ANCIENT DNA

Long-distance genetic relatedness in megalithic central Europe

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Megalithic monuments in Late Neolithic Europe are often viewed as symbols of shared ancestry. In this study, we analyzed genome-wide data of 203 individuals buried in six megalithic grave complexes associated with the Western Funnel Beaker and Wartberg groups. Despite being considered archaeologically distinct, our results show that the studied individuals from both groups form a genetically homogeneous population. Moreover, we identified first- and second-degree relationships spanning up to 225 km, revealing unexpectedly long-distance ties and sustained intersite and intergroup mobility. The six grave complexes functioned as communal burial grounds and were not exclusively used for close genetic relatives, indicating that social kinship played an important role. Limited evidence for genetic connections to distant European megalithic populations indicates that monumentality spread culturally rather than through biological networks.

From the Iberian Peninsula to Scandinavia, megalithic monuments formed a large-scale architectural and cultural phenomenon during the Late Neolithic (~4500 to 2800 BCE). Various agricultural groups constructed dolmens, passage graves, stone circles, and avenues, among other massive stone structures (*1*, *2*). Although these monuments express distinct local and regional identities, they also signify broader supraregional networks that connected communities across vast distances (*3*).

One of the megalithic societies is represented by the Western Funnel Beaker group [Trichterbecherkultur-West (TRB-West); 3600 to 2800 BCE] (Fig. 1). Archaeologically, it is known for graves with a stone-lined passage leading to a central burial chamber and pottery vessels with a rounded or slightly conical body and a wide, flaring, funnel-shaped rim. The deeply incised pottery is typically richly decorated, displaying specific design schemes dominated by horizontal or vertical bands. Weaponry is characterized by transverse arrowheads (supplementary text 1) (*4*, *5*). So far, no comprehensive genomic data of TRB-West individuals has been analyzed, leaving questions about their genetic affinities with other megalithic societies unanswered. The only TRB-West site where well-preserved human remains have been recovered to date is Sorsum (3350 to 3100 BCE), located in present-day Germany (*6*). Sorsum differs from other TRB-West sites in that it consists of an underground burial chamber carved into the bedrock, rather than a typical aboveground passage grave. This feature and the elongated burial chamber show similarities to those of its geographically closest megalithic neighbors associated with the archaeologically distinct Wartberg group (WBC; 3500 to 2800 BCE) (Fig. 1). WBC is renowned for subterranean gallery graves and a ceramic repertoire dominated by largely undecorated barrel-shaped vessels (supplementary text 1) (*5*, *7*, *8*). Like other Late Neolithic communities, WBC resulted from admixture between Middle Neolithic farmers (e.g., from the Michelsberg context) and local western hunter-gatherers (WHG), but with a comparatively higher contribution from the latter (*9*–*12*).

The archaeological similarities and geographic proximity between Sorsum and WBC (Fig. 1) prompted us to investigate to what extent these two groups were genetically related. To this end, we analyzed genome-wide data of 203 individuals from Sorsum and five WBC sites (table S1 and supplementary text 1). Given that the nearest WBC gallery grave presented in this study is more than 80 km away from Sorsum—much greater than distances reported for genetic links between other megalithic sites (*13*)—we did not expect to observe close relatives (up to the second degree).

In addition, we explored broader social dynamics within the six groups. Previous research on megalithic communities from Sweden, Ireland, England, and France has predominantly inferred relatedness through the male line (*13*–*16*) and, in some instances, female mobility within a radius of up to 8 km (*13*). Therefore, we examined whether comparable patterns were also present in Sorsum/WBC. Lastly, we assessed how the Sorsum/WBC individuals fit within the wider context of the European megalithic phenomenon by integrating published data from other contemporaneous groups.

The investigation was not designed to selectively target isolated individuals. Instead, the aim was to capture biological structures at the level of entire local populations. Consequently, all accessible skeletal assemblages from megalithic tombs within the study region were included. The selection of sites analyzed thus reflects the available archaeological record rather than any prior sampling preference. The tombs associated with the six sites contain inhumations of complete bodies. They represent collective graves, in which earlier skeletal remains were partially disarticulated and displaced to accommodate subsequent interments, as required by burial activity over several generations.

