finestructure/finestructureR.html). For the Procrustes analysis to evaluate the correlation between various combinations of PCs with the geographic coordinates of the samples, we used the "vegan" package in R with procrustes() and protest() commands (*120*).

To obtain input files for SOURCEFIND v2 (*86*) and fastGLOBETROTTER (*88*) and haplotype donation profiles, we ran ChromoPainter v2 with 10 iterations of EM to infer parameters on chromosomes 1, 8, 15, and 22. Subsequently, the copy vector and painting sample files were generated for the 22 autosomes on one hand and for the X chromosome on the other hand using the inferred parameters. To identify the haplotype donation from northern and southern France, we used two groups of individuals from the contemporary Late Neolithic sites of Mont-Aimé (2H10, 2H07, 1H13) and Rouquet (ROUQE, ROUQF, ROUQV) (*65*), respectively, as the donor populations in the ChromoPainter v2 run. Neolithic individuals from Bréviandes were used as recipient groups, alongside, as controls, two individuals not used in the initial donor populations, one from Mont-Aimé (1H04) and one from Rouquet (ROUGH), another southern France Late Neolithic individual from a distinct site in the vicinity of Rouquet (GBVPL), and a Chalcolithic sample from Northern Spain (I5838). Using the coancestry matrix of chunk lengths, the expected length of haplotypes that the given recipient individual copies from two Late Neolithic donor populations were normalized by the average values for each recipient individual to show their haplotype donation profile. For SOURCEFIND and fastGLOBETROTTER analyses, the ancestral groups, ANF (Bar31, Bar8, I0707, I0745, I0708, I1580), WHG (Loschbour, Bichon, R15, La Brana, KO1, SC2), and Yamnaya (I2105, RISE548, RISE552, Yamnaya) (see table S4), were used as donor populations to paint recipient individuals. For SOURCEFIND estimations on the X chromosome, individual-based datasets were prepared including only one test individual together with ANF, WHG, and Yamnaya groups. This allowed us to keep only shared genomic positions between tested individuals and ancestral groups after genotype probabilities (GP) and missingness filtrations without any loss of data due to unshared positions between tested individuals. For fastGLOBETROTTER inferences, we prepared a subset of the dataset used in ChromoPainter/fineSTRUCTURE analysis by including only the recipient individuals (see table S8) and donor populations to reduce the loss of data after GP and missingness filtrations, thus using 4,281,610 site sets for analysis. We ran fastGLOBETROTTER to infer the admixture dates for each individual by using Yamnaya and Late Neolithic (1H13, 2H10, ROUQE, ATP2, Koszyce_3_10, Koszyce_3_1) ancestral groups as surrogate populations followed by a jackknife resampling step dropping one of the 22 autosomes at a time as described (*88*) to calculate the confidence intervals. These confidence intervals were calculated using the delete-mj jackknife variance estimator formula of Busing *et al.* (*121*). Density curves were computed using admixture dates calculated from the number of inferred generations per autosome subset of individuals that were estimated by the jackknife resampling step of fastGLOBETROTTER, corresponding to 22 estimations from each chromosome subsets per individual from a total of 20 individuals or grouped individuals, thus using 440 date estimations for density plot analyses. Since the data distribution indicated the presence of distinct pulses of steppe ancestry admixture, we used a GMM probabilistic clustering approach for representing the presence of subpopulations. To do this, we used two R packages, mclust (*122*) and AdaptGauss (*123*). Using mclust, we identified the most likely mixture model as three Gaussian of unequal variance using the BIC for parameterized mixture models given the log likelihood, the dimension of the data, and number of mixture components in the model. We explored it further using AdaptGauss that also estimated the three-Gaussian model as most likely after deriving the Pareto density estimation represented in Fig. 5B and using the expectation maximization algorithm to find the local maximum of the likelihood. The resulting three Gaussian curves (Fig. 5B) had a mean, SD, and proportion estimated at 2611 ± 130 BCE (49.9%), 2947 ± 92 BCE (42.5%), and 3266 ± 82 BCE (7.6%). The null hypothesis that the estimated data distribution does not differ significantly from the GMM was not rejected using a Pearson's chi-squared goodness of fit test ($\chi^2 = 0.86295$), whereas it was clearly rejected when using two ($\chi^2 = 0.000445$) or a single Gaussian ($\chi^2 = 0$).

qpAdm (*87*) was performed using the Admixtools package (*124*) on the 1240k dataset for individuals coming from both shotgun sequencing and in-solution target capture data (*125*). We used Mbuti, Ust'-Ishim, Kostenki14, Sunghir3, Karelia, Motala12, and Iranian Neolithic genomes as the reference groups (see references in table S4). Target individuals that could not be modeled as the product of a three-way admixture event were modeled as the product of a two-way admixture event. Local polynomial regression of relative steppe ancestry proportions using the LOESS method was plotted versus mean radiocarbon dating values using geom_smooth() from ggplot2 that also allowed representation of the 95% confidence interval. DATES (*89*) was applied on the 1240k dataset for individuals from France that were used in fastGLOBETROTTER runs.

Supplementary Materials

This PDF file includes:
Supplementary Text
Figs. S1 to S17
Table S12
Legends for tables S1 to S11
References

Other Supplementary Material for this manuscript includes the following:
Tables S1 to S11

