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### Article

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# Megalithic tombs in western and northern Neolithic Europe were linked to a kindred society

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**Paleogenomic and archaeological studies show that Neolithic lifeways spread from the Fertile Crescent into Europe around 9000 BCE, reaching northwestern Europe by 4000 BCE. Starting around 4500 BCE, a new phenomenon of constructing megalithic monuments, particularly for funerary practices, emerged along the Atlantic façade. While it has been suggested that the emergence of megaliths was associated with the territories of farming communities, the origin and social structure of the groups that erected them has remained largely unknown. We generated genome sequence data from human remains, corresponding to 24 individuals from five megalithic burial sites, encompassing the widespread tradition of megalithic construction in northern and western Europe, and analyzed our results in relation to the existing European paleogenomic data. The various individuals buried in megaliths show genetic affinities with local farming groups within their different chronological contexts. Individuals buried in megaliths display (past) admixture with local hunter-gatherers, similar to that seen in other Neolithic individuals in Europe. In relation to the tomb populations, we find significantly more males than females buried in the megaliths of the British Isles. The genetic data show close kin relationships among the individuals buried within the megaliths, and for the Irish megaliths, we found a kin relation between individuals buried in different megaliths. We also see paternal continuity through time, including the same Y-chromosome haplotypes reoccurring. These observations suggest that the investigated funerary monuments were associated with patrilineal kindred groups. Our genomic investigation provides insight into the people associated with this long-standing megalith funerary tradition, including their social dynamics.**

paleogenomics | population genomics | migration | megalithic tombs

Investigations of the genetic relationships among humans from multiple Neolithic sites across western Eurasia have shown that Neolithic lifeways dispersed across Europe via a large-scale process of migration (1–6) starting from Anatolia and the areas of the Aegean at ca. 7000–6500 (cal) BCE (7–10). In Europe, migrating people and Neolithic lifeways dispersed along two main routes: an inland route (partly along the Danube River) and a route along Mediterranean coastal areas (11–13). Around 4000 BCE, Neolithic farming communities reached the northwestern fringes of Europe, including the British Isles (14, 15) and Scandinavia (1, 2, 16, 17). A marked hunter-gatherer (HG) admixture has been observed in the later farmer groups compared with the Early Neolithic farmers on the continent (2, 10, 12).

During this period of important social and demographic change, a new phenomenon of constructing megalithic monuments emerged, starting around 4500 BCE in France (18), 3700 BCE in the British Isles (14, 19–26), and 3600 in Scandinavia (16, 27). These

Neolithic megalithic tombs are concentrated along the Atlantic coastal areas, stretching from the Mediterranean to Scandinavia, including the British Isles and regions in the northern European plain (28), but also in southern France, northern Italy, and on the Islands of Corsica and Sardinia (Fig. 1) (19, 27).

The emergence of these megaliths was closely associated with the development of farming communities (14, 23, 25, 27, 29), but the origin and the social structure of the groups are largely unknown. The similarities in the construction and design of some types of megaliths (i.e., dolmens and passage graves) from Iberia to southern Scandinavia, Britain, and Ireland is compelling. Interregional interaction has been evidenced in the same period from the dispersal of domesticated resources, raw materials, and artifacts, possibly reflecting shared social and cultural systems as well as shared cosmology of the groups (21, 27, 28, 30). Although it is clear

## Significance

**A new phenomenon of constructing distinctive funerary monuments, collectively known as megalithic tombs, emerged around 4500 BCE along the Atlantic façade. The megalithic phenomenon has attracted interest and speculation since medieval times. In particular, the origin, dispersal dynamics, and the role of these constructions within the societies that built them have been debated. We generate genome sequence data from 24 individuals buried in five megaliths and investigate the population history and social dynamics of the groups that buried their dead in megalithic monuments across northwestern Europe in the fourth millennium BCE. Our results show kin relations among the buried individuals and an overrepresentation of males, suggesting that at least some of these funerary monuments were used by patrilineal societies.**

Author contributions: A.G., J.S., and M.J. designed research; F.S.-Q., H.M., M.F., L.G.-F., E.M.S., L.G.S., R.G., N.H., A.G., J.S., and M.J. performed research; H.M., M.F., L.G.-F., G.B., G.N., K.B., S.T., N.C., H.B., R.S., and J.S. contributed samples and conducted archaeological analyses; F.S.-Q., H.M., and M.F. analyzed data; and F.S.-Q., H.M., M.F., J.S., and M.J. wrote the paper with input from all authors.