Sorsum as part of the genetic WBC spectrum

We analyzed genomes of 203 individuals, including 129 newly generated genomes, from one TRB-West site (Sorsum) and five WBC sites (Altendorf, Niedertiefenbach, Rimbeck, Warburg, and Züschen) (Fig. 1, supplementary text 1, tables S1 to S3, and data S1). The samples included a large proportion of all WBC-associated human remains uncovered so far (*17*). The results of the population genetic analyses are described in detail in supplementary text 2, including figs. S1 to S15 and data S2 to S5. The principal components analysis reveals that WBC individuals group together, in line with what was previously shown on a smaller subset (*11*, *12*) (Fig. 2). Notably, Sorsum clusters with WBC rather than with the TRB-North or -East subgroups. In addition, Sorsum exhibits a high level of WHG ancestry (25 to 48%; mean: 33%) that falls within the range observed for WBC (22 to 56%; mean: 35%) (data S2). Furthermore, analogous to the pattern observed in WBC (*12*), Sorsum individuals display male-biased WHG admixture (supplementary text 2 and figs. S10 to S12). They also show a mode and date of admixture (between Middle Neolithic farmers and WHG) that are akin to those of WBC populations (supplementary text 2, figs. S1 to S4, and data S3). The similarities between Sorsum and the WBC communities are additionally reflected in the shared identity-by-descent (IBD) segments identified using ancIBD (*18*) (Fig. 3, supplementary text 2, data S5, and figs. S13 to S15). They have more IBD segments in common with each other than with any other Late Neolithic European group, including megalithic communities (fig. S16 and data S5). By contrast, there are no IBD links connecting Sorsum (TRB-West) to other TRB-associated groups [≥20-centimorgan (cM) segments; data S5].

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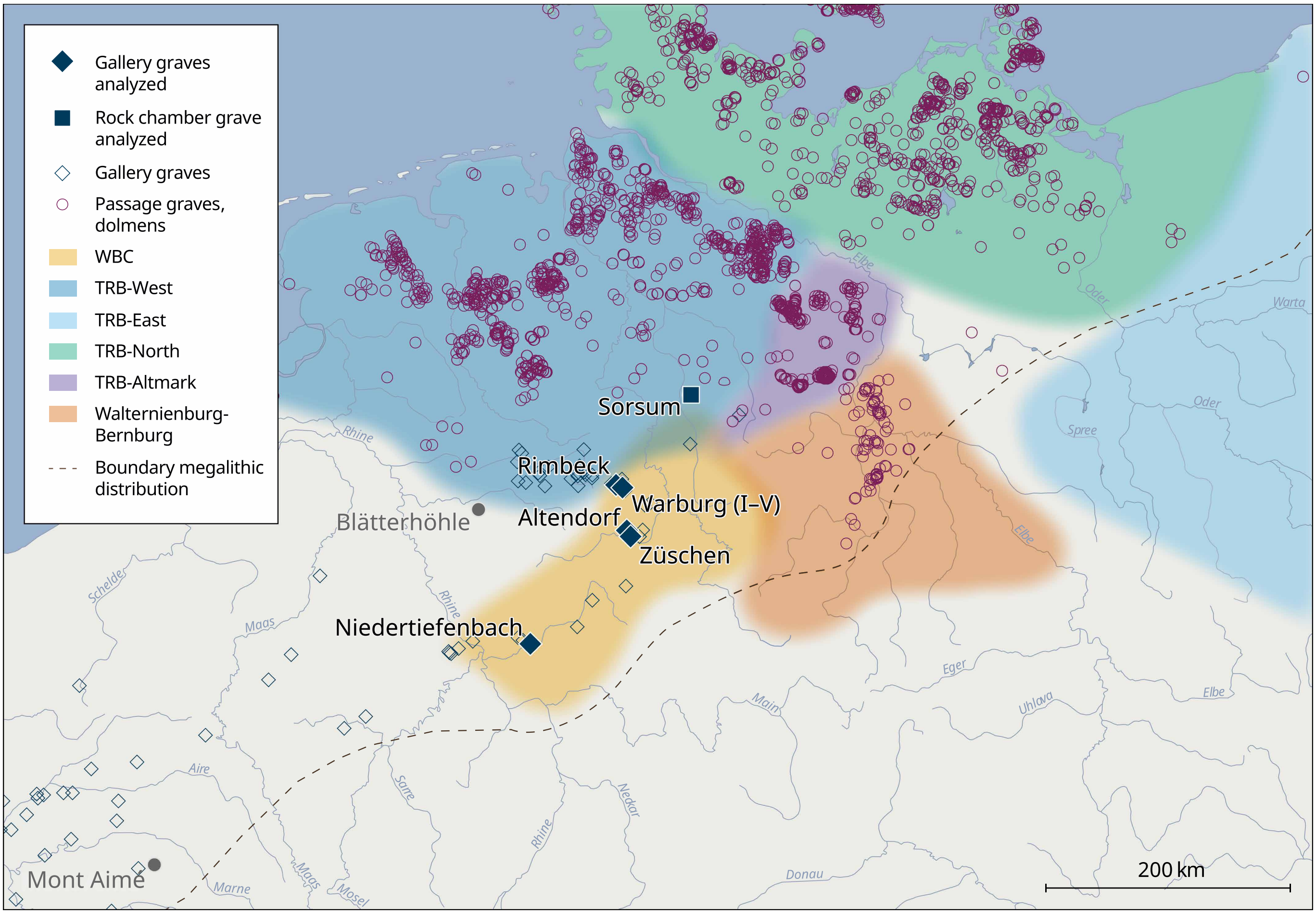