REFERENCES AND NOTES

1. Q. Fu, M. Hajdinjak, O. T. Moldovan, S. Constantin, S. Mallick, P. Skoglund, N. Patterson, N. Rohland, I. Lazaridis, B. Nickel, B. Viola, K. Prüfer, M. Meyer, J. Kelso, D. Reich, S. Pääbo, An early modern human from Romania with a recent Neanderthal ancestor. *Nature* **524**, 216–219 (2015).
2. Q. Fu, C. Posth, M. Hajdinjak, M. Petr, S. Mallick, D. Fernandes, A. Furtwangler, W. Haak, M. Meyer, A. Mittnik, B. Nickel, A. Peltzer, N. Rohland, V. Slon, S. Talamo, I. Lazaridis, M. Lipson, I. Mathieson, S. Schiffels, P. Skoglund, A. P. Derevianko, N. Drozdov, V. Slavinsky, A. Tsybankov, R. G. Cremonesi, F. Mallegni, B. Gely, E. Vacca, M. R. Morales, L. G. Straus, C. Neugebauer-Maresch, M. Teschler-Nicola, S. Constantin, O. T. Moldovan, S. Benazzi, M. Peresani, D. Coppola, M. Lari, S. Ricci, A. Ronchitelli, F. Valentin, C. Thevenet, K. Wehrberger, D. Grigorescu, H. Rougier, I. Crevecoeur, D. Flas, P. Semal, M. A. Mannino, C. Cupillard, H. Bocherens, N. J. Conard, K. Harvati, V. Moiseyev, D. G. Drucker, J. Svoboda, M. P. Richards, D. Caramelli, R. Pinhasi, J. Kelso, N. Patterson, J. Krause, S. Paabo, D. Reich, The genetic history of Ice Age Europe. *Nature* **534**, 200–205 (2016).
3. S. Shennan, *The First Farmers of Europe: An Evolutionary Perspective* (Cambridge Univ. Press, 2018).
4. C. Gamba, E. R. Jones, M. D. Teasdale, R. L. McLaughlin, G. Gonzalez-Fortes, V. Mattiangeli, L. Domboroczki, I. Kovari, I. Pap, A. Anders, A. Whittle, J. Dani, P. Raczky, T. F. Higham, M. Hofreiter, D. G. Bradley, R. Pinhasi, Genome flux and stasis in a five millennium transect of European prehistory. *Nat. Commun.* **5**, 5257 (2014).
5. W. Haak, I. Lazaridis, N. Patterson, N. Rohland, S. Mallick, B. Llamas, G. Brandt, S. Nordenfelt, E. Harney, K. Stewardson, Q. Fu, A. Mittnik, E. Banffy, C. Economou, M. Francken, S. Friederich, R. G. Pena, F. Hallgren, V. Khartanovich, A. Khokhlov, M. Kunst, P. Kuznetsov, H. Meller, O. Mochalov, V. Moiseyev, N. Nicklisch, S. L. Pichler, R. Risch, M. A. Rojo Guerra, C. Roth, A. Szecsenyi-Nagy, J. Wahl, M. Meyer, J. Krause, D. Brown, D. Anthony, A. Cooper, K. W. Alt, D. Reich, Massive migration from the steppe was a source for Indo-European languages in Europe. *Nature* **522**, 207–211 (2015).
6. I. Lazaridis, D. Nadel, G. Rollefson, D. C. Merrett, N. Rohland, S. Mallick, D. Fernandes, M. Novak, B. Gamarra, K. Sirak, S. Connell, K. Stewardson, E. Harney, Q. Fu, G. Gonzalez-Fortes, E. R. Jones, S. A. Roodenberg, G. Lengyel, F. Bocquentin, B. Gasparian, J. M. Monge, M. Gregg, V. Eshed, A. S. Mizrahi, C. Meiklejohn, F. Gerritsen, L. Bejenaru, M. Bluher, A. Campbell, G. Cavalleri, D. Comas, P. Froguel, E. Gilbert, S. M. Kerr, P. Kovacs, J. Krause, D. McGettigan, M. Merrigan, D. A. Merriwether, S. O'Reilly, M. B. Richards, O. Semino, M. Shamoon-Pour, G. Stefanescu, M. Stumvoll, A. Tonjes, A. Torroni, J. F. Wilson, L. Yengo, N. A. Hovhannisyan, N. Patterson, R. Pinhasi, D. Reich, Genomic insights into the origin of farming in the ancient Near East. *Nature* **536**, 419–424 (2016).
7. A. Omrak, T. Gunther, C. Valdiosera, E. M. Svensson, H. Malmstrom, H. Kiesewetter, W. Aylward, J. Stora, M. Jakobsson, A. Gotherstrom, Genomic evidence establishes Anatolia as the source of the European Neolithic gene pool. *Curr. Biol.* **26**, 270–275 (2016).
8. Z. Hofmanova, S. Kreutzer, G. Hellenthal, C. Sell, Y. Diekmann, D. Diez-Del-Molino, L. van Dorp, S. Lopez, A. Kousathanas, V. Link, K. Kirsanow, L. M. Cassidy, R. Martiniano, M. Strobel, A. Scheu, K. Kotsakis, P. Halstead, S. Triantaphyllou, N. Kyparissi-Apostolika, D. Urem-Kotsou, C. Ziota, F. Adaktylou, S. Gopalan, D. M. Bobo, L. Winkelbach, J. Blocher, M. Unterlander, C. Leuenberger, C. Cilingiroglu, B. Horejs, F. Gerritsen, S. J. Shennan, D. G. Bradley, M. Currat, K. R. Veeramah, D. Wegmann, M. G. Thomas, C. Papageorgopoulou, J. Burger, Early farmers from across Europe directly descended from Neolithic Aegeans. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 6886–6891 (2016).
9. M. Lipson, A. Szecsenyi-Nagy, S. Mallick, A. Posa, B. Stegmar, V. Keerl, N. Rohland, K. Stewardson, M. Ferry, M. Michel, J. Oppenheimer, N. Broomandkhoshbacht, E. Harney, S. Nordenfelt, B. Llamas, B. Gusztav Mende, K. Kohler, K. Oross, M. Bondar, T. Marton, A. Osztas, J. Jakucs, T. Paluch, F. Horvath, P. Csengeri, J. Koos, K. Sebok, A. Anders, P. Raczky, J. Regenye, J. P. Barna, S. Fabian, G. Serlegi, Z. Toldi, E. Gyongyver Nagy, J. Dani, E. Molnar, G. Palfi, L. Mark, B. Melegh, Z. Banfai, L. Domboroczki, J. Fernandez-Eraso, J. Antonio Mujika-Alustiza, C. Alonso Fernandez, J. Jimenez Echevarria, R. Bollongino, J. Orschiedt, K. Schierhold, H. Meller, A. Cooper, J. Burger, E. Banffy, K. W. Alt, C. Lalueza-Fox, W. Haak, D. Reich, Parallel palaeogenomic transects reveal complex genetic history of early European farmers. *Nature* **551**, 368–372 (2017).
10. I. Mathieson, S. Alpaslan-Roodenberg, C. Posth, A. Szecsenyi-Nagy, N. Rohland, S. Mallick, I. Olalde, N. Broomandkhoshbacht, F. Candilio, O. Cheronet, D. Fernandes, M. Ferry, B. Gamarra, G. G. Fortes, W. Haak, E. Harney, E. Jones, D. Keating, B. Krause-Kyora, I. Kucukkalipci, M. Michel, A. Mittnik, K. Nagele, M. Novak, J. Oppenheimer, N. Patterson, S. Pfrengle, K. Sirak, K. Stewardson, S. Vai, S. Alexandrov, K. W. Alt, R. Andreescu, D. Antonovic, A. Ash, N. Atanassova, K. Bacvarov, M. B. Gusztav, H. Bocherens, M. Bolus, A. Boroneant, Y. Boyadzhiev, A. Budnik, J. Burmaz, S. Chohadzhiev, N. J. Conard, R. Cottiaux, M. Cuka, C. Cupillard, D. G. Drucker, N. Elenski, M. Francken, B. Galabova, G. Ganetsovski, B. Gely, T. Hajdu, V. Handzhyiska, K. Harvati, T. Higham, S. Iliev, I. Jankovic, I. Karavanic, D. J. Kennett, D. Komso, A. Kozak, D. Labuda, M. Lari, C. Lazar, M. Leppek, K. Leshtakov, D. L. Vetro, D. Los, I. Lozanov, M. Malina, F. Martini, K. McSweeney, H. Meller, M. Mendusic, P. Mirea, V. Moiseyev, V. Petrova, T. D. Price, A. Simalcsik, L. Sineo, M. Slaus, V. Slavchev, P. Stanev, A. Starovic, T. Szeniczey, S. Talamo, M. Teschler-Nicola, C. Thevenet, I. Valchev, F. Valentin, S. Vasilyev, F. Veljanovska, S. Venelinova, E. Veselovskaya, B. Viola, C. Virag, J. Zaninovic, S. Zauner, P. W. Stockhammer, G. Catalano, R. Krauss, D. Caramelli, G. Zarina, B. Gaydarska, M. Lillie, A. G. Nikitin, I. Potekhina, A. Papathanasiou, D. Boric, C. Bonsall, J. Krause, R. Pinhasi, D. Reich, The genomic history of southeastern Europe. *Nature* **555**, 197–203 (2018).
11. S. Brunel, E. A. Bennett, L. Cardin, D. Garraud, H. B. Emam, A. Beylier, B. Boulestin, F. Chenal, E. Ciesielski, F. Convertini, B. Dedet, S. Desbrosse-Degobertiere, S. Desenne, J. Dubouloz, H. Duday, G. Escalon, V. Fabre, E. Gailledrat, M. Gandelin, Y. Gleize, S. Goepfert, J. Guilaine, L. Hachem, M. Ilett, F. Lambach, F. Maziere, B. Perrin, S. Plouin, E. Pinard, I. Praud, I. Richard, V. Riquier, R. Roure, B. Sendra, C. Thevenet, S. Thiol, E. Vauquelin, L. Vergnaud, T. Grange, E. M. Geigl, M. Pruvost, Ancient genomes from present-day France unveil 7,000 years of its demographic history. *Proc. Natl. Acad. Sci. U.S.A.* **117**, 12791–12798 (2020).
12. M. Rivollat, C. Jeong, S. Schiffels, I. Kucukkalipci, M. H. Pemonge, A. B. Rohrlach, K. W. Alt, D. Binder, S. Friederich, E. Ghesquiere, D. Gronenborn, L. Laporte, P. Lefranc, H. Meller, H. Reveillas, E. Rosenstock, S. Rottier, C. Scarre, L. Soler, J. Wahl, J. Krause, M. F. Deguilloux, W. Haak, Ancient genome-wide DNA from France highlights the complexity of interactions between Mesolithic hunter-gatherers and Neolithic farmers. *Sci. Adv.* **6**, eaaz5344 (2020).
13. K. Kristiansen, The decline of the Neolithic and the rise of Bronze Age society, in *The Oxford Handbook of Neolithic Europe*, C. Fowler, J. Harding, D. Hofmann, Eds. (Oxford Univ. Press, 2014), chap. 56, pp. 1093–1118.
14. V. Heyd, in *Yamnaya Interactions. The Yamnaya Impact of Prehistoric Europe 2*, V. Heyd, G. Kulcsár, B. Preda-Bălănică, Eds. (Archaeolingua, 2021), vol. 44, pp. 383–414.
15. I. Olalde, S. Brace, M. E. Allentoft, I. Armit, K. Kristiansen, T. Booth, N. Rohland, S. Mallick, A. Szecsenyi-Nagy, A. Mittnik, E. Altena, M. Lipson, I. Lazaridis, T. K. Harper, N. Patterson, N. Broomandkhoshbacht, Y. Diekmann, Z. Faltyskova, D. Fernandes, M. Ferry, E. Harney, P. de Knijff, M. Michel, J. Oppenheimer, K. Stewardson, A. Barclay, K. W. Alt, C. Liesau, P. Rios, C. Blasco, J. V. Miguel, R. M. Garcia, A. A. Fernandez, E. Banffy, M. Bernabo-Brea, D. Billoin, C. Bonsall, L. Bonsall, T. Allen, L. Buster, S. Carver, L. C. Navarro, O. E. Craig, G. T. Cook, B. Cunliffe, A. Denaire, K. E. Dinwiddy, N. Dodwell, M. Ernee, C. Evans, M. Kucharik, J. F. Farre, C. Fowler, M. Gazenbeek, R. G. Pena, M. Haber-Uriarte, E. Haduch, G. Hey, N. Jowett, T. Knowles, K. Massy, S. Pfrengle, P. Lefranc, O. Lemercier, A. Lefebvre, C. H. Martinez, V. G. Olmo, A. B. Ramirez, J. L. Maurandi, T. Majo, J. I. McKinley, K. McSweeney, B. G. Mende, A. Modi, G. Kulcsar, V. Kiss, A. Czene, R. Patay, A. Endrodi, K. Kohler, T. Hajdu, T. Szeniczey, J. Dani, Z. Bernert, M. Hoole, O. Cheronet, D. Keating, P. Veleminsky, M. Dobes, F. Candilio, F. Brown, R. F. Fernandez, A. M. Herrero-Corral, S. Tusa, E. Carnieri, L. Lentini, A. Valenti, A. Zanini, C. Waddington, G. Delibes, E. Guerra-Doce, B. Neil, M. Brittain, M. Luke, R. Mortimer, J. Desideri, M. Besse, G. Brucken, M. Furmanek, A. Haluszko, M. Mackiewicz, A. Rapinski, S. Leach, I. Soriano, K. T. Lillios, J. L. Cardoso, M. P. Pearson, P. Wlodarczak, T. D. Price, P. Prieto, P. J. Rey, R. Risch,

M. A. R. Guerra, A. Schmitt, J. Serralongue, A. M. Silva, V. Smrcka, L. Vergnaud, J. Zilhao, D. Caramelli, T. Higham, M. G. Thomas, D. J. Kennett, H. Fokkens, V. Heyd, A. Sheridan, K. G. Sjogren, P. W. Stockhammer, J. Krause, R. Pinhasi, W. Haak, I. Barnes, C. Lalueza-Fox, D. Reich, The Beaker phenomenon and the genomic transformation of northwest Europe. *Nature* **555**, 190–196 (2018).