The authors declare no conflict of interest.

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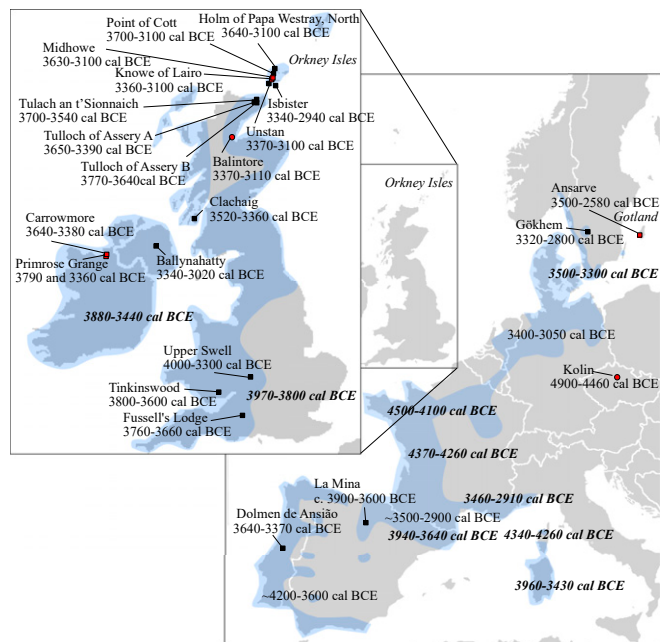
Data deposition: Raw sequencing reads produced for this study have been deposited in the European Nucleotide Archive (accession no. [PRJEB31045](https://www.ebi.ac.uk/ena/record/PRJEB31045)).

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**Fig. 1.** Map of Europe with megalithic burial sites (red squares) and nonmegalithic sites (red circles) from this study, and comparative published data from megalithic sites (black squares) sequenced to date in Europe (Dataset S1.3). The date range represents the 95% CI of available samples from these sites, except for La Mina in Spain. Blue shading represents the estimated distribution of early megalithic burials. Bold italic type indicates dates (95% CI) estimated for the start of dolmens and passage grave monuments, based on samples from these contexts. Regular text indicates time interval associated with the earliest cultural material in the megaliths (27, 45).

that many megaliths were used for collective burials (27, 29, 31), it has been difficult to evaluate which members of the communities were buried in the tombs. Some assemblages include males, females, juveniles, and children, implying familial burials. Many tombs have poorly preserved human remains and also show secondary usage in later times, complicating assessments. The use of megaliths as burial grounds for the community as a whole would imply some level of shared ideology over vast geographical areas (31, 32). However, it has also been argued that the monumental burials and associated rich material culture reflect the emergence of social differentiation or stratification (33–36; see ref. 37 on segmentally structured societies), with the monuments perhaps symbolizing status and territorial markers (37–40).

Some scholars hypothesize that the people buried in the megalithic structures were kin related (41–43). Analyses of mitochondrial data (mtDNA) from megalithic burials at Falbygden and Gotland in modern-day Sweden have revealed a large lineage variation, and thus the groups did not seem to have been organized matrilineally (44, 45; however, contra ref. 43). Genomic data are necessary to provide deeper information on kin relations and the social dynamics and general social structure of the societies or groups. However, as genomic data have been available from only a few individuals from megalithic burials, the origin and dispersal dynamics of the funerary practices, as well as the population history of the people that used the burial constructions, have also remained uncertain.