Fig. 1. Map of northwestern Europe showing the locations of the six archaeological sites analyzed in this study. The broader distribution areas of TRB-West and WBC, to which these sites belong, are shown. Other relevant archaeological groups are highlighted. Additionally, the locations of characteristic megalithic structures are marked. The sites of Blätterhöhle cave and Mont Aimé (hypogeum) are also indicated.

Given the genetic affinities between Sorsum and the WBC populations, we investigated close biological relations (i.e., first- and second-degree) across the six sites using a conservative approach that integrates results from three independent methods (READv2, KIN, and NGSRelate2) (*19*–*21*). We identified six genetic cross-site relationships, five of which involve individuals from Sorsum, including a male subadult (361.0201/b) who is connected to his biological father (NT30) in Niedertiefenbach (Fig. 4 and data S6). In addition, Sorsum is linked to both Niedertiefenbach and Warburg through two second-degree relationships each. The other cross-site pair (second-degree) ties Niedertiefenbach with Warburg. Sorsum is located ~225 km from Niedertiefenbach (Fig. 1), marking both the greatest separation among the six sites and the longest distance between first- and second-degree relatives reported for the Neolithic period to date. Overall, our findings suggest a pattern of sporadic movements or sexual reproduction of people across the sites (involving 11 of the 203 individuals). This level of cross-site relatedness is notably high in light of the distances between respective sites (80 to 225 km) and in view of what was previously reported (*13*).

Our results support the view that Sorsum and the WBC communities are a genetically continuous population, as demonstrated by their close genetic affinities in multiple analyses (supplementary text 2 and figs. S1 to S16). One possible explanation is that Sorsum was the northernmost location of a WBC site, adopting some TRB material culture [e.g., grave architecture, pottery types, and arrowheads (*8*, *22*, *23*)] while staying in contact with the other WBC groups in this fluid contact zone. Alternatively, TRB-West and WBC may have had a common origin, with Sorsum preserving genetic continuity and exchange with WBC over time.

Intersite mobility and integration

A notable case of mobility involves a cross-site biological father-son relationship, with the father buried at Niedertiefenbach and his subadult son at Sorsum (Fig. 4). IBD analysis shows that both the father and son share no genetic segments (>20 cM) with other individuals from Sorsum but have multiple IBD connections with individuals from Niedertiefenbach (Fig. 3). This result suggests that the son probably originated from Niedertiefenbach but was interred in Sorsum. A plausible scenario could be that he may have been residing in Sorsum, possibly as a fostered or adopted child or as an apprentice, which could explain his burial there. In addition, there are five more instances of cross-site connections involving nine second-degree relatives (supplementary text 3). These cases, along with the IBD results both among the WBC sites and between the WBC and Sorsum groups (Fig. 4), underscore that intersite mobility and integration did occur regularly, perhaps as part of a social exchange that helped maintain genetic continuity across the Sorsum/WBC communities.