16. D. M. Fernandes, D. Strapagiel, P. Borowka, B. Marciniak, E. Zadzinska, K. Sirak, V. Siska, R. Grygiel, J. Carlsson, A. Manica, W. Lorkiewicz, R. Pinhasi, A genomic Neolithic time transect of hunter-farmer admixture in central Poland. *Sci. Rep.* **8**, 14879 (2018).
17. L. Papac, M. Ernee, M. Dobes, M. Langova, A. B. Rohrlach, F. Aron, G. U. Neumann, M. A. Spyrou, N. Rohland, P. Veleminsky, M. Kuna, H. Brzobohata, B. Culleton, D. Danecek, A. Danielisova, M. Dobisikova, J. Hlozek, D. J. Kennett, J. Klementova, M. Kostka, P. Kristuf, M. Kucharik, J. K. Hlavova, P. Limbursky, D. Malykova, L. Mattiello, M. Pecinovska, K. Petriscakova, E. Pruchova, P. Stranska, L. Smejtek, J. Spacek, R. Sumberova, O. Svejcar, M. Trefny, M. Vavra, J. Kolar, V. Heyd, J. Krause, R. Pinhasi, D. Reich, S. Schiffels, W. Haak, Dynamic changes in genomic and social structures in third millennium BCE central Europe. *Sci. Adv.* **7**, eabi6941 (2021).
18. M. Furholt, Pottery, cultures, people? The European Baden material re-examined. *Antiquity* **82**, 617–628 (2008).
19. M. Furholt, *Die nördlichen Badener Keramikstile im Kontext des mitteleuropäischen Spätneolithikums (3650–2900 v. CHr.)* (Dr. Rudolf Habelt GmbH, 2009).
20. M. Furholt, Upending a "totality": Re-evaluating Corded Ware variability in Late Neolithic Europe. *Proc. Prehist. Soc. Lond.* **80**, 67–86 (2014).
21. M. Furholt, Mobility and social change: Understanding the European Neolithic period after the archaeogenetic revolution. *J. Archaeol. Res.* **29**, 481–535 (2021).
22. K. Wentink, *Stereotype: The Role of Grave Sets in Corded Ware and Bell Beaker Funerary Practices* (Sidestone Press, 2020).
23. L. Salanova, V. Heyd, Du collectif à l'individu, de la région à l'Europe du IIIe millénaire avant J.-C. entre le Bassin Parisien et la Vallée Rhénane. *Archaeol. Mosellana* **7**, 469–490 (2007).
24. J. Chapman, M. Y. Videiko, D. Hale, B. Gaydarska, N. Burdo, K. Rassmann, C. Mischka, J. Müller, A. Korvin-Piotrovskiy, The second phase of the trypillia mega-site methodological revolution: A new research agenda. *Eur. J. Archaeol.* **17**, 369–406 (2014).
25. Y. Boyadzhiev, K. Boyadzhiev, L. Brandtstätter, R. Krauss, Chronological modelling of the Chalcolithic settlement layers at Tell Yunatsite, Southern Bulgaria. *Doc. Praehist.* **48**, 252–275 (2021).
26. A. G. Nikitin, M. Videiko, N. Patterson, V. Renson, D. Reich, Interactions between Trypillian farmers and North Pontic forager-pastoralists in Eneolithic central Ukraine. *PLOS ONE* **18**, e0285449 (2023).
27. M. Furholt, Translocal communities—Exploring mobility and migration in sedentary societies of the European Neolithic and Early Bronze Age. *Prähist. Z.* **92**, 304–321 (2018).
28. M. Furholt, Re-integrating archaeology: A contribution to aDNA studies and the migration discourse on the 3rd millennium BC in Europe. *Proc. Prehist. Soc.* **85**, 115–129 (2019).
29. M. Furholt, Social Worlds and Communities of Practice: A polythetic culture model for 3rd millennium BC Europe in the light of current migration debates. *Préhist. Méditerranéennes* **8**, 1–24 (2020).
30. V. Heyd, Families, prestige goods, warriors and complex societies: Beaker groups of the 3rd millennium cal BC along the Upper and Middle Danube. *Proc. Prehist. Soc.* **73**, 321–370 (2007).
31. K. Kristiansen, M. E. Allentoft, K. M. Frei, R. Iversen, N. N. Johannsen, G. Kroonen, L. Pospieszny, T. D. Prise, S. Rasmussen, K.-G. Sjögren, M. Sikora, E. Willerslev, Re-theorising mobility and the formation of culture and language among the Corded Ware Culture in Europe. *Antiquity* **91**, 334–347 (2017).
32. J. Ryan-Despraz, *Practice and Prestige. An Exploration of Neolithic Warfare, Bell Beaker Archery, and Social Stratification from an Anthropological Perspective* (Archaeopress Publishing LTC, 2022).
33. A. Immel, S. Terna, A. Simalcsik, J. Susat, O. Sarov, G. Sirbu, R. Hofmann, J. Muller, A. Nebel, B. Krause-Kyora, Gene-flow from steppe individuals into Cucuteni-Trypillia associated populations indicates long-standing contacts and gradual admixture. *Sci. Rep.* **10**, 4253 (2020).
34. D. W. Anthony, *The Horse, the Wheel, and Language: How Bronze-Age Riders from the Eurasian Steppes Shaped the Modern World* (Princeton Univ. Press, 2007).
35. H. Fokkens, F. Nicolis, *Background to Beakers. Inquiries into Regional Cultural Backgrounds of the Bell Beaker Complex* (Sidestone, 2012).
36. J. N. Lantin, J. D. Van der Waals, in *Glockenbechersymposium 1974* (Bussum, 1976), pp. 1–80.
37. L. Salanova, Y. Tchérémissinoff, Gallia Préhistoire supplément, *Les sépultures individuelles campaniformes en France*, CNRS Éditions, Paris vol. 41, (2011).
38. E. Ihuel, N. Mallet, J. Pelegrin, C. Verjux, The dagger phenomenon: Circulation from the Grand-Pressigny region (France, Indre-et-Loire) in western Europe, in *The Bell Beaker Transition in Europe—Mobility and Loca Evolution During the 3rd Millennium BC*, M. P. Prieto Martinez, L. Salanova, Eds. (Oxbow Books, 2015), pp. 113–126.
39. S. Chauvin, P. Allard, G. Fronteau, N. Garnier, L. Hachem, N. Mazzucco, A. Monnier, M.-P. Petitdidier, S. Thiol, Une sépulture campaniforme en plaine du Briennois (Blignicourt, Aube). *Internéo* **12**, 149–158 (2018).
40. L. Hachem, P. Allard, F. Convertinie, B. Robert, L. Salanova, I. Sidéra, C. Thevent, La sépulture campaniforme de Ciry-Salsogne "La Bouche à Vesle" (Aisne), in *Les sépultures individuelles campaniformes en France*, L. Salanova, Y. Tchérémissinoff, Eds. (Gallia Préhistoire, 2011), vol. XLIe Supplément, pp. 21–35.
41. H. Fokkens, Background to Dutch Beakers. A critical review of the Dutch model, in *Background to Beakers. Inquiries into Regional Cultural Backgrounds of the Bell Beaker Complex*, H. Fokkens, F. Nicolis, Eds. (Sidestone Press, 2012), pp. 9–35.
42. L. Salanova, *Chronologie et facteurs d'évolution des sépultures individuelles campaniformes dans le Nord de la France* (Les Sépultures Individuelles Campaniformes en France, Supplément à Gallia Préhistoire, CNRS, 2011), vol. 41.
43. O. Lemercier, in *XXVIIIe Congrès Préhistorique de France: La fin du Néolithique et la genèse du Bronze ancien dans l'Europe du nord-ouest*, N. Buchez, O. Lermercier, I. Praud, M. Talon, Eds. (Société Préhistorique Française, 2019), vol. session 5, pp. 239–250.
44. O. Lemercier, Think and act. Local data and global perspectives in bell beaker archaeology. *J. Neolithic Archaeol.* **20**, 77–96 (2018).
45. M. Besse, E. Derenne, L. Anchieri, A. Baumberger, A. Caminada, M. Piguet, Continuity or rupture? Investigating domestic structures during the Final Neolithic and the Bell Beaker culture in central-eastern France and western Switzerland, in *Bell Beaker Settlement of Europe: The Bell Beaker Phenomenon from a Domestic Perspective*, A. M. Gibson, Ed. (Oxbow Books, 2019), vol. 9, pp. 151–116.
46. Q. Favrel, in *The Bell Beaker Culture in All Its Forms. 22nd Meeting of 'Archéologie et Gobelets' 2021*, C. Abegg, D. Carloni, F. Cousseau, E. Derenne, J. Ryan-Despraz, Eds. (Archaeopress, 2022), pp. 81–95.
47. M. P. P. Martinez, L. Salanova, *The Bell Beaker Transition in Europe: Mobility and Local Evolution During the 3rd millennium BC* (Oxbow Books, 2015).
48. M. Furholt, *Die absolutchronologische Datierung der Schnurkeramik in Mitteleuropa und Südskandinavien* (Universitätsforschungen zur Prähistorischen Archäologie, Dr. Rudolf Habelt GmbH, 2003).
49. L. Salanova, Le rôle de la façade atlantique dans la genèse du Campaniforme en Europe. *Bull. Soc. Préhist. Française* **101**, 223–226 (2004).
50. J. L. Cardoso, Os mais antigos vasos maritimos e sua difusao a partir do estuario do Tejo (Portugal). *Estudos Arqueol. Oeiras* **25**, 47–74 (2019).
51. E. Derenne, V. Ard, M. Besse, Potters' mobility contributed to the emergence of the Bell Beaker phenomenon in third millennium BCE alpine Switzerland: A diachronic technology study of domestic and funerary traditions. *Open Archaeol.* **8**, 925–955 (2022).
52. T. D. Price, J. H. H. Burton, R. A. Bentley, The characterization of biologically available strontium isotope ratios for the study of prehistoric migration. *Archaeometry* **44**, 117–135 (2002).
53. M. Besse, M. Piguet, F. Cattin, J. Desideri, L'imbloglio campaniforme: Une céramique, des céramiques, in *De Méditerranée et d'ailleurs: Mélanges offerts à Jean Guilaine* (Archives d'Écologie Préhistorique, 2009), pp. 97–115.
54. J. L. Cardoso, Absolute chronology of the Beaker phenomenon north of the Tagus estuary: Demographic and social implications. *Trab. Prehist.* **71**, 56–75 (2014).
55. J. Guilaine, La question campaniforme: Sur quelques débats d'hier et d'aujourd'hui. *Estudos Arqueol. Oeiras* **25**, 9–46 (2019).
56. T. D. Price, C. Knipper, G. Grupe, V. Smrchka, Strontium isotopes and prehistoric human migration: The bell beaker period in Central Europe. *Eur. J. Archaeol.* **7**, 9–40 (2004).
57. O. Lemercier, La question campaniforme, in *La Protohistoire de la France*, J. Guilaine, D. Garcia, Eds. [Hermann (Histoire et Archéologie), Paris, 2018], pp. 205–217.
58. J. Turek, Bell Beaker stone wrist-guards as symbolic male ornament. The significance of ceremonial warfare in 3rd millennium BC central Europe, in *The Bell Beaker Transition in Europe—Mobility and Loca Evolution During the 3rd Millennium BC*, M. P. Prieto Martinez, L. Salanova, Eds. (Oxbow Books, 2015), pp. 28–40.
59. R. Grossmann, *Das dialektische Verhältnis von Schnurkeramik und Glockenbecher zwischen Rhein und Saale* (Universitätsforschungen zur prähistorischen Archäologie, Graduiertenschule "Human Development in Landscapes" 8 der Christian-ALbrechts-Universität Kiel, Verlag Dr. Rudolf Habelt GmbH, 2016), vol. 287, p. 281.
60. C. C. Wang, S. Reinhold, A. Kalmykov, A. Wissgott, G. Brandt, C. Jeong, O. Cheronet, M. Ferry, E. Harney, D. Keating, S. Mallick, N. Rohland, K. Stewardson, A. R. Kantorovich, V. E. Maslov, V. G. Petrenko, V. R. Erlikh, B. C. Atabiev, R. G. Magomedov, P. L. Kohl, K. W. Alt, S. L. Pichler, C. Gerling, H. Meller, B. Vardanyan, L. Yeganyan, A. D. Rezepkin, D. Mariaschk, N. Berezina, J. Gresky, K. Fuchs, C. Knipper, S. Schiffels, E. Balanovska, O. Balanovsky, I. Mathieson, T. Higham, Y. B. Berezin, A. Buzhilova, V. Trifonov, R. Pinhasi, A. B. Belinskij, D. Reich, S. Hansen, J. Krause, W. Haak, Ancient human genome-wide data from a 3000-year interval in the Caucasus corresponds with eco-geographic regions. *Nat. Commun.* **10**, 590 (2019).
61. S. Penske, A. B. Rohrlach, A. Childebayeva, G. Gnecchi-Ruscone, C. Schmid, M. A. Spyrou, G. U. Neumann, N. Atanassova, K. Beutler, K. Boyadzhiev, Y. Boyadzhiev, I. Bruyako,

A. Chohadzhiev, B. Govedarica, M. Karaucak, R. Krauss, M. Leppek, I. Manzura, K. Privat, S. Ross, V. Slavchev, A. Sobotkova, M. Toderas, T. Valchev, H. Ringbauer, P. W. Stockhammer, S. Hansen, J. Krause, W. Haak, Early contact between late farming and pastoralist societies in southeastern Europe. *Nature* **620**, 358–365 (2023).