In the present study, we investigated the genetic structure and demographic affinities of people buried within megaliths to shed light on this burial phenomenon, the social dynamics of the people buried in the monuments, and their demographic history. We generated and examined genome sequence data from 24 individuals from five megalith burial sites located in Ireland, the Orkney Isles, and the Island of Gotland in the Baltic Sea dated between ca. 3800 and 2600 cal BCE encompassing wide-ranging examples from the megalithic tradition in northern Europe. The study also incorporated three individuals from nonmegalith contexts

from mainland Scotland (3370–3100 cal BCE) and the Czech Republic (4825–4555 cal BCE) (Table 1).

## Results

We present genome data from 27 individuals excavated from European Neolithic contexts, of whom 24 were buried in megaliths; Primrose Grange ( $n = 11$ ) and Carrowmore ( $n = 1$ ) in Ireland; Lairo ( $n = 1$ ) and Midhowe ( $n = 2$ ) in the Orkney Islands, Scotland; and Ansarve ( $n = 9$ ) in the island of Gotland, Sweden (16, 45, 46) (Table 1 and SI Appendix, section S2). Individuals from the Scottish “short cist” burial Balintore ( $n = 1$ ) and the Czech Republic Kolin Rondel site ( $n = 2$ ) (46), associated with the Stroked Pottery culture, were also investigated. These individuals were all radiocarbon-dated to between 4825 and 2580 cal BCE (Table 1). We compared our data with genetic data previously generated from 36 individuals from 16 megalithic sites (Fig. 1 and Dataset S1.3), as well as with farmer groups of nonmegalithic contexts (Dataset S1.3), to investigate the population history of people buried in megaliths.

The individuals buried in these megaliths from the British Isles and Scandinavia show an ancestry similar to other contemporaneous farmer groups (Fig. 24), with a majority of their ancestry related to early Neolithic farmers and a partial admixture component related to European Mesolithic HGs (Fig. 2B) (1, 2, 5–7, 10, 16, 46).

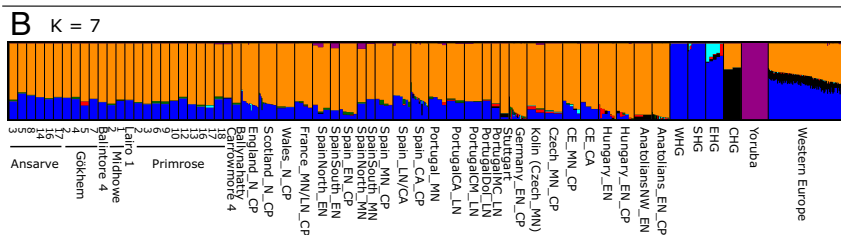
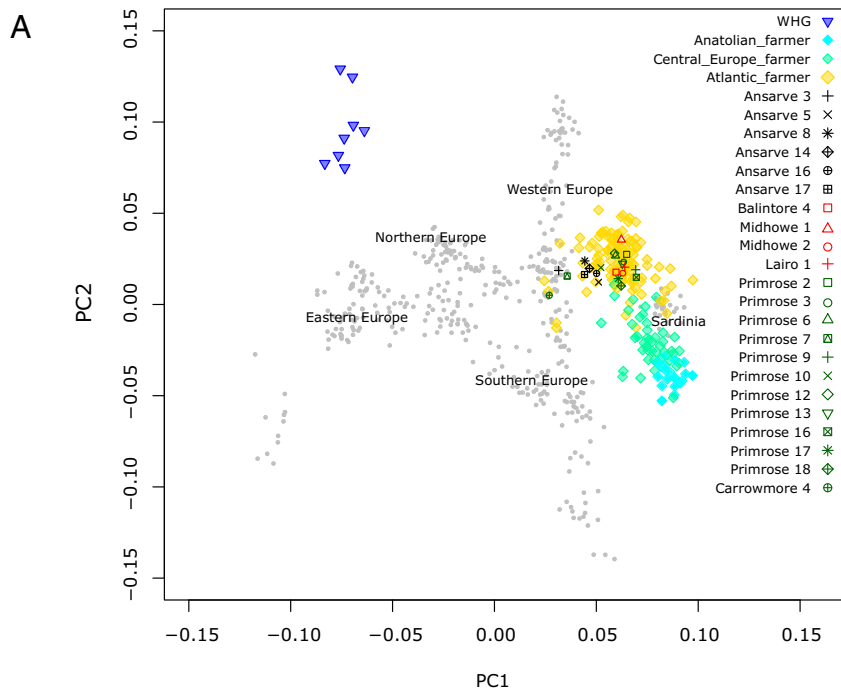
To further explore the demographic history of the individuals buried in the megaliths, we investigated the genetic affinities among sets of individuals and groups, using an  $f_3$  outgroup test for groups of individuals buried in megalithic or nonmegalithic contexts, as well as between individuals from Atlantic coastal and inland Neolithic sites (SI Appendix, section S11.3 and Fig. S19). These analyses showed genetic associations between individuals from the same/similar geographic region and time period (Fig. 24 and SI Appendix, Figs. S16 and S17). However, some tests (SI Appendix, Fig. S19) indicated similar trends as shown in our principal component analysis (PCA) and previous studies (5, 11, 15, 47, 48) and suggested a demic connection among western European Neolithic groups to the exclusion of central European Neolithic groups, as well as a connection between the British Isles and Iberian groups (SI Appendix, section S11.4 and Figs. S20–S22). These results were not driven by greater levels of HG ancestry among the populations at the fringes of the Neolithic expansion (11, 12, 15, 16) (SI Appendix, section S11.4).