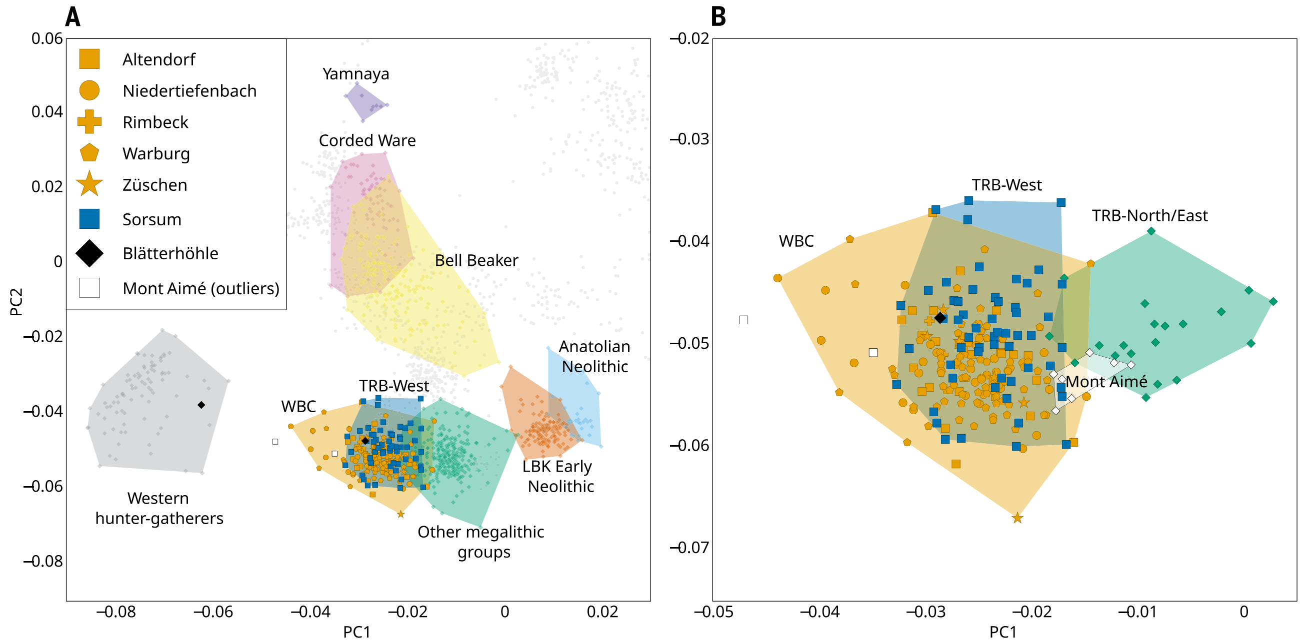

Fig. 2. Principal components analysis (PCA). (**A**) PCA of ancient individuals projected onto the genetic variation of present-day West Eurasian populations (light gray). (**B**) Zoomed-in view of the space occupied by individuals from WBC and TRB communities. Samples from Blätterhöhle and Mont Aimé are highlighted. LBK, Linearbandkeramik (Linear Pottery Culture).

Communal burial places

Within the six communities analyzed, we identified 123 close genetic pairs, comprising 44 first-degree and 79 second-degree relationships (Fig. 4 and data S6). In addition, we detected 39 third-degree related pairs (fig. S17 and data S6). Within the study population of 203 individuals, about half (52%) have a first- or second-degree relative (data S7 and fig. S18).