62. V. Heyd, Kossinna's smile. *Antiquity* **91**, 348–359 (2017).
63. S. Brace, Y. Diekmann, T. J. Booth, L. van Dorp, Z. Faltyskova, N. Rohland, S. Mallick, I. Olalde, M. Ferry, M. Michel, J. Oppenheimer, N. Broomandkhoshbacht, K. Stewardson, R. Martiniano, S. Walsh, M. Kayser, S. Charlton, G. Hellenthal, I. Armit, R. Schulting, O. E. Craig, A. Sheridan, M. Parker Pearson, C. Stringer, D. Reich, M. G. Thomas, I. Barnes, Ancient genomes indicate population replacement in Early Neolithic Britain. *Nat. Ecol. Evol.* **3**, 765–771 (2019).
64. A. Linderholm, G. M. Kilinc, A. Szczepanek, P. Wlodarczak, P. Jarosz, Z. Belka, J. Dopieralska, K. Werens, J. Gorski, M. Mazurek, M. Hozer, M. Rybicka, M. Ostrowski, J. Baginska, W. Koman, R. Rodriguez-Varela, J. Stora, A. Götherstrom, M. Krzewinska, Corded Ware cultural complexity uncovered using genomic and isotopic analysis from south-eastern Poland. *Sci. Rep.* **10**, 6885 (2020).
65. A. Seguin-Orlando, R. Donat, C. Der Sarkissian, J. Southon, C. Theves, C. Manen, Y. Tcheremissinoff, E. Crubezy, B. Shapiro, J. F. Deleuze, L. Dalen, J. Guilaine, L. Orlando, Heterogeneous Hunter-Gatherer and steppe-related ancestries in late neolithic and bell beaker genomes from present-day france. *Curr. Biol.* **31**, 1072–1083.e10 (2021).
66. M. E. Allentoft, M. Sikora, A. Refoyo-Martinez, E. K. Irving-Pease, A. Fischer, W. Barrie, A. Ingason, J. Stenderup, K. G. Sjogren, A. Pearson, B. S. da Mota, B. S. Paulsson, A. Halgren, R. Macleod, M. L. S. Jorkov, F. Demeter, L. Sorensen, P. O. Nielsen, R. A. Henriksen, T. Vimala, H. McColl, A. Margaryan, M. Ilardo, A. Vaughn, M. F. Mortensen, A. B. Nielsen, M. U. Hede, N. N. Johannsen, P. Rasmussen, L. Vinner, G. Renaud, A. Stern, T. Z. T. Jensen, G. Scorrano, H. Schroeder, P. Lysdahl, A. D. Ramsoe, A. Skorobogatov, A. J. Schork, A. Rosengren, A. Ruter, A. Outram, A. A. Timoshenko, A. Buzhilova, A. Coppa, A. Zubova, A. M. Silva, A. J. Hansen, A. Gromov, A. Logvin, A. B. Gotfredsen, B. H. Nielsen, B. Gonzalez-Rabanal, C. Lalueza-Fox, C. J. McKenzie, C. Gaunitz, C. Blasco, C. Liesau, C. Martinez-Labarga, D. V. Pozdnyakov, D. Cuenca-Solana, D. O. Lordkipanidze, D. En'shin, D. C. Salazar-Garcia, T. D. Price, D. Boric, E. Kostyleva, E. V. Veselovskaya, E. R. Usmanova, E. Cappellini, E. B. Petersen, E. Kannegaard, F. Radina, F. E. Yediay, H. Duday, I. Gutierrez-Zugasti, I. Merts, I. Potekhina, I. Shevnina, I. Altinkaya, J. Guilaine, J. Hansen, J. E. A. Tortosa, J. Zilhao, J. Vega, K. B. Pedersen, K. Tunia, L. Zhao, L. N. Mylnikova, L. Larsson, L. Metz, L. Yepiskoposyan, L. Pedersen, L. Sarti, L. Orlando, L. Slimak, L. Klassen, M. Blank, M. Gonzalez-Morales, M. Silvestrini, M. Vretemark, M. S. Nesterova, M. Rykun, M. F. Rolfo, M. Szmyt, M. Przybyla, M. Calattini, M. Sablin, M. Dobisikova, M. Meldgaard, M. Johansen, N. Berezina, N. Card, N. A. Saveliev, O. Poshekhonova, O. Rickards, O. V. Lozovskaya, O. Gabor, O. C. Uldum, P. Aurino, P. Kosintsev, P. Courtaud, P. Rios, P. Mortensen, P. Lotz, P. Persson, P. Bangsgaard, P. de Barros Damgaard, P. V. Petersen, P. P. Martinez, P. Wlodarczak, R. V. Smolyaninov, R. Maring, R. Menduina, R. Badalyan, R. Iversen, R. Turin, S. Vasilyev, S. Wahlin, S. Borutskaya, S. Skochina, S. A. Sorensen, S. H. Andersen, T. Jorgensen, Y. B. Serikov, V. I. Molodin, V. Smrcka, V. Merts, V. Appadurai, V. Moiseyev, Y. Magnusson, K. H. Kjaer, N. Lynnerup, D. J. Lawson, P. H. Sudmant, S. Rasmussen, T. S. Korneliussen, R. Durbin, R. Nielsen, O. Delaneau, T. Werge, F. Racimo, K. Kristiansen, E. Willerslev, Population genomics of post-glacial western Eurasia. *Nature* **625**, 301–311 (2024).
67. M. E. Allentoft, M. Sikora, A. Fischer, K. G. Sjogren, A. Ingason, R. Macleod, A. Rosengren, B. Schulz Paulsson, M. L. S. Jorkov, M. Novosolov, J. Stenderup, T. D. Price, M. Fischer Mortensen, A. B. Nielsen, M. Ulfeldt Hede, L. Sorensen, P. O. Nielsen, P. Rasmussen, T. Z. T. Jensen, A. Refoyo-Martinez, E. K. Irving-Pease, W. Barrie, A. Pearson, B. Sousa da Mota, F. Demeter, R. A. Henriksen, T. Vimala, H. McColl, A. Vaughn, L. Vinner, G. Renaud, A. Stern, N. N. Johannsen, A. D. Ramsoe, A. J. Schork, A. Ruter, A. B. Gotfredsen, B. Henning Nielsen, E. Brinch Petersen, E. Kannegaard, J. Hansen, K. Buck Pedersen, L. Pedersen, L. Klassen, M. Meldgaard, M. Johansen, O. C. Uldum, P. Lotz, P. Lysdahl, P. Bangsgaard, P. V. Petersen, R. Maring, R. Iversen, S. Wahlin, S. Anker Sorensen, S. H. Andersen, T. Jorgensen, N. Lynnerup, D. J. Lawson, S. Rasmussen, T. S. Korneliussen, K. H. Kjaer, R. Durbin, R. Nielsen, O. Delaneau, T. Werge, K. Kristiansen, E. Willerslev, 100 ancient genomes show repeated population turnovers in Neolithic Denmark. *Nature* **625**, 329–337 (2024).
68. A. Juras, M. Chylenski, E. Ehler, H. Malmstrom, D. Zurkiewicz, P. Wlodarczak, S. Wilk, J. Peska, P. Fojtik, M. Kralik, J. Libera, J. Baginska, K. Tunia, V. I. Klochko, M. Dabert, M. Jakobsson, A. Kosko, Mitochondrial genomes reveal an east to west cline of steppe ancestry in Corded Ware populations. *Sci. Rep.* **8**, 11603 (2018).
69. L. Saag, L. Varul, C. L. Scheib, J. Stenderup, M. E. Allentoft, L. Saag, L. Pagani, M. Reidla, K. Tambets, E. Metspalu, A. Kriiska, E. Willerslev, T. Kivisild, M. Metspalu, Extensive farming in Estonia started through a sex-biased migration from the steppe. *Curr. Biol.* **27**, 2185–2193.e6 (2017).
70. A. Furtwängler, A. B. Rohrlach, T. C. Lamnidis, L. Papac, G. U. Neumann, I. Siebke, E. Reiter, N. Steuri, J. Hald, A. Denaire, B. Schnitzler, J. Wahl, M. Ramstein, V. J. Schuenemann, P. W. Stockhammer, A. Hafner, S. Lösch, W. Haak, S. Schiffels, J. Krause, Ancient genomes reveal social and genetic structure of Late Neolithic Switzerland. *Nat. Commun.* **11**, 1915 (2020).