Interestingly, we also found a significant farmer-specific genetic affinity between the British Isles Neolithic populations and the Scandinavian populations (Ansarve and Gökhem; Fig. 1) to the exclusion of central European farmers (SI Appendix, Figs. S21 and S22). This observation is compatible with a further migration of farming groups along the European Atlantic coast, as has been suggested by the archaeological record (21, 49, 50).

We found that significantly more males than females were buried in the British Isles megaliths (31 of 42 randomly sampled individuals;  $P = 0.0014$ , binomial test) and at the Primrose megalith alone (9 of 11;  $P = 0.032$ ) (SI Appendix, section S8). However, other megalithic tombs with at least four individuals investigated, including Ansarve (6 of 9;  $P = 0.25$ ), Gökhem (1 of 4;  $P = 0.93$ ), La Mina (2 of 4;  $P = 0.68$ ), Holm of Papa Westray (2 of 4;  $P = 0.68$ ), and Isbister (Tomb of the Eagles) (8 of 10;  $P = 0.054$ ), did not show the same striking pattern, nor did nonmegalithic burials from the British Isles (15) (nonmegalithic burials: 6 of 10;  $P = 0.27$ , cave burials: 10 of 15;  $P = 0.27$ , both nonmegalithic and cave burials: 16 of 25;  $P = 0.11$ ). Overall, genetic data from all individuals from megalithic contexts suggest a higher male-to-female ratio in these burial chambers (41 of 60;  $P = 0.0031$ ) (SI Appendix, Table S3), although the tendency is similar (but not significant) for nonmegalithic burials (SI Appendix, section S8).

We found greater macrohaplogroup mtDNA diversity than Y-chromosomal (YDNA) diversity. Whereas mtDNA lineages from megalithic burials harbor haplogroups K, H, HV, V, U5b, T, and J (among others), males from megalith burials belong almost exclusively to YDNA haplogroup I, more specifically to the I2a sublineage, which has a time to most recent common ancestor of ~15000 BCE (51). This pattern of uniparental marker diversity is