In total, we observed 19 clusters of close genetic relatedness (fig. S19). Although a few clusters contain more than a dozen individuals, most are small, ranging from isolated pairs to groups of up to seven people. These compact groups represent distinct biological units that may have lived as families in nearby settlements [usually <1.5 km away (*24*)] and used the gallery graves as communal burial grounds. However, about half of the individuals studied (~48%) do not belong to any cluster and appear as singletons (data S7 and fig. S18). This percentage is substantially higher than what was observed at megalithic sites in Sweden (14%) and the British Isles (26%), where interments were largely restricted to one lineage (*13*, *14*). The abundance of singletons observed in our dataset is unlikely to be solely the result of preservation bias and could instead point to the importance of social kinship in determining burial eligibility. Building on interpretations developed for megalithic tombs in Ireland (*16*), the placement of human remains in such monuments may not have been governed exclusively by biological relatedness (*25*). Rather, those buried together could have been part of a kinwork (kinship network) that included, but also exceeded, genetic ties (*25*). Such kinwork may be actively created and maintained through shared social or cultural practices and beliefs, including communal childcare, the construction of megalithic monuments, and funerary rituals (*25*, *26*). The importance of nonbiological ties has also been shown for Neolithic groups in Anatolia not associated with the megalithic phenomenon (*26*, *27*). It is necessary to acknowledge that, although ancient DNA provides valuable insights into biological relatedness, it alone cannot capture the full complexity of social kinship.

Pedigrees reflecting genetic relatedness through the male line

We were able to partially draw pedigrees for three large clusters in Niedertiefenbach ($n = 1$) and Sorsum ($n = 2$) (figs. S19 and S20 and supplementary text 4). One of the genetic trees from Sorsum comprises six generations. This corresponds well with the documented period of use for the collective burial, 150 to 250 years (*6*, *28*). The pedigrees point to a genetic structure characterized by the transmission of identical Y-chromosome haplogroups across generations, whereas associated females display diverse mitochondrial haplogroups. Two of the trees show a marked excess of males, with many of the females inferred rather than directly sampled (fig. S20, B and C). The lack of buried females is observed for all six sites. Overall, they make up only about 40% of the individuals analyzed (fig. S21). This imbalance is seen across various age groups (fig. S22) and has also been observed in other megalithic grave communities (*13*, *14*, *16*). It is possible that females were buried elsewhere owing to social status or ritual customs, potentially in settlements—a special burial form present since the Early Neolithic that may have accommodated individuals of diverse sociocultural backgrounds (*29*).

In Sorsum, one male is identified as the biological father of five offspring by four different women (fig. S20B), while in Niedertiefenbach, another man has children with two women (fig. S20C). This observation could reflect a variety of social arrangements, including multiple female partners, either sequential or concurrent, or additional nonprimary relationships.

Although the two Sorsum pedigrees initially appear as distinct biological units (figs. S19 and S20), the IBD analysis, capturing relatedness up to approximately the sixth degree, reveals broader genetic links between them (Fig. 3, fig. S23, and data S5). The distant relatedness and the shared Y-chromosome haplogroup I2a2a across both clusters suggest that the two pedigrees may represent related branches of a larger genetic network within the Sorsum community.

Lastly, for Warburg, although no pedigrees could be reconstructed, close genetic ties spanning two of the three burial complexes (Warburg I