71. I. Mathieson, I. Lazaridis, N. Rohland, S. Mallick, N. Patterson, S. A. Roodenberg, E. Harney, K. Stewardson, D. Fernandes, M. Novak, K. Sirak, C. Gamba, E. R. Jones, B. Llamas, S. Dryomov, J. Pickrell, J. L. Arsuaga, J. M. de Castro, E. Carbonell, F. Gerritsen, A. Khokhlov, P. Kuznetsov, M. Lozano, H. Meller, O. Mochalov, V. Moiseyev, M. A. Guerra, J. Roodenberg, J. M. Verges, J. Krause, A. Cooper, K. W. Alt, D. Brown, D. Anthony, C. Lalueza-Fox, W. Haak, R. Pinhasi, D. Reich, Genome-wide patterns of selection in 230 ancient Eurasians. *Nature* **528**, 499–503 (2015).
72. I. Olalde, S. Mallick, N. Patterson, N. Rohland, V. Villalba-Mouco, M. Silva, K. Dulias, C. J. Edwards, F. Gandini, M. Pala, P. Soares, M. Ferrando-Bernal, N. Adamski, N. Broomandkhoshbacht, O. Cheronet, B. J. Culleton, D. Fernandes, A. M. Lawson, M. Mah, J. Oppenheimer, K. Stewardson, Z. Zhang, J. M. Jimenez Arenas, I. J. Toro Moyano, D. C. Salazar-Garcia, P. Castanyer, M. Santos, J. Tremoleda, M. Lozano, P. Garcia Borja, J. Fernandez-Eraso, J. A. Mujika-Alustiza, C. Barroso, F. J. Bermudez, E. Viguera Minguez, J. Burch, N. Coromina, D. Vivo, A. Cebria, J. M. Fullola, O. Garcia-Puchol, J. I. Morales, F. X. Oms, T. Majo, J. M. Verges, A. Diaz-Carvajal, I. Ollich-Castanyer, F. J. Lopez-Cachero, A. M. Silva, C. Alonso-Fernandez, G. Delibes de Castro, J. Jimenez Echevarria, A. Moreno-Marquez, G. Pascual Berlanga, P. Ramos-Garcia, J. Ramos-Munoz, E. Vijande Vila, G. Aguilella Arzo, A. Esparza Arroyo, K. T. Lillios, J. Mack, J. Velasco-Vazquez, A. Waterman, L. B. de Lugo Enrich, M. B. Sanchez, B. Agusti, F. Codina, G. de Prado, A. Estalrrich, A. Fernandez Flores, C. Finlayson, G. Finlayson, S. Finlayson, F. Giles-Guzman, A. Rosas, V. Barciela Gonzalez, G. Garcia Atienzar, M. S. Hernandez Perez, A. Llanos, Y. Carrion Marco, I. Collado Beneyto, D. Lopez-Serrano, M. Sanz Tormo, A. C. Valera, C. Blasco, C. Liesau, P. Rios, J. Daura, M. J. de Pedro Micho, A. A. Diez-Castillo, R. Flores Fernandez, J. F. Farre, R. Garrido-Pena, V. S. Goncalves, E. Guerra-Doce, A. M. Herrero-Corral, J. Juan-Cabanilles, D. Lopez-Reyes, S. B. McClure, M. Merino Perez, A. O. Foix, M. Sanz Borras, A. C. Sousa, J. M. V. Encinas, D. J. Kennett, M. B. Richards, K. W. Alt, W. Haak, R. Pinhasi, C. Lalueza-Fox, D. Reich, The genomic history of the Iberian Peninsula over the past 8000 years. *Science* **363**, 1230–1234 (2019).
73. V. Villalba-Mouco, C. Oliart, C. Rihuete-Herrada, A. Childebayeva, A. B. Rohrlach, M. I. Fregeiro, E. Celdran Beltran, C. Velasco-Felipe, F. Aron, M. Himmel, C. Freund, K. W. Alt, D. C. Salazar-Garcia, G. Garcia Atienzar, M. P. de Miguel Ibanez, M. S. Hernandez Perez, V. Barciela, A. Romero, J. Ponce, A. Martinez, J. Lomba, J. Soler, A. P. Martinez, A. Aviles Fernandez, M. Haber-Uriarte, C. R. de Togores Munoz, I. Olalde, C. Lalueza-Fox, D. Reich, J. Krause, L. Garcia Sanjuan, V. Lull, R. Mico, R. Risch, W. Haak, Genomic transformation and social organization during the Copper Age-Bronze Age transition in southern Iberia. *Sci. Adv.* **7**, eabi7038 (2021).
74. N. Patterson, M. Isakov, T. Booth, L. Buster, C. E. Fischer, I. Olalde, H. Ringbauer, A. Akbari, O. Cheronet, M. Bleasdale, N. Adamski, E. Altena, R. Bernardos, S. Brace, N. Broomandkhoshbacht, K. Callan, F. Candilio, B. Culleton, E. Curtis, L. Demetz, K. S. D. Carlson, C. J. Edwards, D. M. Fernandes, M. G. B. Foody, S. Freilich, H. Goodchild, A. Kearns, A. M. Lawson, I. Lazaridis, M. Mah, S. Mallick, K. Mandl, A. Micco, M. Michel, G. B. Morante, J. Oppenheimer, K. T. Ozdogan, L. Qiu, C. Schattke, K. Stewardson, J. N. Workman, F. Zalzala, Z. Zhang, B. Agusti, T. Allen, K. Almassy, L. Amkreutz, A. Ash, C. Baillif-Ducros, A. Barclay, L. Bartosiewicz, K. Baxter, Z. Bernert, J. Blazek, M. Bodruzic, P. Boissinot, C. Bonsall, P. Bradley, M. Brittain, A. Brookes, F. Brown, L. Brown, R. Brunning, C. Budd, J. Burmaz, S. Canet, S. Carnicero-Caceres, M. Causevic-Bully, A. Chamberlain, S. Chauvin, S. Clough, N. Condic, A. Coppa, O. Craig, M. Cresnar, V. Cummings, S. Czifra, A. Danielisova, R. Daniels, A. Davies, P. de Jersey, J. Deacon, C. Deminger, P. W. Ditchfield, M. Dizdar, M. Dobes, M. Dobisikova, L. Domboroczki, G. Drinkall, A. Dukic, M. Ernee, C. Evans, J. Evans, M. Fernandez-Gotz, S. Filipovic, A. Fitzpatrick, H. Fokkens, C. Fowler, A. Fox, Z. Gallina, M. Gamble, M. R. Gonzalez Morales, B. Gonzalez-Rabanal, A. Green, K. Gyenesei, D. Habermehl, T. Hajdu, D. Hamilton, J. Harris, C. Hayden, J. Hendriks, B. Hernu, G. Hey, M. Hornak, G. Ilon, E. Istvanovits, A. M. Jones, M. B. Kavur, K. Kazek, R. A. Kenyon, A. Khreisheh, V. Kiss, J. Kleijne, M. Knight, L. M. Kootker, P. F. Kovacs, A. Kozubova, G. Kulcsar, V. Kulcsar, C. Le Pennec, M. Legge, M. Leivers, L. Loe, O. Lopez-Costas, T. Lord, D. Los, J. Lyall, A. B. Marin-Arroyo, P. Mason, D. Matosevic, A. Maxted, L. McIntyre, J. McKinley, K. McSweeney, B. Meijlink, B. G. Mende, M. Mendusic, M. Metlicka, S. Meyer, K. Mihovilic, L. Milasinovic, S. Minnitt, J. Moore, G. Morley, G. Mullan, M. Musilova, B. Neil, R. Nicholls, M. Novak, M. Pala, M. Papworth, C. Paresys, R. Patten, D. Perkic, K. Pesti, A. Petit, K. Petriscakova, C. Pichon, C. Pickard, Z. Pilling, T. D. Price, S. Radovic, R. Redfern, B. Resutik, D. T. Rhodes, M. B. Richards, A. Roberts, J. Roefstra, P. Sankot, A. Sefcakova, A. Sheridan, S. Skae, M. Smolikova, K. Somogyi, A. Somogyvari, M. Stephens, G. Szabo, A. Szecsenyi-Nagy, T. Szeniczey, J. Tabor, K. Tanko, C. T. Maria, R. Terry, B. Terzan, M. Teschler-Nicola, J. F. Torres-Martinez, J. Trapp, R. Turle, F. Ujvari, M. van der Heiden, P. Veleminsky, B. Veselka, Z. Vytlacil, C. Waddington, P. Ware, P. Wilkinson, L. Wilson, R. Wiseman, E. Young, J. Zaninovic, A. Zitnan, C. Lalueza-Fox, P. de Knijff, I. Barnes, P. Halkon, M. G. Thomas, D. J. Kennett, B. Cunliffe, M. Lillie, N. Rohland, R. Pinhasi, I. Armit, D. Reich, Large-scale migration into Britain during the Middle to Late Bronze Age. *Nature* **601**, 588–594 (2022).