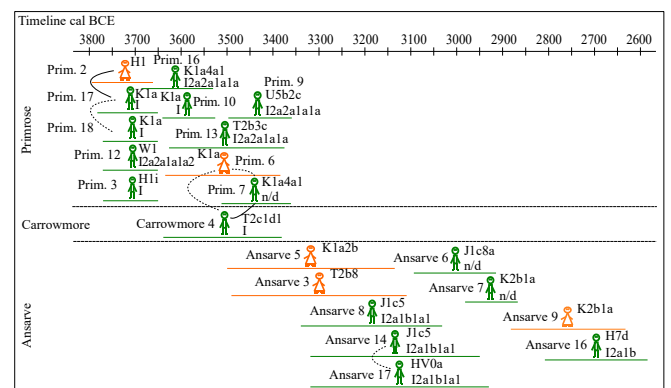
**Fig. 2.** (A) PCA of 429 present-day west Europeans (gray dots) with previously published Western HG (WHGs), Atlantic coast and Central European Neolithic farmer samples (filled symbols), and the samples from the present study (shaded symbols) projected onto the first two principal components (more details in *SI Appendix, Section S11.1*). (B) Inferred ancestry components (assuming seven clusters) of ancient individuals (*Methods* and *SI Appendix, Section S11.2*). All individuals to the left of Yoruba are prehistoric individuals, all of which are shotgun-sequenced unless marked with “CP” for SNP capture data. In the label names, the following letters indicate an archaeological context: CA, Chalcolithic; EN, Early Neolithic; N, Neolithic; MN, Middle Neolithic; LN, Late Neolithic. The LN individuals from Portugal come from different sites (key provided in *Dataset S1.3*).

of three individuals from Primrose Grange (Tomb 1; individuals Primrose 2, 17, and 18), which overlap broadly in time (Fig. 3). Primrose 2 and 17 were predicted to be related in the first degree, representing a father-daughter relationship. Primrose 17 and 18 were predicted to be second-degree relatives (harboring the same mtDNA lineage but with possibly different YDNA haplogroups) and thus could have been half-siblings or double cousins. However, the YDNA prediction is hindered by low coverage and few informative markers, and thus a grandfather-grandson or uncle-nephew relationship cannot be fully excluded.

The other Irish putative pedigree structure was integrated by two individuals from Tomb 1 (Primrose 6 and 7) and one individual from Carrowmore 4 (from the Lishogil Tomb at the Carrowmore site in close vicinity), who harbored different mtDNA lineages. While the 95% CI dating range of Primrose 6 and Carrowmore 4 overlap, Primrose 7 might be slightly younger than the other two individuals. The Carrowmore 4 and Primrose 7 males were inferred to be at least second-degree related (3.14 SE below the expected value for two unrelated individuals), and the best prediction was a first-degree relation (1.79 SE below the value for a second-degree relation, although not statistically significant at the 95% level; *SI Appendix, section S10*). If a first-degree relation is assumed, then the sole possible kin connection is a father-son relationship, because the individuals are not maternally linked. In the case of a second-degree relationship, any paternally related second-degree familial connection is possible. The other two READ-predicted second-degree kin relationships in the Irish burials (Primrose 6-Primrose 7 and Primrose 6-Carrowmore 4; 1.04 SE and 0.50 SE below the threshold for an unrelated pair, respectively) involved a familial connection of the male individuals to Primrose 6 (female).

Within the Ansarve megalith, we identify a second-degree relationship between the contemporaneous males Ansarve 14 and Ansarve

17 (Fig. 3 and *SI Appendix, section S10*). Both males have the same YDNA haplotype but different mtDNA lineages, suggesting that they could be related through any second-degree paternal kin relationship. Morphologically, Ansarve 14 was predicted to be an adult, and Ansarve 17 was predicted to be a juvenile (*SI Appendix, section S2*). Such observations might favor a grandfather-grandson or uncle-nephew relatedness over half-siblings or double cousins; however, the latter alternatives are still compatible with the data (*SI Appendix, Fig. S12*). READ analyses from other megalith burials



**Fig. 3.** Kinship relationships in the Primrose, Carrowmore, and Ansarve burials. Solid line, first degree; dashed line, second degree. Males are displayed in green; females, in orange. The MtDNA and YDNA haplogroups are presented to the right of the figures. Bars underneath figures represent calibrated dating, with 95% CI (details in Table 1 and *SI Appendix, Table S1*).



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