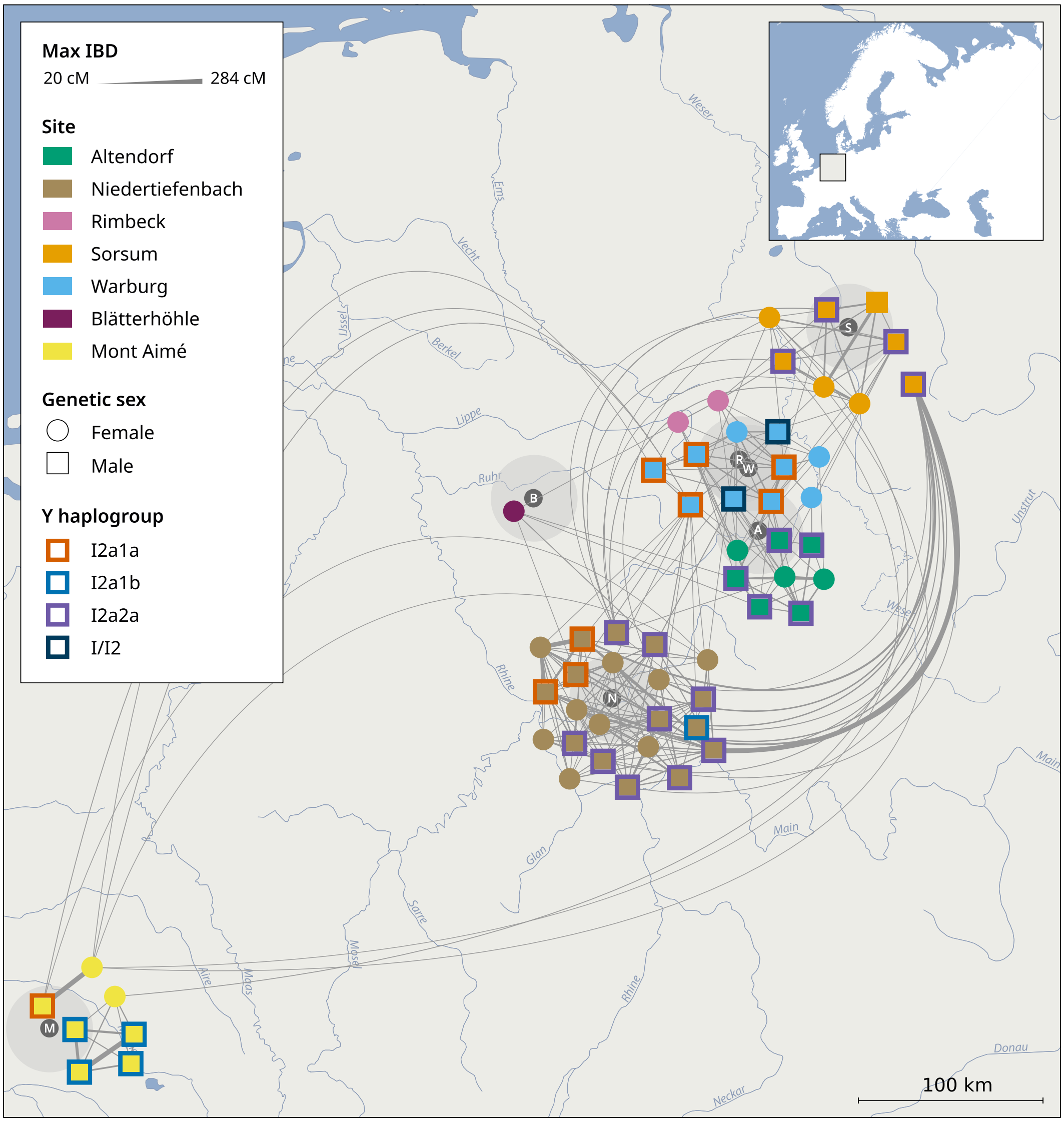

Fig. 3. Identity-by-descent (IBD) network showing genetic connections between individuals analyzed in this study and published previously. Each node represents an individual, with the edge width indicating the maximum shared IBD segment length [in centimorgans (cM)]. Nodes are positioned roughly according to the geographic locations of their respective sites, illustrating the spatial distribution of genetic ties. Single letters mark the precise location of the sites. Individuals from Blätterhöhle and Mont Aimé who are connected to members of the six burial communities are shown. We display only those pairs related up to approximately the sixth degree (i.e., those sharing at least one IBD segment >20 cM). Male individuals are outlined with colored borders indicating their Y-chromosome haplogroups.

and Warburg III) indicate that they were used contemporaneously by related groups (data S6).

Sex-biased mobility pattern

The reconstructed pedigrees show transmission of the same Y-chromosome lineage across generations and different incoming mitochondrial DNA haplogroups (fig. S20). This pattern may be indicative of differences in mobility between the two biological sexes. To follow up on this observation within the WBC and Sorsum populations, we analyzed pairwise mismatch rates (PMR) between same-sex pairs (male-male and female-female). In the three larger communities—Sorsum, Niedertiefenbach, and Warburg—female pairs consistently exhibit significantly higher genetic diversity than male pairs, with small to moderate effect sizes (Cliff's $\delta = 0.21$ to 0.46; figs. S24 and S25 and data S8). The nonsignificant result in Altendorf may be due to the low number of individuals. Züschen and Rimbeck were excluded from the analysis because of their very small sample sizes. The PMR results provide further evidence for a sex-biased mobility pattern in which females moved more than males. This may be inferred to reflect social behavior in line with some degree of virilocality (men preferentially remaining with their parents) and female exogamy (women tending to form partnerships outside their birth unit). Our finding is consistent with previous studies of megalithic groups, including those from TRB-North and Neolithic Britain (*13*, *14*). Whereas uniparental markers and PMR results suggest higher female mobility, direct kinship and IBD analyses indicate that both sexes migrated within Sorsum/WBC.