75. A. Goldberg, T. Gunther, N. A. Rosenberg, M. Jakobsson, Ancient X chromosomes reveal contrasting sex bias in Neolithic and Bronze Age Eurasian migrations. *Proc. Natl. Acad. Sci. U.S.A.* **114**, 2657–2662 (2017).
76. I. Lazaridis, D. Reich, Failure to replicate a genetic signal for sex bias in the steppe migration into central Europe. *Proc. Natl. Acad. Sci. U.S.A.* **114**, E3873–E3874 (2017).
77. A. Mittnik, K. Massy, C. Knipper, F. Wittenborn, R. Friedrich, S. Pfrengle, M. Burri, N. Carlichi-Witjes, H. Deeg, A. Furtwangler, M. Harbeck, K. von Heyking, C. Kociumaka, I. Kucukkalipci, S. Lindauer, S. Metz, A. Staskiewicz, A. Thiel, J. Wahl, W. Haak, E. Pernicka, S. Schiffels, P. W. Stockhammer, J. Krause, Kinship-based social inequality in Bronze Age Europe. *Science* **366**, 731–734 (2019).
78. P. Chambon, *Les morts dans les sépultures collectives néolithiques en France; du cadavre aux restes ultimes* (Gallia Préhistoire, CNRS, 2003), vol. XXXV° supplément.
79. L. Bonnabel, G. Basset, S. Desbrosse-Degobertière, C. Laurelut, R. Nasri, C. Paresys, S. Thiol, E. Vauquelin, in *Occupations et exploitations néolithiques: Et si on parlait des plateaux. Actes du 31° colloque Internéo*, C. Laurelut, J. Vanmoerkerke, Eds. (Bulletin de la Société Archéologique Champenoise, 2015), vol. 107-4, pp. 407–421.
80. K. Hanghoj, I. Moltke, P. A. Andersen, A. Manica, T. S. Korneliussen, Fast and accurate relatedness estimation from high-throughput sequencing data in the presence of inbreeding. *Gigascience* **8**, giz034 (2019).
81. J. M. Monroy Kuhn, M. Jakobsson, T. Gunther, Estimating genetic kin relationships in prehistoric populations. *PLOS ONE* **13**, e0195491 (2018).
82. H. Ringbauer, J. Novembre, M. Steinrucken, Parental relatedness through time revealed by runs of homozygosity in ancient DNA. *Nat. Commun.* **12**, 5425 (2021).
83. B. L. Beard, C. M. Johnson, Strontium isotope composition of skeletal material can determine the birth place and geographic mobility of humans and animals. *J. Forensic Sci.* **45**, 1049–1061 (2000).
84. M. Willmes, C. P. Bataille, H. F. James, I. Moffat, L. McMorrow, L. Kinsley, R. A. Armstrong, S. Eggins, R. Grün, Mapping of bioavailable strontium isotope ratios in France for archaeological provenance studies. *Appl. Geochem.* **90**, 75–86 (2018).
85. D. J. Lawson, G. Hellenthal, S. Myers, D. Falush, Inference of population structure using dense haplotype data. *PLOS Genet.* **8**, e1002453 (2012).
86. J. C. Chàcon-Duque, K. Adhikari, M. Fuentes-Guajardo, J. Mendoza-Revilla, V. Acuna-Alonzo, R. Barquera, M. Quinto-Sanchez, J. Gomez-Valdes, P. Everardo Martinez, H. Villamil-Ramirez, T. Hunemeier, V. Ramallo, C. C. Silva de Cerqueira, M. Hurtado, V. Villegas, V. Granja, M. Villena, R. Vasquez, E. Llop, J. R. Sandoval, A. A. Salazar-Granara, M. L. Parolin, K. Sandoval, R. I. Penaloza-Espinosa, H. Rangel-Villalobos, C. A. Winkler, W. Klitz, C. Bravi, J. Molina, D. Corach, R. Barrantes, V. Gomes, C. Resende, L. Gusmao, A. Amorim, Y. Xue, J. M. Dugoujon, P. Moral, R. Gonzalez-Jose, L. Schuler-Faccini, F. M. Salzano, M. C. Bortolini, S. Canizales-Quinteros, G. Poletti, C. Gallo, G. Bedoya, F. Rothhammer, D. Balding, G. Hellenthal, A. Ruiz-Linares, Latin Americans show wide-spread Converso ancestry and imprint of local Native ancestry on physical appearance. *Nat. Commun.* **9**, 5388 (2018).
87. E. Harney, N. Patterson, D. Reich, J. Wakeley, Assessing the performance of qpAdm: A statistical tool for studying population admixture. *Genetics* **217**, iyaa045 (2021).
88. P. Wangkumhang, M. Greenfield, G. Hellenthal, An efficient method to identify, date, and describe admixture events using haplotype information. *Genome Res.* **32**, 1553––1564 (2022).
89. M. Chintalapati, N. Patterson, P. Moorjani, The spatiotemporal patterns of major human admixture events during the European Holocene. *eLife* **11**, e77625 (2022).
90. C. Knipper, A. Mittnik, K. Massy, C. Kociumaka, I. Kucukkalipci, M. Maus, F. Wittenborn, S. E. Metz, A. Staskiewicz, J. Krause, P. W. Stockhammer, Female exogamy and gene pool diversification at the transition from the Final Neolithic to the Early Bronze Age in central Europe. *Proc. Natl. Acad. Sci. U.S.A.* **114**, 10083–10088 (2017).
91. M. Rivollat, A. B. Rohrlach, H. Ringbauer, A. Childebayeva, F. Mendisco, R. Barquera, A. Szolek, M. Le Roy, H. Colleran, J. Tuke, F. Aron, M. H. Pemonge, E. Spath, P. Telouk, L. Rey, G. Goude, V. Balter, J. Krause, S. Rottier, M. F. Deguilloux, W. Haak, Extensive pedigrees reveal the social organization of a Neolithic community. *Nature* **620**, 600–606 (2023).
92. S. Cveček, Why kinship still needs anthropologists in the 21st century. *Anthopol. Today* **40**, 3–6 (2024).
93. L. Chaitanya, K. Breslin, S. Zuñiga, L. Wirken, E. Pośpiech, M. Kukla-Bartoszek, T. Sijen, P. Knijff, F. Liu, W. Branicki, M. Kayser, S. Walsh, The HIrisPlex-S system for eye, hair and skin colour prediction from DNA: Introduction and forensic developmental validation. *Forensic Sci. Int. Genet.* **35**, 123–135 (2018).
94. N. Marchi, L. Winkelbach, I. Schulz, M. Brami, Z. Hofmanova, J. Blocher, C. S. Reyna-Blanco, Y. Diekmann, A. Thiery, A. Kapopoulou, V. Link, V. Piuz, S. Kreutzer, S. M. Figarska, E. Ganiatsou, A. Pukaj, T. J. Struck, R. N. Gutenkunst, N. Karul, F. Gerritsen, J. Pechtl, J. Peters, A. Zeeb-Lanz, E. Lenneis, M. Teschler-Nicola, S. Triantaphyllou, S. Stefanovic, C. Papageorgopoulou, D. Wegmann, J. Burger, L. Excoffier, The genomic origins of the world's first farmers. *Cell* **185**, 1842–1859.e18 (2022).
95. D. M. Fernandes, A. Mittnik, I. Olalde, I. Lazaridis, O. Cheronet, N. Rohland, S. Mallick, R. Bernardos, N. Broomandkhoshbacht, J. Carlsson, B. J. Culleton, M. Ferry, B. Gamarra, M. Lari, M. Mah, M. Michel, A. Modi, M. Novak, J. Oppenheimer, K. A. Sirak, K. Stewardson, K. Mandl, C. Schattke, K. T. Ozdogan, M. Lucci, G. Gasperetti, F. Candilio, G. Salis, S. Vai, E. Camaros, C. Calo, G. Catalano, M. Cueto, V. Forgia, M. Lozano, E. Marini, M. Micheletti, R. M. Micciche, M. R. Palombo, D. Ramis, V. Schimmenti, P. Sureda, L. Teira, M. Teschler-Nicola, D. J. Kennett, C. Lalueza-Fox, N. Patterson, L. Sineo, A. Coppa, D. Caramelli, R. Pinhasi, D. Reich, The spread of steppe and Iranian-related ancestry in the islands of the western Mediterranean. *Nat. Ecol. Evol.* **4**, 334–345 (2020).
96. T. Saupe, F. Montinaro, C. Scaggion, N. Carrara, T. Kivisild, E. D'Atanasio, R. Hui, A. Solnik, O. Lebrasseur, G. Larson, L. Alessandri, I. Arienzo, F. De Angelis, M. F. Rolfo, R. Skeates, L. Silvestri, J. Beckett, S. Talamo, A. Dolfini, M. Miari, M. Metspalu, S. Benazzi, C. Capelli, L. Pagani, C. L. Scheib, Ancient genomes reveal structural shifts after the arrival of Steppe-related ancestry in the Italian Peninsula. *Curr. Biol.* **31**, 2576–2591.e12 (2021).
97. J. Rio, C. S. Quilodran, M. Currat, Spatially explicit paleogenomic simulations support cohabitation with limited admixture between Bronze Age Central European populations. *Commun. Biol.* **4**, 1163 (2021).
98. I. Lazaridis, S. Alpaslan-Roodenberg, A. Acar, A. Acikkol, A. Agelarakis, L. Aghikyan, U. Akyuz, D. Andreeva, G. Andrijasevic, D. Antonovic, I. Armit, A. Atmaca, P. Avetisyan, A. I. Aytek, K. Bacvarov, R. Badalyan, S. Bakardzhiev, J. Balen, L. Bejko, R. Bernardos, A. Bertsatos, H. Biber, A. Bilir, M. Bodruzic, M. Bonogofsky, C. Bonsall, D. Boric, N. Borovinic, G. B. Morante, K. Buttinger, K. Callan, F. Candilio, M. Caric, O. Cheronet, S. Chohadzhiev, M. E. Chovalopoulou, S. Chryssoulaki, I. Ciobanu, N. Condic, M. Constantinescu, E. Cristiani, B. J. Culleton, E. Curtis, J. Davis, T. I. Demcenco, V. Dergachev, Z. Derin, S. Deskaj, S. Devejyan, V. Djordjevic, K. S. D. Carlson, L. R. Eccles, N. Elenski, A. Engin, N. Erdogan, S. Erir-Pazarci, D. M. Fernandes, M. Ferry, S. Freilich, A. Frinculeasa, M. L. Galaty, B. Gamarra, B. Gasparyan, B. Gaydarska, E. Genc, T. Gultekin, S. Gunduz, T. Hajdu, V. Heyd, S. Hobosyan, N. Hovhannisyan, I. Iliev, L. Iliev, S. Iliev, I. Ivgin, I. Jankovic, L. Jovanova, P. Karkanas, B. Kavaz-Kindigili, E. H. Kaya, D. Keating, D. J. Kennett, S. D. Kesici, A. Khudaverdyan, K. Kiss, S. Kilic, P. Klostermann, S. K. B. N. Valdes, S. Kovacevic, M. Krenz-Niedbala, M. K. Skrivanko, R. Kurti, P. Kuzman, A. M. Lawson, C. Lazar, K. Leshtakov, T. E. Levy, I. Liritzis, K. O. Lorentz, S. Lukasik, M. Mah, S. Mallick, K. Mandl, K. Martirosyan-Olshansky, R. Matthews, W. Matthews, K. McSweeney, V. Melikyan, A. Micco, M. Michel, L. Milasinovic, A. Mittnik, J. M. Monge, G. Nekhrizov, R. Nicholls, A. G. Nikitin, V. Nikolov, M. Novak, I. Olalde, J. Oppenheimer, A. Osterholtz, C. Ozdemir, K. T. Ozdogan, N. Ozturk, N. Papadimitriou, N. Papakonstantinou, A. Papathanasiou, L. Paraman, E. G. Paskary, N. Patterson, I. Petrakiev, L. Petrosyan, V. Petrova, A. Philippa-Touchais, A. Piliposyan, N. P. Kuzman, H. Potrebica, B. Preda-Balanica, Z. Premuzic, T. D. Price, L. Qiu, S. Radovic, K. R. Aziz, P. R. Sikanjic, K. R. Raheem, S. Razumov, A. Richardson, J. Roodenberg, R. Ruka, V. Russeva, M. Sahin, A. Sarbak, E. Savas, C. Schattke, L. Schepartz, T. Selcuk, A. Sevim-Erol, M. Shamoon-Pour, H. M. Shephard, A. Sideris, A. Simalcsik, H. Simonyan, V. Sinika, K. Sirak, G. Sirbu, M. Slaus, A. Soficaru, B. Sogut, A. Soltysiak, C. Sonmez-Sozer, M. Stathi, M. Steskal, K. Stewardson, S. Stocker, F. Suata-Alpaslan, A. Suvorov, A. Szecsenyi-Nagy, T. Szeniczey, N. Telnov, S. Temov, N. Todorova, U. Tota, G. Touchais, S. Triantaphyllou, A. Turker, M. Ugarkovic, T. Valchev, F. Veljanovska, Z. Videvski, C. Virag, A. Wagner, S. Walsh, P. Wlodarczak, J. N. Workman, A. Yardumian, E. Yarovoy, A. Y. Yavuz, H. Yilmaz, F. Zalzala, A. Zettl, Z. Zhang, R. Cavusoglu, N. Rohland, R. Pinhasi, D. Reich, R. Davtyan, The genetic history of the Southern Arc: A bridge between West Asia and Europe. *Science* **377**, eabm4247 (2022).
99. M. E. Allentoft, M. Sikora, K. G. Sjogren, S. Rasmussen, M. Rasmussen, J. Stenderup, P. B. Damgaard, H. Schroeder, T. Ahlstrom, L. Vinner, A. S. Malaspinas, A. Margaryan, T. Higham, D. Chivall, N. Lynnerup, L. Harvig, J. Baron, P. Della Casa, P. Dabrowski, P. R. Duffy, A. V. Ebel, A. Epimakhov, K. Frei, M. Furmanek, T. Gralak, A. Gromov, S. Gronkiewicz, G. Grupe, T. Hajdu, R. Jarysz, V. Khartanovich, A. Khokhlov, V. Kiss, J. Kolar, A. Kriiska, I. Lasak, C. Longhi, G. McGlynn, A. Merkevicius, I. Merkyte, M. Metspalu, R. Mkrtchyan, V. Moiseyev, L. Paja, G. Palfi, D. Pokutta, L. Pospieszny, T. D. Price, L. Saag, M. Sablin, N. Shishlina, V. Smrcka, V. I. Soenov, V. Szeverenyi, G. Toth, S. V. Trifanova, L. Varul, M. Vicze, L. Yepiskoposyan, V. Zhitenev, L. Orlando, T. Sicheritz-Ponten, S. Brunak, R. Nielsen, K. Kristiansen, E. Willerslev, Population genomics of Bronze Age Eurasia. *Nature* **522**, 167–172 (2015).
100. W. Haak, M. Furholt, M. Sikora, A. B. Rohrlach, L. Papac, K.-G. Sjögren, V. Heyd, M. Fischer Mortensen, A. B. Nielsen, J. Müller, I. Feeser, G. Kroonen, K. Kristiansen, The corded ware complex in Europe in light of current archaeogenetic and environmental evidence, in *The Indo-European Puzzle Revisited Integrating Archaeology, Genetics, and Linguistics*, K. Kristian Kristiansen, G. Kroonen, E. Willerslev, Eds. (Cambridge Univ. Press, 2023), pp. 63–80.
101. N. Clément, The prestige of warriors: Bell Beaker archers' equipment in Central Europe. *Préhist. Méditerranéennes* **8**, (2020).
102. J. Cauliez, The Bell Beaker complex: A vector of transformations? Stabilities and changes of the indigenous cutures in south-east France at the end of the Neolithic, in *The Bell Beaker Transition in Europe—Mobility and Local Evolution During the 3rd Millennium BC*, M. P. Prieto Martinez, L. Salanova, Eds. (Oxbow Books, 2015), pp. 88–112.
103. E. Sangmeister, in *Premier Colloque Atlantique*, P. R. Giot, Ed. (Laboratoire d'Anthropologie Préhistorique Rennes, 1961), vol. Les Civilisations Atlantiques du Néolithique à l'âge du Fer, pp. 25–56.