Long-distance connection of Sorsum/WBC to individuals with high WHG ancestry

Sorsum/WBC show their closest external genetic connections (33 to 75 cM total IBD in segments >20 cM, which is consistent with distant relatedness likely beyond the sixth degree) with one individual from

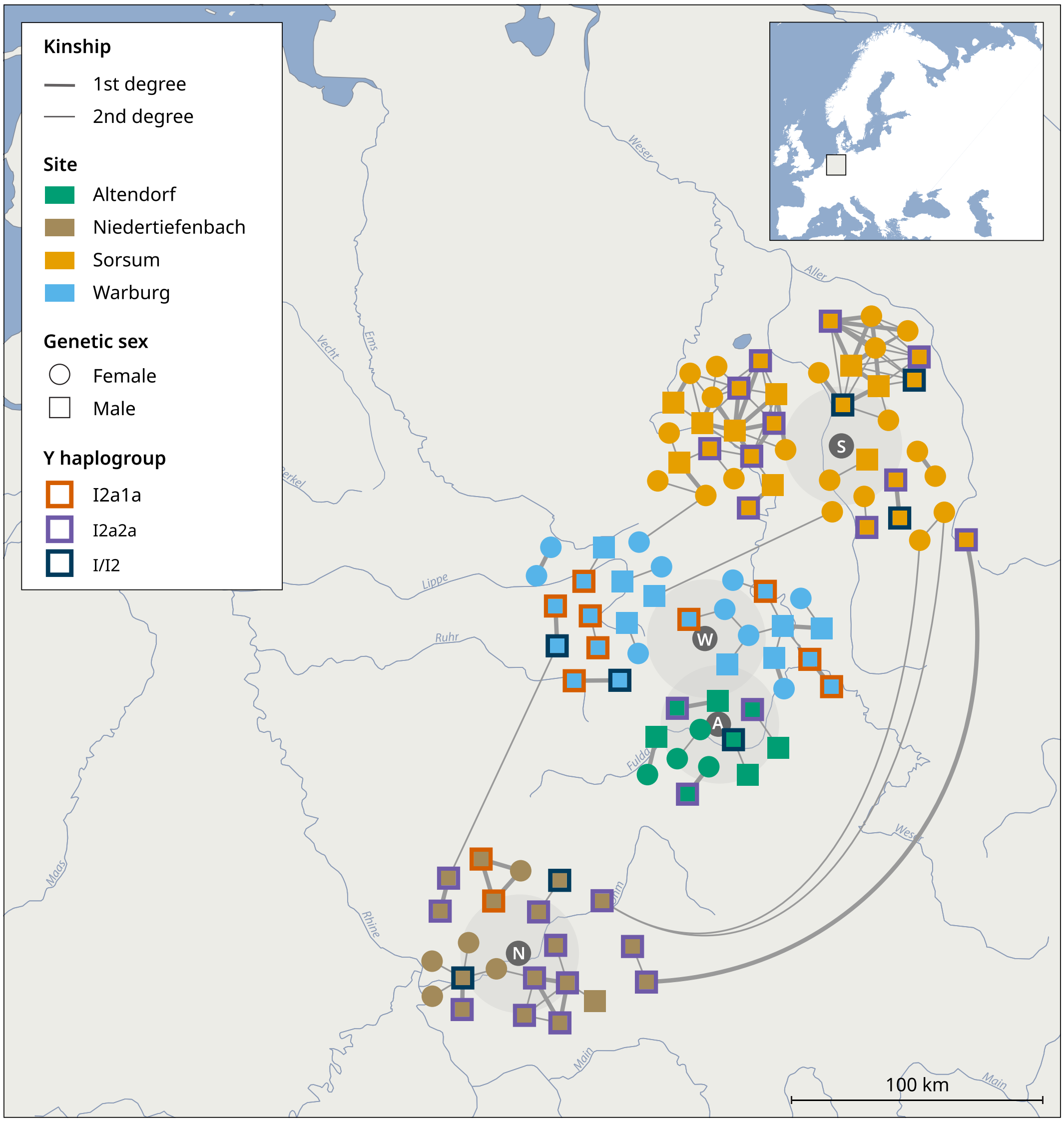

Fig. 4. Network of individuals identified as first- and second-degree relatives. Each node represents an individual, and the edge width denotes the degree of the genetic relationship. Clusters are positioned approximately according to the geographic locations of their respective sites, illustrating the spatial distribution of close genetic ties across the region. Male individuals are depicted with colored borders indicating their Y-chromosome haplogroups. Single letters mark the precise location of the sites.

the Blätterhöhle cave in northwestern Germany (I1563) and three individuals from Mont Aimé in the Paris Basin (Figs. 2 and 3 and data S5) (*9*, *30*). The shared segments are enriched for WHG ancestry (fig. S26). Owing to limited genomic data from contemporaneous populations west of our study area, the extent of wider interactions remains unresolved, and broader networks cannot be excluded. Among the Mont Aimé individuals, two (2H11 and 1H06) have been classified as outliers because of their elevated WHG ancestry, and the third (1H04) is a female with more intermediate WHG ancestry levels (*30*). f_4 statistics reveal that the WHG ancestry in Sorsum and WBC cannot be distinguished from that present in Blätterhöhle and Mont Aimé (fig. S27). IBD-sharing individuals who lived contemporaneously (supplementary text 5) but were distributed across a wide geographic area could reflect sustained long-distance mobility and interaction. Another explanation may be that a group of WHG admixed with Middle Neolithic farmers, whose offspring then moved to Sorsum, WBC, Blätterhöhle, and Mont Aimé.

Limited ties between Sorsum/WBC and other megalithic groups

When considering additional published contemporaneous megalithic groups across Europe, we detected only two other large clusters of individuals sharing IBD segments (fig. S16 and data S5). The first one comprises individuals from British, Irish, and Scottish sites belonging to the Atlantic megalithic tradition (data S5 and S9). Long-distance genetic relatedness among some of these groups has been previously reported (*16*), reflecting cultural continuity and interaction across the British Isles. The second cluster includes individuals from southern Scandinavian sites associated with the TRB-North and Pitted Ware cultures (data S5 and S9). The two clusters do not show connections to each other or to the Sorsum/WBC network. These observations indicate that although megalithic societies may have shared architectural styles and certain cultural practices, genetic exchange did not extend across vast distances or across the English Channel. Instead, genetic networks appear to have been maintained among more local or regional populations.

Conclusions

Our study reveals a complex interaction pattern in central Europe during the Late Neolithic. The presence of first- and second-degree relationships spanning several sites indicates that there was substantial contact between megalithic communities that not only were far apart (more than 200 km) but also had cultural differences in ceramic styles (TRB-West versus WBC). Their close genetic relatedness is further substantiated by the archaeological record, which shows similarities in burial construction (rock-cut chamber of Sorsum and WBC gallery graves) (*28*). The 225-km distance between biological father (Niedertiefenbach) and son (Sorsum) is much larger than previously observed for first-degree relationships (*13*, *31*). However, Sorsum and WBC lack close genetic ties with more distant megalithic populations in the British Isles or Scandinavia, likely reflecting the considerable geographic separation rather than restricted mating practices. These observations add an important layer to our understanding of megalithic societies.

Although the use of large blocks and collective burial practices is a common feature across regions with megalithic structures, our findings, together with results from previous studies, show considerable variations in the degrees of genetic relatedness among the deceased at the different sites across Europe (*13*–*16*). Contrasting burial practices imply that the same social sphere may have held distinct meanings for the various groups. The Sorsum/WBC collective graves served as communal burial grounds for at least 19 different biological units. Together with the relatively high proportion of unrelated individuals, this suggests an inclusive burial practice, indicating that social kinship may have played an important role.

Our findings highlight both the spatial extent of genetic networks in the Neolithic and the complexity of the supraregional megalithic phenomenon.

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SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.aeb2926
Material and Methods; Supplementary Texts 1 to 6; Figs. S1 to S30; Tables S1 to S3; References (*32*–*71*); Data S1 to S10; Reproducibility Checklist

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