104. E. A. Bennett, I. Crevecoeur, B. Viola, A. P. Derevianko, M. V. Shunkov, T. Grange, B. Maureille, E. M. Geigl, Morphology of the Denisovan phalanx closer to modern humans than to Neanderthals. *Sci. Adv.* **5**, eaaw3950 (2019).
105. E. A. Bennett, J. Weber, W. Bendhafer, S. Champlot, J. Peters, G. M. Schwartz, T. Grange, E. M. Geigl, The genetic identity of the earliest human-made hybrid animals, the kungas of Syro-Mesopotamia. *Sci. Adv.* **8**, eabm0218 (2022).
106. S. Guimaraes, B. S. Arbuckle, J. Peters, S. E. Adcock, H. Buitenhuis, H. Chazin, N. Manaseryan, H. P. Uerpmann, T. Grange, E. M. Geigl, Ancient DNA shows domestic horses were introduced in the southern Caucasus and Anatolia during the Bronze Age. *Sci. Adv.* **6**, eabb0030 (2020).
107. J. Dabney, M. Knapp, I. Glocke, M. T. Gansauge, A. Weihmann, B. Nickel, C. Valdiosera, N. Garcia, S. Paabo, J. L. Arsuaga, M. Meyer, Complete mitochondrial genome sequence of a Middle Pleistocene cave bear reconstructed from ultrashort DNA fragments. *Proc. Natl. Acad. Sci. U.S.A.* **110**, 15758–15763 (2013).
108. N. Rohland, I. Glocke, A. Aximu-Petri, M. Meyer, Extraction of highly degraded DNA from ancient bones, teeth and sediments for high-throughput sequencing. *Nat. Protoc.* **13**, 2447–2461 (2018).
109. G. Renaud, U. Stenzel, J. Kelso, leeHom: Adaptor trimming and merging for Illumina sequencing reads. *Nucleic Acids Res.* **42**, e141 (2014).
110. H. Li, R. Durbin, Fast and accurate short read alignment with Burrows-Wheeler transform. *Bioinformatics* **25**, 1754–1760 (2009).
111. H. Li, B. Handsaker, A. Wysoker, T. Fennell, J. Ruan, N. Homer, G. Marth, G. Abecasis, R. Durbin, The sequence alignment/map format and SAMtools. *Bioinformatics* **25**, 2078–2079 (2009).
112. A. Jagadeesan, S. S. Ebenesersdóttir, V. B. Guðmundsdóttir, E. L. Thordardottir, K. H. S. Moore, A. Helgason, HaploGrouper: A generalized approach to haplogroup classification. *Bioinformatics* **37**, 570–572 (2021).
113. H. Weissensteiner, L. Forer, L. Fendt, A. Kheirkhah, A. Salas, F. Kronenberg, S. Schoenherr, Contamination detection in sequencing studies using the mitochondrial phylogeny. *Genome Res.* **31**, 309–316 (2021).
114. H. Weissensteiner, D. Pacher, A. Kloss-Brandstatter, L. Forer, G. Specht, H. J. Bandelt, F. Kronenberg, A. Salas, S. Schonherr, HaploGrep 2: Mitochondrial haplogroup classification in the era of high-throughput sequencing. *Nucleic Acids Res.* **44**, W58–W63 (2016).
115. T. S. Korneliussen, A. Albrechtsen, R. Nielsen, ANGSD: Analysis of next generation sequencing data. *BMC Bioinformatics* **15**, 356 (2014).
116. S. Rubinacci, D. M. Ribeiro, R. J. Hofmeister, O. Delaneau, Efficient phasing and imputation of low-coverage sequencing data using large reference panels. *Nat. Genet.* **53**, 120–126 (2021).
117. B. S. da Mota, S. Rubinacci, D. I. Cruz Dávalos, C. E. G. Amorim, M. Sikora, N. N. Johannsen, M. H. Szmyt, P. Włodarczak, A. Szczepanek, M. M. Przybyła, H. Schroeder, M. E. Allentoft, E. Willerslev, A.-S. Malaspinas, O. Delaneau, Imputation of ancient human genomes. *Nat. Commun.* **14**, 3660 (2023).
118. R. Yaka, I. Mapelli, D. Kaptan, A. Dogu, M. Chylenski, O. D. Erdal, D. Koptekin, K. B. Vural, A. Bayliss, C. Mazzucato, E. Fer, S. S. Cokoglu, V. K. Lagerholm, M. Krzewinska, C. Karamurat, H. C. Gemici, A. Sevkar, N. D. Dagtas, G. M. Kilinc, D. Adams, A. R. Munters, E. Saglican, M. Milella, E. M. J. Schotsmans, E. Yurtman, M. Cetin, S. Yorulmaz, N. E. Altinisik, A. Ghalichi, A. Juras, C. C. Bilgin, T. Gunther, J. Stora, M. Jakobsson, M. de Kleijn, G. Mustafaoglu, A. Fairbairn, J. Pearson, I. Togan, N. Kayacan, A. Marciniak, C. S. Larsen, I. Hodder, C. Atakuman, M. Pilloud, E. Surer, F. Gerritsen, R. Ozbal, D. Baird, Y. S. Erdal, G. Duru, M. Ozbasaran, S. D. Haddow, C. J. Knusel, A. Gotherstrom, F. Ozer, M. Somel, Variable kinship patterns in Neolithic Anatolia revealed by ancient genomes. *Curr. Biol.* **31**, 2455–2468 e18 (2021).
119. S. Leslie, B. Winney, G. Hellenthal, D. Davison, A. Boumertit, T. Day, K. Hutnik, E. C. Royrvik, B. Cunliffe; Wellcome Trust Case Control Consortium 2; International Multiple Sclerosis Genetics Consortium, D. J. Lawson, D. Falush, C. Freeman, M. Pirinen, S. Myers, M. Robinson, P. Donnelly, W. Bodmer, The fine-scale genetic structure of the British population. *Nature* **519**, 309–314 (2015).
120. J. Oksanen, G. Simpson, F. Blanchet, R. Kindt, P. Legendre, P. Minchin, R. O'Hara, P. Solymos, M. Stevens, E. Szoecs, H. Wagner, M. Barbour, M. Bedward, B. Bolker, D. Borcard, G. Carvalho, M. Chirico, M. De Caceres, S. Durand, H. Evangelista, R. FitzJohn, M. Friendly, B. Furneaux, G. Hannigan, M. Hill, L. Lahti, D. McGlinn, M. Ouellette, E. Ribeiro Cunha, T. Smith, A. Stier, C. Ter Braak, J. Weedon, Vegan: Community Ecology Package. (2022); https://cran.r-project.org/package=vegan.
121. F. M. T. A. Busing, E. Meijer, R. V. D. Leeden, Delete-m jackknife for unequal m. *Stat. Comput.* **9**, 3–8 (1999).
122. L. Scrucca, C. Fraley, T. B. Murphy, A. E. Raftery, *Model-Based Clustering, Classification, and Density Estimation Using mclust in R* (Chapman & Hall/CRC, 2023).
123. A. Ultsch, M. C. Thrun, O. Hansen-Goos, J. Lotsch, Identification of molecular fingerprints in human heat pain thresholds by use of an interactive mixture model R toolbox (AdaptGauss). *Int. J. Mol. Sci.* **16**, 25897–25911 (2015).
124. N. Patterson, P. Moorjani, Y. Luo, S. Mallick, N. Rohland, Y. Zhan, T. Genschoreck, T. Webster, D. Reich, Ancient admixture in human history. *Genetics* **192**, 1065–1093 (2012).
125. S. Mallick, A. Micco, M. Mah, H. Ringbauer, I. Lazaridis, I. Olalde, N. Patterson, D. Reich, The Allen Ancient DNA Resource (AADR) a curated compendium of ancient human genomes. *Sci. Data* **11**, 182 (2024).
126. M. Kunst, in *Bell Beakers Today: Pottery, People, Culture, Symbols in Prehistoric Europe*, F. Nicolis, Ed. (Provincia Autonoma di Trento Servizio Beni Culturali Ufficio Beni Archeologici, 2001), pp. 81–90.
127. R. Harrison, V. Heyd, The transformation of Europe in the third millennium BC: The example of 'Le Petit-Chasseur I+III' (Sion, Valais, Switzerland). *Praehist. Z.* **82**, 129–214 (2007).
128. L. Salanova, *La question du Campaniforme en France et dans les Îles anglo-normandes: Productions, chronologie et rôles d'un standard céramique* (Société préhistorique française et Comité des travaux historiques et scientifiques, 2000).
129. M. Vander Linden, Bell Beaker pottery and society, in *The Oxford Handbook of Neolithic Europe*, C. Fowler, J. Harding, D. Hofmann, Eds. (Oxford University Press, 2015), pp. 605–620.
130. P. Reimer, W. Austin, E. Bard, A. Bayliss, P. Blackwell, C. B. Ramsey, M. Butzin, H. Cheng, R. L. Edwards, M. Friedrich, P. M. Grootes, T. P. Guilderson, I. Hajdas, T. J. Heaton, A. G. Hogg, K. A. Hughen, B. Kromer, S. W. Manning, R. Muscheler, J. G. Palmer, C. Pearson, J. van der Plicht, R. W. Reimer, D. A. Richards, E. M. Scott, J. R. Southon, C. S. M. CTurney, L. Wacker, F. Adolphi, U. Büntgen, M. Capano, S. M. Fahrni, A. Fogtmann-Schulz, R. Friedrich, P. Köhler, S. Kudsk, F. Miyake, J. Olsen, F. Reinig, M. Sakamoto, A. Sookdeo, S. Talamo, The IntCal20 Northern Hemisphere radiocarbon age calibration curve (0–55 cal kBP). *Radiocarbon* **62**, 725–757 (2020).
131. G. Bräuer, Osteometrie, in *Anthropologie: Handbuch der Vergleichenden Biologie des Menschen*, R. Knussmann, Ed. (G. Fischer, 1988), pp. 160–232.
132. L. Laporte, H. Guy, F. Blaizot, La sepulture à mobilier campaniforme de Jablines Le Haut-Château, in *L'exploitation du silex néolithique: l'Exemple de la minière du Haut-Château à Jablines (Seine-et-Marne)*, F. Bostyn, Y. Lanchon, Eds. (Editions de la Maison des Sciences de l'Homme, 1992), pp. 224–230.
133. V. Blouet, J.-C. Brénon, J. K. Franck, T., P.-P. Koenig, P. Pernot, M.-P. Petitdidier, F. Thiériot, L. Thomashausen, J. Vanmoerkerke, in *28e Congrès préhistorique de France: Préhistoire de l'Europe du Nord-Ouest: Mobilité, climats et identités culturelles. 2016*, C. Montoya, J.-P. Fagnart, J.-L. Locht, Eds. (Société Préhistorique française, 2019), vol. La fin du Néolithique et la genèse du Bronze ancien dans l'Europe du nord-ouest, pp. 321–344.
134. P. Lefranc, L. Vergnaud, A. Denaire, F. Chenal, C. Féliu, J.-M. Treffort, in *28e Congrès préhistorique de France: Préhistoire de l'Europe du Nord-Ouest: Mobilité, climats et identités culturelles. 2016*, C. Montoya, J.-P. Fagnart, J.-L. Locht, Eds. (Société Préhistorique française, 2019), vol. La fin du Néolithique et la genèse du Bronze ancien dans l'Europe du nord-ouest, pp. 235–238.
135. C. Domenech-Jaulneau, A. Corona, in *InterNéo 12, Journée d'information du 6 novembre 2018* (Association pour les Etudes Interrégionales sur le Néolithique et Société Préhistorique Française, 2018), pp. 159–169.
136. J. E. Ericson, Strontium isotope characterization in the study of prehistoric human ecology. *J. Hum. Evol.* **14**, 503–514 (1985).
137. R. A. Bentley, Strontium isotopes from the earth to the archaeological skeleton: A review. *J. Archaeol. Method Theory* **13**, 135–187 (2006).
138. L. J. Raggatt, N. C. Partridge, Cellular and molecular mechanisms of bone remodeling. *J. Biol. Chem.* **285**, 25103–25108 (2010).
139. M. M. Ash, S. J. Nelson, *Wheeler's Dental Anatomy, Physiology, and Occlusion* (Saunders, W.B., 2003).
140. M. L. Antonio, Z. Gao, H. M. Moots, M. Lucci, F. Candilio, S. Sawyer, V. Oberreiter, D. Calderon, K. Devitofranceschi, R. C. Aikens, S. Aneli, F. Bartoli, A. Bedini, O. Cheronet, D. J. Cotter, D. M. Fernandes, G. Gasperetti, R. Grifoni, A. Guidi, F. La Pastina, E. Loreti, D. Manacorda, G. Matullo, S. Morretta, A. Nava, V. F. Nicolai, F. Nomi, C. Pavolini, M. Pentiricci, P. Pergola, M. Piranomonte, R. Schmidt, G. Spinola, A. Sperduti, M. Rubini, L. Bondioli, A. Coppa, R. Pinhasi, J. K. Pritchard, Ancient Rome: A genetic crossroads of Europe and the Mediterranean. *Science* **366**, 708–714 (2019).
141. P. de Barros Damgaard, R. Martiniano, J. Kamm, J. V. Moreno-Mayar, G. Kroonen, M. Peyrot, G. Barjamovic, S. Rasmussen, C. Zacho, N. Baimukhanov, V. Zaibert, V. Merz, A. Biddanda, I. Merz, V. Loman, V. Evdokimov, E. Usmanova, B. Hemphill, A. Seguin-Orlando, F. E. Yediay, I. Ullah, K. G. Sjogren, K. H. Iversen, J. Choin, C. de la Fuente, M. Ilardo, H. Schroeder, V. Moiseyev, A. Gromov, A. Polyakov, S. Omura, S. Y. Senyurt, H. Ahmad, C. McKenzie, A. Margaryan, A. Hameed, A. Samad, N. Gul, M. H. Khokhar, O. I. Goriunova, V. I. Bazaliiskii, J. Novembre, A. W. Weber, L. Orlando, M. E. Allentoft, R. Nielsen, K. Kristiansen, M. Sikora, A. K. Outram, R. Durbin, E. Willerslev, The first horse herders and the impact of early Bronze Age steppe expansions into Asia. *Science* **360**, eaar7711 (2018).
142. S. Freilich, H. Ringbauer, D. Los, M. Novak, D. T. Pavicic, S. Schiffels, R. Pinhasi, Reconstructing genetic histories and social organisation in Neolithic and Bronze Age Croatia. *Sci. Rep.* **11**, 16729 (2021).
143. G. Gonzalez-Fortes, E. R. Jones, E. Lightfoot, C. Bonsall, C. Lazar, A. Grandal-d'Anglade, M. D. Garralda, L. Drak, V. Siska, A. Simalcsik, A. Boroneant, J. R. Vidal Romani,

M. Vaqueiro Rodriguez, P. Arias, R. Pinhasi, A. Manica, M. Hofreiter, Paleogenomic evidence for multi-generational mixing between Neolithic farmers and Mesolithic hunter-gatherers in the Lower Danube Basin. *Curr. Biol.* **27**, 1801–1810.e10 (2017).

144. I. Lazaridis, N. Patterson, A. Mittnik, G. Renaud, S. Mallick, K. Kirsanow, P. H. Sudmant, J. G. Schraiber, S. Castellano, M. Lipson, B. Berger, C. Economou, R. Bollongino, Q. Fu, K. I. Bos, S. Nordenfelt, H. Li, C. de Filippo, K. Prufer, S. Sawyer, C. Posth, W. Haak, F. Hallgren, E. Fornander, N. Rohland, D. Delsate, M. Francken, J. M. Guinet, J. Wahl, G. Ayodo, H. A. Babiker, G. Bailliet, E. Balanovska, O. Balanovsky, R. Barrantes, G. Bedoya, H. Ben-Ami, J. Bene, F. Berrada, C. M. Bravi, F. Brisighelli, G. B. Busby, F. Cali, M. Churnosov, D. E. Cole, D. Corach, L. Damba, G. van Driem, S. Dryomov, J. M. Dugoujon, S. A. Fedorova, I. G. Romero, M. Gubina, M. Hammer, B. M. Henn, T. Hervig, U. Hodoglugil, A. R. Jha, S. Karachanak-Yankova, R. Khusainova, E. Khusnutdinova, R. Kittles, T. Kivisild, W. Klitz, V. Kucinskas, A. Kushniarevich, L. Laredj, S. Litvinov, T. Loukidis, R. W. Mahley, B. Melegh, E. Metspalu, J. Molina, J. Mountain, K. Nakkalajarvi, D. Nesheva, T. Nyambo, L. Osipova, J. Parik, F. Platonov, O. Posukh, V. Romano, F. Rothhammer, I. Rudan, R. Ruizbakiev, H. Sahakyan, A. Sajantila, A. Salas, E. B. Starikovskaya, A. Tarekegn, D. Toncheva, S. Turdikulova, I. Uktveryte, O. Utevska, R. Vasquez, M. Villena, M. Voevoda, C. A. Winkler, L. Yepiskoposyan, P. Zalloua, T. Zemunik, A. Cooper, C. Capelli, M. G. Thomas, A. Ruiz-Linares, S. A. Tishkoff, L. Singh, K. Thangaraj, R. Villems, D. Comas, R. Sukernik, M. Metspalu, M. Meyer, E. E. Eichler, J. Burger, M. Slatkin, S. Paabo, J. Kelso, D. Reich, J. Krause, Ancient human genomes suggest three ancestral populations for present-day Europeans. *Nature* **513**, 409–413 (2014).

145. R. Martiniano, L. M. Cassidy, R. O'Maolduin, R. McLaughlin, N. M. Silva, L. Manco, D. Fidalgo, T. Pereira, M. J. Coelho, M. Serra, J. Burger, R. Parreira, E. Moran, A. C. Valera, E. Porfirio, R. Boaventura, A. M. Silva, D. G. Bradley, The population genomics of archaeological transition in west Iberia: Investigation of ancient substructure using imputation and haplotype-based methods. *PLOS Genet.* **13**, e1006852 (2017).

146. I. Olalde, M. E. Allentoft, F. Sanchez-Quinto, G. Santpere, C. W. Chiang, M. DeGiorgio, J. Prado-Martinez, J. A. Rodriguez, S. Rasmussen, J. Quilez, O. Ramirez, U. M. Marigorta, M. Fernandez-Callejo, M. E. Prada, J. M. Encinas, R. Nielsen, M. G. Netea, J. Novembre, R. A. Sturm, P. Sabeti, T. Marques-Bonet, A. Navarro, E. Willerslev, C. Lalueza-Fox, Derived immune and ancestral pigmentation alleles in a 7,000-year-old Mesolithic European. *Nature* **507**, 225–228 (2014).

147. H. Schroeder, A. Margaryan, M. Szmyt, B. Theulot, P. Wlodarczak, S. Rasmussen, S. Gopalakrishnan, A. Szczepanek, T. Konopka, T. Z. T. Jensen, B. Witkowska, S. Wilk, M. M. Przybyla, L. Pospieszny, K. G. Sjogren, Z. Belka, J. Olsen, K. Kristiansen, E. Willerslev, K. M. Frei, M. Sikora, N. N. Johannsen, M. E. Allentoft, Unraveling ancestry, kinship, and violence in a Late Neolithic mass grave. *Proc. Natl. Acad. Sci. U.S.A.* **116**, 10705–10710 (2019).

148. C. Valdiosera, T. Gunther, J. C. Vera-Rodriguez, I. Urena, E. Iriarte, R. Rodriguez-Varela, L. G. Simoes, R. M. Martinez-Sanchez, E. M. Svensson, H. Malmstrom, L. Rodriguez, J. M. B. de Castro, E. Carbonell, A. Alday, J. A. Hernandez Vera, A. Gotherstrom, J. M. Carretero, J. L. Arsuaga, C. I. Smith, M. Jakobsson, Four millennia of Iberian biomolecular prehistory illustrate the impact of prehistoric migrations at the far end of Eurasia. *Proc. Natl. Acad. Sci. U.S.A.* **115**, 3428–3433 (2018).

149. L. M. Cassidy, R. Martiniano, E. M. Murphy, M. D. Teasdale, J. Mallory, B. Hartwell, D. G. Bradley, Neolithic and Bronze Age migration to Ireland and establishment of the insular Atlantic genome. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 368–373 (2016).

150. E. R. Jones, G. Gonzalez-Fortes, S. Connell, V. Siska, A. Eriksson, R. Martiniano, R. L. McLaughlin, M. Gallego Llorente, L. M. Cassidy, C. Gamba, T. Meshveliani, O. Bar-Yosef, W. Muller, A. Belfer-Cohen, Z. Matskevich, N. Jakeli, T. F. G. Higham, M. Currat, D. Lordkipanidze, M. Hofreiter, A. Manica, R. Pinhasi, D. G. Bradley, Upper Palaeolithic genomes reveal deep roots of modern Eurasians. *Nat. Commun.* **6**, 8912 (2015).

Acknowledgments: We are grateful to D. Reich and his team for providing access to the Allen Ancient Genome Diversity Project/John Templeton Ancient DNA Atlas. We thank T. D. Price and P. D. Fullagar for performing the strontium isotope analysis and E. Vauquelin for providing the iconographic representation of burial 445 of Bréviandes. We thank all the staff from the Imagine genomic core facility for advice and technical assistance and C. Masson from the Bioinformatic Core Facility for the data transfer. We are very grateful to O. Lemercier, E. Patin, and G. Hellenthal for stimulating discussions and to M. Willmes who produced the isoscape map for this study. We extend thanks to A. Nafplioti for discussion of the strontium isotope results. We express our gratitude to L. C. Martin and M. Ilett for critical reading of the manuscript and for corrections of the English language. **Funding:** We acknowledge support from the French national research center CNRS. The paleogenomic facility of the Institut Jacques Monod obtained support from the University Paris Diderot within the program "Actions de recherches structurantes." The sequencing facility of the Institut Jacques Monod, Paris, was supported by grants from the University Paris Diderot, the Fondation pour la Recherche Médicale (DGE20111123014), and the Région Ile-de-France (11015901). We acknowledge EUR G.E.N.E. (ANR-17-EURE-0013; IdEx #ANR-18-IDEX-0001 l'Université de Paris; Programme d'Investissements d'Avenir) for support of O.P. **Author contributions:** E.-M.G. and T.G. conceptualized and supervised the project. O.P., T.G., and E.-M.G. performed the laboratory work. O.P. and T.G. performed the formal data analyses. O.P., T.G., and E.-M.G. analyzed and interpreted the data. C.L., C.P., L.B., C.D.-J., and A.C. provided the archaeological samples. C.L. and C.D.-J. provided the archaeological contexts. L.B., A.C., C.P., and I.R. provided anthropological data. C.B. supervised the sequencing platform. C.L. contributed to the discussion. E.-M.G. and T.G. wrote the paper with help from O.P. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** Sequence data generated for this study are available from EBI European Nucleotide Archive PRJEB73626. All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials.

Submitted 7 October 2023
Accepted 16 May 2024
Published 19 June 2024
10.1126/sciadv.adl2468